The Condor 102:838–847

ARTIFICIAL NEST PREDATION AND ABUNDANCE OF BIRDS ALONG AN URBAN GRADIENT[1]

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Abstract. We studied nest predation pressure on birds along an urban gradient in urban parks in three Finnish towns. Artificial ground nests with Japanese Quail (*Coturnix coturnix japonicus*) eggs were depredated more in the urban area than in the adjacent forest area. Within each town, the nest predation rate was higher in the town center than in the less urbanized area of detached houses. Predation rates did not vary from year to year or between study towns. Abundances of generalist avian predators were higher in the town center than in the area of detached houses and in the surrounding forest area. Most of the nests in the town center were destroyed by avian predators. Predation rate of artificial nests in each of the town areas was higher in managed parks than in unmanaged parks, presumably due to the less dense vegetation in the managed than the unmanaged parks. A test involving covering nests revealed that artificial nests covered by adjacent vegetation survived better than nests with less cover. In our study, artificial nest loss reflected the distribution of avian nest predators. Ground nesters were present at lower abundances in areas where concealing vegetation was missing and avian nest predation was high. Apparently, nest predation is one of the several possible mechanism affecting urban bird assemblages.

Key words: *avian nest predators, community structure, habitat choice, nest predation, urbanization.*

INTRODUCTION

Urban areas may play an important role in addressing concerns for the conservation of biological diversity. Most research directed towards determining the habitat needs of various bird species has centered on natural ecosystems, whereas urban ecosystems have been largely ignored (Gilbert 1989, Jokimäki 1996). However, with the rapid expansion of urban and suburban development and the associated modification of habitats, the importance of understanding the relationship between birdlife and urban habitats is quite evident (Blair 1996, Clergeau et al. 1998). Several factors such as food, the availability of suitable nest sites, and interspecific competition have been recognized to be important in determining avian habitat selection and community structure. Predation has also been added to this context (Osborne and Osborne 1980, Sih et al. 1985, Suhonen et al. 1994). Nest predation, in particular, is assumed to influence avian population density, reproductive ecology, and life history, but there are few empirical studies on how nest predation pressure affects the structure of bird communities (Tomiałojc 1978, 1982, Sieving 1992).

Most nest predation studies have been conducted in forested or agricultural landscapes, with only a few studies in urban landscapes (Sasvári et al. 1995, Major et al. 1996, Gering and Blair 1999, Matthews et al. 1999). However, predation pressure in any landscape depends on the response of different predator species to landscape structure, and the relative effects of these predators on different bird species. Comparisons of nest predation pressures between different kinds of landscapes may lead to a more holistic understanding of the impacts of man-made changes in landscape structure on nest predation, and consequently in bird community structure. The disturbance of the environment through human-induced changes commonly is thought to increase nest predation (Wilcove 1985, Sieving 1992). During the past few decades, many avian nest predators have expanded their distribution into urban environments

[1] Received 8 December 1999. Accepted 6 July 2000.
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(Gregory and Marchant 1996, Jokimäki 1996). The increase of these predators in urban environments is expected to result in elevated nest predation rates, which in turn may result in the decline of some prey species.

The aim of this study was to explore the intensity of nest predation pressure on birds, and patterns among nest predation risk and avian assemblage organization along the spatial gradient of urbanization in three towns in northern Finland. We conducted artificial nest predation experiments and nest predator surveys to assess the relative risk of nest predation along an urban gradient from an uninhabited forest to the town center.

METHODS

STUDY AREA

The study was conducted in northern Finland in the towns of Rovaniemi (66°32′N, 24°12′E), Oulu (65°00′N, 25°28′E), and Kemijärvi (66°45′N, 27°30′E). The human population of Rovaniemi is approximately 35,000 (density of people in the town center being about 1,000 km^{-2}), in Oulu it is approximately 110,000 (2,000 km^{-2}), and in Kemijärvi approximately 12,300 (500 km^{-2}). In each of the towns studied, we divided the town area into two separate study sites: the town center and the area of detached houses based on the level of urbanization using aerial photographs (scale 1:5,000). This classification was based on building structure (block-of-flats or detached houses), proportion of green areas, and location (town center or residential periphery). The town centers were the most urbanized areas, consisting of blocks of flats (3–7 stories high), streets, and urban parks. The areas of detached houses were less urbanized areas located at the periphery of the town and comprised of one-story houses, gardens, parks, and streets. Each of the three towns had two categories of parks: managed (that is, parks which have shrub and small tree plantations, hedges, etc., and that are continuously tended as regards lawn mowing and shrub clipping by gardeners) and unmanaged parks (green areas with more natural vegetation; grasses, shrubs, and trees). In general, unmanaged parks were characterized by their higher numbers of trees and shrubs, and their higher field layer vegetation and its coverage relative to managed parks (Table 1). Parks were bounded by roads and buildings. The size range of the study parks used in the artificial nest experiment was 0.25–11.5 ha ($\bar{x} \pm SD = 1.7 \pm 2.4$ ha, $n = 53$) in Rovaniemi, 0.1–20.0 ha (2.1 $\pm$ 3.7 ha, $n = 52$) in Oulu, and 0.1–3.0 ha (0.8 $\pm$ 0.8 ha, $n = 32$) in Kemijärvi. Park size did not differ between study towns ($F_{2,137} = 2.1$, $P > 0.10$). The surrounding forest areas of the town were used as comparisons at Rovaniemi and at Kemijärvi. These forests were dominated by scots pine (*Pinus sylvestris*) (Table 1).

URBANIZATION AND NEST PREDATION RISK

At Rovaniemi, artificial nest experiments were carried out in 1993 and 1996–1998. In 1993, the town area (town center and the area of detached houses) and the surrounding uninhabited forest area were used in the study. In 1996–1998, the experiment was carried out only within the town area. In Oulu, these experiments were carried out in the town area in 1995. In Kemijärvi, they were carried out in the town area in 1996–1997 and also in the surrounding forest area in 1996. Thus, not all experiments were performed in all sites at the same time. Most of the work was conducted in the town of Rovaniemi and the other two towns were used as confirmation studies.

One nest with a Japanese Quail (*Coturnix coturnix japonicus*) egg was placed in the center of each park in the town center and in the area of the detached houses, except in 1993 in Rovaniemi where two eggs were placed in each nest. Nests in the forest area were placed both at the forest edge and in the interior (200 m from the edge) of large ($\geq$12 ha) blocks of forest. A nest was a handmade cup in the soil without any particular constructions. Nests were placed on leaf litter, directly on the ground, under a small tree or shrub, which covered nests directly from above and exposed the nests in the other directions. The nest sites mimicked the nest sites of many ground-breeding birds (e.g., buntings). No nest markers were used. To reduce human scent at nests, we wore rubber boots and gloves when setting nests and checking them. All the experiments were started at the beginning of June, which is the laying time of most bird species in the study region. The situation prevailing after 21 days of exposure was considered to be the final result in all the experiments. This period included 7 days of laying and 14 days of incubation, typical for many ground-nesting passerines in Finland (Solonen 1985). A nest was scored as having been preyed upon if one or

TABLE 1. Means (± SD) of the vegetation characteristics in the surroundings of each artificial nest in the Rovaniemi area. P values are reported after using the sequential Bonferroni technique.

	Town center (n = 35)	Detached houses area (n = 18)	Forest area (n = 20)	Managed parks (n = 34)	Unmanaged parks (n = 19)	Mann-Whitney U-tests		
						P^a	P^b	P^c
Park area (ha)	1.0 ± 1.3	3.1 ± 3.6	—	1.2 ± 1.6	2.8 ± 3.6	—	ns	ns
Scots pine	0.2 ± 0.6	1.3 ± 1.8	3.0 ± 2.7	0.2 ± 0.7	1.3 ± 1.7	<0.01	<0.05	<0.01
Norway spruce	0.2 ± 0.9	0.2 ± 0.5	0.3 ± 0.6	0.0 ± 0.2	0.4 ± 1.2	ns	ns	ns
Deciduous trees	1.4 ± 1.6	4.6 ± 4.7	0.2 ± 0.7	1.4 ± 1.9	4.4 ± 4.5	<0.01	ns	<0.05
Deciduous shrubs	7.5 ± 7.8	10.4 ± 9.8	1.0 ± 2.7	4.8 ± 6.0	15.6 ± 8.1	<0.01	ns	<0.01
Herbs (%)	16.4 ± 33.0	52.2 ± 37.2	80.8 ± 24.7	12.3 ± 28.9	57.6 ± 35.8	<0.01	<0.01	<0.01
Bare ground (%)	51.2 ± 39.0	6.1 ± 12.0	4.8 ± 16.0	24.5 ± 37.0	5.5 ± 10.7	ns	ns	ns
Distance to 5 nearest trees from nest (m)	6.8 ± 5.3	3.9 ± 4.0	3.5 ± 2.6	7.5 ± 5.5	2.8 ± 1.8	ns	ns	<0.01
Tree layer 2–5 m	0.5 ± 0.9	3.1 ± 4.9	2.4 ± 2.1	0.4 ± 0.8	3.1 ± 4.7	<0.01	ns	ns
Tree layer >5–10 m	0.9 ± 1.0	1.9 ± 3.0	1.0 ± 1.1	1.0 ± 1.8	1.7 ± 2.5	ns	ns	ns
Tree layer >10 m	0.5 ± 1.0	1.0 ± 1.5	0.2 ± 0.4	0.4 ± 0.9	1.2 ± 1.4	ns	ns	ns
No. trees	1.8 ± 1.8	6.1 ± 4.8	3.5 ± 2.6	1.7 ± 2.1	6.0 ± 4.4	ns	<0.01	<0.01
Tree cover (%)	35.3 ± 30.1	38.1 ± 25.6	20.8 ± 17.8	29.0 ± 27.5	49.1 ± 26.0	ns	ns	ns
Shrub cover (%)	34.7 ± 28.3	40.0 ± 23.5	9.4 ± 15.1	30.9 ± 28.1	46.6 ± 21.1	<0.01	ns	ns
Nest cover (%)	64.6 ± 36.5	76.7 ± 31.4	48.9 ± 38.3	65.4 ± 35.2	74.5 ± 35.0	ns	ns	ns
Ground layer (cm)	15.8 ± 21.9	41.9 ± 27.3	13.9 ± 7.1	12.6 ± 19.4	46.3 ± 24.6	ns	<0.01	<0.01
Visibility of nest (m)	3.2 ± 2.7	1.1 ± 0.4	1.4 ± 1.0	3.2 ± 2.7	1.2 ± 0.6	ns	<0.01	<0.01

[a] Denotes comparisons between town (town center and areas of detached houses pooled) and forest area.
[b] Denotes comparisons between town center and area of detached houses within a town.
[c] Denotes comparisons between managed and unmanaged parks.

both eggs had disappeared or had been broken. Artificial nest experiments were not repeated during the breeding season because in the study areas birds seldom breed twice during one season.

In order to obtain data on the predators responsible for consuming eggs from artificial nests, we carried out a test in the town of Rovaniemi in 1998 by using plasticine eggs. Each nest (n = 50) contained one such quail-sized egg painted to resemble a brown spotted quail egg. The study design was the same as in the other experiments of this study. Plasticine fragments left in the nests were examined and compared with a reference collection of plasticine eggs attacked by known predators (Groom 1993).

VEGETATION MEASUREMENTS

We collected information on the vegetation characteristics of the urban and forest sites only from Rovaniemi, but the vegetation structure of the variously urbanized areas in the towns was basically similar in Oulu and Kemijärvi (pers. observ.). All the vegetation measurements were made in July 1993, immediately following the nest predation experiment and by the same researcher. The vegetation measurements were made using a nest-centered circular plot (3-m radius, area 28 m^2) on all the nest sites in the parks included in the study (n = 35 for town center, and n = 18 for detached house area) and in 20 randomly selected nest sites in the surrounding forest area. The tree-stem frequency distribution series for pine, spruce, and deciduous trees were determined by height class (2–5 m, >5–10 m, and >10 m). The numbers of pine, spruce, and deciduous saplings or shrubs (<2 m) were determined. The distances to the five nearest trees from the nests were measured and their average was determined. The canopy cover of the trees (%) and nest cover (%) above each nest were estimated through a cardboard tube (10 cm long × 4 cm in diameter) by looking directly up from a height of 1.7 m. The canopy cover of trees was measured in four main directions from the arc of the 3-m radius vegetation measurement plots; these four measures were then averaged. The area covered by herbs and grasses, and the proportion of bare ground in the surroundings of the nest site were estimated by using 1 m × 1 m plot centered on the nest. The height of the ground layer vegetation also was measured. The horizontal visibility of each nest was measured by walking along transects starting from the nest site along the four main compass directions and noting when the nest disappeared from view (measured in meters). The mean value of these four measurements was used as the visibility index for each nest. In general, deciduous trees and shrubs dominated the urban study sites, and the shrub cover was greater in the parks than in the forests (Table 1). The total amount of trees and herb cover were lower in the town center than in the area of detached houses (Table 1). The visibility of artificial nests was greater in the town center than in the area of detached houses (Table 1).

In Rovaniemi in 1997, we studied the relationship between nest visibility and predation risk by setting up three different types of nests (covered, uncovered, and control nests; n = 38 for the each type of nest) baited with one Japanese Quail egg and placed in each of the study parks. The distance between the different types of nests in these parks was about 50 m. All the nests were placed on the ground at the base of a tree or a shrub. The covered nests were hidden by the field layer of vegetation, the uncovered nests were placed without any or with little covering vegetation, whereas the control nests were placed in a normal position as in the other experiments in this study (i.e., sites partly covered from the side, from above, etc.). The horizontal visibility of the nests was measured by human eye after the establishment of the experiments. The horizontal visibility was lower in the covered nests ($\bar{x} \pm SD = 1.4 \pm 0.6$ m, n = 38) than in the control nests (3.6 ± 0.8 m, n = 38) or in the uncovered nests (5.0 ± 1.0 m, n = 38, Kruskal–Wallis one-way ANOVA, $\chi^2_2 = 90.7$, $P < 0.001$, pairwise comparisons by Tukey-type nonparametric test, $P < 0.05$; Zar 1984).

BIRD SURVEYS

Birds were surveyed in Rovaniemi (1996–1997), Oulu (1995), and Kemijärvi (1997) in the parks used in the nest predation experiments. Bird abundance was determined by the point-count method (Hildén et al. 1991). One survey station was located in the center of each park, and all birds seen or heard within the park boundaries were recorded during a 5-min count between 04:00 and 08:00. Whenever we were sure that a bird had already been observed, it was not included in the results for the second time. Overflying birds that did not land in the study area and obvious feeding visitors also were excluded. In order to avoid interobserver bias, all the surveys were made by the same person (J. Jokimäki).

Data on the regional abundance (i.e., abundances of birds in the surrounding forest area of the town) of the breeding bird species were collected from the forest area in Rovaniemi in 1990–1995 using the point-count census method as described above. A total of 93 census points were visited each year, and the same census points were used each year. Censuses in the forest were carried out between 4 June and 2 July between 04:00 and 08:00. Data from six years were then combined, and an average value was obtained for each species. A detailed description of the forest study area and study design can be found elsewhere (Jokimäki and Huhta 1996). The bird species recorded in each survey were grouped according to their breeding habits into three nesting guilds: ground-nesters, shrub- or tree-nesters, and hole-nesters (Harrison 1975). These raw data are available by request from the authors.

NEST PREDATORS AND HUMAN ACTIVITY

Potential nest predators, including the Magpie (*Pica pica*), the Hooded Crow (*Corvus corone cornix*), the Great-spotted Woodpecker (*Denrocopus major*), gulls (*Larus* spp.), and the red squirrel (*Sciurus vulgaris*), were surveyed in Rovaniemi (1996–1997), Oulu (1995), and Kemijärvi (1997) in the parks where the artificial nest experiments had been set up. Nest predators were counted in the center of each park by single-visit point-count method lasting 5 min between 04:00 and 08:00. Gulls and red squirrels were not encountered in Oulu.

In Finland, foxes (*Vulpes vulpes*), shrews (*Sorex* spp.), and voles (*Microtus* spp.) occur only seldom in town areas (Liukko 1990). No special night-time surveys or other suitable samplings for foxes, stray cats, or small predatory mammals were performed. Humans and their domestic animals (dogs) also can destroy nests. Assessments of human activity were made only in Rovaniemi (1996) in the parks used in the nest predation experiments. The level of human activity was assessed in each park in the course of 5-min counts focusing on number of visiting people and dogs at 09:00–16:00. To eliminate the day-of-the-week effect on the data recorded, all these counts were done on the same day, 19 June. To avoid interobserver bias, all the census were made by the same person.

Data on the abundances of avian nest predators (Hooded Crow, Magpie, Common Raven *Corvus corax,* Siberian Jay *Perisoreus infaustus,* Eurasian Jay *Garrulus glandarius,* and Great-spotted Woodpecker) in the surrounding forest area of Rovaniemi were collected during 1990–1995 by means of a single-visit point-count method between 04:00 and 08:00.

STATISTICAL ANALYSES

Nonparametric tests were used in comparing the abundance of breeding bird assemblages, nest predator abundances, and habitat structure between town centers, detached house areas, and forest areas. When using multiple tests, the Bonferroni correction was made to minimize tablewise errors (Rice 1989). In the nest predation experiments, the effects of park location and park type on nest predation were examined using the *G*-test. The effects of vegetation characteristics on nest loss were analyzed using stepwise logistic regression (Hosmer and Lemeshow 1989, Trexler and Travis 1993). Two, forward stepwise logistic-regression models were constructed, one for habitat structure and one for vegetation composition. The variables used in the first model were area of park, management status of park (managed/unmanaged), number of trees in the three height categories surrounding the nest site, mean distance of the five nearest trees to the nest, vegetation cover above the nest, canopy cover provided by trees, cover provided by shrubs, visibility of the nest, number of shrubs, and height of the field layer surrounding the nest site. The variables in the second model included the numbers of pine, spruce, and deciduous trees, numbers of pine, spruce, and deciduous shrubs, coverage of herbs and grasses, and proportion of bare ground. The significance level required for each variable to enter the analysis was 0.10 in both models.

The relationships between park location, park status (managed vs. unmanaged), and nest type (covered, control, uncovered) on nest predation were studied using multiple logistic-regression analysis. The values reported below in the Results section are mean ± SD if not otherwise stated.

TABLE 2. The percentage (and sample size) of the artificial ground nests preyed upon in the three study towns.

Study town	Urbanization level: Town center	Urbanization level: Detached houses area	G_1	P
Rovaniemi[a]	79.3 (95)	20.7 (83)	48.4	<0.001
Oulu	76.7 (30)	36.4 (22)	8.7	<0.01
Kemijärvi	69.2 (10)	22.2 (22)	7.0	<0.01

[a] At Rovaniemi, pooled data from different study years are used.

RESULTS

URBANIZATION AND NEST PREDATION RISK

Nest predation rates in both Rovaniemi and Kemijärvi were higher in the town area than in the surrounding forest area (Rovaniemi: 40%, $n = 53$ and 4%, $n = 53$, respectively; $G_1 = 20.1$, $P < 0.001$; Kemijärvi: 70%, $n = 33$ and 0%, $n = 30$; $G_1 = 36.7$, $P < 0.001$). At the town of Rovaniemi, nest predation rate did not differ between study years (33%, 50%, 56%, and 53%; $G_3 = 5.4$, $P = 0.15$) and quail eggs suffered same rates of predation as plasticine eggs (quail eggs 46%, plasticine eggs 52%; $G_1 < 0.1$, $P = 0.85$). Therefore, we pooled the data from different study years for subsequent analyses. Nest predation rate did not differ between study towns (Rovaniemi 48%, Oulu 57%, and Kemijärvi 46%; $G_2 = 4.0$, $P > 0.10$). Nest predation rate in all three towns was higher in the town center than in the area of detached houses (Table 2).

At Rovaniemi, nest predation rate was higher in managed than in unmanaged parks during each year (1993: managed parks 53%, $n = 34$, and unmanaged parks 16%, $n = 19$, $G_1 = 7.0$, $P < 0.01$; 1997: 92%, $n = 24$ and 14%, $n = 14$, $G_1 = 24.8$, $P < 0.001$; 1998: 66%, $n = 32$ and 22%, $n = 18$, $G_1 = 9.1$, $P < 0.01$). The data for 1996 did not allow this kind of comparison. Similar results also were obtained both in Oulu and Kemijärvi (Oulu: managed parks 72%, $n = 29$ and unmanaged parks 44%, $n = 23$, $G_1 = 4.5$, $P < 0.05$; Kemijärvi: 67%, $n = 10$ and 26%, $n = 22$, $G_1 = 5.0$, $P < 0.05$).

In Oulu and Kemijärvi, the proportion of managed and unmanaged parks did not differ between the town center and the area of detached houses. In the case of Rovaniemi, there may have been some interaction between the park location and park status on nest predation rate because the distribution of managed and unmanaged parks differed between study sites (the proportion of managed parks in the town center was 74%, $n = 35$, and that in the area of detached houses 39%, $n = 18$, $G_2 = 9.2$, $P < 0.05$). Consequently, at Rovaniemi, we compared predation risk in managed and unmanaged parks separately in relation to park location. The predation rate in the managed parks was higher in the town center than in the area of detached houses (1993: town center 63%, $n = 27$ and area of detached houses 14%, $n = 7$ preyed upon, $G_1 = 5.3$, $P < 0.05$; 1997: 95%, $n = 19$, and 41%, $n = 5$, $G_1 = 7.1$, $P < 0.05$; 1998: 81.0%, $n = 21$ and 36.4%, $n = 11$, $G_1 = 6.3$, $P = 0.01$). Among unmanaged parks, predation rate did not differ between town center and the area of detached houses in Rovaniemi.

The class of predator (avian, mammalian, human) could be identified from imprints left in plasticine eggs for 42% (11 of 26) of nests attacked. There was a significant difference between the town center and the area of detached houses in the number of plasticine eggs destroyed by avian and mammalian predators (town center: birds 35.3%, mammals 0%, $n = 17$; area of detached houses: birds 11.1%, mammals 44.4%, $n = 9$, $G_1 = 9.4$, $P < 0.01$). Plasticine eggs in three nests located in the area of detached houses and one nest in the town center bore marks left by humans. Plasticine eggs were missing from 10 nests in the town center and from 1 nest in the area of detached houses.

VEGETATION STRUCTURE AND NEST PREDATION

According to the stepwise logistic regression analysis, a high field layer of vegetation ($\beta \pm SE = -0.52 \pm 0.02$, Wald $\chi^2 = 7.1$, $P < 0.01$) decreased the frequency of nest loss. High numbers of pines ($\beta \pm SE = -0.94 \pm 0.53$, Wald $\chi^2 = 3.0$, $P < 0.1$) and deciduous trees ($\beta \pm SE = -0.25 \pm 0.15$, Wald $\chi^2 = 3.0$, $P < 0.1$) de-

TABLE 3. The mean (± SE) numbers (pairs park^{-1} 5-min^{-1}) of birds according to their breeding habit and nest type in the different study sites. Statistical differences tested by the Kruskal-Wallis ANOVA and a Tukey-type nonparametric test (paired comparisons, $P < 0.05$) in Rovaniemi and by Mann-Whitney U-test in Kemijärvi and Oulu. C = town center, D = area of detached houses, F = forest area in paired comparisons.

	Urbanization level				
Study site	Town center	Area of detached houses	Forest area	P	Paired comparisons
Rovaniemi[a]	$n = 19$	$n = 17$	$n = 93$		
Ground nesters	0.03 ± 0.03	1.32 ± 0.18	3.66 ± 0.07	<0.001	F > C, F > D, D > C
Hole nesters	0.59 ± 0.15	1.22 ± 0.21	1.30 ± 0.05	<0.001	F > C
Tree or shrub nesters	0.89 ± 0.15	2.86 ± 0.66	3.82 ± 0.09	<0.001	F > C, F > D, D > F
Kemijärvi	$n = 10$	$n = 22$			
Ground nesters	0.30 ± 0.15	1.50 ± 0.23	—	<0.001	D > C
Hole nesters	0.80 ± 0.33	1.00 ± 0.22	—	ns	
Tree or shrub nesters	2.50 ± 0.62	2.36 ± 0.42	—	ns	
Oulu	$n = 30$	$n = 22$			
Ground nesters	0.62 ± 0.12	1.80 ± 0.46	—	0.02	D > C
Hole nesters	0.87 ± 0.15	1.67 ± 0.40	—	ns	
Tree or shrub nesters	2.49 ± 0.68	3.60 ± 0.89	—	ns	

[a] At Rovaniemi, pooled data from different study years are used.

creased predation risk (whole model $G_2 = 11.5$, $P < 0.01$).

The nest cover experiment revealed that covered nests were preyed upon less frequently than uncovered and control nests (nest type: $\beta \pm$ SE $= 1.79 \pm 0.45$, Wald $\chi^2 = 16.1$, $P = 0.001$). However, based on the main-effect model of the logistic regression analyses, park location ($\beta \pm$ SE $= 1.90 \pm 0.68$, Wald $\chi^2 = 7.7$, $P < 0.01$) and park type ($\beta \pm$ SE $= -2.66 \pm 0.75$, Wald $\chi^2 = 12.4$, $P < 0.001$) also affected nest predation rate (whole model $G_2 = 70.1$, $P < 0.001$). Therefore, we conducted a second analysis with interaction terms. In this analysis, interaction terms park location × nest type and park type × nest type were nonsignificant, indicating that nest cover affected nest predation rate similarly and was independent of park location and park type. Thus, nests were significantly more vulnerable to predation if they were situated in managed parks in the town center and if the nest was inadequately covered by vegetation.

BREEDING BIRD COMMUNITY STRUCTURE

A total of 30 species were found to breed in the three towns studied, and only 6 of them were ground-nesters. At Rovaniemi, the abundance of ground-nesters was lower in the town center than in the area of detached houses and the forest (Table 3). In Oulu and Kemijärvi, the abundances of ground nesters also were lower in the town centers than in the areas of detached houses (Table 3). The abundance of hole nesters did not differ between the town center and the area of detached houses in any study town (Table 3). The results did not change if we adjusted abundances by the area sampled. Only three ground-breeding species were found nesting in the town centers: Wheatear (*Oenanthe oenanthe*), Willow Warbler (*Phylloscopus trochilus*), and Yellowhammer (*Emberiza citrinella*).

ABUNDANCE OF NEST PREDATORS

The abundance (individuals park^{-1} 5-min^{-1}; $\bar{x} \pm$ SE) of Magpies was higher in the town center than in the area of detached houses in each of the three towns studied (Rovaniemi 0.76 ± 0.10 vs. 0.27 ± 0.07, respectively; Oulu 0.85 ± 0.14 vs. 0.29 ± 0.11; Kemijärvi 1.10 ± 0.23 vs. 0.32 ± 0.10, Mann–Whitney U-tests, $P < 0.05$, $P < 0.02$, and $P < 0.01$, respectively). In Oulu, the Hooded Crow was more abundant in the town center (1.10 ± 0.14) than in the area of detached houses (0.47 ± 0.12, $P < 0.05$). No such difference was observed in other study towns. In both Rovaniemi and Kemijärvi, where Black-headed Gulls were surveyed, gulls were more abundant in the town center (Rovaniemi 1.86 ± 0.42, Kemijärvi 0.30 ± 0.21) than in the area of detached houses (0.00 ± 0.00, $P < 0.001$; 0.00 ± 0.00, $P < 0.05$, respectively). Abundance of the red squirrel (Rovaniemi and Kemijärvi; not surveyed in Oulu), visiting people (Rovaniemi; not surveyed in other study towns), and dogs

(Rovaniemi; not surveyed in other study towns) did not differ between the town center and the area of detached houses. No stray cats were observed in the towns.

The abundances of Magpies, Hooded Crows, and Black-headed Gulls were lower in the forest area surrounding Rovaniemi than in the town area of Rovaniemi (Magpies: forest 0.02 ± 0.01, center 0.76 ± 0.10, and area of detached houses 0.27 ± 0.07; Hooded Crows: forest 0.15 ± 0.02, center 0.38 ± 0.10, and area of detached houses 0.27 ± 0.09; Black-headed Gulls: forest 0.00 ± 0.00, center 1.86 ± 0.42, and area of detached houses 0.00 ± 0.00; all $P < 0.05$, except Black-headed Gulls comparison between the forest and area of detached houses, where $P > 0.05$). The abundances of Raven, Siberian Jay, Eurasian Jay, and Great-spotted Woodpecker did not differ between the town center, area of detached houses, and forest area in Rovaniemi.

DISCUSSION

NEST PREDATION RATE IN URBAN ENVIRONMENTS

Nest predation rates measured by artificial nests were higher in the towns than in the adjacent forest. Within the town area, nest predation risk increased from the less urbanized areas towards the town center. These observations were similar in each of the three towns studied. Furthermore, we found that predation patterns in the urban study sites were constant from year to year. According to Sasvári et al. (1995), Major et al. (1996), Matthews et al. (1999), and our results, nest predation risk may be very high in highly urbanized areas. Gering and Blair (1999) concluded that predation pressure on artificial nests decreased with urbanization. However, they looked at different land uses (a business district, apartment complex, residential areas, etc.) but not a similar habitat type (parks) surrounded by different land uses (town center, detached houses) as we did. Apparently, nest predation pressure also is influenced by the structure of the local predator community.

Based on the plasticine egg experiment, most of the nest damage in the town centers was attributed to avian nest predators. In the other studies, avian nest predators have been identified as main nest predators in urban environments (Groom 1993, Major et al. 1996, Matthews et al. 1999). Mammalian nest predators, such as stray cats (*Felis domesticus*) and foxes, have been shown to reduce the nesting success of ground-nesting birds in many towns (Gilbert 1989). However, no stray cats or foxes were detected in the towns included in our study, and they are, in general, also rare in other Finnish towns (Liukko 1990). The red squirrel was the only mammalian nest predator detected in our surveys. The abundance of red squirrels did not differ between the town center and the detached houses area in our study. However, our experiment with the plasticine eggs showed that mammals destroyed nests mainly in the areas of detached houses, and so their importance in nest predation might be more pronounced in less urbanized areas and in forests. Unfortunately, we were unable to identify mammalian predators responsible for nest losses.

Thus, in this study, the increased nest predation rate focusing on the ground-nesting birds in our town center sites was mainly due to avian nest predators. In all towns studied, the numbers of generalist avian nest predators (magpies and gulls) were higher in the town center than in the areas of detached houses and in the uninhabited forests. There was no marked temporal variation in this pattern as revealed by our comparison of consecutive years in Rovaniemi. Anthropogenic wastes and feeding in urban landscapes may help to maintain high densities of corvids (Väisänen 1994). Our results clearly indicate that nest predation pressure on artificial ground nests increased in parallel with avian nest predator abundance.

Nest predation rates were higher in managed than in unmanaged parks. 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, correspondingly, enhanced nest predation risk in managed parks relative to unmanaged parks. The structural simplicity of the vegetation may increase nest predation rates in town parks as well as a consequence of intensive park management. Our results on the role of nest visibility in regard to predation risk also support this view. Because we placed the artificial nests, vegetation characteristics and visibility measurements were influenced by human placement. The relative exposure of real nests may be lower than our artificial nests (1–5 m). Thus, our method was perhaps not fully appropriate when assessing conspicuousness of nests to different predator groups.

In urban areas, where the sparse vegetation cover provides little protection, the high visibility of nests may increase the risk of predators discovering the nests. The results obtained underline the importance of sheltering vegetation and nest cover in birds selecting their nest sites and of nest-predation risk. However, in the managed parks, nest predation rates were higher in town centers than in the areas of detached houses. This indicates that there was a clear location effect in nest predation, and this was associated with extremely high nest losses caused by avian nest predators in managed parks located in heavily-urbanized areas.

The use of artificial nests in predation studies has been criticized because predation intensity may differ from that of natural nests (Haskell 1995a). However, standardized sampling with artificial nests provides reasonable information on the potential risk of nest predation in different habitats (Wilcove 1985). In the present study, we used artificial nests of a similar design in the different study areas, and we assumed that the effect of our experimental procedure was more or less the same between the study sites. Furthermore, we used artificial nests because they provide information on the potential risk of nest predation in different habitats even though the relative predation rate may not be similar for natural and artificial nests. Another controversy surrounding the use of quail eggs is that they could be too large for some potential nest predators (Haskell 1995b). However, in our study towns, the main nest predators were large-gaped animals (magpies, crows, and squirrels), which certainly are able to take quail eggs.

NEST PREDATION RISK AND URBAN BIRD COMMUNITIES

Birds have been shown to avoid breeding areas characterized by high direct predation risk (Suhonen et al. 1994). Nest predation also has been suggested to influence bird assemblages, although direct evidence is somewhat lacking (Martin 1988). Our results agree with these ideas. Artificial nest predation rates were high and the abundance of ground-breeding birds was low in parks in town centers. Low numbers of ground breeders in urban bird communities also have been observed in other studies (Suhonen and Jokimäki 1988, Jokimäki 1996, 1999). These studies have indicated that many ground-nesting bird species are more abundant in the surrounding forest area than in the town, and within the town, ground nesters are more abundant in unmanaged parks than in managed parks.

The lack of coexisting species in the nesting guilds of ground nesters in areas with apparently high intensities of nest predation support this conclusion. Ground-nesting species, such as buntings (*Emberizidae*) and the Tree Pipit (*Anthus trivialis*), are practically absent from most urbanized study sites (Jokimäki 1996). The only abundant ground-breeder in the town centers was the Willow Warbler. Buntings and Tree Pipit, with their covered nest type, may suffer less intensive nest predation than other ground-nesters with open cup nests (Møller 1989). The same apparently is true of the Wheatear, which mainly breeds in protected holes in rock cavities. However, exploration of the hypothesis that nest predation is a reasonable mechanism for breeding-habitat selection by ground breeding birds in northern Finnish towns does not exclude alternatives. For instance, disturbance by humans, amount of food, food-based competition, lack of suitable nest sites, high management level of the parks, and recreational activities may work in concert to increase nest predation and affect bird populations in urban environments.

ACKNOWLEDGMENTS

R. Blair, B. Forbes, P. Helle, M. Mönkkönen, and an anonymous reviewer provided insightful comments on the manuscript. The study was financially supported by the Emil Aaltonen Foundation (support granted to E.H.) and by the Finnish Cultural Foundation (support granted to J.J.).

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