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Effects of urbanization on nest site selection and nesting success of the Greenfinch *Carduelis chloris* in Krotoszyn, Poland

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Nest success was studied in relation to nest-height and urban gradient at 313 Greenfinch nests in Krotoszyn (western Poland). The nests were grouped according to three height-categories: low (≤ 2.5 m), medium (2.5 m < h ≤ 3.5 m) and high (> 3.5 m). The three sites were selected to represent different intensities of human development (low, medium and high). Nesting success estimated by Mayfield and the 'traditional' method was highest in the height-interval above 3.5 metres. The probability of nest survival was 37% and 39% in low and medium nests and 82% in high nests. The daily survival rate of low and medium nests was significantly lower than in high nests. This preference could serve the nests to evade mammalian predators, most probably domestic cats. Nest success estimated across an urban gradient was higher in the site of high intensity human development than in other sites. The differences estimated using the 'traditional' method were significant. However, the daily survival rate between these three sites was non-significant. There were more nests than expected in the site of high intensity human development, and less than expected in the site of lower intensity urban gradient. These data confirm the 'safe zones' hypothesis that as the intensity of urbanization increases the frequency of predation decreases.

1. Introduction

Populations of some birds may reach distinctly higher densities in urban areas than in more natural sites (Tomiałojć 1980, 1982, 1998, Mills *et al.* 1989, Jokimäki *et al.* 1996, Gering & Blair 1999). This phenomenon could be attributed to the ability to adapt to some features of urbanization in spite of the negative aspects of habitat patchiness, scarcity of natural components of ecosystems and human activity. Urbanization offers more positive elements such as increased volume of exotic vegetation and as a consequence, abundant roosting and nesting sites, winter feeding and a lack of natural predators (Bessinger & Osborne 1982, Mills *et al.* 1989, Tomiałojć 1998). Predation is the most important cause of reduced nesting success in land birds (Ricklefs 1969). The frequency of nest predation has been shown to be related to nest-height (Dyrcz 1969, Martin 1993, Ludvig *et al.* 1995), size of habitat patches, plant type and nest concealment (Furrer 1980, Martin & Roper 1988, Møller 1988, 1991, Tryjanowski *et al.* 2000), as well as distance from human disturbance (Osborne & Osborne 1980). Urban environments are considered as 'safe zones' with low predation pressures, as an effect of the low abundance of natural predators (Tomiałojć 1982, Gering & Blair 1999). On the other hand, Sasvári *et al.* (1995), Matthews *et al.* (1999) and Jokimäki and Huhta (2000) found, on the basis of artificial nests, that the nest predation risk was higher in highly urbanized areas. However, these studies may give a false picture of predation pressure (Major & Kendal 1996, Wilson *et al.* 1998, King *et al.* 1999, but see Martin 1987) and therefore a study of natural nests would be valuable.

In this paper, the nesting success of Greenfinches *Carduelis chloris* according to nest-height and urban gradient was investigated. According to the 'safe zones' hypothesis two predictions were tested: 1) if urbanized areas are 'safe zones' the nesting success should increase as the intensity of urbanization increases; and 2) the density of breeding pairs should increase as urbanization intensity increases, while other factors which may determine breeding density e.g. food availability and number of suitable nest sites are equal.

2. Materials and methods

2.1. Study area

The study was carried out in Krotoszyn (51°41′N, 17°26′E, western Poland). Krotoszyn is a town of medium-size with an area of 23 km^2 and is inhabited by nearly 29 000 people. A detailed study on Greenfinch ecology was carried out on a 44 ha plot. This area presents a mosaic of variously aged housing estates and built-up industrial areas (19 ha, 56.8% of the total area), tree-covered areas, e.g. taller greenery of a park-like character, alleys and street trees, small squares (13 ha, 29.5%) and barren (rural) areas (6 ha, 13.6%). The most characteristic element of plant coverage are the street trees and alleys with hawthorn *Crataegus* sp. up to 4.5 metres in height. The total length of streets with this type of vegetation is ca 1 km. Additionally, ca 0.15 km of street trees are covered by Norway maple *Acer platanoides* and False acacia *Robinia pseudoacacia*. These trees are distributed evenly ca every 4.5 meters. The hawthorn crowns were cut off yearly in mid July, except 1998. After that the crowns took on a spherical shape. The diameters of the crowns were no more than 2.5 m. The study plot was limited or crossed by communication routes with high vehicular traffic and a railway line.

Data was collected between 1994 and 1998. Regular searches of the study area from mid April to the end of July resulted in the collection of data from 342 nests, from which 313 were considered as completed (since females started egg laying). Nests abandoned by females before egg-laying were not included in the analysis of nesting success. The position of each nest was marked on a map, the tree species was identified and the heights of the nests were measured using the metre stick to the nearest 5 cm under 4 m and to the nearest 0.5 m above it. To avoid excessive disturbance of nests they were checked no more than twice a week.

To determine the effect of intensity of urbanization on nest success, three sites representing different intensities of human development (low, medium and high) were selected within the study area using an aerial photograph (scale 1:3500, see Kosiński 2000a). As 89% of all nests (n = 342) were built on similar arranged street trees (Kosiński 2001), the selection of sites was based on the immediate surroundings: proportion and building structure adjoining the street trees, proportion of green areas and location (from periphery to center). The proportion of built-up and green areas was measured in a 50 m strip along both sides of the streets using a digitising pad. Jokimäki (1999) has suggested that local habitat factors appear to be more important than broad-scale landscape variables for Greenfinch nest site selection. In the present study habitat factors should be considered as local. The following list contains the description of these sites:

Site I (total length of streets ca 0.41 km) — low intensity human development, situated on the edge of a densely built up area; the street trees surrounded by housing estates (blocks of flats — 4 stories high) on one side and by lawns and rural areas with single low buildings on the other side. The percentage of area covered by built-up and green areas comprised 42% and 58% of the total area, respectively. Rural areas may act as corridors for mammalian predators from suburban areas.

Site II (ca 0.32 km) — medium intensity of human development; a wide strip of greenery (up to 100 meters), small squares and park-like patches adjoined throughout its length by street trees. The percentage of built-up and green areas was 40% and 60%, respectively. The area is surrounded by a railway, a bus station, housing estates (blocks of flats — 5 stories) and industrial built-up areas and thus isolated from suburban areas.

Site III (ca 0.42 km) — high intensity of human development, situated nearest to the city center; the street trees surrounded by housing estates (blocks of flats — 3–4 stories), industrial built-up areas and one isolated park-like patch (ca. 1 ha) adjoining the city center. The percentage of built-up and green areas was 80% and 20%, respectively.

2.2. Data analysis

According to the distribution of the nests, three height-categories were used: low (≤ 2.5 m), medium (2.5 m < h ≤ 3.5 m) and high (> 3.5 m). Nests with a known history were considered in the analysis (n = 299). In both the cases of nest-height and urban gradient, the effects of the year and season were taken into consideration. On the basis of the phenology of the breeding season and observations of individually marked birds, the breeding season was divided into two parts (Kosiński 2001). It was assumed that clutches produced until 25 May were first clutches and after this date were second (this includes replaced clutches).

Nest success was estimated by the 'traditional' method, as the percentage of observed nests which were successful. A nest was considered to be successful if at least one nestling survived 12 days. The most frequent cause of nest loss was predation (39% of 313 nests). Though the predation events were not recorded directly the identifyng of the predators was inferred from nest appearance and the presence or absence of eggs/nestling remains. Nest abandonment accounted for 14% of failure and infertility for only 1%. A detailed description of nesting failures is given by Kosiński (2001). The 'traditional' estimator of nest success may be severely biased because unsuccessful nests are less likely to be found than successful nests. A second measure of nest success was estimated using the Mayfield method (Mayfield 1975). This method takes into account the time span of observation (exposure in nest-days) and allows the calculation of daily survival rate and the probability of the nest's survival from the start of egg laying to the fledging of young. In this case only nests with more than one visit were included in the analysis. To calculate the probability of nest survival, it was assumed that the mean length of the nesting period was 33 days (Kosiński 2001). Error terms (standard error and confidence limit) were calculated from Johnson (1979). Daily survival rates between nest height-categories and sites of different intensities of human development were analysed with the two-tailed z-test. As the repeated use of a statistical test increases the probability of committing a type I error, the level of significance was adjusted to 0.02 using the Bonferroni method. To determine the overall effect of nest-height (NEHEI), intensity of urbanization (URB), year (YEAR) and season (SEAS) on nesting success, as the dependent variable, the logistic regression analysis was used (Hosmer & Lemeshow 1989). In a later analysis, the two-way interactions between significant variables were added into the model. The models were calculated with backward stepwise method. The significance of each variable included in the model was based on the Log Likelihood ratio. As nesting success was significantly lower in 1994 (Kosiński 2001), a double analysis was performed, the first excluding this year, the second using data from all the years. In this way, four logistic regression models were constructed.

The densities of breeding pairs were not measured directly but expressed as a frequency of breeding attempts to the number of the most suitable nest places (number of hawthorns). An examination was made as to whether the distribution of nest frequencies between different zones was evenly spread according to the number of suitable nest places. The expected number of nests was calculated using the contingency table.

The statistics were performed on the basis of the statistical software package STATISTICA (StatSoft, Inc. 2000). The logistic regression analysis was performed using SPSS statistical package (Norusis 1986). Values reported are means ± 1 standard deviations except otherwise stated.

3. Results

3.1. The effects of the predictive variables on nesting success

The logistic regression analysis based on the pooled data from the all years showed that the year, degree of urbanization and nest-height were the important factors affecting nesting success (Table 1). However, when the breeding attempts from 1994 were excluded from the analysis, the only predictive variables were nest height and intensity of urbanization. Nesting success increased with the degree of urbanization and nest height. Both these factors appear to affect nesting success independently. The interaction URB × NEHEI did not affect nesting success. Hence, in further analysis the effect of nest height and the intensity of urbanization on nesting success was estimated separately.

3.2. Nest site characteristics

Of the 299 Greenfinch nests with a known history, 245 (82%) were built in hawthorn. Nine other plant species were adopted; a minority (6%) were placed in maple and a further 6% were built in coniferous trees, mainly on spruce *Picea* spp. The heights of the nests varied slightly over the years from 2.93 ± 0.46 m to 3.24 ± 1.50 m (ANOVA, $F_{4,294} = 0.870$, $P = 0.482$). However, no differences in nest-height between sites which differed in intensity of urbanization were observed (Kruskal-Wallis ANOVA, H = 2.409, P = 0.30). Nest-heights changed from 2.98 ± 0.46 m in the site with a high intensity of urbanization, 3.15 ± 1.49 m in the site with a medium intensity of urbanization to 3.08 ± 0.66 in the site with a low intensity of urbanization. As nest height did not differ between study years and intensity of urbanization, pooled data from the different study years were used in subsequent analyses.

3.3. The effect of nest-height on nesting success

It was found that, independent of the method used and sample size, the nesting success was highest in the height-interval above 3.5 metres (Table 2). The differences between nesting success across the height-categories estimated using the traditional method were insignificant ($\chi^2_2 = 5.24$, P = 0.073). Daily survival rates were similar in low and medium height-categories (z = 0.023, P = 0.982). However, the value calculated for nests found above 3.5 metres differed significantly from both the low (z = 5.03, P < 0.001) and medium placed nests (z = 3.59, P < 0.001). However, some of the higher nests were checked directly only once owing to their inaccessibility and in some cases the duration and outcome of breeding attempts were recorded by observations from the ground. As a result, the analysis presented here may be subject to error. When nesting success for the same nests of known history (n = 26) was compared using both methods, this difference was less marked (probability of nest's survival = 0.81 vs. nesting success = 0.73).

Table 1. Results of the logistic regression analysis of nesting success according to the year, season, intensity of urbanization and nest-height. The significance of each variable is based on Log Likelihood ratio (* = P < 0.1, ** = P < 0.05, *** = P < 0.01).

Variables included/ retained in the model	Variables excluded	χ^2	df	P
All years				
URB*, YEAR***, NEHEI**	SEAS	24.612	3	< 0.0001
NEHEI**, YEAR × URB***	URB, NEHEI × URB, YEAR, NEHEI × YEAR	26.637	2	< 0.0001
1994 excluded				
URB***, NEHEI**	YEAR, SEAS	11.682	2	< 0.01
URB***, NEHEI**	NEHEI × URB	11.682	2	< 0.01

3.4. The effect of urbanization on nesting success

Nesting success showed similar patterns across an urban gradient, independent of the method used, being highest in the site of high intensity human development (Table 3). Daily survival rates between three sites which differed in intensity of urbanization were not significantly different (Low vs. Medium: z = 1.25, P = 0.210, Medium vs. High: z = 0.23, P = 0.819, Low vs. High: z = 1.30, P = 0.195). However, the probability of the nest's survival was clearly higher in the site of high, than in sites with low and medium intensity human development (Table 3). Moreover, the differences between nesting success estimated using the 'traditional' method were statistically significant (χ^2_2 = 7.02, P = 0.03). This pattern was similar over four years, with the exception of 1994. In this year the low frequency of nest success was noted in all parts of the urban gradient and the overall nesting success was markedly lower than in other years (Fig. 1).

3.5. Distribution of nests according to the urban gradient

The way the nests were placed with respect to the intensity of human development deviated significantly from the expected even distribution according to the number of suitable nest sites (χ^2_2 = 7.31, P = 0.05). There were more nests than expected in the site of high intensity human development and fewer than expected in the site of low intensity urban gradient (Table 4).

4. Discussion

4.1. Nest site characteristics and nest success

The results suggested that the frequency of nesting success was higher in the high nests. In most studies where the vertical distribution of nests has been studied it has been found that frequency of nest predation depends on nest height (Dhindsa *et al.* 1989, Martin 1993, Ludvig *et al.* 1995,

Table 2. Nest success calculated using the Mayfield method and the 'traditional' method according to nest-height (see Data analysis). Daily survival rates (DSR), standard errors (SE) and 95% confidence limits (CL) are given. The numbers of clutches inspected are shown in brackets.

Height categories	Mayfield method			Traditional method
	DSR ± SE	95% CL	Probability of survival	Nesting success
h ≤ 2.5 m	97.21 ± 0.005 (50)	96.11–98.31	0.39	40.0 (55)
2.5 m < h ≤ 3.5 m	97.07 ± 0.003 (188)	96.46–97.67	0.37	43.5 (209)
h > 3.5 m	99.40 ± 0.003 (28)	98.70–100.09	0.82	62.9 (35)
Total	97.35 ± 0.002 (266)	96.88–97.83	0.41	45.2 (299)

Table 3. Nest success calculated using the Mayfield method and the 'traditional' method according to intensity of urbanization (see Data analysis). Daily survival rates (DSR), standard errors (SE) and 95% confidence limits (CL) are given. The numbers of clutches inspected are shown in brackets.

Intensity of urbanization	Mayfield method			Traditional method
	DSR ± SE	95% CL	Probability of survival	Nesting success
Low	96.87 ± 0.005 (65)	95.79–97.94	0.35	37.0 (81)
Medium	97.02 ± 0.004 (100)	96.20–97.84	0.37	38.9 (113)
High	97.69 ± 0.003 (106)	97.01–98.38	0.46	53.8 (119)
Total	97.26 ± 0.002 (271)	96.78–97.74	0.40	44.1 (313)

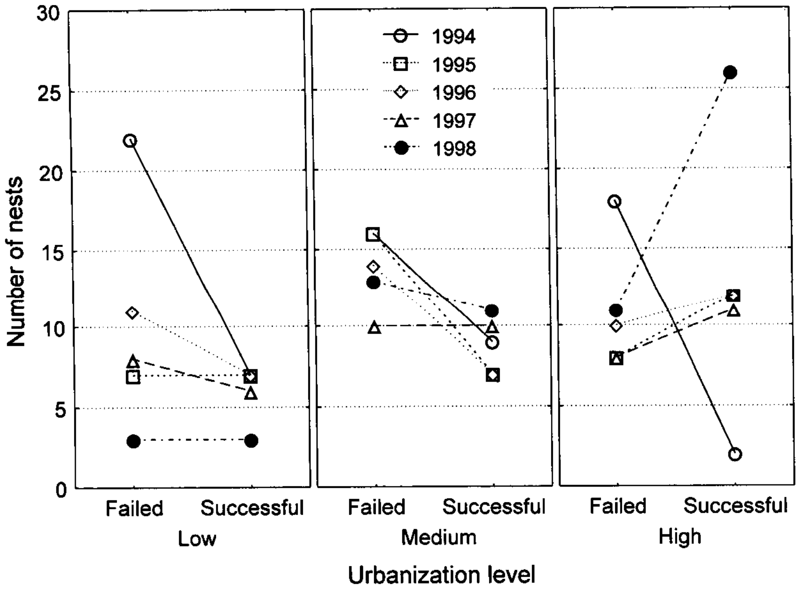

Fig. 1. The number of failed and successful breeding attempts across sites of different intensities of human development (see Materials and methods).

Osborne & Osborne 1980). It has been suggested that nesting at greater heights may make the nests less vulnerable to predation, especially from mammals. On the other hand, some data suggest that lower nests may have greater success (Dyrcz 1969, Møller 1988). These patterns of nesting success could be determined by a trade-off between the influence of mammalian and avian predators and/or depend upon the most common predator species (Ludvig *et al.* 1995). It was found that Greenfinches change their choice of nest site preferences during the breeding season from the evergreens to broad-leaf trees (Kosiński 2001). The preference for nesting in coniferous trees at the beginning of the season enables birds to begin breeding early, nests being less easily detected by predators. However, the preference for coniferous trees at the beginning of the season may not result in higher nesting success (Furrer 1980, Ludvig *et al.* 1995, Tryjanowski *et al.* 2000, Kosiński 2001, but see Møller 1988). Before the tree leafing nests were placed at the base or in the central part of the crown probably to avoid the risk of predation from avian predators. It is worth noting that birds, especially corvids, were not responsible for the nest failures, since some potential nest predators, e.g. Magpie *Pica pica*, Hooded Crow *Corvus corone* and Jay *Garrulus glandarius* were absent from the study area (Kosiński 2001). As the development of foliage increased most birds placed nests in the dense and thorny peripheral part of the crown. This preference could serve

Table 4. The distribution of Greenfinch nests according to the number of hawthorns *Crataegus* sp. in the three sites of urban gradient. Nests from all the years were pooled. Expected number of nests along urbanization gradient is calculated using the contingency table (*see* Materials and methods).

Intensity of urbanization	Number of suitable hawthorn trees for nesting	Number of nests	
		Observed	Expected
Low	104	88	102.3
Medium	63	76	74.0
High	84	122	109.7
Total	251	286	

the nests in the evasion of mammalian predators, most probably domestic cats *Felis catus*. Thus, the selective pressure of mammals and lack of avian predators could favour high-placed nests. One could expect that nest-height was affected by the height of available trees, especially in the site of medium intensity human development (Site II). Unfortunately, availability of different sized trees was not measured. It should be emphasized that three nests on poplars (*Populus* spp.) were responsible for the highest mean and SD values of nest height in site II. However, the number of suitable nest sites in the study area was limited by the height of the most frequently used hawthorns.

4.2. Intensity of urbanization and nest success

The comparison of frequency of nest success between sites, which differed in intensity of human development, supports the 'safe zones' hypothesis which suggests that the frequency of predation decreases as the intensity of urbanization increases. Moreover, it was found that Greenfinches more frequently placed nests in the site of high intensity and fewer in the site of low intensity of urban gradient. It should be emphasized that 52% (n = 67) of the nests in the site of high intensity of urban gradient were found in street trees and park adjoining the city center and cross-roads where traffic was heavy. It could be expected that difference in bird densities would depend more on the trophic factor (Lancaster & Rees 1979). However, the occurrence of potential feeding sites (lawns, rural areas) adjoining the breeding sites were more abundant in the site of medium and low intensity of urban gradient. Moreover, Greenfinches feed their young on seeds, which are clumped and available for only a short period. In consequence birds forage over a wide area, far from their nests (Newton 1972). These findings suggest that lower predation pressure leads to higher densities of breeding pairs (Tomiałojć 1998, Gering & Blair 1999).

The pattern of nest predation in urban gradients is attributed to the number of predators. It was suggested that urban environments contain fewer natural predators than natural areas (Tomiałojć 1982). However, several studies have found that nesting success can decrease with urbanization (Sasvári *et al.* 1995, Matthews *et al.* 1999, Jokimäki & Huhta 2000). In Finnish towns, the high predation rate on artificial ground nests in town center sites was mainly due to avian predators — corvids (Jokimäki & Huhta 2000). As stated earlier, cats probably caused most breeding failures in Krotoszyn (Kosiński 2001). Earlier studies suggested that catches of birds by cats were related to habitat, being higher in more urban areas. Moreover, the proportion of birds in the diet of domestic cats is greater in spring and summer, coinciding with the time of first broods and fledging period (Carss 1995, Churcher & Lawton 1987).

It is possible that lower predation rates in the site of high intensity urban gradient are simply a result of the supplemental feeding and the presence of an artificial food source (e.g. in refuse containers). In consequence, adult birds as well as eggs and fledglings could be less important in the diet of free-roaming domestic cats. However, these results do not exlude that alternative food availability is the cause of reduced predation pressure. However, Osborne & Osborne (1980) found that in nests placed near buildings the rate of predation was lower than in the distant nest type. The areas with low and medium intensity human development may be more frequently penetrated by feral cats and other predators, e.g. stone marten *Martes foina* (Kosiński 2001). Thus, the diet of predator(s) and the intensity of predation in the different sites of the urban gradient may be a reflection of the patterns of abundance and availability of their prey and artificial food sources, as well as the distance from buildings. Recent studies have documented that rodents and noncorvid birds may destroy nests or eggs at artificial open nests (DeGraaf *et al.* 1999, Purcell & Verner 1999, Maier & DeGraaf 2000), as well as hatchlings at natural nests (Majer 1987). It is likely that the low and medium sites of urban gradient, rich in rural vegetation and shelter and placed on the perimeter of close building, contain the highest diversity of predator guilds, e.g. rodents and mustelids.

My results confirm data suggesting that the Greenfinch could be identified as an 'urban exploiter' based on its pattern of density along the urban gradient (Zalewski 1994, Kosiński 2000b), its commonness in urban parks and other urban habitats (Suhonen & Jokimäki 1988, Jokimäki *et* *al.* 1996) and its ability to utilize small patches of vegetation in urban landscapes (Górski & Górska 1979, Jokimäki 1999, Kosiński 2001).

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Selostus: **Kaupungistumisen vaikutukset viherpeipon pesimäpaikanvalintaan ja pesimämenestykseen Puolassa**

Eräät lintulajit esiintyvät runsaampina kaupungistuneilla alueilla kuin luonnontilaisemmilla alueilla. Kyseiset lajit ovat yleensä sopeutuneet kaupunkiympäristöön paremmin kuin muut lajit. Kaupunkeihin lintuja houkuttelevat mm. talviruokinta, petojen vähäinen määrä ja eksoottiset kasvilajit. Linnunpesiin kohdistuva predaatio on yksi tärkeimmistä pesimämenestykseen vaikuttavista tekijöistä. Useat muutkin tekijät, kuten pesän sijaintikorkeus, habitaattilaikun koko ja etäisyys ihmisen aiheuttamista häiriötekijöistä, vaikuttavat pesimämenestykseen. Kaupungeissa esiintyy yleensä vähän petoeläinlajeja. Kaupunkeja voidaankin pitää eräänlaisina "turvavyöhyke" alueina. Artikkelin kirjoittaja tutki Puolassa kaupungistumisen ja pesän sijaintikorkeuden vaikutusta viherpeipon pesimämenestykseen. "Turvavyöhyke"-hypoteesiin liittyen kirjoittaja testasi seuraavia oletuksia: 1) jos kaupungistuneet alueet ovat "turvavyöhykkeitä", viherpeipon pesimämenestyksen tulisi kasvaa kaupungistumisen myötä ja 2) vastaavasti viherpeipon pesimätiheyden pitäisi kasvaa kaupungistumisasteen kasvaessa, mikäli muut pesimätiheyteen vaikuttavat tekijät pysyvät vakioina. Tutkimusaineisto koostui vuosina 1994–1998 löydetyistä 313 pesästä, joista valtaosa sijaitsi orapihlajissa (82 %). Pesät jaoteltiin sijaintikorkeuden mukaisesti kolmeen luokkaan: matalalla sijaitsevat pesät (kork. ≤ 2.5 m), keskikorkeudella sijaitsevat pesät (2.5 m < kork. ≤ 3.5 m) ja korkealla sijaitsevat pesät (kork. > 3.5 m). Pesät jaoteltiin myös voimakkaasti kaupungistuneella, keskimääräisesti kaupungistuneella ja vähäisesti kaupungistuneella alueella sijaitseviin pesiin. Predaatio aiheutti suurimman osan tutkimuksessa havaituista viherpeipon pesätuhoista (39 %). Viherpeipon pesimämenestys oli paras korkealla sijaitsevissa pesissä. Oletettavasti korkealla sijaitsevat pesät olivat paremmassa suojassa tutkimusalueen pesiä tuhoavilta pedoilta. Tässä tutkimuksessa pääasiallisia petoja olivat nisäkkäät. Pesimämenestys havaittiin paremmaksi voimakkaasti kaupungistuneella alueella kuin vähemmän kaupungistuneella alueella. Sen sijaan kaupungistumisen ei havaittu vaikuttavan viherpeipon pesän sijaintikorkeuteen. Voimakkaimmin kaupungistuneella alueella oli oletettua enemmän pesiä, kun taas vähiten kaupungistuneella alueella oli oletettua vähemmän pesiä. Tulokset viittaavat siihen, että "turvavyöhyke"-hypoteesi voisi päteä viherpeipon kohdalla.

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