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Nest predation in Blackbirds (*Turdus merula*) and the influence of nest characteristics

Arnaud Grégoire, Stéphane Garnier, Noël Dréano & Bruno Faivre*

*Université de Bourgogne, UMR CNRS 5561 Biogéosciences, 6 Boulevard Gabriel, 21000 Dijon, France. (*Corresponding author's e-mail: Bruno.Faivre@u-bourgogne.fr)*

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Various studies have shown that predation rates depend on several factors, such as nest site and nest characteristics, nest defense and clutch size. However, the relative contribution of each factor in determining the observed patterns of nest predation remains an important question. We studied nest predation in a population of Blackbirds (*Turdus merula*) in an urban park located in Dijon (Eastern France) over two consecutive years. We used both natural and artificial nests (filled with dummy eggs). Overall, predation rate did not differ between natural (50%) and artificial nests (53%). Few species of predators were identified in the study site, and the red squirrel was the main predator (88% of the predation cases). Blackbirds used a large number of plant species as nest sites, but predation was not associated with this characteristic. A significant effect of nest characteristics (nest height, nest external diameter) on nest predation was detected for artificial nests but not for natural ones. These two factors may influence nest visibility, and may be important characteristics of nest exposure. Our results are consistent with those of previous studies and underline the importance of nest charcteristics on nest predation rate.

1. Introduction

Nest predation is a major cause of breeding failure in bird species (Skutch 1949, Ricklefs 1969, Loiselle & Hoppes 1983, Martin 1992), especially in passerines (Martin & Roper 1988, Holway 1991, Filliater *et al.* 1994), and is thought to have an important influence on avian life-history evolution (Slagsvold 1982, Martin & Li 1992, Martin 1993a, b, Martin & Clobert 1996) and bird community structure (e.g. Osborne & Osborne 1980, Sih *et al.* 1985, Suhonen *et al.* 1994, Jokimäki & Huhta 2000). Nest vulnerability to predation depends on a combination of specific factors, including nest type and visibility (Cresswell 1997, Huhta *et al.* 1998), nest defense (Barash 1975, Andersson *et al.* 1980, Cresswell 1997), and clutch size (Perrins 1977, Ricklefs 1977, Slagsvold 1982, Lundberg 1985). In addition, external factors such as habitat (Huhta & Jokimäki 2001), predator community (Huhta *et al.* 1996, 1998, Jokimäki & Huhta 2000, Dion *et al.* 2000, Twedt *et al.* 2001) and human disturbance (Huhta *et al.* 1996, Martin & Clobert 1996, Tryjanowski & Kuźniak 1999, Jokimäki & Huhta 2000) can contribute to breeding success. An important question, however, is the relative contribution of each factor in determining the observed patterns of nest predation, particularly if one aims at understanding the evolution of life-history traits (Lessells 1991, Cresswell 1997). In this context, Cresswell (1997) emphasized the difficulty inherent to the fact that any measured factor under birds' control can be itself dependent upon the risk of predation. If birds do compensate for the perceived risk of predation, then there will be no observable variation in the risk of predation according to a specific trait (Møller 1989, Cresswell 1997). Indeed, studies differ markedly in their appreciation of the role of nest site characteristics. Several studies have found that nest site characteristics have a direct influence on predation (Nias 1986, Møller 1988, Seitz & Zegers 1993, Martin 1993c, Wada 1994, Jokimäki & Huhta 2000, Kosiński 2001), whereas others have failed to demonstrate such an effect (Zimmerman 1984, Holway 1991, Colwell 1992, Filliater *et al.* 1994). However, correlational studies suffer from several limitations, and only experimental works can identify the relevant factors affecting nest predation. Particularly, study of nest predation rate by using artificial nests is able to detect the influence of nest characteristics independently of adult nest defense behaviour. In addition, adult nest defense is indirectly detectable by comparing the issues of the same nest during a breeding attempt and as "artificial nest", without adults.

In this study, we analyse the role of nest characteristics on nest predation in an urban population of European blackbird *Turdus merula*. Following Cresswell (1997), we hypothesize that nest characteristics influence predation, and that breeding adults can compensate for a higher nest exposure with a more active defense. We compare predation rates for two successive years on natural and artificial nests containing dummy eggs that allow identification of the predators.

2. Methods

2.1. Study area

Predation on blackbird nests was studied in an urban park located in Dijon (France, 47°19'N 5°02'E, about 150 000 inhabitants), from April to August 1997 and 1998. The total area covered by parkland in this town is about 700 ha. A study of Blackbird biology and demography was carried out in a 5.5 ha park in the center of the town. This study site is managed by the local Natural History Museum. It is open daily to visitors (300–500/day) for walking and visiting the botanical garden. The total cover of the study park is divided in lawns (15%), bushes (2%), hedges (3%), botanical garden (15%), woodlands (38%) and artificial cover (27%). The park is surrounded by a historic monument, a railway station and a street to the north, and by blocks of flats (4 to 8 stories) and individual houses (2 to 3 stories) to the other directions.

2.2. Nest census and monitoring

Before the onset of the breeding season, we captured birds using mist nets and ringed them with combinations of colour rings allowing individual identification. Once pair formation had occurred, we checked nests by following females that were carrying nest material (with binoculars). Once a week, we checked nests in all bushes, hedges and small trees. Nests in high trees could not be monitored and therefore our study is based on a subsample of the park population. All the nests were found before or during laying and from then were regularly visited each two days. Thus, laying date and clutch size were accurately determined. Once incubation had started, nests were not visited for ten days, but the presence of the female on the eggs was daily checked by careful observations. After ten days, a daily visit allowed the determination of hatching date. The presence of chicks was then regularly checked from the behaviour of parents bringing prey to the nest. In case of breeding failure, we checked for the presence of eggs and chicks in order to evaluate the evidence for predation or nest desertion.

We studied 27 and 23 breeding pairs of blackbirds in 1997 and 1998 respectively. Among the 23 breeding pairs observed in 1998, 5 had not been recorded during the preceding year. Within all the 18 remaining pairs, at least one mate belonged to one of the 27 breeding pairs recorded in 1997. Ninety-six nests with full clutches and identification of the breeding pair were monitored during the two breeding seasons.

2.3. Nest characteristics and sites

At the end of the breeding season, we visited all nests that had been monitored and recorded nest characteristics (see Table 1). Plant species used as nest site were grouped in three categories for statistical analysis. The first category corresponded to yew (*Taxus baccata*) and coniferous (mainly *Thuja* sp.). The second category corresponded to evergreen broadleaved plants (*Prunus laurocerasus, Aucuba japonica, Mahonia* sp., *Buxus sempervirens* etc.). The last category consisted of deciduous broadleaved plants (*Prunus* sp., *Tilia* sp., *Morus* sp., *Aesculus hippocastanum* etc.). Within the total sample of monitored nests, we analysed only breeding attempts followed by a second breeding attempt after nest predation to consider nest site selection after a first predation event.

2.4. Experimental procedure

At the end of both breeding seasons, we reused nests that had been used by blackbirds during the 1997 and 1998 seasons as artificial nests in situ. Nests that had been damaged were not retained for experiments. Following previous studies (Gottfried & Thompson 1978, Martin 1987, Møller 1988, Cresswell 1997), we placed two quail eggs in each artificial nest. Our procedure differed from that used by Cresswell (1997) as one egg was a dummy egg filled with wax: 5 cm of a 30 cm long nylon thread were inserted in each egg previously cleaned out and hot liquid wax was injected inside the egg with a warmed syringe. The second egg was a natural quail egg. Each dummy egg was attached to the nest by the nylon thread. The natural egg was supposed to provide reward to the predator. The dummy egg would conserve imprints of predators and thus help to identify them (Ribaut 1964). Artificial nests were set up on 7 July, and each nest was monitored each two days until 4 August or until it experienced a predation attempt.

2.5. Predator abundance and identification

In order to assess the variation in nest predator abundance during the breeding season and during the experimental phase, we regularly censused all potential predators that could be seen in the park. We used the same constant route covering the entire study area, and each detected predator was located on a map. Potential predators included the Magpie (*Pica pica*), the Carrion crows (*Corvus corone*), the Domestic cat (*Felis domesticus*) and the Red squirrel (*Sciurus vulgaris*). Overflying predators were not included in the data. Censuses were always performed between 9.00–9.30 a.m. For each survey, the abundance of a nest predator species corresponded to the number of mapped individuals. In both years, seven censuses were performed during the breeding season (June), and nine censuses during the experimental phase (July–August).

Table 1. Description of nest characteristics recorded.

Nest characteristics	Measurement unit, and accuracy
1. Nest site (species of tree or bush in which the nest was located)	–
2. Height of the nest above the ground	Meter, ±0.1
3. Height of the nest material (distance from the base to the top rim of the nest)	Centimeter, ±0.5
4. External diameter of the nest	Centimeter, ±0.5
5. Horizontal distance from the nearest edge of the nest to the edge of the bush or structure in which it was located	Meter, ±0.1
6. Vertical distance from the top of the nest to the top of the bush or structure in which it was located	Meter, ±0.1
7. Percentage of sky visible (amount of foliage above the nest), evaluated by using reversed 10 × 50 binoculars in order to obtain wide-angle lens view (see Cresswell 1997)	Percentage, ±5
8. Maximum horizontal distance from which a red card marker measuring 5 × 5 cm attached to the north, east, south and west sides of the nest could be seen. An index of detectability was then obtained from summing the four measurements	Meter, ±0.5
9. Distance to the nearest nest	Meter, ±0.5

2.6. Statistical analysis

Within one year, nests from the same pair cannot be considered as statistically independent data, and the same is true for nests from the same pair in consecutive years. Therefore, to avoid pseudoreplication, we randomly selected only one nest per breeding pair over the two study years for statistical analyses. The same nests were however used as natural (i.e. when occupied by a pair) and artificial (at the end of the breeding season). Nineteen nests were included in analyses for 1997 and 13 for 1998.

Characteristics of the nests between the three categories of plant species were compared by using Kruskal-Wallis tests (Siegel & Castellan 1988). We used a Fisher exact test for r*k table (Louis & Dempster 1987, Raymond & Rousset 1995) to compare (i) predation rate between clutch sizes and (ii) the proportion of pairs that changed nest site category according to the issue of the attempt.

We studied the influence of nest characteristics (Table 1) and year on natural and artificial nest outcomes (depredated versus non-depredated) using two logistic regressions with a stepwise omission of non significant terms (P value < 0.05), beginning from the maximum model. The same technique was used to compare the outcomes between natural and artificial nests and between years.

Predator abundance was compared between breeding and experimental periods using Mann-Whitney U-tests (Siegel & Castellan 1988). The same statistic was used to compare predator abundances between 1997 and 1998.

Logistic regressions were performed using GLIM procedures (Aitkin *et al.* 1994), and other tests were performed using Statistica (Statsoft, version 5.1., 1997).

3. Results

3.1. Nest characteristics and nest sites

Blackbirds used a large number of plant species as nest sites: the 32 nests presently analysed were found in 15 different species. Eighteen nests were built in the first category of nest site (i.e. yews and coniferous), 8 in the second category (Cherry-Laurel *Prunus laurocerasus*, Boxwood *Buxus sempervirens* and Ivy *Hedera helix*), and 6 in the third category (deciduous trees or bushes). Meas-

Table 2. Characteristics of blackbird nests for different categories of nest sites (upper values = medians; lower values in brackets = interquartile). Nest site categories: (1) Yew + coniferous, (2) Evergreen broadleaved plants and (3) Deciduous broadleaved plants.

	Nest site category			Kruskal-Wallis H	P
	1	2	3		
Height above ground (m)	1.93 (1.36)	1.40 (1.30)	2.05 (0.95)	2.54	0.28
Height of nest material (cm)	14.50 (1.88)	11.60 (4.73)	14.50 (3.25)	2.83	0.24
External diameter of nest (cm)	16.50 (4.53)	14.90 (1.50)	15.50 (1.13)	0.90	0.64
Horizontal distance to edge (m)	0.48 (0.78)	0.50 (0.49)	0.58 (0.72)	0.08	0.96
Vertical distance to edge (m)	0.50 (1.90)	0.70 (2.50)	1.50 (9.59)	2.33	0.31
Percentage of sky visible	15.00 (32.50)	10.00 (20.00)	10.00 (0.00)	1.61	0.44
Index of detectability (m)	31.05 (27.08)	13.60 (28.38)	20.30 (8.98)	2.87	0.23
Distance to nearest nest (m)	15.25 (10.38)	10.50 (10.25)	8.00 (16.75)	0.74	0.69

ured nest characteristics were not related to the category of plant species inside which nests were built (Table 2). Proportion of pairs that changed nesting site category following a depredation event did not differ significantly between nesting site category (Fisher exact test for r*k tables, P = 0.60): 2 pairs among 5 breeding in yews and conifers have changed nesting site after depredation, 5 pairs within 9 breeding in evergreen broadleaved have changed nesting site after depredation, and 2 pairs within 4 breeding in deciduous broadleaved plants have changed nesting site after depredation.

3.2. Nest predation rates

About 50% of natural and artificial nests were depredated (Table 3). Predation rates were not significantly different between 1997 and 1998, or between natural and artificial nests (logistic regression, Maximum model, $\chi^2_3 = 0.310$, $P = 0.96$, proportion of deviance explained = 0.3%). In addition, clutch size had no significant effect on nest predation: Proportions of predated natural nest with two eggs (2/2), 3 eggs (3/5), 4 eggs (10/22) and 5 eggs (2/3) were not significantly different (Exact test for r*k tables, P = 0.62).

According to the artificial nest experiment, red squirrels caused most of the nest losses (88% out of 17 scored). The morphology and size of imprints conserved on the wax of dummy eggs corresponded to squirrel imprints. The two remaining predation cases seem to be due to other mammal species (probably *Mustellidae*), but without absolute evidence.

3.3. Nest characteristics and predation rates

Logistic regression did not reveal any significant predictor of natural nest outcomes (Maximum model, $\chi^2_{15} = 21.685$, $P = 0.12$). On the other hand, artificial nests located at a higher elevation or with a higher external diameter suffered from higher nest predation. In addition, a significant interaction between year and height of nest material was detected (Table 4). Nests with larger nest material height were more prone to predation than nests with smaller nest material height in 1997 only.

3.4. Predator abundance

For both years, the abundance of Common Crow did not vary significantly between the breeding season and the experimental period (Table 5, 1997: U = 28.5, P = 0.74; 1998: U = 29, P = 0.78). However, crow abundance was significantly higher in 1997 than in 1998 (U = 73.5, P = 0.035). No Magpie was observed during the study period in both years. For both years, the abundance of red squirrel did not vary significantly between the

Table 3. Outcomes of natural and artificial nests over the study period.

	Natural nests		Artificial nests	
	n	Predation rate (%)	n	Predation rate (%)
1997	19	47.37	19	57.89
1998	13	53.85	13	46.15

Table 4. A logistic regression model of the relationship between nest characteristics, year and outcome of the artificial nests.

	Dev (Change in)	df (Change in)	P
Null Model	44.33	31	
External diameter of nest	7.94	1	0.008
Height of the nest above ground	8.79	1	0.003
Year × Height of the nest material	19.96	1	< 0.001

breeding season and the experimental period (Figure 5, 1997: U = 29, P = 0.77; 1998: U = 27.5, P = 0.63). Finally, domestic cats were occasionally observed in the study area: one individual only during the census in 1997, and 3 in 1998 (one during the breeding period and two during the experimental phase).

4. Discussion

In this study, we found that blackbirds built their nests in several plant species. The diversity of plant species as nest sites has been previously mentioned in other studies (Snow 1958, Cramp 1988). Besides, Cresswell (1997) found that predation exposure was dependent on vegetation type in which nest was placed. Our data do not confirm the existence of a relationship between nest site and risk of predation, since all nest characteristics associated with increased predation risk were independent of our defined nest site categories. Blackbirds could thus benefit from placing their nests in various vegetation types through preventing predators from associating the presence of nests with particular vegetation types.

However, nest predation during a first breeding attempt did not systematically result in a change of nesting site category. Thus, it seems that nest predation does not influence the choice of nesting site in consecutive breeding attempts. However, we could not avoid two potential biases (i) the elimination of highly placed nests from our sample may have excluded a particular nest site category from the analysis, and (ii) the measurement of nest characteristics took place at the end of the breeding season (during the experimental phase). The period of measurement is an important point (see Burhans & Thompson 1998) that could reduce differences between nest characteristics from one site category to an other. However, these two biases are probably negligible because a small number (less than 4 %) of nests were highly located (nest height > 5 m); in addition, bushes, hedges and the main part of trees were regularly trimmed to maintain their shape and volume.

The predation rate observed in our study (about 50%) is in the same order as those estimated for the same species by Snow (1958). However, predation rate has been found to fluctuate within urban habitats from one location to the other, from 31% (Havlin 1963) to 94.44% (Groom 1993). Other studies on the Blackbird in rural habitats mentioned a higher predation rate with roughly 80% of nests depredated (Snow 1958, Frochot *et al.* 1968, Hatchwell *et al.* 1996). However, this contrast is not observed for all species breeding in habitats ranging from rural to urbanized sites. For example, Jokimäki & Huhta (2000) found a higher predation rate in more urbanized places by using artificial nests mimicking those of ground-breeding birds.

Similarity between predation rates in natural nests and artificial nests has been already observed in other studies (Gottfried & Thompson 1978, Møller 1988, Cresswell 1997). However, if birds were able to reduce nest predation rates by displaying or producing other behaviours, the predation rates should be higher on experimental than on natural nests (Møller 1988). Therefore, the observed similarities in predation rates between natural and artificial nests suggested that nest defense is not efficient, or compensated by other strategies, in blackbirds.

In our study, the Red squirrel has been identified as the main predator. Previous works have shown that small mammals can be the most frequent nest predators (Ribaut 1964, Schmidt *et al.* 2001, Carigan & Villard 2002). In addition, sev-

Table 5. Predator abundance during breeding and experimental periods. Medians are presented with interquartile ranges in brackets. The sample sizes correspond to the number of censuses performed.

	1997		1998	
	Breeding (n = 7)	Experiment (n = 9)	Breeding (n = 7)	Experiment (n = 9)
Common Crow	3(4)	3(4)	1(1.5)	1(1.5)
Red squirrel	1(1)	1(1)	1(0)	1(1)

eral species can potentially depredate blackbird nests: corvids, several raptor species, squirrels and other mammals are among the most common nest predators in blackirds (Ribaut 1964, Cresswell 1997). However, even if predator density may be particularly high in towns (Haskell *et al.* 2001, Sorace 2002), the predator community structure varies between areas (Jokimäki & Huhta 2000). As consequence, predator community may be reduced (low species number) in some urban parks, as it is the case in our study site where the Red squirrel was the most frequently observed predator.

Our results are partially consistent with those obtained by Cresswell (1997), who found that height and nest detectability were determinant factors of predation on artificial nests. In addition, the importance of nest characteristics on predation probability has been reported in previous studies on different species of open-cup nesting passerines including blackbirds (Osborne & Osborne 1980, Martin & Roper 1988, Møller 1988, 1989, Wada 1994, Ludvig *et al.* 1995, Wilson & Cooper 1998). Although nest detectability did not appear as a significant predictor of the outcomes of artificial nests in our study, it seems obvious that nest height and nest external diameter can influence nest visibility, and may be important characteristics of nest exposure. This is particularly relevant because red squirrel (the main predator species in our study) shows a diurnal activity, and relies on vision to detect their food (Saint-Girons 1973). Some studies considered that nest predation rate depended greatly on concealment inside nest site (Martin & Roper 1988, Martin 1993c), while others have not found any relationship between this characteristic and nest failure by predation (Holway 1991, Filliater *et al.* 1994, Howlett & Stuchbury 1996, Burhans & Thompson 1998, Huhta *et al.* 1998). As proposed by Cresswell (1997), these opposite results suggest the existence of two strategies among birds. Firstly, a strategy based on nest concealment with carefully placed nests to avoid predators. Secondly a strategy based on nest defense with nest less carefully concealed or placed in relation to defense abilities (Ricklefs 1977, Wilson & Cooper 1998). The choice may vary according to species or individuals in the same species (Cresswell 1997, Mallory *et al.* 1998). Comparison of the outcomes for the same nests used as natural and experimental sets, seems to be a reliable approach to explore this hypothesis. Indeed, the absence of predictive variables of predation risk in the case of natural nests, contrasting with the significant predictors of predation risk of artificial nests, tends to support the existence of a nest defense behaviour in blackbirds.

Another discrepancy between our results and those of some other works (Cresswell 1997, Kosiński 2001) is that nest predation rate and nest elevation were positively associated in our study case whereas they were negatively associated in the other studies. This difference may result from differences in predator communities between study sites. In our case, the main predator was the Red squirrel, which scarcely explores the lower parts of bushes and trees. Thus, local predators identification might be of interest to discuss the difference observed between sites.

Finally, many studies have analyzed the influence of nest site and characteristics (e.g. distance to nearest trees from nest, tree layer, visibility of nest) on predation by using only artificial nests (for instance Loiselle & Hoppes 1983, Martin 1987, Marini & Weale 1997, Keyser *et al.* 1998, Jokimäki & Huhta 2000). However, our results show that the importance of nest characteristics on predation rate depends on the type of nest considered (artificial vs. natural). In addition, hypothesing that adults can compensate a higher exposure of their nest (and consequently modify conclusions of analyses), further studies are required to estimate directly the nest defense behaviour of birds and its importance in nest outcome.

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Selostus: **Mustarastaiden pesiin kohdistuva predaatio ja pesätuhoihin vaikuttavat tekijät**

Petojen aiheuttamat pesätuhot ovat yksi tärkeimmistä tekijöistä, jotka aiheuttavat varpuslintujen pesinnän epäonnistumisen. Pesän alttiuteen joutua pesärosvojen tuhon kohteeksi vaikuttavat muun muassa pesän sijainti, pesätyyppi ja emojen puolustuskäyttäytyminen. Kirjoittajat tutkivat petojen mustarastaiden pesille aiheuttamia tuhoja sekä pesätappioihin liittyviä tekijöitä ranskalaisessa Dijonin kaupungissa vuosina 1997–1998. Kaupungin keskustassa sijaitsevasta 5.5 hehtaarin kokoisesta puistosta pyrittiin vuosittain kartoittamaan kaikki mustarastaiden pesät. Korkealla puiden yläosissa sijainneet pesät jätettiin tutkimuksen ulkopuolelle. Tutkimuksessa kerättiin tiedot haudonnan alkamispäivästä, pesän munaluvusta, munien kuoriutumispäivästä ja poikasten esiintymisestä. Mikäli pesintä jostain syystä epäonnistui, kirjoittajat pyrkivät määrittämään epäonnistumisen syyn. Emolinnut pyydystettiin ja ne rengastettiin värirenkailla. Tutkimusalueella pesi vuonna 1997 kaikkiaan 27 mustarastasparia ja vuonna 1998 yhteensä 23 paria. Tutkimusalueella oli tutkimusvuosina seurannassa kaikkiaan 96 pesää. Pesinnän päätyttyä mustarastaiden pesiltä tehtiin kasvillisuuskuvaukset ja pesiä käytettiin tekopesäkokeessa. Ehjänä säilyneisiin pesiin aseteltiin kaksi viiriäisen munaa, joista toinen oli täytetty muovailuvahalla. Vahamunat kiinnitettiin pesään nailonnarulla. Tekopesän tuhonnut peto määritettiin muovailuvahaan jääneiden jälkien perusteella. Tekopesäkoe kesti noin kuukauden. Tutkimuksen yhteydessä laskettiin tutkimuspuiston petomäärät sekä mustarastaiden pesimäaikana että tekopesäkokeen aikana. Mustarastaat hyväksyivät pesimäpaikoikseen monia eri kasvilajeja, joista useimmat olivat havupuita tai -pensaita. Pesäpredaation voimakkuus ei eronnut luonnonpesien ja tekopesien välillä. Pedot tuhosivat tutkimuspesistä noin puolet. Tulos viittaa siihen, että tekopesiä voitaisiin käyttää arvioitaessa petojen aiheuttamien pesätuhojen määrää. Tässä tutkimuksessa orava oli tärkein pesien tuhoaja, 88% havaituista pesätuhoista oli oravan aiheuttamia. Pesän sijaintia ja laatua kuvaavat ympäristömuuttujat eivät selittäneet luonnonpesiin kohdistuvan pesäpredaation määrää. Tekopesäkokeissa havaittiin sen sijaan, että korkealla sijaitsevat pesät ja suurikokoiset pesät kärsivät voimakkaasta pesäpredaatiosta. Oletettavasti pesän sijaintikorkeus ja koko vaikuttavat pesän näkyvyyteen ja siten pesän alttiuteen joutua ryöstetyksi. Arvioitaessa pesän ryöstetyksi tulemiseen vaikuttavia tekijöitä, tuleekin kirjoittajien mukaan huomioida tutkimuksessa käytetty pesätyyppi. Saadut tulokset luonnonpesistä ja tekopesistä voivat erota toisistaan. Lisäksi tutkimusalueen petoyhteisön rakenne voi vaikuttaa pesätuhojen määrään ja syihin.

References

Aitkin, M., Anderson, D., Francis, B. & Hinde, J. 1994: Statistical modelling in GLIM. — Oxford Statistical Sciences Series 4. Clarendon Press, Oxford.

Andersson, M., Wiklund, G. & Rundgren, H. 1980: Parental defense of offspring: a model and an example. — Anim. Behav. 28: 536–542.

Barash, D. P. 1975: Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. — Wilson Bull. 87: 367–373.

Burhans, D. E. & Thompson, F. R. 1998: Effects of time and nest-site characteristics on concealment of songbird nests. — Condor 100: 663–672.

Carigan, V. & Villard, M. A. 2002: Effects of variations in micro-mammal abundance on artificial nest predation in conifer plantations and adjoining decideous forests. — For. Ecol. Manage. 157: 255-265.

Colwell, M. 1992: Wilson's phalarope nest success not influenced by vegetation concealment. — Condor 94: 767–772.

Cramp, S. 1988: Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Palearctic. Vol. V: Tyrant Flycatchers to Thrushes. — Oxford University Press, Oxford.

Cresswell, W. 1997: Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. — Anim. Behav. 53: 93–103.

Dion, N., Hobson, K. A. & Lariviere, S. 2000: Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. — Condor 102: 629–634.

Filliater, T. S., Breitwisch, R. & Nealen, P. M. 1994: Predation on northern cardinal nests: does choice of nest site matter? — Condor 96: 761–768.

Frochot, B., Petitot, F. & Dufour, H. 1968: La reproduction du merle en Bourgogne. — Le Jean-le-Blanc 7: 4–17.

Gottfried, B. M. & Thompson, C. F. 1978: Experimental analysis of nest predation in an old-field habitat. — Auk 95: 304–312.

Groom, D. W. 1993: Magpie Pica pica predation on blackbirds Turdus merula nests in urban areas. — Bird Study 40: 55–62.

Hatchwell, B. J., Chamberlain, D. E. & Perrins, C. M. 1996: The demography of blackbirds Turdus merula in rural habitats: is farmland a sub-optimal habitat. — J. Appl. Ecol. 33: 1114–1124.

Havlin, J. 1963: Breeding Density in the Blackbird, Turdus merula. — L. Folia Zoologica 12: 1–18.

Holway, D. A. 1991: Nest-site selection and the importance of nest concealment in the black-throated blue warbler. — Condor 93: 575–581.

Howlett, J. S. & Stuchbury, B. J. 1996: Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. — Auk 113: 1–9.

Huhta, E. & Jokimäki, J. 2001: Breeding occupancy and success of two hole-nesting passerines: the impact of fragmentation caused by forestry. — Ecography 24: 431–440.

Huhta, E., Jokimäki, J. & Helle, P. 1998: Predation on artificial nests in a forest dominated landscape — the effects of nest type, patch size and edge structure. — Ecography 21: 464–471.

Huhta, E., Mappes, T. & Jokimäki, J. 1996: Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. — Ecography 19: 85–91.

Jokimäki, J. & Huhta, E. 2000: Artificial nest predation and abundance of birds along an urban gradient. — Condor 102: 838–847.

Keyser, A. J., Geoffrey, E. H. & Soehren, E. C. 1998: Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passerine birds. — Conserv. Biol. 12: 986–994.

Kosiński, Z. 2001. Effects of urbanization on nest site selection and nesting success of the Greenfinch Carduelis chloris in Krotoszyn, Poland. — Ornis Fenn. 78: 175–183.

Lessells, C. M. 1991: The evolution of life histories. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioral Ecology: An Evolutionary Approach: 137–168. Blackwell Scientific, Oxford.

Loiselle, B. A. & Hoppes, W. G. 1983: Nest predation in insular and mainland lowland rainforest in Panama. — Condor 85: 93–95.

Louis, E. G. & Dempster, E. R. 1987: An exact test for Hardy-Weinberg and multiple alleles. — Biometrics 43: 805–811.

Ludvig, E., Vanicsek, L., Török, J. & Csörgö, T. 1995: The effect of nest-height on the seasonal pattern of breeding success in Blackbirds Turdus merula. — Ardea 83: 411–418.

Lundberg, S. 1985: The importance of egg hatchability and nest predation in clutch size evolution in altricial birds. — Oikos 45: 110–117.

Mallory, M. L., McNicol, D. K., Walton, R. A. & Wayland, M. 1998: Risk-taking by incubating common goldeneyes and hooded mergansers. — Condor 100: 694–701.

Marini, M. A. & Weale., M. E. 1997: Density- and frequency-dependent predation of artificial bird nests. — Biol. J. Linn. Soc. 62: 195–208.

Martin, T. E. 1987: Artificial nest experiments: effects of nest appearance and type of predator. — Condor 89: 925–928.

Martin, T. E. 1992: Interaction of nest predation and food limitation in reproductive strategies. — Curr. Ornithol. 9: 163–197.

Martin, T. E. 1993a: Nest predation among vegetation layers and habitat types: revising the dogmas. — Am. Nat. 141: 896–913.

Martin, T. E. 1993b: Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? — Am. Nat. 142: 937–946.

Martin, T. E. 1993c: Nest predation, nest sites, and birds: new perspectives on old patterns. — Biosciences 43: 523–532.

Martin, T. E. & Clobert., J. 1996: Nest predation and avian life-history evolution in Europe versus North America: a possible role of humans? — Am. Nat. 147: 1028–1046.

Martin, T. E. & Li, P. 1992: Life history traits of open- vs. cavity-nesting birds. — Ecology 73: 579–592.

Martin, T. E. & Roper, J. J. 1988: Nest predation and nest-site selection of a western population of hermit thrush. — Condor 90: 51–57.

Møller, A. P. 1988: Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. — Oikos 53: 215–221.

Møller, A. P. 1989: Nest predation selects for small nest size in the blackbird. — Oikos 57: 237–240.

Nias, R. C. 1986: Nest site characteristics and reproductive success in the superb fairy-wren. — Emu 86: 139–144.

Osborne, P. & Osborne, L. 1980: The contribution of nest characteristics to breeding success among blackbirds Turdus merula. — Ibis 122: 512–517.

Perrins, C. M. 1977: The role of predation in the evolution of clutch size. — In: Stonehouse, B. & Perrins, C. M. (eds.), Evolutionary Ecology: 181–191. Macmillan, London.

Raymond, M. & Rousset, F. 1995: An exact test for population differentiation. — Evolution 49: 1280–1283.

Ribaut, J. P. 1964: Dynamique d'une population de Merle noir, Turdus merula L. — Rev. Suisse Zool. 71: 816–902.

Ricklefs, R. E. 1969: An analysis of nesting mortality in birds. — Smithson. Contrib. Zool. 9: 1–48.

Ricklefs, R. E. 1977: The role of predation in the evolution of clutch size. — In: Stonehouse, B. & Perrins, C. M. (eds.), Evolutionary Ecology: 194–214. Macmillan, London.

Saint-Girons, M. C. 1973: Les Mammifères sauvages de France et du Bénélux. — Doin, Paris.

Schmidt, K. A., Goheen, J. R., Naumann, R., Ostfeld, R. S., Schauber, E. M. & Berkowitz, A. 2001: Experimental removal of strong and weak predators: mice and chipmunks preying on songbird nests. — Ecology 82: 2927–2936.

Seitz, L. C. & Zegers, D. A. 1993: An experimental study of nest predation in adjacent deciduous, coniferous and successional habitats. — Condor 95: 297–304.

Siegel, S. & Castellan, N. J. 1988: Non Parametric Statistics for the Behavioral Sciences. (2nd Ed.). — Mc Graw-Hill Book Company, New York.

Sih, A., Crowley, P., Mc Peek, M, Petrenka, J. & Strohmeier, K. 1985: Predation, competition, and prey communities: a review of field experiments. — Annu. Rev. Ecol. Syst. 16: 269–311.

Skutch, A. F. 1949: Do tropical birds rear as many young as they can nourish? — Ibis 91: 430–455.

Slagsvold, T. 1982: Clutch size variation in passerines birds: the nest predation hypothesis. — Oecologia 54: 159–169.

Snow, D. W. 1958: A Study of Blackbirds. — Allen & Unwin, London.

Suhonen, J., Norrdhal, K. & Korpimäki E. 1994: Avian predation risk modifies breeding bird community on a farmland area. — Ecology 75: 1626–1634.

Tryjanowski, P. & Kuźniak, S. 1999: Effect of research activity of Red-backed Shrike Lanius collurio nests. — Ornis Fenn. 76: 41–43.

Twedt, D. J., Wilson, R. R., Henne-Kerr, J. L. & Hamilton, R. B. 2001: Nest survival of forest birds in the Mississippi alluvial valley. — J. Wild. Manag. 65: 450–460.

Wada, T. 1994: Effects of height and neighbouring nests on nest predation in the rufous Turtle-dove (Streptopelia orientalis). — Condor 96: 812–816.

Wilson, R. R. & Cooper, R. J. 1998: Acadian flycatcher nest placement: does placement influence reproductive success? — Condor 100: 673–679.

Zimmerman, J. L. 1984: Nest predation and its relationship to habitat and nest density in dickcissels. — Condor 86: 68–72.