Factors affecting nest predation in the Great Crested Grebe: field observations, experiments and their statistical analysis

Veikko Salonen & Antti Penttinen

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Factors affecting predation by crows on nests of Great Crested Grebes (*Podiceps cristatus*) were studied during 1983–85 in Finland. The material consists of observations of grebes' nests and controlled experiments with artificial nests. During the study period, 39% of all grebes' nests were robbed at least once. The nesting success of natural nests did not depend statistically significantly on nest density. For the artificial nests used in the experiments, the occurrence of grebes' nests in the neighbourhood decreased the survival probability. The number of other artificial nests in the vicinity did not alone explain the observed degree of predation, but the robbery of a nearby artificial nest had a strong effect, decreasing the survival probability. The most successful nests, natural or artificial, were those situated in very dense vegetation ($\geq$ 90 reeds/m^2) or in the vicinity of a gull's nest. The proportion of experimental nests destroyed by crows decreased when the egg was covered. By contrast, brown colouring of the eggs did not have any effect on predation. Logistic regression models for survival probabilities are given. The fact that in the experimental study the spatial distribution of nests is taken into account in the statistical analysis constitutes a methodological advance.

Veikko Salonen, University of Jyväskylä, Department of Biology, Seminaarinkatu 15, SF-40100 Jyväskylä, Finland; Antti Penttinen, University of Jyväskylä, Department of Statistics, Seminaarinkatu 15, SF-40100 Jyväskylä, Finland

Introduction

Studies of predation on waterfowl nests have mainly dealt with ducks (e.g. Bengtson 1970, Dwernychuk & Boag 1972, Schranck 1972, Livezey 1981, Hill 1984a and 1984b). Grebes differ from most ducks and other waterfowl in their habit of building floating nests, often far from the shore, which reduces predation by mammals. The major threat to the nests of grebes is avian predators. In particular, the Hooded Crow (*Corvus corone*) is known to rob nests of the Great Crested Grebe (Tenovuo 1963, von Haartman 1975).

The relationship between nest density and predation has been discussed in many papers. In some studies, especially those using artificial nests, predation was found to be higher when nest density increased (e.g. Göransson et al. 1975, Andersson & Wiklund 1978, Page et al. 1983, Sugden & Beyersbergen 1986). Hill (1984a) reached a similar conclusion after studying natural nests of two duck species. There are, however, many nest predation studies which have yielded different results (e.g. Gottfried 1978, Götmark & Andersson 1984, Zimmerman 1984). The effect of concealment on nest success is another subject frequently treated in predation studies. In many of them increasing nest cover has been shown to reduce predation (e.g. Schranck 1972, Livezey 1981, Hill 1984b). On the other hand, in some studies no relationship between predation and nest cover has been observed (Dwernychuk & Boag 1972, Erikstad et al. 1982).

The present study is both observational and experimental: applying data from natural nests of Great Crested Grebes and artificial nests used in controlled experiments, we have examined how vegetation and nest cover affect predation by Hooded Crows. As a new feature, we have also taken account of the spatial arrangement of grebes' nests and the heterogeneity of the study area using statistical methods developed in spatial statistics. The dependence of predation on nest density will also be discussed.

Material and methods

Observations about natural nests

Predation on natural nests was investigated in 1983–85 in the northern part of Lake Päijänne in Finland (62°06′N, 25°40′E). The Great Crested Grebe is common in the study area (approximate size 7.5 km^2 with 30 km shoreline) and 40–50 breeding pairs have been observed in recent years. In 1985, however, the population consisted of only 32 breeding pairs. About ten pairs of Hooded Crows were breeding in the vicinity of the shore during the study years. Crows patrolling along the shores could be observed in all parts of the area. There are numerous stands of varying size of emergent macrophytes, the dominant, and often the only species being the common reed (*Phragmites australis*). Most of the Great Crested Grebe pairs start breeding in one-year-old reed stands in May. The majority of the breeding pairs are solitary.

Nests were located by surveying every emergent macrophyte stand several times during the breeding period. The distance of one inhabited nest from another was measured with an accuracy of 5 m. Nests less than 50 m apart were regarded as neighbours. The density of the reed stand protecting a nest was measured in three sample plots of 0.25 m^2 right beside the nest, using four density classes. These measurements were made in one-year-old reed stands. The eggs in a clutch were marked according to the laying order, which allowed us to record even the theft of a single egg during the laying period. The nests were visited on average twice a week, during the laying period even more frequently. Traces of the visits in the stands were removed as carefully as possible. We use the term "robbed nest" if one or more eggs in the nest had been stolen. A nest is said to have survived (untouched) if it was not tampered with during the study period, i.e. the nest escaped detection by predatory birds or was otherwise saved from robbing.

Experiments with artificial nests

Experiments with artificial nests were carried out in 1984–85 in the part of the lake where the density of grebes' nests was greatest. A total of 90 artificial nests were built on small (40 cm × 40 cm) rafts made of wood and polystyrene. In imitation of the natural nests, the artificial ones were made of pieces of reed, water mosses and other aquatic plants. The rafts were anchored to the lake bed. The resemblance to natural nests was apparently good, since in 1984 one grebe pair and in 1985 three pairs gave up their nest building and laid their eggs in an artificial nest.

All artificial nests were placed in over one-year-old common reed stands, which varied in density. A total of 30 nests were placed in very sparse stands (10–40 reeds/m^2), where natural nests are uncommon. Another 30 nests were placed in the stands used for breeding by most of the pairs of Great Crested Grebes in the study area (50–80 reeds/m^2). Finally, 30 artificial nests were placed in very dense stands (over 90 reeds/m^2), also favoured by grebes. The densities of the reed stands were estimated in the same way as for the natural nests, using three density classes. One half of the nests were placed in the vicinity of one or several natural nests. The total number of natural and artificial nests in these groups was at least five. A few artificial nests were situated near nests of Common Gulls (*Larus canus*) or Common Terns (*Sterna hirundo*). The artificial nests were left empty for the first 24 hours, after which one small-sized hen's egg was put in the nest. The nests were checked after 24, 48 and 72 hours. After 72 hours all the nests were removed for a week and were then put back in the same places. No nest markers were used between or during the experiments.

In the first experiment in 1984, a white (undyed) egg was put in the nest. To imitate the behaviour of a disturbed adult grebe, the egg was covered with nest material. In the second experiment, the white egg was left uncovered. In the third experiment, the egg was dyed brown by boiling it in onion water and left uncovered in the nest. The purpose of dyeing the eggs was to imitate the darkening of eggs in natural nests caused by decaying nest material. In 1985 the series of experiments was carried out in the reverse order. In both study years the first experiment took place at the beginning of the laying period of grebes.

Statistical analysis

The probability that a single nest located in the coordinate point t will remain untouched over a time period is a natural theoretical parameter in the description of the predation of a single nest. This probability is called the survival probability and is denoted by π_t. Thus, a low value for π_t indicates a high degree of predation. This probability is subject to environmental factors, which may be controlled or observed variables. In the present study we assume that the survival probability has the form

$$\pi_t = 1/(1 + \exp(-a_o - a_1x_{1,t} - \ldots - a_px_{p,t})),$$

where the explanatory variables $x_{1,t}, x_{2,t}, \ldots, x_{p,t}$ are environmental factors such as reed density. This model is known as the linear logistic regression model (Cox 1970) and is widely applied for contingency table analysis. For an example of the ecological applications of the logistic regression model, see the reanalysis of Schoener's (1970) data on the habitat preference of lizards in McCullagh & Nelder (1983).

If the robbings of nests are assumed to be independent of each other, our hypotheses can be reformulated in terms of the logistic model. If the assumption of independence is not true, the probability π_t will be replaced by the conditional probability $\pi_{t/\partial t}$ this being the probability that the nest on site t will remain untouched over the time period conditioned by the information about robbings of the nearby nests in the set of artificial nests in the neighbourhood of site t, denoted by ∂t. The logistic form will be applied. This spatial modification suggested by Besag (1974) is known as the auto-logistic model (see also Ripley 1981:94–95).

As an estimation method, the maximum likelihood approach for π_t and the so called pseudo-likelihood method (Besag 1975) for $\pi_{t/\partial t}$ have been applied. All calculations have been carried out using the GLIM program (Baker & Nelder 1978).

Results

Natural nests

On an average, 38.5% of all nests were robbed at least once during the study period in 1983–85. The proportion of nests remaining untouched, called the survival rate, was less than 70% in each of the study years (Table 1). Note that the time period is the whole nesting season for natural nests, as against 1–3 days for artificial ones.

Table 1. Predation on natural nests: survival of nests in 1983–85.

Year	Total	Survived	Survival rate
1983	44	26	0.59
1984	42	28	0.67
1985	31	18	0.58

Isolated and non-isolated nests did not show statistically significant differences in survival probabilities (P=0.60). By contrast, both the density of vegetation and the distance from gulls' nests had an effect (Table 2). The survival rates for nests situated in the vicinity of gulls' nests seem to be high, although our empirical data are not sufficient to give reliable estimates. For the nests which were far from gulls' nests, the survival rate increased with increasing reed density. The difference between the density classes 30–60 and 60–90 (reeds/m^2) is not statistically significant (P=0.51). As a reasonable description of the survival probability when there are no gulls' nests in the vicinity, we obtain

$$\pi_t = 1/(1 + \exp(-0.29 - 1.52\, D_t)),$$

where $D_t = -1, 0$ or 1 when the reed density on site t is very low (10–30), medium (30–90) or very high (over 90), respectively. For this model, fitted to the frequencies in Table 2, the (scaled) deviance, which is the statistic for the likelihood ratio test and approximately chi-square distributed, is 1.11 with 2 degrees of freedom (P=0.57). The observed and predicted survival probabilities can be found in Fig. 1.

Table 2. Survival of natural nests classified according to reed density and the proximity of gull nests in 1984–85.

	Reed density (reeds/m^2) 10–30		30–60		60–90		over 90	
Gull nests	Total	Survived	Total	Survived	Total	Survived	Total	Survived
not near	7	1	27	15	20	13	10	8
near	1	1	1	1	2	2	5	4

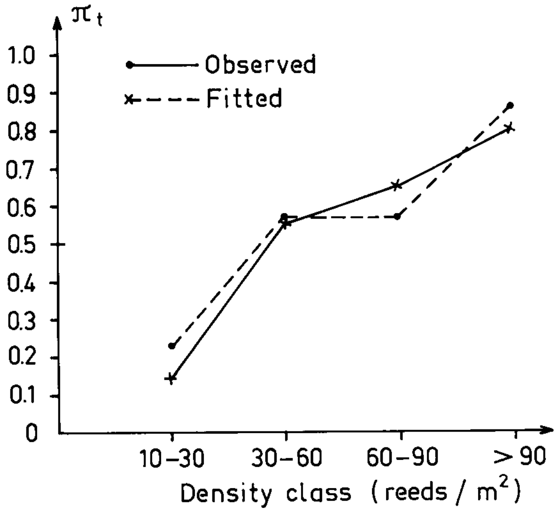

Fig. 1. Observed and fitted survival probabilities for natural nests not in the vicinity of gulls' nests during the period 1984–1985.

The linearity of the effect of reed density was also studied using linear contrast instead of Dt. This model was also statistically plausible (P=0.46), but gave poor agreement with the data when the reed density was low.

The usual likelihood ratio tests were applied in these analyses, the P values being the tail probabilities of the test statistics. These tests are asymptotic. In particular, all the P values are large-sample approximations only. Further, the analysis assumes that robbings of nests are independent events. Care is required in the interpretation of the tests, because the data do not allow verification of the mutual independence of the robbings.

Experiments with artificial nests

The controlled factors used in the experiment are reed density with three classes (10–40, 50–80 and over 90 reeds/m^2), and treatment of the eggs with three classes (covered and white, uncovered and white, and uncovered and brown).

Predation during 3 days

Assuming homogeneity in predation and independence between robbings of different nests, the data can be reduced to the two-way contingency table shown in Table 3.

Table 3 indicates that the colouring of eggs had no statistically significant effect on the survival probabilities (P=0.39). Similarly, no difference exists between the density classes 10–40 and 50–80 (P=0.90). On the other hand, in the highest density class (over 90) the survival rates were higher than in the two lower ones and the difference is statistically significant (P=0.006). Covering the eggs also had a statistically significant positive effect on the survival of the nest (P=0.01). The estimated survival probabilities can be expressed as follows: Let us introduce the dummy variables $D_t = 1$ if the reed density on site t is over 90 (otherwise) and $E_t=1$ if the nest on t is covered (otherwise). Then the estimated survival probabilities can be presented in the form

$$\pi_t = 1/(1 + \exp(1.82 - 1.37\,E_t - 1.42\,D_t)),$$

which we call Model 1. For this model the agreement with the frequencies in Table 3 is satisfactory, deviance = 6.87 with 6 degrees of freedom (P=0.36). The study of the standardized residuals shows, however, that they form spatial patterns (see also Fig. 2a).

Table 3. Survival of artificial nests during 3 days classified according to egg treatment and density of vegetation.

	Reed density (reeds /m²)					
	10–40		50–80		over 90	
Treatment	Total	Survived	Total	Survived	Total	Survived
Covered/white egg	8	2	9	4	9	7
Uncovered/white egg	10	1	10	0	9	4
Uncovered/brown egg	10	3	10	2	10	3

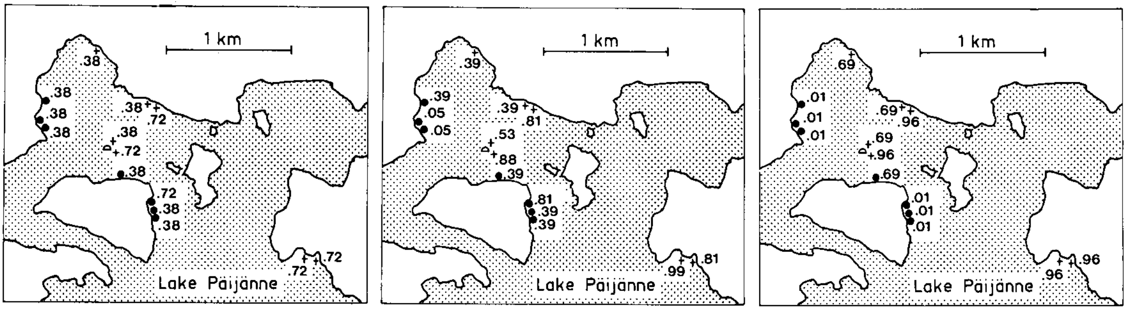

Fig. 2. Performance of the Models 1 – 3 in the prediction of survival of artificial nests in the experiment n:o 3/1985 (eggs white and covered): survival probabilities calculated from a) Model 1 b) Model 2 and c) Model 3. (black dot = robbed nest, + = intact nest).

Table 4. Survival of artificial nests during 3 days classified according to reed density, treatment of egg and the two heterogeneity factors (proximity of gull nests and proximity of natural nests).

		Natural nests in the neighbourhood							
		at most one				more than one			
		reed density low		reed density high		reed density low		reed density high	
Gull nests	Treatment	Total	Survived	Total	Survived	Total	Survived	Total	Survived
not near	Covered	7	2	6	5	6	0	1	0
	Uncovered	16	2	14	5	10	0	2	0
near	Covered	1	1	1	1	4	3	1	1
	Uncovered	6	3	2	2	8	1	1	0

Indeed, the prediction ability of this model is low in clusters of nests. This indicates that information is lost in the reduction of the data to the form of Table 3. A more precise statistical analysis is needed.

One explanation of the spatial patterns formed by the residuals is that they are due to heterogeneity which is not controlled by the experimental design. Examples of observed sources of heterogeneity are the proximity of gulls' nests and natural nests of grebes. These two variables are used as covariates in the modification of Model 1. The independence assumption can now be expressed thus: the robbings of nests are conditionally independent given the environmental variables describing heterogeneity.

With the new model assumption, the data can be reduced to the four-way contingency table shown in Table 4. The model obtained with the assumption of heterogeneity is

$$\pi_t =$$

$$1/[1+\exp(2.58-2.14\ E_t-1.89\ D_t+2.62\ L_t-3.17\ S_t)]$$

called Model 2, where $L_t = 1$ if there are two or more natural nests in the vicinity of nest t (0 otherwise) and $S_t = 1$ if there are one or more gulls' nests in the vicinity of nest t (0 otherwise). The variables E_t and D_t are as before. This model agrees well with the data (Table 4; deviance=5.68, df=11, P =0.89), whereas Model 1 is not satisfactory (deviance=23.11, df=13, P=0.04). Also, the standardized residuals do not show clear spatial patterns, as did those calculated from Model 1. Note that the factors controlled in the experiment (covering of eggs, vegetation) are of the

Table 5. Survival of artificial nests during 3 days classified according to reed density, treatment of eggs and the fate of nearby artificial nests.

		Reed density (reeds/m^2)			
		less than 90		over 90	
Robbed neighbours	Treatment	Total	Survived	Total	Survived
0	Covered	9	6	5	5
	Uncovered	14	6	7	5
1	Covered	3	0	3	2
	Uncovered	11	0	6	2
2	Covered	5	0	1	0
	Uncovered	15	0	6	0

same magnitude as in Model 1, but that some additional information will now be obtained: the existence of natural grebes' nests in the vicinity decreases the survival probability and that of gulls' nests increases it.

So far we have assumed that robbings of nests are independent or conditionally independent (conditioned by the environmental variables). Another explanation of pattern formation is interdependence of robbings. We now assume that the survival probability of a nest on site t depends on the condition of the nests on nearby sites ∂t within an approximate radius of 50 m. All the interdependences are introduced into the model in terms of this definition of neighbourhood relation only. Let us denote the number of robbed nests on ∂t by $Y_{\partial t}$. The autologistic scheme will be applied as the conditional model. Using the pseudo-likelihood method, we obtain the conditional survival probabilities when the number of robbed neighbours is known and these are

$$\pi_{t|\partial t}(Y_{\partial t}) =$$
$$1/[1+\exp(0.54 - 1.34\ E_t - 2.38\ D_t + 3.02\ Y_{\partial t})]$$

(Table 5; Model 3). We cannot apply any likelihood ratio test now because the observations are allowed to be dependent.

This model performs slightly better in the prediction of survival of nests than Model 2, but the difference is rather small (Fig. 2). In particular, Model 3 is better for non-isolated nests. Note that the covariates L_t and S_t have a negligible effect. The reason is that $Y_{\partial t}$ is strongly collinear with L_t and S_t, explaining the major part of the heterogeneity in addition to dependence. The effect of reed density and the treatment of the eggs is of the same magnitude as in Model 2. The comparison of the two models is based not on statistical tests but on quantitative inspection of residuals and prediction ability.

Predation during the first and second days

The artificial nests in the experiments were checked at intervals of one day and the models were constructed for survival probabilities after the 1st and 2nd days separately. The factors explaining the survival of nests were the same, with one exception: in Model 2 the effect of natural nests was negligible after the first day but not after the second day.

Discussion

The survival rate of artificial nests was much lower than that of natural nests of the Great Crested Grebe. The most probable explanation is that natural nests can be robbed by crows only when they are unprotected. This rarely occurs, especially during the later part of the incubation period. The natural nests, receive almost constant protection during the whole of the laying and incubating periods, whereas the artificial nests were unprotected and exposed to predation during a period of 1–3 days. Hence, the possibility of predation lasted much longer for artificial nests. For this reason the predation rates of artificial nests are not really comparable with those of natural nests.

Many authors have suggested that predation is more frequent when nest density is high (e.g. Göransson et al. 1975, Hill 1984a, Sugden & Beyersbergen 1986). Our data for grebes' nests do not support this hypothesis. By contrast, the predation on artificial nests indicated slight dependence on the density of natural nests in the neighbourhood. The effect of the number of nearby artificial nests seemed to be of the same kind, but was not statistically significant. The difference observed between natural and artificial nests can be, at least partly, explained by natural nests occurring among the non-isolated artificial nests. In these mixed groups of nests, the adult birds on natural nests may have served to reveal the unprotected artificial nests. In the case of natural nests, real nest colonies might have yielded density dependent survival rates.

An increase in the vegetation cover has a positive effect on the survival of grebes' nests. Many other studies on nest predation have yielded similar results (Livezey 1981, Hill 1984b, Sugden & Beyersbergen 1986). As a result of the growth of new shoots in midsummer, the reed stands become much denser. Owing to their long breeding period, the Great Crested Grebes are forced to start breeding in reed stands from the previous year and thus cannot make full use of these denser stands. A reduction in predation rates has been observed for nests of late-nesting pairs (V. Salonen, unpubl.). This reduction in predation may to some extent compensate for the lower number of eggs of late and re-nesters.

From a methodological point of view, the estimation of survival probabilities π_t as a function of controlled and environmental variables is a natural choice as well as the logistic form of π_t. The weakness of this approach is the idea of mutual independence of robbings, which has usually been assumed in other predation studies as well.

For artificial nests we observed that nearby nests tend to suffer the same fate (robbed or surviving), which is partially explained by the heterogeneity of the surroundings, e.g. the proximity of gulls' nests and natural grebes' nests. Indeed, our Model 2 permits a clear interpretation. A slightly better explanation was achieved in terms of the result of nearby experimental nests when no independence was assumed. This may be an indication of actual dependence in nest predation and accords with the observations of some authors that the predation rate increases with increasing nest density. An explanation is that a predatory bird which has robbed one nest will search the surroundings intensively (Croze 1970, Sonerud & Fjeld 1987). Although in our experimental data the effect of the number of nearby artificial nests was not statistically significant, the information that some of the nearby nests have been robbed gives a much better explanation of predation.

In this study, two models offering different explanations were obtained: heterogeneity of the surroundings and interdependence between nest robbings. We cannot separate these two hypotheses using statistical reasoning only. Instead, new field observations about the behaviour of predatory birds are needed.

Our conclusion from the statistical analysis of the experimental data is that interdependence between robbings should be taken into account if the nests are located in groups and, in general, interpretations of statistical tests which assume independence should be treated with care if some of the nests are grouped together.

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Selostus: **Silkkiuikun pesäpredaatioon vaikuttavia tekijöitä**

Varisten silkkiuikkujen munapesiin kohdistaman predaation määrää ja siihen vaikuttavia tekijöitä tutkittiin vuosina 1983–85 Päijänteen pohjoisosassa sijaitsevalla tutkimusalueella. Alueen silkkiuikkupopulaation pesien lisäksi tutkimusaineistoa kerättiin pesäjäljitelmien avulla. Yhteensä 90 tekopesästä puolet sijoitettiin muutaman pesän rykelminä ja puolet yksittäispesinä järviruokokasvustoihin, joiden tiheys vaihteli. Kokeissa pesiin sijoitettiin pienikokoinen kananmuna, jonka väriä ja suojausta pesäaineksilla vaihdeltiin.

Sekä luonnonpesäaineston että kokeellisen havaintoaineiston tilastollisessa analysoinnissa käytettiin logistista ja autologistista regressiomallia predaatiotodennäksisyyksien selittämisessä. Metodinen valinta salli heterogeenisuuden ja mahdollisen predaatiotapahtumien keskinäisen riippuvuuden huomioonottamisen aineiston tilastollisessa analysoinnissa.

Keskimäärin 39% alueen silkkiuikkupopulaation pesistä ryöstettiin kokonaan tai osittain. Vuosien välinen vaihtelu ryöstettyjen pesien osuudessa oli vähäistä (taulukko 1). Ryöstettyjen pesien osuudessa ei havaittu tilastollisesti merkitsevää eroa yksittäin ja ryhmissä sijainneiden pesien välillä. Lähellä sijainneiden muiden tekopesien määrän ei todettu vaikuttaneen tekopesän predaatioon tilastollisesti merkitsevästi. Sen sijaan lähellä olevilla silkkiuikunpesillä oli tekopesään kohdistuvaa predaatiota lisäävä vaikutus, samoin yhdellä tai useammalla naapuristossa sijainneella ryöstetyllä tekopesällä (taulukko 5). Pesää suojaavan järviruokokasvuston tiheyden kasvulla ja lokkilintujen pesien lähesyydellä oli selvä positiivinen vaikutus pesien säilymiseen (kuva 1, taulukot 2–4). Pesäaineksien alle kätketyt munat säilyivät paremmin kuin suojattomat munat. Suojattomien munien värillä ei sen sijaan ollut vaikutusta (taulukot 3–5).

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