Nest predation in Meadow Pipits *Anthus pratensis* nesting in natural conditions

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Predation was the most important cause of nest failures in a population of Meadow Pipits *Anthus pratensis* breeding in a natural fen mire in Biebrza marshes (NE Poland). According to the Mayfield method, in two breeding seasons, predators interrupted 47% of all breeding attempts (95% confidence limits: 36%–55%). Other mortality agents (e.g. desertion of nests, flooding) eliminated another 5% of nests. Predators reduced production of fledglings by about 50% and introduced most of the variability in the number of fledglings produced in a single reproductive bout. There was a significant annual and within-season variation in the probability of nest predation. When seasonal changes in vulnerability were controlled for, the analysis revealed that in all stages of the breeding cycle the nest was equally likely to be depredated. A review of the data on survival of nests in four populations of Meadow Pipits, indicates that even though nest failure rates are similar (around 50%), the species must cope with different agents of mortality. In natural habitats predators pose a greater threat to nests than in habitats strongly modified by human activity.

1. Introduction

Typically, in small altricial species of birds, predators take about a half of all clutches and broods (Martin 1993, Hanski et al. 1996). It is hypothesised that from an evolutionary perspective, nest predation shapes the life history of birds (Bosque & Bosque 1995, Martin 1995).

Most of the data on frequency of nest predation were gathered in environments strongly affected by human activity. The extensive changes in habitat, e.g. elongation of ecotones (Wilcove 1985), introduction of new predatory species (Caughley 1994) or removing of some natural predators (Newton 1993), can influence causal mechanisms determining survival of eggs and nestlings. Research suggests that such human-induced changes could evoke some evolutionary shifts in life histories of small altricial nesters (Martin & Clobert 1996). To test this hypothesis we need more data from the "control" populations living in habitats where mechanisms and effects of nest predation were not disturbed by factors associated with human settlements.

In this paper I investigated the pattern of annual and seasonal changes in the intensity of nest predation and its effects on reproductive success in Meadow Pipits *Anthus pratensis* nesting in natural conditions.

2. Material and methods

Data were collected between May and July of 1990 and 1991 in the Biebrza marshes (NE Poland), a large lowland fen mire. In the 19th century at-

tempts were made to drain some marshy areas within the Biebrza river valley; however efforts were generally not successful. In areas which were relatively easier to access, sedges were scythed for hay once a year, but even this practice ceased in the 1980s. In the early 1990s, the national park was established.

The 40 ha study plot was located in the southernmost Biebrza basin, 5 km from the river, in a sedge *Carex spp.* meadow with some sparse concentrations of small bushes *Salix spp.* The ground was covered by prominent tussocks of *Carex appropinquata* and moss. In some places (about 7% of the research plot) the scattered reed *Phragmites communis* occurred. Early in the breeding season the water level was at its highest (in 1991 it approached about 40 cm) and thereafter gradually decreased, so that in July the surface water was only a few centimetres deep.

In the 1990 and 1991 seasons the earliest breeding attempt started between 10 and 20 of April. Therefore, I assumed that the phenology in both breeding seasons was similar.

The most important nest predators of small passerines were Harriers *Circus spp*, which, while hunting for nests, apparently use visual cues (Halupka 1998a, 1998b).

Nests of Meadow Pipits were randomly distributed within the study plot (Halupka K., unpubl.). The population reached a density of 9.8 pairs per 10 ha in 1990 and 9.2 in 1991 (one of the highest found for this species; cf. Hötker 1990).

The same research methods were used in 1990 and 1991. To assure that at any period of time the number and characteristics of sampled nests reflected the number and characteristics of all active nests in the marsh, I checked the area each day to find all nests within the study plot.

Nests found during the incubation period were checked daily to determine the hatching day. In the nestling period, nests were checked on the 4th, 6th and 8th day (hatching day is day 0) and, thereafter, daily up to fledging. If the nest was found to be empty, there were some signs of predation (e.g., disturbed nest cover, blood, feathers, etc.) and parental activities were not observed, the nest was classified as depredated. In order to estimate the date on which the nest was attacked, I checked whether remains left by the predator were fresh. If the exact date of nest failure was indetermina-

ble I used Mayfield's (1975) rule that predation, on average, occurred in the middle of the period between consecutive nest checks. Nests attacked after day 8 were checked once again on the following day to determine whether or not the entire brood was taken, since some nestlings could leave the nest and escape from the predator. In the present study, I classify such partially depredated broods as successful (see Halupka 1998c for details).

I assumed that the number of fledglings was equal to the number of nestlings on the day preceding the fledging day. The number of fledglings in partially depredated nests (Halupka 1998c) was assigned as 50% of the nestlings present in the nest during the previous nest check.

Survival rates of nests were calculated with Mayfield's (1975) method. Mayfield's estimators were compared using the test proposed by Johnson (1979; known as Johnson's test). Only a few nests were found during egg-laying. Therefore, I calculated the nest success for the 27-day period from the beginning of incubation to modal day (13) of fledging. While preparing the survival curve (Fig. 2), I pooled all data from the incubation period. As there is no "ANOVA-like" procedure to compare more than two Mayfield's estimators (see Figs. 2 & 3), I selected groups with homogenous survival rates on the basis of 95% confidence intervals (if there was no overlapp, I concluded that the difference was statistically significant).

Some descriptive statistics are given with their 95% confidence limits (referred to as "c.l."). Chi-squared tests with one degree of freedom were calculated with Yates's correction. If the same null hypothesis was multiple tested on different subsets of data, I applied Bonferroni's correction (Sokal & Rohlf 1995) in order to keep the type I error rate constant (at $P = 0.05$). Unplanned pair-wise comparisons of proportions within the same two-way contingency table were done with the method proposed by Sokal and Rohlf (1995, p. 741).

3. Results

3.1. Breeding success: general statistics

During the two breeding seasons I found 189 nests in various stages of the breeding cycle. Of those, 54 (29%) did not fledge young. The majority
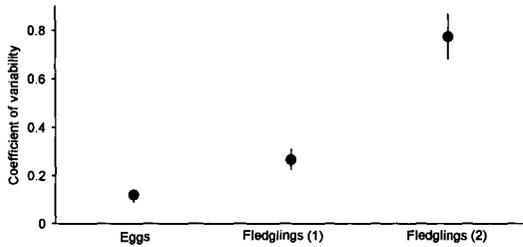
Fig. 1. Coefficients of variability and their 95% confidence intervals (calculated with the 5000 iterations bootstrap percentile method; Efron i Tibshirani 1993) for clutch size (Eggs), production of fledglings in nests which were not attacked by predators (Fledglings 1) and production of fledglings in all nests in the study area (including depredated nests; Fledglings 2).

Fig. 2. Daily survival rates of nests of Meadow Pipits in consecutive months of the breeding season in 1990 and 1991.

(85%) of unsuccessful nests failed because of predation. Desertion of adult birds, flooding, trampling by animals and some unknown factors caused the remaining 15% of nest failures. A null hypothesis that nest predation and other mortality agents cropped the same proportion of nests from the general population, was rejected (χ^2 = 26.704, df = 1, P < 0.001).

According to the Mayfield method, 48.2% (c.l.: 39.4–58.8) of all nests in which incubation began were successful. A large proportion of nests, 46.5% (c.l.: 35.7–55.4), were depredated and 5.3% failed owing to other factors listed above.

The variation in breeding success would be negligible if predators were not present in the study area. It is also clear that nest predators contributed to variations in the production of fledglings more than other mortality factors (Fig. 1).

The potential production of fledglings per nest (assuming that all eggs would yield fledglings) equalled 4.9. On average 1.1 young died of non-predation causes (intristic factors, e.g. unhatched eggs, deaths of nestlings owing to competition between sibs, and the external ones listed above). Predators took another 1.9 young and this gave the average final production of 1.9 fledglings per nest.

3.2. Nest predation: between- and within-season variation

According to Mayfield's method, in 1990 predators interrupted only 19.5% of all breeding attempts. The same statistic calculated for 1991
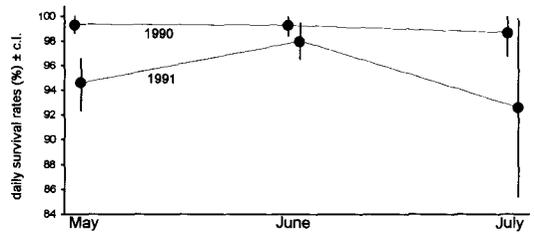
equalled 64.5%. Respective daily rates of survival were estimated as 99.20% (c.l.: 98.64–99.76) and 96.24%, (c.l.: 95.04 – 97.44) and differed significantly (Johnson's test: z = 4.483, P < 0.001). This annual variation in vulnerability seemed to arise as a result of a dramatically low survival rate in May 1991 (Fig. 2).

In 1991, the survival of nestlings in May was significantly lower than in June (Fig. 2). Such a phenomenon did not occur in 1990, when the probability of predation was similar throughout the entire season.

3.3. Probability of nest predation vs. stage of the breeding cycle

About 16% of all nests were depredated during incubation (585 successful nest-days and 8 nest-days with predation, daily survival rate: 98.65%; c.l.: 97.70–99.60) and 32% during the nestling period (1382 and 38; daily survival: 97.32%; c.l.: 96.47–98.18). This difference was statistically significant (Johnson's test: z = 2.078, P = 0.038). However, it seems to reflect some overlap of breeding phenology with seasonal changes in predation rate (see above) rather than the generally higher vulnerability of nests in the nestling feeding stage. When the effect of seasonal changes was controlled for, that is the analysis was performed with nests sampled when nest predation rate was homogenous (1990 and June–July 1991; Fig. 2), the shape of the survival curve and an overlapp between the 95% confidence intervals for daily survival rates (Fig. 3) indicated that the probability of nest predation did not vary within the breeding cycle.
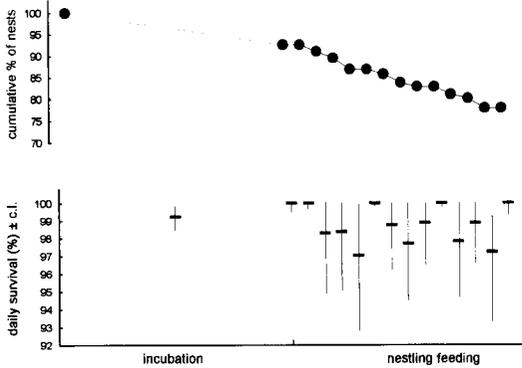
Fig. 3. Cumulative percentage of active nests of Meadow Pipits (upper graph) and daily rates of survival of clutches/broods in consecutive days of the breeding cycle (lower graph). Tick mark on the horizontal axis represents the hatching day. Data from incubation period were pooled together. Number of sampled nests in each day of the cycle varied from 41 to 91 (average = 71).

4. Discussion

Production of fledglings in Meadow Pipits is a good estimator of individual fitness (Hötker 1989). Therefore, the present study demonstrated that nest predation in the Biebrza population was a powerful factor of natural selection. Predators strongly contributed to the reduction in the number of fledglings and caused a large variability in this parameter.

Results suggest that predation pressure is not constant: it varied considerably both within and between breeding seasons. However, it is not clear what factors contributed to this variation. It could

be hypothesised that some factors might be associated with changes in the proportion of vulnerable nests (Halupka 1998a) or the density of harriers (Witkowski 1989).

When the influence of seasonal factors determining vulnerability was controlled for, the probability of brood destruction appeared to be more or less constant throughout the breeding cycle (cf. Cresswell 1997). It should be noted, however, that the analysis concerned the frequency of nest failures and not the frequency of predatory attacks. The latter significantly increased in the last quarter of the nestling period (Halupka 1998c). This phenomenon was not parallel with an increase in the rate of total breeding failures, since young Pipits escaped during the approach of a predator and only 40% of attacks resulted in destruction of the entire brood (Halupka 1998c).

The proportion of unsuccessful nests in the Biebrza marshes, when compared with data from other populations, seems to be quite typical. Figures found in all research were around 50% (Table 1). However, the relative importance of nest predation as a mortality agent varied considerably between areas. There were significant differences in proportions of nests that failed owing to predation and to all other factors ($\chi^2 = 13.438$, df = 2, P = 0.001). Pair-wise comparisons between areas revealed that the proportion of depredated nests among all unsuccessful nests was significantly lower in the human-modified habitat in Germany than in the natural fen in Poland. In the coastal area in Sweden the impact of nest predators was moderate: the proportion of depredated nests did not differ significantly (after Bonferroni's correc-

Table 1. Percentage of nests which did not produce fledgling(s) in four populations of the Meadow Pipit and the relative importance of nest predation. The table consists of information gathered in studies which gave comparable estimators of nest predation rate, were carried out for at least two seasons in the same location and included more than 50 nests.

Habitat and location	Unsuccessful nests (%)	Number of failed nests (% depredated)
Pastures, N Wales (Seel & Walton 1979)	53	20 ([a])
Pastures, meadows and arable lands in NW Germany (Hötker & Sudfeldt 1982)	54	181 (65.7)
Coastal moorland in SW Sweden (T. Elfström, personal comm.)	51	19 (89.5)
Fen in a river valley NE Poland (this study)	52	54 (85.2)

[a] not estimated in the study

tion) from that found in other studies. These results could suggest that the pressure of nest predators is lower in human-modified habitats, while the importance of other mortality agents (in Hötker's and Sudfeldt's study: nest abandonment, deaths of entire broods, human influences) is greater. As a result, the probability of nest success in Meadow Pipits was more or less even across various areas.

Selostus: **Niittykirvisen pesiin kohdistu-va saalistus Koillis-Puolassa**

Predaatio oli tärkein pesätappioita aiheuttava tekijä Koillis-Puolassa pesivässä niittykirvispopulaatiossa. Kahden pesimäkauden (1990–91) aineiston mukaan saalistus tuhosi lähes puolet (47%) kaikista aloitetuista pesinnöistä (kaikkiaan 189 pesää). Muut tekijät (pesien hylkääminen, tulva) aiheuttivat lisäksi 10 pesän tuhoutumisen (5% aloitetuista pesinnöistä). Pesiin kohdistuva saalistus alensi populaatiossa tuotettujen lentopoikasten määrää 50%:lla ja oli suurin pesintöjen välisen vaihtelun lähde lentopoikasten määrässä. Pesäpredaation määrä vaihteli merkitsevästi vuosien välillä ja myös yhden pesimäkauden sisällä eri kuukausina (kuva 2). Kun kesän mittaan vaihteleva saalistupaine huomioitiin eri pesinnän vaiheiden (muninta, haudonta, pesäpoikasvaihe) välillä ei ollut eroa tuhoutumisriskissä. Kirjoittajan tekemän katsauksen mukaan tuhoutuneiden pesien osuus on eri niittykirvispopulaatioissa jotakuinkin samanlainen. Populaatioiden välillä on kuitenkin eroja tuhoutumisen syissä. Luonnollisissa elinympäristöissä petojen pesiin kohdistama saalistus näyttäisi olevan merkittävämpi pesien tuhoutumista aiheuttava tekijä kuin ihmisen voimakkaasti muokkaamissa elinympäristöissä (Taulukko 1).

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