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Interacting effects of vegetation structure and breeding patterns on the survival of Great Reed Warbler *Acrocephalus arundinaceus* nests

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We studied the rate of predation on artificial and natural nests of Great Reed Warbler *Acrocephalus arundinaceus* in two contrasting vegetation types, reed *Phragmites australis* and reed mace *Typha angustifolia* beds. Reed provided thinner and taller stems to attach a nest to than reed mace, and reed mace provided more cover in late spring, but not in early spring. Nest density, the distance of nests from the water edge, and the timing of breeding differed considerably between vegetation types. However, there were no differences in survival rates of natural nests between both habitats. Artificial nests, on the contrary, were more frequently depredated in reed beds. Based on peck marks left on plasticine eggs, 74% of identified nest predators were large birds in both reed and reed mace beds. There was no correlation between the predicted predation rate of natural nests (derived from a logistic regression model using artificial nests) and the observed predation rate of natural nests, suggesting parental nest defence behaviour or subtle differences between actual nest sites and artificial nest sites might account for the observed discrepancy between natural and artificial predation rates. We suggest that interactions between vegetation structure, nest site choice and parental behaviour may have influenced nest predation rates in the Great Reed Warbler.

Key words: *Acrocephalus arundinaceus*, nests, predation, edge effect, timing of breeding

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INTRODUCTION

The vegetation structure around a nest may profoundly influence the nesting success of birds (Seitz & Zegers 1993, Thompson & Burhans 2003). Birds selecting nests sites within more dense vegetation may diminish the likelihood of predation by minimising the transmission of visual, olfactory or auditory cues to predators (Martin 1993). Additionally, dense plant cover may discourage predators from searching for nests, e.g. due to a reduced hunting efficiency in such habitats (Martin 1993, Seitz & Zegers 1993). Parent birds have evolved

various anti-predator strategies to increase nest success. Predation rate between habitats may be influenced by decisions made by parents about where and when to breed (Martin 1998, Weidinger 2002). Indeed, Forstmeier & Weiss (2004) demonstrated that Dusky Warblers *Phylloscopus fuscatus* chose their nest site according to the actual predation risk.

Although several studies have noted that onset of breeding in birds may be shifted by food availability (Poulin *et al.* 1992, Eeva *et al.* 2000) and weather (Finch 1991), nest predation and vegetation surrounding the nest site may play important roles as well. The

visibility of nests in each habitat is largely affected by concealment within the surrounding vegetation (San-tisteban *et al.* 2002, Gregoire *et al.* 2003), thus the phenology of the vegetation during nest site selection may influence the timing of breeding initiation. Interactive effects of timing of breeding, vegetation and breeding experiences on reproductive success were found by Thyen & Exo (2005) in salt-marsh breeding Redshank *Tringa totanus*. Other studies found close relations between nest density and nest predation (Hoi & Winkler 1994, Schmidt & Whelan 1999, Ackerman *et al.* 2004). Similarly, nest predation rate has also been linked with proximity to the boundary of the nesting vegetation ('edge effect'). In their meta-analysis of 64 artificial and natural nest experiments, Batáry & Báldi (2004) showed a significant edge effect on nest predation in marsh and deciduous forest habitats. However, it is important to recognise that rates of predation on artificial nests were usually higher than on natural nests (Mezquida & Marone 2003, Burke *et al.* 2004).

Although some of these patterns have been studied frequently in marsh habitats, little attention has been paid to predation of reed passerine nests in Small Reed Mace *Typha angustifolia* that presumably differs in vegetation structure from Common Reed *Phragmites australis*. One of the reed passerines that breeds in both reed and reed mace habitats is the Great Reed Warbler *Acrocephalus arundinaceus* (Glutz & Bauer 1991). Because vegetation structure, nest position and nest density are known to be important factors influencing nest predation in this species (Hoi & Winkler 1988, 1994, Hoi *et al.* 2001, Batáry *et al.* 2004, Batáry & Báldi 2005, Báldi & Batáry 2005) survival of Great Reed Warbler nests is expected to differ between the contrasting habitats of reed and reed mace beds. The objectives of this study were three-fold. First, we compared vegetation structure and its seasonal changes between the two types of vegetation to determine which of them offers better opportunities for concealing nests. We predicted that reed beds are the better habitat in the early breeding season, whereas reed mace offers more protection late in the season. Second, we compared breeding parameters and the rate of predation on natural Great Reed Warbler nests between the habitat types. We predicted that the nests of Great Reed Warbler are more often predated in the reed mace than in the reed because of less opportunities to conceal a nest in reed mace vegetation in the early season. Third, we determined predation rates on artificial nests to obtain a standard measure of predation rate for each habitat type.

METHODS

Study site

The study was conducted during the breeding season in 2005 at ponds near Trnava, SW Slovakia (48°21'N, 17°33'E). Five ponds extend over an area of about 60 ha and are surrounded by large areas of water and terrestrial reed beds containing Common Reed and Small Reed Mace. The ponds have a stable water level during the breeding period due to management in this protected area.

Vegetation structure

Vegetation structure was measured at the beginning of the Great Reed Warbler's nesting period (mid May) and at the end of July, after the reed growth period. Density and proportion of dry (old) and green (new) reeds or reed maces were determined by counting all stems within five 0.25m² quadrates randomly located in each habitat. Additionally, height and diameter of five randomly chosen stems in each square were measured. In order to examine vegetation cover of reed and reed mace, the cover at the same quadrates using a scale from 0 (no cover, total transparency) to four (total opacity) were assessed. These measurements were done at three lower (30, 60 and 90 cm above ground) and three upper height levels (120, 150 and 180 cm) in spring (20 May) and summer (30 July).

Natural nests

In both reed and reed mace beds, natural Great Reed Warbler nests were searched for systematically, stand by stand, in parallel lines across the entire vegetation at 4–5 day intervals from mid May to late June. In reeds we moved slowly and discreetly trying to avoid reed stems damage and disturbance of breeding birds or potential predators. We were confident that we located 90–95% of the nests in the study area. Nests were visited at the same intervals until hatching or until complete nest predation. We measured for each nest the height above the water surface (in cm), the distance from the edge of open water surface (in m) and distances between individual nests (in m). First broods, second broods and replacement broods were all treated equally. Nests located in the experimental study plots (see below) were not included into the analyses, because their success might have been influenced by the surrounding artificial nests. Because the study area was checked every 4–5 days, almost all nests were located during the nest building or egg laying periods. Based on these data we calculated the laying date of each clutch.

Artificial nests

Handmade artificial nests resembling in size and appearance the nests of Great Reed Warblers were used. Two plots were selected for the experiment: one was located in the north-western part of a pond covered exclusively by reed (with a total area of 1.6 ha), the other was located in the northern part of pond 3, covered by reed mace only (total area was 1.8 ha). The breadth of the experimental reed bed plot was from land to water edge about 35–45 m; the length approximately 400 m. The reed mace plot was 40–60 m in width and the length was about 350–400 m. Distance between study plots was approximately 800 m. According to direct observations, there were comparable predator communities in both study areas.

Based on realistic nest densities and distances between nests of Great Reed Warbler in our study area (A. Trnka, unpubl. data, 2000–2004), in each of three trials 20 artificial nests were placed in each habitat type. Each artificial nest received one fresh Quail *Coturnix coturnix* egg and one plasticine egg. The nests were distributed along linear transects at the water edge (17 nests in reed and 24 nests in reed mace, 0–5 m from open water), grassland edge (18 and 12 nests, 0–5 m from shore) and at the reed interior (25 and 24 nests, 10–45 m from water). Transects ran parallel to the edges. According to our findings (P. Batáry, pers. obs.), there was no seasonal trend in height of Great Reed Warbler nests ($t = 0.933$, $df = 23$, $P = 0.36$). Therefore, during each trial the artificial nests were fixed to four stems at a height of 70 cm above water/ground level in reed and 50 cm in reed mace, similarly to the mean height above water level of natural Great Reed Warblers nests in these habitats (A. Trnka, pers. obs.). The distance between neighbouring nests was 40 m. Corresponding to the course of breeding of Great Reed Warbler in the study area, the experiments started on 15 May, and were repeated on 8 June and 22 June.

Because of high predation rates of artificial nests compared to natural Great Reed Warbler nests (Batáry & Báldi 2005), artificial nests were exposed for 7 days only, i.e. shorter than the duration of incubation in this species, and checked at one day intervals. A nest was considered predated if any of the eggs was missing or appeared damaged. The predators were identified on the basis of peck marks left on the plasticine eggs. Three predator categories were distinguished: large birds (large triangular bill marks), small birds (small triangular bill marks) and mammals (incisor marks).

Statistical analyses

The daily survival rate of natural and artificial nests were calculated by using the Mayfield method (Mayfield 1975) and compared with the z -test (Hensler & Nichols 1981). The number of exposure days per nest was the interval between the day when the first egg was laid (for natural nests) or when the nest was placed (artificial nests) until the day the eggs were predated, divided by two. In the case of survived nests we used the whole exposure time. All artificial nests were exposed during 7 days and success was measured at day 7, so we additionally computed a logistic regression model of success (predated coded zero and survived coded one) depending on vegetation characteristics and 'laying date' (day 0 of the quail egg exposed). This logistic regression model was used to predict the success rate of natural nests based on vegetation and laying date, and to compare this against observed success rate of these same nests. Simple comparisons between two variables were performed using Mann-Whitney U-tests. Number of new stems per plot was compared by Chi-square test. ANOVA was used for comparison of vegetation cover. All statistical analyses were conducted using STATISTICA, ver. 7.0. Mean values are presented with standard errors (SE).

RESULTS

Vegetation structure

The structure of vegetation differed considerably between reed and reed mace habitats (Table 1). Stems of reed were significantly thinner and taller than stems of reed mace both in spring (Mann-Whitney test, $z = -5.676$ and $z = -6.066$, $P < 0.001$, respectively) and summer ($z = -4.332$ and $z = -5.012$, $P < 0.001$, respectively). The density of vegetation, however, was season dependent; no differences were found between reed and reed mace habitats in spring (Mann-Whitney test, $z = -0.943$, $P = 0.421$), but in summer the vege-

Table 1. Characteristics of vegetation in reed and reed mace habitats in spring (mid May) and in summer (end of July) (mean \pm SE).

Habitat	Date	Diameter stems (mm) ($n = 25$)	Height (cm) ($n = 25$)	Density stems (per 0.25 m ²) ($n = 5$)
Reed	Spring	8.6 \pm 0.5	233.8 \pm 7.9	21.2 \pm 2.4
	Summer	8.5 \pm 0.6	321.6 \pm 4.9	43.8 \pm 2.2
Reed mace	Spring	14.9 \pm 0.5	130.3 \pm 7.9	24.6 \pm 4.6
	Summer	15.7 \pm 0.6	158.6 \pm 4.9	67.4 \pm 3.2

tation of reed mace was more dense than that of reed (Mann-Whitney test, $z = -2.635$, $P = 0.008$). The number of new vs. old stems in summer was biased toward new growth in both reed ($\chi^2 = 31.8$, $P < 0.001$) and reed mace ($\chi^2 = 30.4$, $P < 0.001$).

Vegetation cover significantly changed over the season ($F_{1,112} = 28.758$, $P < 0.001$, mean vegetation cover in spring vs. summer: 0.69 ± 0.11 vs. 1.53 ± 0.11 , $n_1 = n_2 = 60$), but did not differ between the two habitats ($F_{1,112} = 2.709$, $P = 0.103$, reed mace vs. reed: 1.24 ± 0.12 vs. 0.98 ± 0.12 , $n_1 = n_2 = 60$), nor differed between the upper and the lower part of the vegetation ($F_{1,112} = 2.371$, $P = 0.126$, upper vs. lower part: 0.991 ± 0.12 vs. 1.233 ± 0.12 , $n_1 = n_2 = 60$). However, lower parts of reed maces (as measured at the three lower height levels) were significantly denser than those in reed, while reed were denser in their upper parts (three upper height levels; interaction between vegetation type \times upper and lower part of the vegetation: $F_{1,112} = 96.486$, $P < 0.001$).

Breeding patterns

Nest density, timing of breeding and distance from the water edge of Great Reed Warbler nests differed considerably between reed and reed mace. In reed, nest density reached 3.89 nests/ha, with only 1.98 nests/ha in reed mace, and hence mean distance between two nearest nests was significantly shorter in reed than reed mace habitats (43.5 ± 5.79 m vs. 78.9 ± 12.72 m, $n = 28$ and 17, respectively, Mann-Whitney test, $z = -2.375$, $P = 0.018$).

Comparing the laying date between habitat types, Great Reed Warblers were found to start nesting 11 days earlier in reed than in reed mace (median laying dates of the first egg in reed and reed mace were 28 May and 8 June, $n = 28$ and 17, respectively; Mann-Whitney test, $z = -3.344$, $P = 0.001$; Fig. 1).

While the species tended to nest close to open water in reed, the nests in reed mace were situated further from open water edge (mean distances of nests from open water in reed and reed mace were 1.3 ± 0.19 m and 3.7 ± 0.72 m, $n = 28$ and 17, respectively, Mann-Whitney test, $z = -3.671$, $P < 0.001$; Fig. 2). Similarly, marked differences were found also in the height of nests above water surface; mean nest height in reed ($n = 28$) and reed mace ($n = 17$) was 0.76 ± 0.41 m and 0.55 ± 0.39 m, respectively (Mann-Whitney test, $z = -2.837$, $P = 0.005$).

Nest predation

Overall, 20% of 45 natural Great Reed Warbler nests and 29% of 120 artificial nests were depredated during

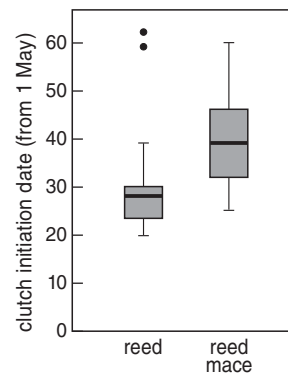


Figure 1. Medians, quartiles and minimum and maximum clutch initiation dates of Great Reed Warblers nesting in reed ($n = 28$) and reed mace ($n = 17$). Outliers are depicted with a dot.

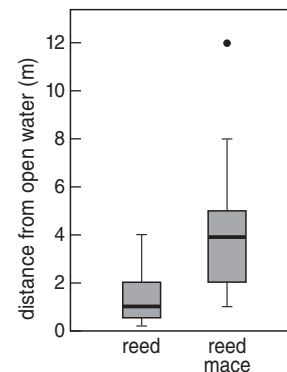


Figure 2. The medians, quartiles and the minimum and maximum distance from open water of Great Reed Warbler nests in reed ($n = 28$) and reed mace ($n = 17$). Outlier is depicted with a dot.

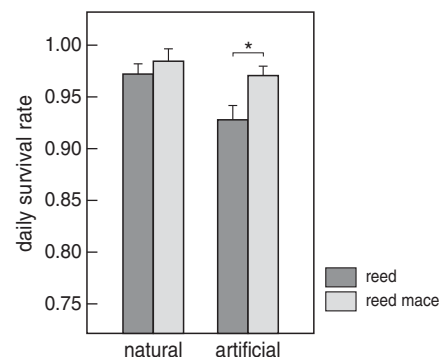


Figure 3. Daily survival rate of natural and artificial Great Reed Warbler nests in reed ($n = 28$ and 60, respectively) and reed mace ($n = 17$ and 60, respectively). Standard error bars are shown. Asterisks indicate significant differences between reed and reed mace beds ($P < 0.05$).

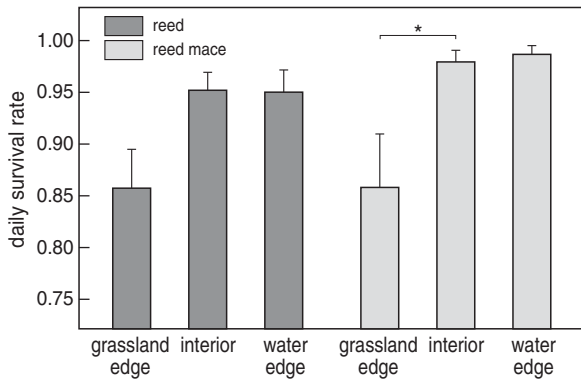


Figure 4. Daily survival rates of artificial nests located in grassland edge, water edge, or interior habitat in reed ($n = 18, 17$ and 25 , respectively) and reed mace ($n = 12, 24$ and 24 , respectively). Standard error bars are shown. Asterisks indicate significant differences between habitats ($P < 0.05$).

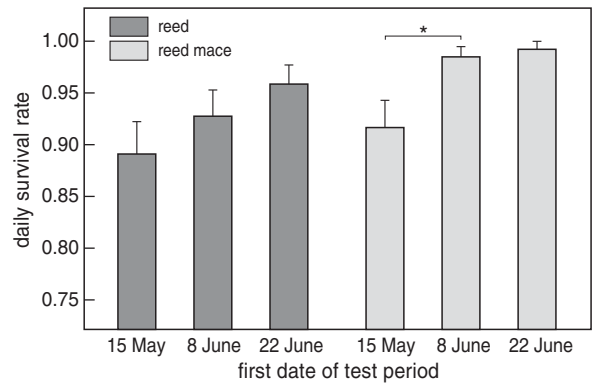


Figure 5. Seasonal differences in daily survival rates in artificial nests in reed ($n = 60$) and reed mace ($n = 60$). Standard error bars are shown. Asterisks indicate significant differences between trials ($P < 0.05$).

the study period ($z = 2.355$, $P = 0.009$). There were no differences in natural nest survival rates in reed versus reed mace ($n = 28$ and 17 , respectively; $z = 0.860$, $P = 0.195$). In contrast, artificial nests in reed had a significantly lower daily survival rate than those in reed mace ($z = 2.588$, $P = 0.005$, Fig. 3). Daily survival rate of artificial nests was also dependent on distance from the edge ($\chi^2_2 = 17.427$, $P < 0.001$) and breeding season ($\chi^2_2 = 9.244$, $P < 0.01$). Survival was significantly lower at the grassland edge in both habitat types, while no edge effect was found at the water edge either in reed or reed mace (Fig. 4). There were conspicuous seasonal trends in artificial nest predation in both habitats (Fig. 5). However, significant differences were found only in reed mace, where survival of artificial nests in May was significantly lower than in early and late June ($z = 2.383$, $P = 0.009$ and $z = 2.753$, $P = 0.003$, respectively).

Taking into consideration that the Great Reed Warbler appears to be an edge breeding species in our population, we compared daily survival rate of natural nests and artificial nests placed in reed-water and reed mace-water edges. In this way, no differences in predation rates were found between natural and artificial nests in reed ($n = 28$ and 17 , respectively, $z = 0.917$, $P = 0.179$) and reed mace ($n = 17$ and 24 , respectively, $z = 0.488$, $P = 0.377$).

Predicted versus observed natural nest predation rates

A logistic regression model showed that the success rate of artificial nests significantly depended on the 'laying date' (exposure date), distance to nearest open

water, diameter of the stems in the vegetation and the density of stems in the vegetation (Table 2), supporting in general the single-factorial analyses given above. In contrast, none of the variables reported in Table 2 significantly affected the success rate of natural nests (all $P > 0.24$). These results did not change when including the number of nest days as a covariate (all $P > 0.09$; with vegetation height $P = 0.098$, laying date $P = 0.11$ and density of stems $P = 0.15$). Consequently, when we used the model reported in Table 2 to predict the probability of success for each natural nest found in our study population and correlate this with actual success, no correlation was found (Spearman rank correlation, $r_s = 0.03$, $P = 0.85$, $n = 45$).

Table 2. Success rate of artificial nests ($n = 120$) by vegetation characteristics and 'laying date' (exposure date). Depicted are results from a logistic regression with the response variable success at day 7 of exposure (coded zero when depredated, or one when survived).

Parameter ^a	Coefficient \pm SE	Wald χ^2	df	P
Constant	1.14 \pm 1.64	0.5	1	0.48
Laying date (1 = 1 May)	0.053 \pm 0.017	9.6	1	0.002
Distance nearest water (m)	-0.047 \pm 0.013	13.2	1	<0.001
Diameter stems (mm)	0.187 \pm 0.060	9.7	1	0.002
Density stems (per 0.25 m ²)	-0.049 \pm 0.024	4.1	1	0.043

^aNon-significant terms were: habitat (reed or mace, $P = 0.98$), edge (water edge, interior or grassland edge, $P = 0.46$), and height above water surface ($P = 0.98$).

Artificial nest predators

Based on peck marks left on 35 predated plasticine eggs, 26 (74%) of the identified predators were large birds, the others were small birds (5) and mammals (4). The most probable large bird predators were Marsh Harrier *Circus aeruginosus*, Little Bittern *Ixobrychus minutus* and Black-headed Gull *Larus ridibundus* that regularly occurred and hunted in the experimental area. Small peckmarks on plasticine eggs were most likely produced by small songbird with pointed bills (probably warblers). There was no difference in predator composition between reed and reed mace beds ($\chi^2=0.95$, $df = 2$, $P = 0.62$).

DISCUSSION

Our results indicate no difference in daily survival rate of Great Reed Warbler nests in reed and reed mace, despite differences in vegetation density and height between the two habitats. However, nests were located further from the water edge but vertically closer to the water surface in reed mace. Additionally, median laying date was earlier in reed, where nest density was also greater. Artificial nests, on the other hand, were more frequently depredated in reed than in reed mace.

Reed and reed mace are considered traditional breeding habitats of Great Reed Warbler in Central Europe, though many studies (see Glutz & Bauer 1991) showed clear preferences for reed. Due to the different vegetation structure between reed and reed mace beds, differences in predation risk of Great Reed Warbler nests were predicted. Although several previous experiments showed a positive correlation between nest concealment (due to reed density and height) and nest survival (Ille *et al.* 1996, Honza *et al.* 1998, Hansson *et al.* 2000b, Batáry *et al.* 2004, Batáry & Báldi 2005), no difference was found in daily survival rates between natural nests in the two habitats in our study. However, vegetation structure appeared to affect significantly the height at which Great Reed Warblers built their nests. Nests were fixed at lower heights above water surface on the shorter and less firm stems of the reed mace habitat, which had denser lower portions of the vegetation than did reed. Similarly, Havlín (1971) found that the mean height of Great Reed Warbler nests above water surface was 0.43 m in reed mace, while Dyrce (1981) and Honza *et al.* (1993) reported 0.74 m and 0.80 m mean nest heights, respectively, in reed. We see this as strong evidence that nest placement is closely related to vegetation cover in this species.

Similarly, vegetation structure may have influenced

timing of breeding in the Great Reed Warbler. In the reed, marked by thinner, taller, stems with more dense upper parts of the vegetation, birds bred earlier and with a higher density of nests situated nearer to the water edge than in reed mace stands. Since the males established territories during the same time period in both habitats (A. Trnka, pers. obs.), delayed breeding in reed mace could have been caused by the structure of old reed mace stems, which may have been too short and soft at the beginning of the breeding season to provide safe shelter and fixture for nests. Therefore, the birds would have to wait until the new stems grew up to the proper height and firmness. Another explanation is that males settling on reed mace are of lower quality and therefore need more time to attract a female. Positive correlation between timing of breeding and nest cover in closely related species, Marsh Warbler *Acrocephalus palustris* and Reed Warbler *Acrocephalus scirpaceus* was shown by Ille *et al.* (1996) and Bergmann (1999). Similarly, Graveland (1999) found that Reed Warblers nested 6–12 days later in cut than uncut reed, which differed noticeably in stem density.

Commencement of breeding may be closely linked to nest predation rates as well. In our study, significantly higher risk of artificial nest predation at the beginning of the breeding period was found in reed mace. This might explain why reed warblers avoid breeding in reed mace in the early season. Changes in daily survival rates of artificial nests during the breeding period were found also by Batáry *et al.* (2004) at Lake Neusiedl, where the nest survival increased from start to mid breeding season. It is possible that predation rates of Great Reed Warbler nests is also related with nest density. Contrary to other habitats (Robinson *et al.* 1995, Keyser *et al.* 1998, Zanette & Jenkins 2000, Winter *et al.* 2006), Hoi *et al.* (2001) found that nest depredation of reed passerines increased with the size of the reed bed. In our study area, density of natural Great Reed Warbler nests was 2 times higher in reed than in reed mace. This could explain that the predation rate was lower in our study area with small plots of reed and reed mace (20% on natural and 29% on artificial nests) compared to large reed areas where depredation of artificial nests ranged from 42% to 96% (Batáry *et al.* 2004, López-Iborra *et al.* 2004). Natural Great Reed Warbler nest predation ranged from 24% to 43% (Bensch & Hasselquist 1994, Batáry & Báldi 2005).

The polygynous mating system of Great Reed Warbler is another factor that could affect breeding density and nest predation rates. Bensch & Hasselquist (1994) and Hansson *et al.* (1997) found that nests of primary females suffered a three times higher rate of

nest loss during the egg-laying period than nests of secondary and monogamous females, and that secondary females commit infanticide on eggs of primary females. Thus, higher rates of nest predation could be expected in populations with a higher rate of polygyny. However, although polygyny is common in our study area (Trnka *et al.* in prep.), rates do not differ between the birds nesting in reed and reed mace beds.

Finally, proximity to the edge may affect predation rates within a habitat type, although much variation exists within and across studies. Batáry *et al.* (2004) found a higher nest predation in artificial nests at the edges of reed beds than in the reed interior. Hansson *et al.* (2000b), on the contrary, found no edge effect in predation on natural Great Reed Warbler nests in reed. Our results are consistent with the latter findings. By comparing the location and survival of artificial nests in our study sites, a significant edge effect was found only at the grassland edge. Although artificial nests generally suffer higher predation rates (Davison & Bollinger 2000, Mezquida & Marone 2003, Burke *et al.* 2004, Batáry & Báldi 2005), we found no differences between natural and artificial nests placed in reed-water and reed mace-water edges, considered to be the preferred nest sites.

Results of our artificial nest predation experiments hinge much on the choice of sites used for the experiments. The rate of nest predation can be influenced – apart by the habitat structure – indirectly also by food availability, quality of breeding pairs, or predator communities. We were limited in possibilities in choosing sites because only few suitable habitat spots were available in the study area. For a firm comparison between reed and reed mace habitat, we plan to replicate the experiments in more sites.

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SAMENVATTING

Om te onderzoeken in hoeverre het broedsucces van de Grote Karekiet *Acrocephalus arundinaceus* afhangt van de structuur van de vegetatie, werd een vergelijking gemaakt tussen de overlevingskansen van nesten in twee verschillende vegetatietypes, de een gedomineerd door Riet *Phragmites australis* en de andere door Kleine Lisdodde *Typha angustifolia*. De stengels van Riet waren dunner en langer dan die van Lisdodde. De dichtheid van stengels in beide vegetatietypes was aanvankelijk gelijk, maar later in het broedseizoen was de dichtheid van Lisdoddes hoger dan van Riet. De nestbouw was 11 dagen eerder in het Riet dan in de lisdoddevegetatie, en de dichtheid aan nesten was in Riet hoger terwijl de nesten bovendien op een kleinere afstand van open water lagen. Echter, de overlevingskans van de nesten verschildte niet tussen beide vegetatietypes. Proeven met kunstnesten lieten zien dat de predatiekans in het Riet het hoogst was. De afdrukken in nepeieren van plasticine wezen erop dat grote vogels verantwoordelijk waren voor 74% van de predatie. De proeven met de kunstnesten toonden aan dat de nestoverleving afhing van de datum, de afstand tot het water, en de diameter en dichtheid van de stengels. Maar deze kennis bleek weinig voorspellende waarde te hebben wanneer toegepast op de echte nesten. Dit was mogelijk het gevolg van het gedrag van de broedvogels om predatoren te verjagen of af te leiden. Ook subtiele verschillen tussen de manier waarop de kunstnesten waren opgehangen in vergelijking met echte nesten kunnen hierbij een rol gespeeld hebben. (DH)

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