

PREDATION ON NORTHERN LAPWING *VANELLUS VANELLUS* NESTS: THE EFFECT OF POPULATION DENSITY AND SPATIAL DISTRIBUTION OF NESTS

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The effects of population density, nest pattern, size of nest aggregations and position of nests within aggregations on predation rates were analysed in two Northern Lapwing *Vanellus vanellus* populations in agricultural landscape in South Bohemia, Czech Republic, 1988-98. Two sites (Arable Land and Meadow) differed in breeding densities but their nest patterns were similarly clumped. While population density negatively correlated with nest predation rate at both sites, the nest pattern demonstrated only a weak effect. Nest predation was not influenced by distance to the nearest neighbouring nest while it was significantly affected by aggregation size in Meadow but not in Arable Land. Decreasing predation from edge to centre of large aggregations supports Lack's protective umbrella hypothesis. However, large aggregations in Arable Land experienced high predation risk, particularly due to extensive loss of marginal nests indicating that the Northern Lapwings' aggregating behaviour may not always reduce predation risk in the group as a whole. Habitat quality and composition of predator guilds are considered to be factors influencing the different predation pattern on nests at the studied sites.

Key words: *Vanellus vanellus* – nesting success – predation risk – Mayfield method – aggregability – nest pattern – density dependence – protective umbrella hypothesis

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INTRODUCTION

Predation constitutes the primary cause of nest failure across a variety of bird species, habitats and geographic locations (Martin 1993). This factor is considered to be one of the reasons for the gregarious behaviour demonstrated by birds during nesting, and this behaviour has been documented in many bird populations (e.g. Horn 1968; Picman *et al.* 1988; Larsen & Moldsvoor 1992).

Nests of the ground-nesting Northern Lapwing *Vanellus vanellus* may be more vulnerable to predators than those of above-ground nesters (Newton 1994; Yanes & Suarez 1995) and preda-

tion of clutches is a major factor limiting Northern Lapwing productivity (e.g. Baines 1990).

In order to defend their nests against predators, Northern Lapwings nest in open, flat country with few shrubs and trees (e.g. Klomp 1954; Imboden 1971; Cramp & Simmons 1983), far away from potential perches for avian predators (Berg *et al.* 1992). Galbraith (1988b) found that the number of Northern Lapwings nesting in an area was negatively correlated with the proximity of predator refuges such as trees and hedgerows. Moreover, Northern Lapwings respond aggressively to predator attacks (Cramp & Simmons 1983). At nesting time, the birds congregate in



groups known as 'loose colonies' (Lack 1968; Larsen *et al.* 1996) where overlapping defence zones around individual nests result in shared protection of clutches. Working together, they have a better chance of successfully excluding predators from the nesting area (Elliot 1985a; Baines 1990).

In central Sweden, Berg *et al.* (1992) found that nests in Northern Lapwing groups containing at least five nests were more likely to survive than nests in smaller groups. The conclusion was that higher local densities of nests may provide more effective protection against predators, and hence a better chance of survival (Göransson *et al.* 1975; Birkhead 1977; Baines 1990). Moreover, experiments with artificial nests have suggested a lower risk of predation within Northern Lapwing colonies than outside and the risks to real Northern Lapwing nests were also examined (Elliot 1985a; Berg 1996).

The aim of this study was to evaluate the nest predation patterns in Northern Lapwings breeding in an agricultural landscape in Central Europe widely affected by human activities; namely, to analyse and compare how susceptibility to predators may be affected by population density and nest clumping, size of aggregations and by positions of nests within these aggregations.

MATERIAL AND METHODS

Northern Lapwing populations were studied at two sites in the northern part of the *České Budějovice Basin* (flat river and fish-pond valley), *South Bohemia, Czech Republic* (49°15'N, 14°05'E). The first site, referred to as *Arable Land* (12.2 km²), varies from a flat basin (370 m a.s.l.) to a gently undulating landscape (390 m). This area comprises of a mosaic of cultivated fields (61% of the area) and meadows (18%), interspersed with small woods (9%) and shrubs (2%). Wetlands (fish-ponds, sedges, bogs) cover less than 7% of the area. The remaining 3% include settlements and roads. The second site, referred to as *Meadow* (5 km²), is adjacent to the first site in flat, open countryside in the floodplain of the *Blanice River*.

It comprises of fields (55% of the area), small patches of shrubs (1.5%) and trees (3.5%), with few settlements and roads (2%) and a high proportion of meadows (30%) and wetlands (8%). The fields at both sites are managed similarly, winter wheat, spring cereals, oilseed rape and clover being the primary crops. Meadows are worked in early spring, generally before or during incubation period and mowed at the end of May or later, well after the hatching period of Northern Lapwings in this area.

Data sampling

Breeding Northern Lapwings were counted from the end of March through mid-May between 1988 and 1998, with the exception of 1990, 1992 and 1995. Each field was surveyed at least once a week, with high density areas being monitored more often. Locations of all observed Northern Lapwings and nests were recorded on a topographic map (scale 1 : 5000). Northern Lapwings of which no nests were found, but that were demonstrating territorial or breeding behaviour (display, mating, guarding, attacking potential predator) in the same field repeatedly for a two-week or longer time period were recorded as probable breeding birds. Nests were monitored from the date of finding throughout the incubation period with approx. 3-10 d intervals. After detection, each nest was marked with a sallow placed at a distance of about 15 m (20 steps) away to re-locate the nest quickly and reduce the chance of attracting predators (cf. Galbraith 1987). The incubation stage of completed clutches was estimated using the floatation test (Van Paasen *et al.* 1984).

For this study, only nests in which the first egg appeared before April 15th were included in the predation analysis. April 15th was found to be the date on which at least 90% of all first clutches in the study area were laid (M. Šálek, unpubl. data). All confirmed and probable breeding pairs recorded until this period were included in the estimation of population density and aggregation size. Clutches after 15 April or replacement clutches of individually marked females were excluded to avoid effects from bird redistribution

after destruction of first clutches, and different survival rates of first and later clutches (cf. Berg 1996). The only exception was 1996 when laying was delayed for about two weeks due to cold weather in early spring; the 90% level of first started clutches was shifted to the end of April. Nest survival was monitored from a distance (presence of incubating adults) or by visiting the nest in 3-10 day intervals so that many were visited during hatching.

Nests found without eggs after the calculated date of hatching were considered to have hatched when only very small eggshell fragments were present in the base of the nest. A nest was considered successful, even if the nest site itself was destroyed, when adults indicated a brood by displaying brood-protection behaviour, e.g. intensive warning. Out of 443 clutches, four (0.9%) with an uncertain fate were excluded from the analysis of nest survival. A nest was also classified as successful if at least one chick hatched (with or without partial clutch loss). Nests were categorised as predated if they were found without eggs before the expected date of hatching, or if there was other evidence of predation such as remains of destroyed eggs in or near the nest (cf. Galbraith 1988a; Berg *et al.* 1992; Blomqvist & Johansson 1995).

Data analysis

Population density was calculated by dividing the number of all (i.e. confirmed and assumed) Northern Lapwing nests by the total area available for nesting in the study area. The total area available for nesting was estimated by including all fields where at least one pair attempted to breed from 1985 (M. Šálek, unpubl. data). This procedure effectively excluded all unsuitable habitat such as forests, shrubland, open waters (fishponds and rivers), roads, human settlements and too small or highly disturbed fields which are avoided by breeding Northern Lapwings.

The nest pattern (nest aggregation rate) in a population was evaluated by the nearest-neighbour method. The index of aggregation R was calculated as a ratio between the mean distance of

nests to their nearest neighbour and the average of the theoretical distances in this population being distributed randomly in a given area. If the spatial pattern is random, then $R = 1$; when clumping occurs, R approaches zero (Krebs 1989). As Northern Lapwings actively defend their nests against avian predators in a radius of 30-50 m from the nest (Elliot 1985a), the maximum distance between neighbouring nests which may be jointly defended is about 100 m. Therefore, a nest aggregation was defined as a group of nests in which each nest is situated within 100 m from any other nest (Berg 1996) unless intersected by shrubs or tree lines. Three nesting group categories were distinguished: solitary nests (> 100 m from the nearest nest), small aggregations (2-9 nests in a group) and large aggregations (> 9 nests in a group).

Each nest within a nesting aggregation was assigned to one of three equally wide concentric rings constructed around the geometric centre of the group. Thus, the central ring included nests in the inner-most area of the aggregation while the marginal ring included all nests in the outer-most third of the radius. Nests placed between these two latter rings are referred to as intermediate nests. As most nests in groups of two or three showed a dubious pattern of their position in terms of the defined rings, they were excluded from the analysis of predation risk in the three positions within aggregations. The nests closer to the aggregation centres were hypothesized to be at less risk than the nests at the margins.

The Mayfield method (Mayfield 1961, 1975) was used to estimate nest success (cf. Blomqvist & Johansson 1995; Berg 1996) because nests varied in the stage of incubation at the time of their finding. The daily predation risk was calculated by dividing the number of predated nests by total exposure (nest-days) of all examined nests. The predated nests do not include those that suffered partial predation. Standard deviations (SD) were derived according to Johnson (1979) and t-statistics were calculated using the formula of Hensler & Nichols (1981). In multi-way comparisons or when three or more categories in one-way clas-

sification were distinguished, the extended Mayfield method was applied using regression analysis (general linear models, GLM) as recommended by Aebischer (1999). Because it was expected that the studied variables (survival rate, population density, nest pattern, aggregation size and distances between nests) are inter-related on a multiplicative scale, their values were log-transformed to adhere to the additivity assumption of the linear regression model. The regression models were fitted using the S-PLUS® (1999) software. The results obtained with a generalised linear model with assumed binomial distribution of response variable were largely consistent with those obtained using the linear model and are not therefore presented in this study.

RESULTS

During the study period, the breeding density of the Northern Lapwing populations varied between 0.7 and 3.4 nests/100 ha in Arable Land, and between 3.7 and 21.2 in Meadow (Table 1).

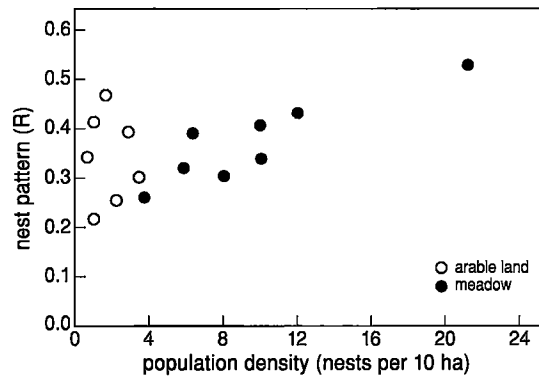


Fig. 1. Relationship between population density and nest pattern in Northern Lapwing populations at the studied sites. For calculation of nest pattern index (R) see Data analysis. R approaching zero indicates a more clumped pattern of nests in a population.

Differences in breeding densities between the sites were significant throughout the study period ($t_{13} = -3.76$, $P = 0.002$) with a 3.5 -19.6 times higher density in Meadow in any one year. Also, the nest pattern (R) fluctuated between 0.22 and 0.47 (median: 0.34) in Arable Land while 0.26

Table 1. Population size, spatial nest distribution and daily nest predation rates (Mayfield) in Lapwings at the study sites between 1988 and 1998. In Total nests, all confirmed and probable nests are included. For calculation of nest pattern index (R) see Data analysis. Number of cases in parentheses. * too small sample size of monitored nests.

Year	1988	1989	1991	1993	1994	1996	1997	1998
Arable Land								
Total nests	42	27	12	12	8	20	35	5
Density (nests/100 ha)	3.4	2.2	1.0	1.0	0.7	1.6	2.9	0.4
Solitary nests	3(3)	3(3)	3(3)	3(3)	3(3)	5(5)	5(5)	1(1)
Small aggregations (2-9 nests)	22(6)	24(6)	9(2)	9(4)	5(2)	15(4)	15(5)	4(2)
Large aggregations (> 9 nests)	17(1)	-	-	-	-	-	15(1)	-
Daily nest predation (%)	1.11	2.85	25.53	7.19	28.57	9.3	7.81	*
Nest pattern (R)	0.30	0.26	0.41	0.22	0.34	0.47	0.39	*
Meadow								
Total nests	108	61	19	30	32	51	51	41
Density (nests/100 ha)	21.2	12.0	3.7	5.9	6.3	10.0	10.0	8.0
Solitary nests	2(2)	1(1)	1(1)	2(2)	1(1)	1(1)	6(6)	7(7)
Small aggregations (2-9 nests)	15(4)	28(5)	18(4)	28(7)	19(5)	25(5)	11(4)	22(8)
Large aggregations (> 9 nests)	91(5)	32(2)	-	-	12(1)	25(2)	34(2)	12(1)
Daily nest predation (%)	1.42	2.64	16.78	7.66	2.65	3.53	2.13	4.63
Nest pattern (R)	0.53	0.43	0.26	0.32	0.39	0.34	0.41	0.30

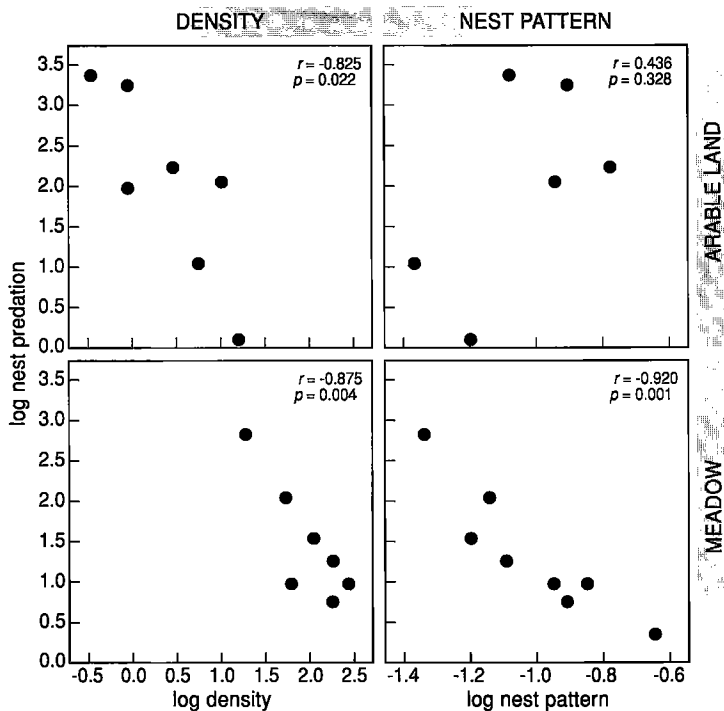


Fig. 2. Relationships between daily predation on Northern Lapwing nests (%) and two population factors at the studied sites: population density and nest pattern (values of R index; for calculation see Data analysis). All values are log-transformed.

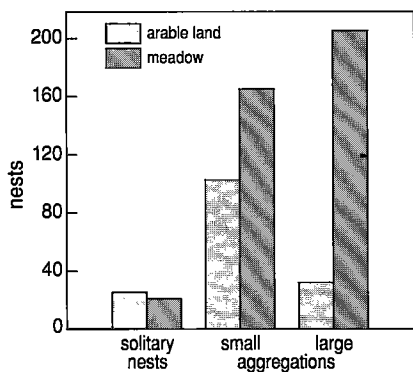


Fig 3. Distribution of Northern Lapwing nests among three types of nesting groups (units) at the studied sites: solitary nests, small aggregations (2-9 nests) and large aggregations (> 9 nests).

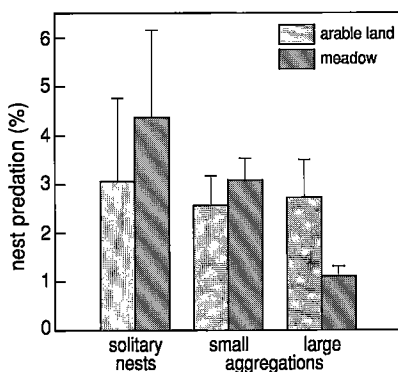


Fig. 4. Daily predation on Northern Lapwing nests (% \pm SD) within three types of nesting groups at the studied sites: solitary nests, small aggregations (2-9 nests) and large aggregations (> 9 nests).

and 0.53 (median: 0.37) in Meadow; the difference between the sites was not significant (Mann-Whitney test, $U_{7,8} = 23.5$, $P = 0.6$; Fig. 1). The nest pattern highly correlated with population

density in Meadow ($r = 0.89$, $R^2 = 76.1\%$, $F_{1,6} = 23.2$, $P = 0.003$) but no such relationship was found in Arable Land ($r = 0.03$, $F_{1,5} = 0.004$, $P = 0.95$; Fig. 1).

Table 2. The GLM models of population density and nest pattern effects on daily nest predation in Lapwings in Arable Land and Meadow. The factors density and nest pattern are nested within the site.

Model	<i>t</i>	<i>P</i>
log(daily nest predation)		
≈ site / log(density)		
Site	1.56	0.147
Arable Land	-4.08	0.002
Meadow	-3.20	0.009
log(daily nest predation)		
≈ site / log(nest pattern)		
Site	-3.08	0.011
Arable Land	1.56	0.147
Meadow	-2.40	0.036

Effect of population density and nest pattern on predation rate

Given that the relationship between population density and nest pattern (aggregation rate) differed largely in Arable Land and Meadow (Fig. 1), effects of both factors were analysed in two separate GLM models where the factors were nested within the site factor (Table 2). While predation rates correlated negatively with breeding densities in both sites in a similar pattern, indicating that nest predation decreased as the population density increased, the relationship between predation and nest pattern was only weak and varied between the sites (Table 2, Fig. 2). While no significant relationship was confirmed in Arable Land, Meadow nests were predated significantly more in years with higher nest clumping. However, this result can be considered as a product of high intercorrelation between aggregation rate and high population density in the area-limited Meadow (Fig. 1).

Aggregation size and its effect on nest predation rate

The most common type of nesting in both sites were small aggregations (52% in Arable Land, 55% in Meadow; Table 1). However, large aggre-

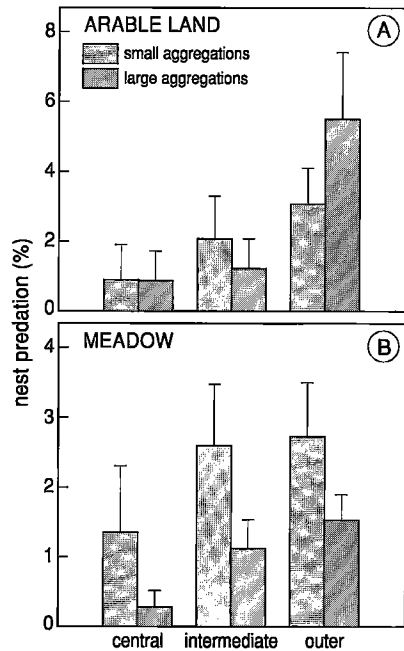


Fig. 5. Daily predation on Northern Lapwing nests (% \pm SD) within central, intermediate and outer positions of small aggregations (2-9 nests) and large aggregations (> 9 nests) in (A) arable land and (B) meadow.

gations appeared more often in Meadow (17% with 52.4% nests) and were more rare in Arable Land (3% with 19.9% nests). It is why the sites differed significantly in nest distribution among the groups ($\chi^2_2 = 55.9$, $P < 0.001$) in favour of small aggregations in Arable Land and large aggregations in Meadow (Fig. 3). The effects of distance to the nearest neighbouring nest and to aggregation size (number of nests within an aggregation) on nest predation rate were analysed by the GLM with the use of separate data from Arable Land and Meadow. Distances to the nearest neighbour did not contribute to the variability of predation rate in Arable Land ($t = 0.38$, $P = 0.7$) nor in Meadow ($t = 0.23$, $P = 0.8$). The size of aggregation played a highly significant role in Meadow ($t_{2,249} = 4.08$, $P < 0.001$) but not in Arable Land ($t = 1.65$, $P = 0.1$). Similarly, the GLM analysis confirmed types of nesting groups (soli-

tary nests, small aggregations and large aggregations) as significant factors of nest survival in Meadow ($t_{2,249} = 3.56$, $P < 0.001$) but not in Arable Land ($t = 1.72$, $P = 0.09$). While the daily predation rate decreased significantly from solitary nests (4.4%) to large aggregations (1.1%) in Meadow, it varied little (between 2.6 and 3.0%) among nesting groups in Arable Land (Fig. 4).

Although only slight differences between sites were found in nest predation risk either on solitary nests or within small aggregations ($P > 0.05$ for both types of nesting groups), large aggregations in Meadow suffered lower predation risk than those in Arable Land ($t_{183} = 2.01$, $P < 0.05$; Fig. 4).

Predation within aggregations

The effect of nest positions within aggregations was analysed separately for Arable Land and Meadow. In general, nests situated in central positions within aggregations were predated less than nests positioned at the edges (Fig. 5). The GLM analysis confirmed, however, that the differences were statistically significant only in large aggregations (Arable Land $R^2 = 13.7\%$, $F_{1,26} = 5.29$, $P = 0.03$; Meadow $R^2 = 4.2\%$, $F_{1,151} = 7.62$, $P = 0.006$) but not in small aggregations (Arable Land: $P = 0.4$; Meadow: $P = 0.8$). A fairly high predation rate was confirmed at the edges of large aggregations in Arable Land (5.5%). This predation was significantly higher than predation on marginal nests in small aggregations in this area ($t_{28} = 2.67$, $P < 0.01$; Fig. 5a). On the contrary, the Meadow nests located at the margins of large aggregations suffered lower predation than those in smaller aggregations in the area ($t_{95} = 1.28$, $P > 0.05$).

DISCUSSION

Nest predation was an important source of Northern Lapwing nest failures in the study sites. This has also been documented in a number of other Northern Lapwing populations (e.g. Matter 1982; Beintema & Müskens 1987; Galbraith 1988b; Baines 1990; Berg *et al.* 1992; Liker 1992; Blomqvist & Johansson 1995) although the proportional loss

due to predation widely varied between 12.5% (West Germany; Grosskopf 1968 in Cramp & Simmons 1983) and 76% (improved grasslands in northern England; Baines 1990). The result of this study, 30.0% nests failed due to predation, is rather similar to 23.5%, 26% and 29% clutches predated in the Switzerland (Glutz von Blotzheim *et al.* 1977; Matter 1982) and 21.7% clutches predated on Hungarian alkaline grasslands (Liker 1992).

Nest predation rate decreased significantly with an increase in population density in a similar way at both sites. Thus the density dependence hypothesis, supposing that higher predation risk on nests may result from predators searching actively for dense nests aggregations, can be rejected. On the contrary, nearest nest distances obviously did not influence the nest predation rate directly. The correlation between clumping and nest predation in Meadow may result from the close relationship between population density and spatial nest pattern in this site, i.e. high numbers of nesting birds in a small site (unlike in Arable Land). The questionable meaning of spatial nest pattern is also documented by the absence of a relationship between predation risk and the distance to the nearest neighbour nest at both sites.

Results from Meadow (unlike Arable Land) pointed out that nest predation can be significantly affected by aggregation size. Observations in this study correspond with the finding of Berg *et al.* (1992) who showed a strong negative correlation between predation rate and the number of Northern Lapwing nests nearby. The most successful nests in Meadow were located within large aggregations with 10 or more nests and the high percentage of nests situated in such aggregations indicated Meadow as the more favourable site for Northern Lapwing nest survival. However, in Arable Land, nests situated within large aggregations suffered high predation similar to those in small aggregations or solitary nests. It suggests that large aggregations may not always be the means to reduce the predation risk in a Northern Lapwing population.

The fact that the nest predation decreased significantly from edge to centre of large nesting

groups in Meadow supports Lack's 'protective umbrella' hypothesis (Lack 1968). The hypothesis assumes that nests located in the centre of aggregations are defended against some predators more effectively than marginal (or solitary) nests. Amazingly, coloniality of Northern Lapwings and predation pattern on their nests differed between two neighbouring breeding sites. High nest predation risk at the edges of large aggregations and lack of protective umbrella, both in Arable Land, can be attributed to a different composition of predator guilds combined with various habitat parameters at particular nesting sites (vegetation cover, amount of bushes and hedgerows, presence of perches for avian predators) which may enhance the efficiency of some predators. For instance, some mammal predators being a serious threat to adults, e.g. Red Foxes *Vulpes vulpes*, are capable to penetrate into aggregations despite active defence of nesting birds (Elliot 1985b).

Carrion Crows *Corvus corone* probably played a major role in the predation of Northern Lapwing nests in the present study area, namely on Meadow, as elsewhere (Elliot 1985a; Galbraith 1988b; Baines 1990; Berg *et al.* 1992). The local crow population was about 6-8 nesting pairs in Arable Land and 4-6 in Meadow and some of these crows were identified as key predators of dumy nests which were installed in one treatment in managed fields nearby the Meadow site in April 1998 (M. Šálek, unpubl. data). However, potential mammalian predators such as foxes and martens (*Martes* sp.) regularly occur in both Arable Land and Meadow (own observations). As no quantitative data on composition of predator fauna in the study area are available, it is impossible to discuss the differences between Meadow and Arable Land from the point of view of predator guild composition.

Large aggregations are certainly beneficial to the breeding success of Northern Lapwings in agricultural landscapes. However, hatching success of nests in these aggregations can be limited for various reasons, such as extent of suitable habitats, number of perches for avian predators or composition of the predator community. Disper-

sion of Northern Lapwings into small breeding groups, frequent solitary nesting and the occasional absence of a protective umbrella in large aggregations all result in high vulnerability of such populations throughout the breeding season. Moreover, generalist predators are more abundant in fragmented agricultural landscapes (Andrén 1992; Hanski *et al.* 1996).

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SAMENVATTING

In Zuid-Bohemen (Tsjechië) varieerde de dichtheid van Kieviten *Vanellus vanellus* van 0,7-3,4 nesten per 100 ha akkerland tot 3,7-21,2 nesten per 100 ha grasland. In beide habitats lagen de nesten overwegend in clusters, waarbij het aantal nesten per cluster grasland groter was dan in akkerland. Predatie van nesten in grasland was het hoogst bij solitaire nesten, minder bij nesten in kleine clusters en het minst bij nesten in grote clusters. In akkerland werd deze correlatie niet gevonden. In grote clusters (10 of meer) in akker- en grasland waren de nesten in het centrum minder onderhevig aan predatie dan nesten aan de randen. Deze gegevens suggereren dat de veronderstelde hogere predatiekansen bij hogere dichtheden (hypothese van dichtheidsafhankelijkheid) niet opgaat. Veel meer lijkt het erop dat gezamenlijke verdediging tegen gevleugelde roofvijanden het best werkt indien wordt gebroed in grote groepen. Variaties op dit thema zijn overigens zeer wel mogelijk naar gelang oppervlakte en kwaliteit van broedgebieden, aan- of afwezigheid van zitposten voor kraaiachtigen en samen-

stelling van de predatorfauna (grondpredatoren als de vos *Vulpes vulpes* kunnen ook grote clusters bejagen). Gemiddeld genomen biedt broeden in grote groepen echter de beste overlevingskansen voor nesten. (RGB)

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