Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes

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Summary

1. Nest site choice and reproductive success of lapwings was studied during 1988–90 at a farmland site dominated by cereal crops in central Sweden.

2. The most important factor causing breeding failures was farming operations, which accounted for 85% of all nest losses. Difference in hatching success between habitats; unsown tillage (9% hatching success), sown tillage (78%), fallow fields (31%) and grassland (67% hatching success) was an effect of different farming practices.

3. Only 13% of the females were estimated to hatch a first clutch, but a majority (66%) of the females that lost the first clutch was estimated to lay a replacement clutch (67% hatching success), giving an estimated proportion of 55% females hatching a clutch.

4. Although most failures were caused by farming practices, predation accounted for 14% of nest losses. Predation risk was negatively correlated to the number of close neighbours ($R^2 = 90\%$), indicating that the density of nests in the colony was very important.

5. There was also a general anti-predator effect in large colonies, which was independent of the number of close neighbours, since nests in large colonies (>5 nests) were less likely to be robbed than solitary nests and nests in small colonies (2–5 nests).

6. Nest survival was higher at sites far (>50 m) from trees or other perches suitable for avian predators than at those situated close to (<50 m) these perches, indicating that birds were important predators of lapwing nests.

7. Lapwings seemed to minimize the influence of avian predators by breeding in aggregations, 92% of the nests were found in colonies (up to 28 nests), and preferring nest sites far away from perches for avian predators.

8. Paradoxically, lapwings preferred to breed on tillage, which (when unsown) was the habitat with most nest losses. However, a majority of the failed breeders laid a replacement clutch and 57% of the females is estimated to hatch a clutch in tillage, which is slightly better than in other habitats.

Key-words: lapwing, farmland, hatching success, farming practices, predation.

Journal of Animal Ecology (1992), **61**, 469–476

Introduction

Reproductive success commonly varies greatly between individuals in a population, and a large part of this variation can often be attributed to complete breeding failures (e.g. Clutton-Brock 1988; Newton 1989). In birds, common causes of failure are predation of eggs, nestlings or incubating adults, and environmental factors, such as poor weather conditions (Newton 1989). Furthermore, in ground-nesting bird species inhabiting areas of farmland, farming practices might have a major impact on the probability of a successful breeding. For example, cultivation and harrowing after the start of breeding have been shown to be a major factor causing complete failures for lapwings *Vanellus vanellus L.* (Kooiker 1984; Galbraith 1988a; Shrubb 1990) and curlews *Numenius arquata L.* (Berg, 1992).

Areas of farmland are usually a mosaic of different habitats, with large differences in the abundance of

food items, risk of predation and nest destruction by farming practices (O'Connor & Shrubb 1986; Galbraith 1988a; Berg 1992). Consequently, the probability of producing fledglings varies between habitats and we would expect birds primarily to choose the most productive sites, i.e. habitat selection by ground-nesting farmland birds is expected to be strong.

Lapwings are large ground-nesting plovers that breed in semi-colonial aggregations in farmland. Previous studies suggest that lapwings prefer nest sites with little or no vegetation (Klomp 1954), but close to fields which are suitable foraging sites for adults and chicks (Galbraith 1988b), such as grasslands. Grasslands seem to be important for successful breeding because the production of chicks at arable sites is correlated to the distance to the nearest grassland (Galbraith 1988a). Lapwings are well known for their anti-predator behaviours (Cramp & Simmons 1983; Elliot 1985a) and experiments with artificial nests suggest that predation risk is lower inside than outside lapwing aggregations (Göransson *et al.* 1975; Baines 1990). Furthermore, probably due to the anti-predator behaviour by lapwing aggregations, ground-nesting passerines have been shown to have higher reproductive success within lapwing territories than elsewhere (Eriksson & Götmark 1982).

We have studied a population of lapwings at a farmland site dominated by cereal crops. The major goal was to identify and investigate the relative importance of factors causing breeding failures in this population and to relate this to nest site choice. Therefore, we evaluated the effect of predation on nests in different habitats, on nest aggregations of different size, and on nests placed at different distances from trees and other perches suitable for avian predators. We also discuss the influence of farming practice on reproductive success and how nest site choice is influenced by predation, spring farming and the position of foraging habitats.

Study site and methods

The study was made during 1988−90 at a farmland site (approximately 59°57′N, 16°17′E) consisting of about 59 km² of mixed farmland (forests and villages excluded) around the village of Västerfärnebo in the province of Västmanland. The site was, with a small extension of 3·5 km², the same as described by Berg (1992). In 1985, when the whole site was mapped, dry tillage was dominant (62·6%), but there were large areas of seasonally flooded tilled fields (9·1% of farmland area in years with maximum flooding, but varying between years). The tillage was mainly ploughed in autumn and sown in spring, when the lapwings incubated. Remnants of old seasonally flooded meadows (12·9% of farmland area) and sown pasture and ley (12·5%)

covered relatively large areas for being in central Sweden. The sown pastures were grazed from beginning of May (incubation phase) and some leys form middle of June (during chick rearing). The remaining 2·9% consisted of scrub.

The nests were mostly checked from a distance (usually >100 m) at intervals of about 4−8 days, but at shorter intervals as the expected date of hatching approached. Nest were recorded as successful when the brood was seen, when the behaviour of the adults indicated the presence of a brood or when there was evidence of a successful hatch in the nest (i.e. the presence of shells from hatched eggs). A nest was assumed to have failed if it was empty before the expected hatch date or if the observer recorded evidence of predation, destruction or desertion. Predation of clutches was identified by the complete disappearance (partial losses were not included since nests mostly were checked from a distance) of the clutch or by the presence of partially eaten eggs in or close to the nest. Clutch destruction due to spring farming was easy to identify since it resulted in the complete disappearance of the nest.

Data on colour-ringed birds (37, 52 and 35 in 1988, 1989 and 1990, respectively) suggest that lapwings usually re-nest after failure within 2 weeks in the close neighbourhood (and same habitat) of the previous nest. Thus, clutches laid by unringed birds were considered to be replacement clutches if a clutch was lost and another appeared in the close proximity (<100 m within 5-15 days (mean time between clutches in 1988 = 9 days). Furthermore, all nests found before the first known replacement clutch in each year were considered to be first clutches, while all nests found after the last known first clutch were classified as replacement clutches. Daily nest survival (P) was calculated according to Mayfield (1961 and 1975) and confidence limits were calculated according to Johnson (1979) and Hensler & Nicholls (1981). Incubation and egglaying were assumed to take 32 days and hatching success was calculated as P^{32}.

The habitat distribution of nests at the mixed farmland site was compared to that of 196 (4 of 200 sites excluded because they were not on farmland) randomly chosen control sites, from coordinates on a 10 × 10 m grid system in the study site. Distance to the nearest tree and water was also measured for nests and control sites.

Results

NEST SITE SELECTION IN RELATION TO HABITAT

Lapwing nests (*n* = 870) were not uniformly distributed at the study site, as the number of lapwing nests in 1-km² squares departed significantly from a uniform distribution (an equal number in all squares,

Kolmogorov Smirnov test, $D = 0.738$, $P < 0.001$). Only 7·8% of the 870 nests were solitary and 92·2% were found in colonies. A nest was defined as belonging to a colony when situated within 200 m of any other active nest (incubated during the same time for at least one day). Thus, nests situated several hundred metres apart could belong to the same colony, if there were other nests between them. Pairs without nests during the same period were not included when the colony size was calculated. Altogether, 35·1% of the 870 nest were found in small colonies (2−5 nests), 29·8% in medium-sized colonies (6−10 nests) and 27·2% of the nests were found in large colonies (>10 nests) up to a maximum of 28 nests.

The habitat distribution of the 870 nests differed significantly from the habitat distribution of the 196 randomly chosen sites ($\chi^2 = 144$, df = 2, $P < 0.001$). Tillage was preferred as nesting habitat, while grassland (meadow and sown grass combined) was used less commonly than expected (Fig. 1). To avoid effects of philopatry, nest site choice was also tested within years. The same preference for tillage was found all years and all differences were significant; 339 nests in 1988 ($\chi^2 = 75$, df = 2, $P < 0.001$), 303 nests in 1989 ($\chi^2 = 69$, df = 2, $P < 0.001$) and 228 nests in 1990 ($\chi^2 = 54$, df = 2, $P < 0.001$). Aggregation of nests was not a result of a preference for a spatially limited nesting habitat since tillage was the most common habitat at the study site and tilled fields were found in all parts of the study site (71·7% of farmland area in 1985).

On average, lapwings nested closer to rivers or flooded areas (mean distances of 870 nests $\pm$ SD = 109 ± 152 m) than expected by chance (mean of 196 random sites $\pm$ SD = 333 ± 387 m, Mann-Whitney test, $U = 437422$, $P < 0.001$), indicating the im-portance of wetness in lapwing habitat selection. Also birds breeding on dry fields preferred to nest closer to flooded fields and rivers than expected by chance ($n = 585$ and 145, respectively (excluding observed and randomized sites on flooded fields) Mann-Whitney test, $U = 19055$, $P < 0.001$), indicating that sites close to flooded fields and rivers were chosen for reasons other than being nest sites, probably because they were good foraging habitats.

DIFFERENCES IN NEST SURVIVAL BETWEEN HABITATS

There were large differences in nest survival probabilities between different habitats (Table 1). Nest survival was significantly higher in sown tillage than in all other habitats, except grassland, and the hatching success in sown tillage was 77·7%. Nest survival in grassland was significantly higher than in fallow fields and unsown tillage and hatching success in grassland was 66·8%. Hatching success in fallow fields was intermediate (31·3%) and nest survival in this habitat was significantly higher than in unsown tillage. Unsown tillage was the habitat with the lowest hatching success (only 8·6%) and nest survival in this habitat was significantly lower than in all other habitats (Table 1). These differences between habitats also incorporate differences between first clutches and replacement clutches, since most first clutches are laid on unsown tillage and most relayings on sown tillage. The two main factors causing all 446 nest losses were farming practices (84·8% of nest losses) and predation (14·1% of nest losses).

EFFECTS OF SPRING FARMING: DIFFERENCES BETWEEN HABITATS AND YEARS

The effects of spring farming activities on nests differed greatly between habitats (Fig. 2). The risk of nest destruction was highest in unsown tillage and lowest in sown tillage and grassland, while birds breeding in fallow fields experienced intermediate levels of nest destruction. All these differences (except grassland-sown tillage) were highly significant (Fig. 2). Although the habitat differences in the risk of nest destruction were consistent between years (Fig. 3), there was some annual variation. For example, in unsown tillage the probability of nest destruction was significantly higher in 1988 than in 1989, while in areas of fallow fields nest destructions were more frequent in 1989 than in the other two years of study (Fig. 3). The main reason for these differences was yearly differences in the starting date of spring farming in relation to the timing of breeding of lapwings. Therefore, some lapwings succeeded in hatching young before the start of spring farming in some years, whereas in other years they did not.
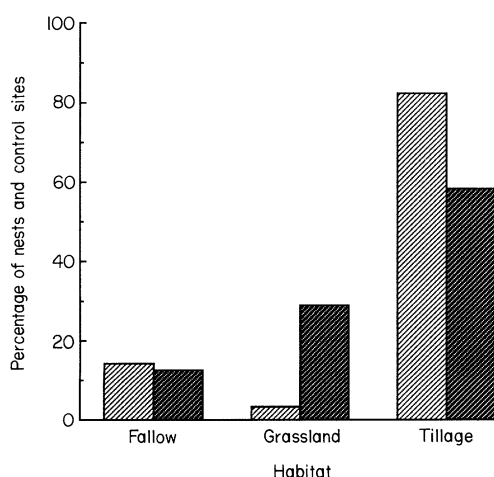

Fig. 1. Percentage of 196 random control sites (dark bars) and 870 lapwing nests (1988−90 combined, light bars) in fallow fields, grasslands and tillage. The difference in habitat distribution between observed and expected was significant ($\chi^2 = 144$, df = 2, $P < 0.001$).

Table 1. Survival of lapwing nests in different farmland habitats (all years combined). Nest days are the number of days for which nests were under observation, P is the daily survival probability, SE its standard error (after Johnsson 1979 and Hensler & Nichols 1981), hatching success is the probability of surviving until hatching after 32 days (P^{32})

Habitat	Nests	Nest days	Losses	P	SE	Hatching success
Unsown tillage	408	5006	339	0·9323	0·00355	0·086
Sown tillage	309	5289	38	0·9928	0·00116	0·777
Fallow fields	124	1928	63	0·9673	0·00405	0·313
Grassland	29	523	6	0·9885	0·00466	0·668

Nest survival was significantly higher in sown tillage than in unsown tillage and fallow fields ($z = 16·21$, $P < 0·001$ and $z = 6·05$, $P < 0·001$, respectively), but nest survival did not differ between sown tillage and grassland ($z = 0·89$, $P > 0·3$). Nest survival was significantly higher in grassland than in unsown tillage and fallow fields ($z = 9·60$, $P < 0·001$ and $z = 3·44$, $P < 0·001$, respectively) and significantly higher in fallow fields than in unsown tillage ($z = 6·51$, $P < 0·001$).
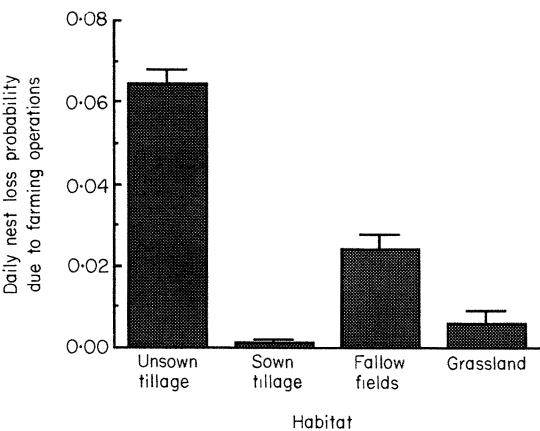

Fig. 2. Daily nest loss probability due to farming practices in different habitats (all years combined). Standard errors after Johnson (1979) and Hensler & Nichols (1981). The number of nests and nest days in different habitats were as follows; unsown tillage (408 & 5289), sown tillage (309 & 5289), fallow fields (124 & 1928) and sown grass (29 & 523). The probability of nest destruction due to farming practices was significantly higher in unsown tillage than in sown tillage, fallow fields and grassland ($z = 17·96$, $P < 0·001$, $z = 8·06$, $P < 0·001$ and $z = 12·21$, $P < 0·001$, respectively), significantly higher in fallow fields than in sown tillage and grassland ($z = 6·50$, $P < 0·001$ and $z = 3·87$, $P < 0·001$, respectively), but there was no significant difference in influence of spring farming between grassland and sown tillage ($z = 1·32$, $P > 0·1$).

FACTORS RELATED TO PREDATION RATE

Although most of the nest losses observed were caused by farming practices, at least 14·1% were due to predation. Birds such as corvids *Corvus* spp. are known to be important predators of eggs and newly hatched young in this species (Heim 1978; Baines 1990). Such predators frequently sit in trees and bushes in order to locate nests, and one would expect lapwings to avoid breeding close to such perches. It was found that lapwings bred further away from trees (mean 852 nests ± SD = 94 ± 64 m) than would be expected by chance (mean 196 random sites ± SD = 60 ± 56 m, Mann-Whitney test, $U = 496564$, $P < 0·001$). It seemed to be advant-
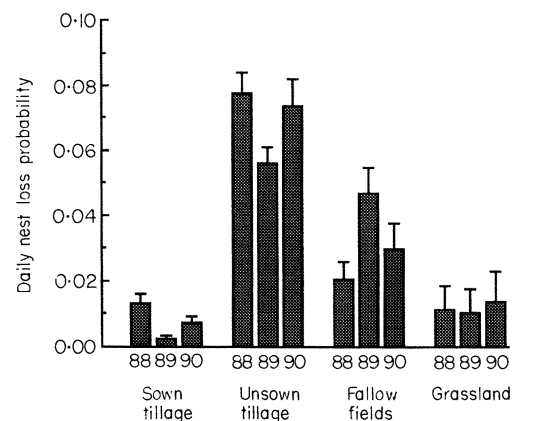

Fig. 3. Daily nest loss probability in unsown tillage, sown tillage, fallow fields and grasslands during the years 1988–90. Standard errors after Johnsson (1979) and Hensler & Nichols (1981). The number of nests and nest days in different categories were as follows for the years 1988–90; sown tillage (103 & 1512, 107 & 1984 and 99 & 1793), unsown tillage (183 & 1943, 145 & 2124 and 79 & 939), fallow fields (51 & 733, 44 & 726 and 29 & 469) and grassland (11 & 182, 10 & 192 and 8 & 149).

ageous to avoid sites close to trees, bushes or other perches, because the risk of predation was significantly higher for nests with trees within a distance of 50 m than for nests with no trees or perches within that distance (all habitats and years combined, Fig. 4).

There was a significant negative relationship between the total number of nests in the colony (all nests within 200 m of any other nest) and predation rate ($t = -2·4$, $n = 20$, $P < 0·05$ and $R^2 = 19·8\%$). However, a more important factor related to predation rate was the number of close neighbours (number of nests within 100 m of a nest site). There was a strong negative correlation between the number of neighbouring nests and daily predation risk (Fig. 5). The number of nests within 100 m of the nest site explained 89·8% of the variation in mean predation risk. The observed relationship between predation and colony size was not only an effect of birds in large colonies also breeding at higher densities (many close neighbours). When the number of
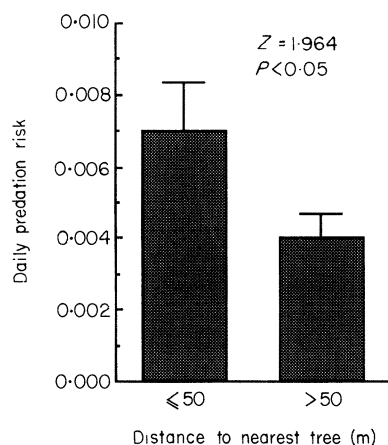
Fig. 4. Daily predation risk for lapwing nests within 50 m of trees (or other perches suitable for avian predators) and nests further away than 50 m from perches. Standard errors after Johnsson (1979) and Hensler & Nichols (1981). The number of nests and nest days in the two groups were as follows; within 50 m of perches (250 & 3860 and further from perches (602 & 8655). The distance to the closest perch was not measured for 18 nests.
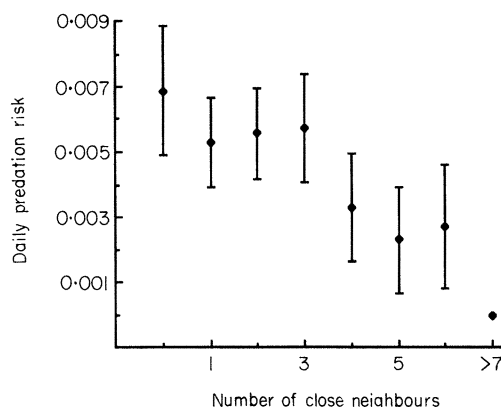

Fig. 5. Daily predation risk in lapwing nests with 1 to >7 close neighbours (nests within 100 m of the nest site). A linear regression analysis showed a significant negative correlation between the number of nests within 100 m and predation risk ($t = -8.46$, $n = 8$, $P < 0.001$, $R^2 = 89.8\%$).

Fig. 6. Daily predation risk in lapwing nests in large colonies (light striped bars) and in small colonies & solitary nests (dark bars) for nests with different number of close neighbours (nests within 100 m of the nest site). Large colonies contained >5 nests and small colonies 2−5 nests. Nests within 200 m of any other nest were considered as belonging to a colony. Predation risk values after Mayfield (1961 and 1975) and standard errors after Johnsson (1979) and Hensler & Nichols (1981). Predation risk was significantly higher for nests in small colonies than for nests in large colonies for nests with 1, 2 and 3 nests within 100 m of the nest site (one-tailed tests; $z = 1.95$, $P < 0.05$, $z = 1.92$, $P < 0.05$ and $z = 3.23$, $P < 0.001$, respectively). There were no differences between large and small colonies for nests with 0 and 4 nests within 100 m of the nest site (one-tailed tests, $z = 0.09$, $P > 0.4$ and $z = 0.71$, $P > 0.2$, respectively).

nests within 100 m was kept constant, there was still an effect of colony size, with lower predation risk in large colonies (>5 nests) than in small ones (Fig. 6).

The effects of the number of nests within 100 m and the distance to the closest tree were independent, as there were no significant differences in the distance to the closest tree between different group sizes (Kruskal-Wallis test, df = 7, $H = 4.96$, $P > 0.6$), nor was there any difference in group sizes between nests close to ($n = 250$) or far away ($n = 602$) from trees (Mann-Whitney test, $U = 76475$, $P > 0.2$).

Distance of nests from trees differed significantly between habitats (Kruskal-Wallis test, df = 3, $H = 20.2$, $P < 0.001$), and therefore predation rate between habitats was compared separately for nests situated close to or far away from trees. The only difference between habitats was that predation rate
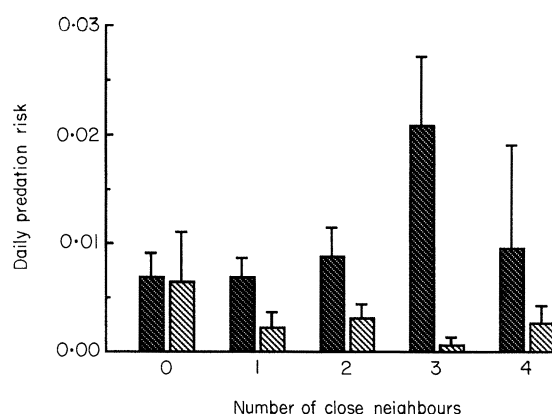
for nests far away from trees was lower in grassland (only 12 nests) than in all other habitats ($z = 2.6$, $P < 0.01$). There were, however, no differences between the major nesting habitats in predation rate, indicating that group size, density of nests within colonies and distance to predator perches were more important factors influencing predation risk than habitat.

HATCHING SUCCESS OF FIRST AND SECOND CLUTCHES

Altogether 430 (49·4%) of the nests were classified as first clutches, 305 (35%) as second clutches and the remaining 15·6% could not be classified. There was a large difference in daily nest survival rate between first clutches (P = 0·9428 ± 0·0030) and second clutches (P = 0·9887 ± 0·0016), which was significant ($z = 13.49$, $P < 0.001$). A large proportion (66·1%) of the destroyed first clutches was, however, estimated to be replaced by a second clutch. This figure is very close to the 64·9% of the individually colour-ringed birds observed renesting ($n = 37$). A total of 12·7% of the females hatched a first clutch and 38·8% of all nesting females were estimated to hatch a second clutch ($0.873 \times 0.661 \times 0.672 = 0.388$) which, together with the ones succeeding in first clutches, gives an estimated proportion of 51·5% females successfully hatching a clutch.

Discussion

Few studies have been able to identify any factors that could explain variation in reproductive success to such great extent as in this study (e.g. Clutton-Brock 1988; Newton 1989), where as much as 98% of the breeding failures observed could be explained by two factors, namely predation and nest destruction due to farming operations. As complete failures probably explain the major part of the variation in reproductive success in this species (Galbraith 1988a), it is likely that the effect of farming practices and predation are the most important determinants of reproductive success.

Farming activities were, by far, the most important causes of nest losses in this population of lapwings. This result is in contrast with several other studies of breeding lapwings, where predation was found to be the most important factor causing nest losses (Matter 1982; Galbraith 1988a; Baines 1990). However, it is likely that the relative influence of farming practices on reproductive success varies greatly depending on the dominating habitat and the date of sowing at the study site. Also, data from other studies suggest that lapwings breeding in areas dominated by grassland seldom fail due to farming practices, but often experience a high predation risk (Table 2). In contrast, the relative importance of farming practices and predation seems to be the opposite in areas dominated by tillage (Table 2).

Predation is in general probably an important factor determining reproductive success of lapwings (Table 2). We present at least two factors related to the risk of predation. First, lapwings breeding far from trees or other perches of avian predators enjoyed a lower predation risk than birds breeding close to such perches. As more than 90% of 108 attacks observed against predators were made against corvids (Å. Berg, unpublished data), the results suggest that birds were the most important predators of lapwing nests at this site. The number of foxes *Vulpes vulpes* L. in central Sweden have declined during the 1980s, probably an effect of mange in the region (Lindström, in press), so foxes were probably not important predators of lapwing nests. Similarly, other studies of lapwings (Heim

1978; Baines 1990) suggest that birds, and especially corvids, are important nest predators.

Second, in terms of predation risk, lapwings benefitted from breeding in aggregations. Although not shown explicitly, other studies also suggest that lapwings might reduce predation risk by breeding in aggregations. For example, Elliot (1985b) showed that the anti-predator behaviour of lapwings towards crows *Corvus corone* L. implied some protection against predation at least within 30−50 m from a lapwing nest. Furthermore, predation rate on artificial nests has been shown to be lower within aggregations of breeding lapwings than outside them (Baines 1990; Göransson *et al.* 1975). Thus, it is very likely that the observed benefits of breeding in aggregations were due to more efficient defence against avian predators.

In contrast, Galbraith (1988a) found no significant effect of the size of aggregations on predation risk. However, the predators were not identified in that study, and other studies suggest that aggregations need not be beneficial if the main predators are mammals. For example, Elliot (1985a) showed that there was no relationship between the size of groups attacking a dummy fox and the size of a lapwing aggregation. He suggests that this was because foxes implied a serious threat to the adults. In fact, if foxes are the most common predator, one would expect it to be disadvantageous to breed in large groups. This is because predator defence of lapwings against foxes probably is less efficient and predators are known to concentrate their search for food close to sites were they have recently had success (Tinbergen, Impekoven & Franck 1967; Croze 1970).

One would expect lapwings to choose nest sites where the influence of predation and farming operations is minimized. Concerning predation, this seems to be the case, because most birds (92%) were breeding in aggregations and because they preferred nest sites far away from potential perches for avian predators. It is unlikely that lapwings were pushed into these aggregation simply to get away from perches, as there were large fields without perches suitable for lapwings, where no nests were found. Therefore, these two adaptations to avoid predation seem to be independent of each other.

Table 2. Percentage of nests robbed and destroyed by farming practices in arable and grassland habitats in three lapwing studies

Study	Site	Number of nests	Destroyed by farming	Robbed
Galbraith 1988a	Arable	273*	29·7	59·3
	Grassland	293*	0·0	89·4
Baines 1990	Arable	88	11·5	24·6
	Grassland	630	5·9	53·2
Shrubb 1990	Arable	2734	26·0	9·0
	Grassland	1021	9·0	20·0

* Refers to number of eggs, partially destroyed nests also included.

Concerning the choice of breeding habitat, lapwings paradoxically seemed to prefer tillage despite the fact that birds breeding in this habitat experienced the highest rates of nest losses due to farming operations. However, after the tillage was sown, lapwings breeding in these fields enjoyed the highest hatching success of all habitats (Table 2). In fact, the total hatching success in tillage (first clutches in unsown tillage and second clutches in sown tillage) was calculated at 57·4%, which is slightly higher than the total hatching success of 52·0% calculated for other habitats (fallow and grasslands combined). This was due to a higher relaying frequency in tillage than other habitats (67·4% and 58·3%, respectively) and higher hatching success in second clutches in sown tillage than in other habitats (79·5% and 53·8%, respectively). Thus, the habitat with the highest total hatching success was indeed chosen. Furthermore, the effect of spring farming on lapwing reproductive success varied between years due to the timing of breeding in relation to the start of spring farming. So in some years there might be a better chance to hatch in unsown tillage.

In addition, the survival of chicks might be lower late in the season in some areas, as has been shown by Galbraith (1988a), making it more advantageous to breed early. It might therefore be worth the risk to breed early and have a small chance to hatch, especially as this chance might be somewhat larger in some years because of differences in the starting date of spring farming in relation to lapwing breeding cycle.

Lapwings also preferred to breed close to rivers and at, or close to, flooded fields. Data on foraging preferences at the same study site showed a strong preference for flooded habitats (especially tillage), which were used for foraging twice as much as expected from its area (Berg, unpublished data). Flooded habitats are limited, so it is possible that the observed aggregations of breeding lapwings were a result both of distribution of food as well as a behavioural avoidance of predation. However, at present it is not possible to estimate the relative importance of each factor.

A total of 51·5% of the females was estimated to hatch if replacement clutches were included, which can be compared to the hatching figures of 35% on improved grassland and 69% on unimproved grassland in the United Kingdom presented by Baines (1988). This indicates that influence of farming practices on hatching success on intensively managed farmland is smaller than could be expected, being an effect of the high replacement rate of lost clutches (a few marked females even laid three clutches) and the high hatching success in replacement clutches. Differences in reproductive success between arable sites and grassland sites might, however, be larger than this. Lapwing chicks have been shown to survive better at grassland sites than at arable sites, where

chick survival was influenced by the distance to grassland (Galbraith 1988a), indicating that there might be differences in production of young between modern farmland and traditional farmland.

To sum up, lapwings seemed to be relatively adapted to breed on farmland because they preferred to nest on tillage, which was the habitat with the highest total hatching success. The high hatching success, despite many nest losses on unsown tillage, was due to the high replacement rate of lost clutches and the high hatching success of clutches on sown tillage. Lapwings also preferred to nest far from perches for avian predators, where hatching success was higher than close to perches. Most lapwings bred in aggregations, probably also an adaptation against avian predators, and predation risk was shown to be negatively correlated with colony size. This was mainly an effect of many close neighbours in large colonies, but there was also a general anti-predator effect which was independent of density within colonies. Studies of mortality rates and production of young are needed to test if these adaptations are sufficient to yield enough fledglings to keep the population stable, or if immigration from other habitats is required.

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