Factors affecting nest-site choice and reproductive success of Curlews *Numenius arquata* on farmland

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Nest-site choice and reproductive success of Curlews *Numenius arquata* in different habitats were studied at a mixed farmland site (grasslands and flooded tilled fields relatively common) and at an arable farmland site (dry tilled fields more dominant than at the mixed site) in central Sweden. At both sites Curlews preferred to nest on grassland and fallow fields, where hatching success was higher than on tillage fields. Nests were also situated further away from forest edges than random sites, but hatching success did not vary with distance to the forest edge. Only 35.6% of the pairs were estimated to hatch young. The main cause of nest loss was predation and the second most important factor was destruction by farming practices, which was an important factor in tillage early in season. Surprisingly, nest survival was higher at the arable than at the mixed farmland site, probably being an effect of the increased proportion of fallowing during recent years. Mortality of chicks was 79.7% before fledgling age (both sites combined) and, surprisingly, chick survival was lower on meadows than on arable fields and leys. The mean production of young was only 0.25 fledglings per pair, which is lower than in areas less affected by farming practice. The low production of young is probably an important factor in the decline of Curlew populations on Swedish farmland. On bogs 1.4 fledglings per pair were produced, indicating that reproductive success of Curlews is higher in more natural habitats.

Extensive modernization of Swedish farmland commenced in the 1940s (Gerell 1988). In many districts cattle farms were replaced with mechanized farms that specialized in cereal crops. The area of grasslands decreased, the old small fields were amalgamated into a few large ones and habitat elements which hindered efficient farming were often removed. Another result of intensification was the increased use of fertilizers and pesticides. This modernization has resulted in relatively homogeneous and intensively managed farmland in large parts of Sweden, especially in the south. These changes in farming practice have resulted in reduction in many farmland bird populations, Curlews *Numenius arquata* among them.

Curlews breed throughout Sweden, except in the mountain areas in the northwest. The highest densities are found on meadows; lower densities are found on bogs and arable farmland (Pettersson 1988). Curlews probably started to breed on farmland when the area of meadows decreased. Surveys from several areas (Pettersson 1988, Berg & Sjöberg in press) indicate that the Curlew population has declined, and most severely in southern Sweden, where the density of Curlews on farmland is now low over large areas (Berg & Sjöberg in press). Although reasons for this decline are not clear, modernization of farmland has probably adversely affected the Curlew populations, but hunting during migration has also been suggested as a possible factor (Meltofte 1986).

This paper describes nest-site choice and reproductive success of Curlews within different habitats at two farmland sites. The influences of farming practices, modernization of farming and predation on the success of nests are discussed.

STUDY SITES AND METHODS

Curlews were studied from 1987 to 1989 at two farmland sites in central Sweden. Most of the study was done at a mixed farmland site where cattle farming was still relatively common but, for comparison, some studies were also made at a more uniformly arable site specializing in cereal production.

The mixed farmland site (approximately 59°57′N, 16°17′E) consisted of 55.5 km^2 farmland around the village of Västerfärnebo in the province of Västmanland. This was a complex study site. Dry tillage was dominant (62.6%), but there were large areas of seasonally flooded tilled fields (9.1% of total farmland area in years with maximum flooding), remnants of old meadows (12.9%) and, compared to the arable site, large areas of sown pasture and ley (12.5%). The remaining 2.9% consisted of rough pastures and scrubland. Parts of the site are considered to be of great conservation interest because of breeding and migrating birds and are therefore included in the Convention on Wetlands (Swedish Environmental Protection Agency 1989). The arable farmland site (approximately 59°41′N, 16°47′E) consisted of 68.3 km^2 farmland and was situated north of the city of Västerås in the province of Västmanland, 20 km southeast of the mixed farmland site. Dry tillage (88.4% of total farmland area) was more dominant than in the mixed farmland site, with only 1.6% of flooded tilled fields, 3.8% of sown pasture/ley and a small area of meadow (3.3%) in this relatively homogeneous area. The remaining 2.9% consisted of rough pasture and scrubland.

Approximately 90% of the cereal crops at the study sites were spring sown and Curlew nests were not found on autumn sown fields, so this paper discusses the effects of farming in spring sown fields. Fallow fields consisted of stubble fields or cultivated tillage. The majority of the fields were cultivated in late May–early June, some were sprayed with herbicides instead and a few were not managed at all.

Bird censuses

The sites were censused 2–5 times a year (more effort being put into areas difficult to census) and the minimum criterion for a territory was observation of a pair or two observations within 1 km. Adults were trapped at the nest with a cage, close to or after hatching. Most of the birds were caught and marked in the years before this study, none of the 25 captures in 1987–89 resulted in Curlews abandoning their nests. Thus nest-trapping during this study did not directly affect the reproductive success of the pairs studied.

Nest-site choice and hatching success

The habitat distribution of 92 nests at the mixed farmland site was compared to that of 100 randomly chosen control sites (from coordinates on a 10 × 10 m grid system in the study site). Areas greater than 1 km^2 without breeding Curlews were excluded when the 100 sites were randomly chosen, so the habitat distribution of nests was compared with the habitat distribution of random control sites in areas where Curlews were breeding. At the arable farmland site the habitat distribution of 15 nests was compared to that of 30 random sites in the same way. In nests which were found before the last egg was laid, the first egg date was calculated on the assumption that the laying interval between the eggs was 2 days, which is only slightly higher than the 1.85 days reported in the literature (Glutz von Blotzheim *et al.* 1977). This gives a laying period of 6 days between the first and fourth egg. Expected hatch date was estimated as 29 days after clutch completion (von Frisch 1956), which gives a total nest period of 35 days when four eggs are laid. The breeding season started during the last days of April and the start of the season was defined as the initiation date of the earliest nest that year. When both first layings and relayings were found, first layings were always initiated during the first 10 days and relaying after the first 10 days of the breeding season ($n = 20$). Nests initiated during the first 10 days of the breeding season (Period I) were therefore assumed to be first clutches; nests initiated after this (Period II) were assumed to be relayings. When only a nest initiated in Period II was found the assumed loss of the first nest was often supported by observations of copulations and breeding behaviour early in the season, indicating that an early breeding attempt had occurred.

The nests were mostly checked from a distance (usually > 150 m) at intervals of 3–4 days, but at shorter intervals as the expected hatch date approached. Nests were visited only on the following occasions: when they were found in order to check the number of eggs, after hatching in order to ring the chicks, and a few times during incubation when it was impossible to check the nest from a distance.

If the risk of predation is constant through time, nests that are found only a few days before hatching are more likely to hatch than nests observed for a longer period, and this might give a bias in the estimate of hatching success. To overcome this, daily nest survival probability ($P = 1 -$ no. failed nests/no. of observation days) and hatching success (P^{35}, probability of surviving 35 days) were calculated according to Mayfield (1961, 1975), which takes the observation time into account and therefore gives a better estimate of hatching success than the proportion of successful nests. Hatching was established by the presence of chicks in or close to the nest or by large eggshell fragments, usually with folded edges, in the nest. Predation was identified by empty nests or by small eggshell fragments in the nest.

Number of fledglings

Broods were checked once a week and, when possible, chicks were counted. If a brood was not found, another three visits were made encompassing several kilometres around the nest. If the brood was still not found, the chicks were considered dead. Since the longest recorded brood movement was 1.5 km, it is improbable that any failed broods were broods that had moved far away and were actually alive. The number of fledglings was counted 35 days after hatching, when most chicks are able to fly short distances (Glutz von Blotzheim *et al.* 1977). The presence of alarm-calling adults made it possible to determine if a clutch had hatched, even if the nest had not been found. Thus all pairs at the study sites were included when the production of fledglings was calculated.

Statistics

Two-tailed tests were used unless otherwise stated. The *G*-test with Williams' correction (Sokal & Rohlf 1981) is designated as G_{adj}. Standard errors and *Z*-tests for comparison of hatching success were calculated according to Johnson (1979) and Hensler & Nichols (1981).

RESULTS

Bird censuses and marked adults

The density of breeding Curlews varied between 0.52 and 0.68 territories/km^2 farmland (patches of forest, villages excluded) in the mixed farmland site during 1987–89. Densities were lower in the arable site and varied between 0.10 and 0.13 territories/km^2 farmland. Altogether, 62 adults were individually marked with colour rings at the two farmland sites and the numbers of marked individuals that could be identified between 1987 and 1989 were 36 (45% of studied adults), 46 (51%) and 37 (38%), respectively. Even when the adults were not marked it was possible to distinguish the different clutches, because the nests were usually separated by several hundred metres (mean ± s.d. = 784 ± 446 m, $n = 26$, data from mixed farmland site 1987) and nest failures markedly decreased the number of clutches and therefore made them easier to separate.

Nest site choice

The habitat distribution of the 92 nests at the mixed farmland site differed significantly from the habitat distribution of the 100 randomly chosen sites (G-test; $G_{adj} = 28.4$, d.f. = 4, $P < 0.001$). Leys, fallow fields, sown pastures and meadows were preferred nest habitats, while tillage was used as nesting habitat less commonly than expected (Fig. 1a). Similarly, the habitat distribution of the 15 nests in the arable farmland site differed significantly from that of 30 random nest sites at the same site (G-test, $G_{adj} = 9.1$, d.f. = 4, $P < 0.005$). Grassland was uncommon at the arable site, so fallow fields were the preferred nesting habitat and again tillage was used less frequently than expected (Fig. 1b).

At the mixed farmland site the median distance to the forest edge was significantly greater for 83 nests (the distance was not measured for 9 of the 92 nests), than for 83 randomly chosen sites (median 150 and 100 m, respectively, Mann-Whitney *U*-test, $z = 3.2$, $P < 0.001$). To avoid effects of differences in distance to the forest edge between habitats the number of random sites in each habitat was constrained to be the same as in the sample of nests. There were no significant differences (Mann-Whitney *U*-test, $z = 1.5$, n.s.) in the distance to rivers or large ditches (median nests 180 m, median random nest sites 160 m).

At the mixed farmland site, the habitat distribution of 49 nests initiated during the first 10 days of the breeding season (Period I) and assumed to be first clutches, did not differ significantly from that of the 26 probable relaid clutches initiated later (Period II, G-test, $G_{adj} = 3.7$, d.f. = 4, n.s.). There was, however, a tendency for fewer nests on sown pasture and more nests on meadows in Period I than Period II.

Causes of nest failure and hatching success

Nests were not more likely to be preyed upon after I visited them than when they were not visited. Of 32 nests which

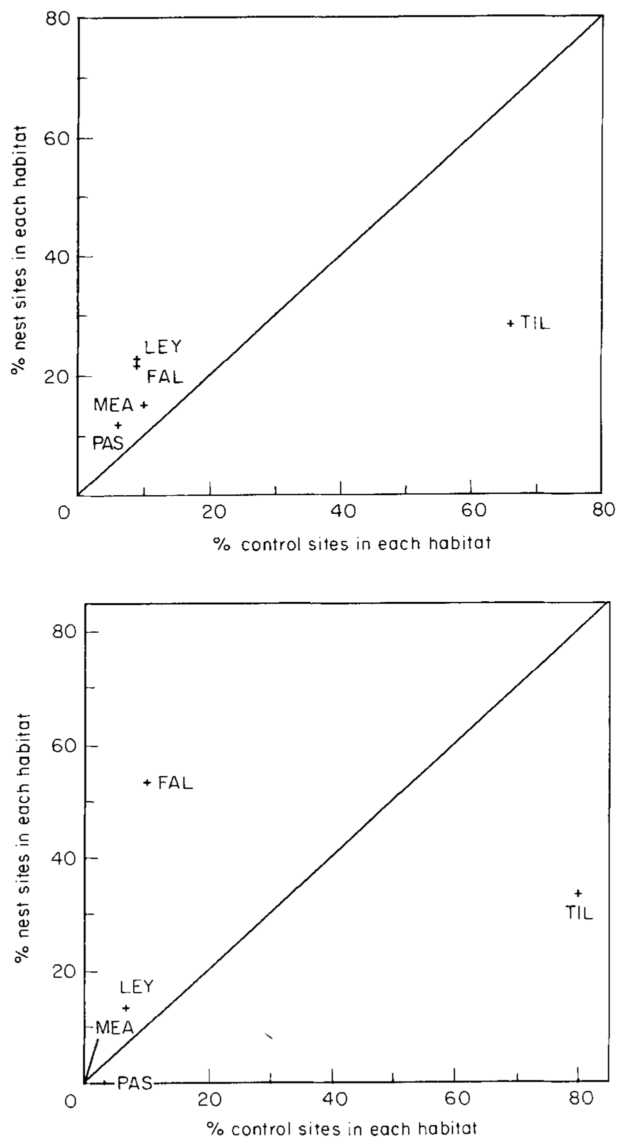

Figure 1. Proportion of Curlew nests and random control sites in different habitats at (a) mixed ($n = 92$ and 100, respectively) and (b) arable farmland sites ($n = 15$ and 30, respectively). Til = tillage (includes both unsown and sown fields), Fal = fallow, Ley = ley, Pas = pasture and Mea = meadow. Unsown and sown fields were grouped together since the area of these habitats changed during spring tillage operations, but the area of arable fields was constant and the number of nests and random sites in arable fields could be compared. The distribution of nests differed significantly from that of the control sites both at the mixed farmland site (G-test, $G_{adj} = 28.4$, d.f. = 4, $P < 0.001$) and the arable farmland site (G-test, $G_{adj} = 9.1$, d.f. = 4, $P < 0.005$).

were checked both by visits (40.3% of checks) and by observations from a distance (59.7% of checks) the number of nests preyed upon after a visit (11) and the number of nests preyed upon after being observed from a distance (21) did not differ significantly from the expected (G-test, $G_{adj} = 2.1$,

Table 1. *Number of Curlew nests destroyed by predation, farming, trampling by stock and other reasons (e.g. disturbance by humans). Nest days is the number of days for which nests were under observation.* p *is the daily survival probability, s.e. its standard error (after Johansson 1979 and Hensler & Nichols 1981), hatching success is the probability of surviving until hatching* ($P^{35} \times 100$)

Habitat	No. of Nests	Destruction due to: Pred.	Farm.	Stock	Other	Total loss	Nest days	p	s.e. × 1000	Hatching success (%)
Mixed farmland site										
Meadow	14	7	0	0	0	7	272	0.974	9.60	39.8
Ley	21	11	0	0	0	11	433	0.975	7.56	41.2
Sown pasture	11	4	1	6	0	11	110	0.900	28.60	2.5
Total	46	22	1	6	0	29	815	0.964	6.49	27.7
Unsown field	15	1	11	0	1	13	101	0.871	3.33	0.8
Fallow	20	11	6	0	0	17	283	0.940	14.12	11.5
Sown field	11	6	1	0	0	7	202	0.965	12.87	28.7
Total	46	18	18	0	1	37	586	0.937	10.05	10.3
All	92	40	19	6	1	66	1401	0.953	5.66	18.5
Arable farmland site										
All	15	2	4	0	1	7	282	0.975	9.26	41.2

d.f. = 1, n.s.). Nests destroyed by farming are excluded from tests, since they were usually exposed to predators only for a short time.

Only 26 (28%) of the 92 nests in the mixed farmland site survived until hatching (Table 1). The main causes of nest destruction were predation, which accounted for 44% of the nests, and spring farming practice which destroyed 21% of the nests, but causes of nest failure varied between habitats (Table 1). Predation was the dominant cause of nest destruction in grasslands (meadow, ley and sown pasture) and was responsible for the destruction of 48% of the grassland nests, but trampling by stock was important in sown pasture and destroyed 54.5% of the pasture nests. Predation was an important cause of nest destruction also in tillage habitats (fallow fields, unsown and sown fields) and destroyed 39% of the nests. In tillage habitats, farming practice was an important cause of nest destruction, especially in unsown fields, and to a lesser degree in fallow fields where 73% and 30% of the nests were destroyed by farming, respectively (Table 1). Of the 19 nests destroyed by farming, the majority (16 nests) were destroyed by cultivation or harrowing. Two nests were destroyed by pesticide spraying and one nest by hay cutting.

Data from 77 pairs were used to study the extent to which Curlews laid a replacement clutch if they lost their first. In some cases, both the first and second nest were found, but a replacement clutch was also assumed to have been laid if adults that lost their first nest were seen giving alarm calls later in the season, or when only a nest initiated in Period II was found. These data show that of the 77 pairs only 22 (29%) succeeded in hatching their first clutch. The majority (76%) of the 55 pairs that lost their first clutch laid a replacement clutch. The proportion of pairs that replaced the lost clutch decreased significantly with the age of the lost nest. As many as 18 (90%) of 20 pairs who lost their nest within 10 days laid a replacement clutch, while only 5 (31%) of 16 pairs that lost their nest after 10 days did so (G-test, $G_{adj} = 13.57$, $P < 0.001$). No pairs that failed at the chick stage produced replacement clutches.

Hatching success is estimated more accurately if the exposure time (number of observation days) of the nests is taken into account (Mayfield 1961, 1975). The Mayfield method assumes a constant risk of nest loss over the whole nest period. The probability of nest loss did not differ between egglaying ($P = 0.957$) and incubation ($P = 0.975$; $z = 0.93$, n.s.), nor between the first ($P = 0.967$) and second half ($P = 0.984$) of the incubation ($z = 1.71$, n.s.), even if there was a tendency for higher survival probabilities in the late period. The hatching success of the first clutches and relayings is estimated at 23.1% and 27.7%, respectively. Since 71% of the pairs are estimated to lose their first clutch and 76% of these pairs laid a second clutch, approximately 12.5% of the pairs hatched a second clutch ($0.71 \times 0.76 \times 0.277 = 0.149$) if the first failed. This means that a total of 38.0% of the pairs successfully hatched at least one chick, but nest survival probability varied greatly between habitats and study sites (Table 1).

At the mixed farmland site daily nest survival was significantly higher in grassland habitats than in tillage (Z-test, $z = 2.3$, $P < 0.05$). The difference in daily nest survival between tillage and grassland habitats was mainly due to the low nest survival in unsown tilled fields (daily survival probability, $P = 0.87$), and if nests in this habitat were excluded from the analysis the difference between grasslands and tillage habitats was no longer significant ($P_{tillage} = 0.95$, $P_{grassland} = 0.96$, $z = 1.1$, n.s.). This difference between tillage

Table 2. *Daily probability* p *of predation and destruction of Curlew nests due to farming activities for different nest types. Early season (≤ 10 May), late season (> 10 May), grassland and arable nests are from the mixed farmland site. Nest-days is the number of days for which nests were under observation, s.e. is the standard error of* p *(after Johnson 1979 and Hensler & Nichols 1981).* $z = |p_1 - p_2| / \sqrt{(s.e._1)^2 + (s.e._2)^2}$ *after Johnson (1979) and Hensler & Nichols (1981). Significance levels* *P < 0.05, **P < 0.01 *and* ***P < 0.001

Nest type	No. of Nests	Nest days	Farming activities: Losses	p	s.e. × 1000	z-test	Predation: Losses	p	s.e. × 1000	z-test
Arable	46	586	18	0.031	7.13	$z=4.2^{***}$	18	0.031	7.13	$z=0.4$
Grassland	46	815	1	0.001	1.23		22	0.027	5.68	
≤10 May	49	218	11	0.050	14.83	$z=2.9^{*}$	7	0.032	11.94	$z=0.2$
>10 May	74	1183	7	0.006	2.23		34	0.029	4.86	
Mixed site	92	1401	19	0.014	3.09	$z=0.0$	40	0.029	4.45	$z=3.3^{**}$
Arable site	15	282	4	0.014	7.04		2	0.007	5.00	

and grassland habitats is mainly due to the fact that the daily probability of being destroyed by farming differed between the two habitats, whereas the probability of nests being preyed upon did not differ (Table 2). There were also differences in daily nest survival within the grassland and tillage habitats. Sown pasture had significantly lower nest survival than meadow and ley ($P_{\text{sown pasture}} = 0.90$, $P_{\text{meadow+ley}} = 0.97$, $z = 2.5$, $P < 0.05$), mainly due to trampling by stock.

The destruction of nests by farming practices was a seasonal effect because of the intensive spring farming during the first weeks of May. The daily survival probability of nests on or before 10 May ($P = 0.92$, s.e. $= 18.6 \times 10^{-3}$) was significantly lower ($z = 2.2$, $P < 0.05$) than after 10 May ($P = 0.96$, s.e. $= 5.7 \times 10^{-3}$). The daily probability of nest destruction due to farming differed significantly between these periods, but nest destruction due to predation did not (Table 2).

Surprisingly, nest survival at the arable farmland site was significantly higher than at the mixed farmland site (Z-test, $z = 2.0$, $P < 0.05$). This was due to a lower predation rate at the arable site. The daily nest probability of nest destruction due to farming was not higher at the arable farmland site, as might be expected (Table 2).

Although Curlews preferred to nest far from forest edges the daily predation rate was not significantly higher close to edges than away from them (Table 3), and there were no differences in daily predation probability close to and far from rivers or large ditches, which are potential corridors for predators (Table 3).

Clutch-size and hatchability

The mean clutch-size ± s.d. of the 83 clutches of known size was 3.87 ± 0.41 eggs. Of these clutches, 74 (89.2%) had four eggs, 7 (8.4%) had three eggs and 2 (2.4%) had two eggs. The clutch-size did not differ significantly between the mixed and the arable farmland sites (Table 4). The difference in clutch-size was significant, however, if nests initiated during Period I (mean 3.95 ± 0.23 eggs) were compared to those initiated in Period II (mean 3.64 ± 0.62 eggs, Table 4). This indicates a lower clutch-size in probable replacement clutches compared to first clutches. Among successful clutches there was a tendency for a higher proportion of eggs to hatch in nests initiated in Period I (mean 96% of eggs in 21 nests) than in nests initiated in Period II (mean 82.7% in 13 nests), but the difference was not significant (Mann-Whitney *U*-test, $z = 1.6$,

Nest site	No. of Nests	Nest days	Predated clutches	p	s.e. × 1000	z-test
≤50 m forest	14	207	6	0.029	11.66	$z=0.16$
>50 m forest	70	1128	31	0.027	4.87	
≤100 m forest	30	486	11	0.023	6.75	$z=0.9$
>100 m forest	54	849	26	0.031	5.91	
≤100 m river/ditch	20	303	12	0.039	11.2	$z=1.2$
>100 m river/ditch	71	1095	28	0.026	4.77	

Table 3. *Daily probability of predation* (p) *of Curlew nests close to and far away from forest edge and river/ditch. All data from the mixed farmland area. Nest-days is the number of days for which nests were under observation, s.e. is the standard error of* p *(after Johnson 1979 and Hensler & Nichols 1981) and* $z = |p_1 - p_2| / \sqrt{(s.e._1)^2 + (s.e._2)^2}$ *after Johnson (1979) and Hensler & Nichols (1981). None of the Z-tests was significant*

Table 4. *Number of Curlew clutches with 1–3 eggs in different farmland sites and periods. Period I includes nests initiated during the first 10 days of the breeding season (first clutches) and Period II includes nests initiated after the first 10 days (relaid clutches). Significance levels* $^{*}P<0.05$

	No. of Nests		
Nest category	1–3 eggs	4 eggs	G-test
Arable site	1	11	$G=0.48$
Mixed site	9	47	
Period I (all areas)	2	35	$G=6.41^{*}$
Period II (all areas)	8	20	

n.s.). The hatchability did not differ between the arable (8 nests, mean 91%) and mixed farmland sites (26 nests, mean 90.6%, Mann-Whitney U-test, $z=0.2$, n.s.).

Number of fledglings

Of the 118 chicks hatched, 24 (20.3%) survived until they were able to fly after 35 days. There was a significant difference in the proportion of fledged chicks between different habitats. Surprisingly, survival was lower in the seven broods on meadows (no chicks survived) compared to the 25 broods on tillage and leys (mean = 25% survival, Mann-Whitney U-test, $z=2.4$, $P<0.05$). Distance to forest edge also affected chick survival. The distance from nest to forest edge was significantly longer (mean 351 ± 64 m) for the 14 successful clutches (at least one fledgling) than for the 18 unsuccessful ones (mean 185 ± 39 m, Mann-Whitney U-test (one-tailed test since predation was expected to be higher close to edges), $U=75$, $P<0.05$), suggesting that chick predation is higher on clutches hatched close to forest edges. There was a small difference in the proportion of fledged chicks in 20 nests initiated in Period I (mean = 23.7%) compared to nine nests initiated in Period II (mean = 16.7%), but the difference was not significant (Mann-Whitney U-test, $U=76$, n.s.).

Influence of different mortality factors on reproductive success

In order to estimate the influence of factors such as farming and predation on the reproductive success of Curlews, destroyed nests which were replaced must be separated from those that were not replaced with new nests. The influence of lowered clutch-size, hatchability and survival of young in relaid clutches must also be taken into account, and the following estimate of reproductive success is therefore made with single eggs as the unit of calculation. Data from 87 nests with known time of initiation, which could be classified as first clutches (56) or relayings (31) are used for these calculations. The hatching success and effect of different mortality factors differ somewhat from the earlier results from all 107 nests. For example, 46.6% of the pairs laid a replacement clutch, which is a somewhat lower figure than the 54% calculated from the initiation time of nests. Nevertheless, these calculations are useful in highlighting the effects of different mortality factors on the reproductive success of Curlews.

We would expect that a total of 100 pairs of Curlews would lay 392 eggs (3.92 egg per first clutch) and they could potentially produce 392 fledged young. Of these eggs, 96.4% are not hatched or killed as chicks in first broods. The major factors reducing reproductive success in first clutches are predation of eggs, mortality of chicks (unknown reasons), destruction of eggs by farming practices, trampling of eggs by cattle, and infertile eggs (Fig. 2). Only 3.6% of eggs in first clutches produce fledglings. Of the eggs destroyed in first layings 46.6% would be replaced by relayings. However, in the replacement clutches the majority of the eggs would also be destroyed as eggs or killed as chicks. The major factors reducing reproductive success are the same as in the first layings; predation of eggs, mortality of chicks, destruction of eggs by farming practice, but trampling of eggs by cattle and infertile eggs (also including reduction of clutch-size in relaid clutches) are more important factors in replacement clutches. Only 5.6% of the eggs produce fledglings (Fig. 2). A higher proportion of eggs produce fledglings in relaid than in first clutches, mainly because of their higher nest survival.

The mean production of young in the mixed farmland site was 0.23 fledglings per pair ($n=113$ pairs) and varied between 0.17 and 0.29 during the study years. The production of young in the arable farmland site was slightly higher, 0.37 fledglings per pair ($n=19$ pairs) during the study years, but the difference was not significant (Mann-Whitney U-test, $z=0.37$, n.s.). These figures also include pairs whose nest was not found, since broods could be found with help of alarm-calling adults. Studies of 12 pairs on bogs in the vicinity of the mixed farmland site showed that 1.4 fledglings per pair were produced, which is significantly higher than the 0.25 fledglings per pair ($n=132$, both sites) on farmland (Mann-Whitney U-test, $z=4.74$, $P<0.001$).

DISCUSSION

Nest site choice and reproductive success

Grassland was a preferred nesting habitat of Curlews and hatching success was higher in grassland than on tillage. It might therefore seem that Curlews have adapted to the influence of modern farming by breeding in habitats where the effects of farming are small. However, a relatively large proportion of the nests (28% at mixed farmland site) were found in tilled fields, while pairs with grassland in their territory did not always breed on grassland. There were also changes between years within territories; a pair might breed successfully on grassland in one year but in the next year breed on tillage where the nest was most probably destroyed. This is difficult to explain, but perhaps the probability of the adult birds being preyed upon is lower on tillage where, at

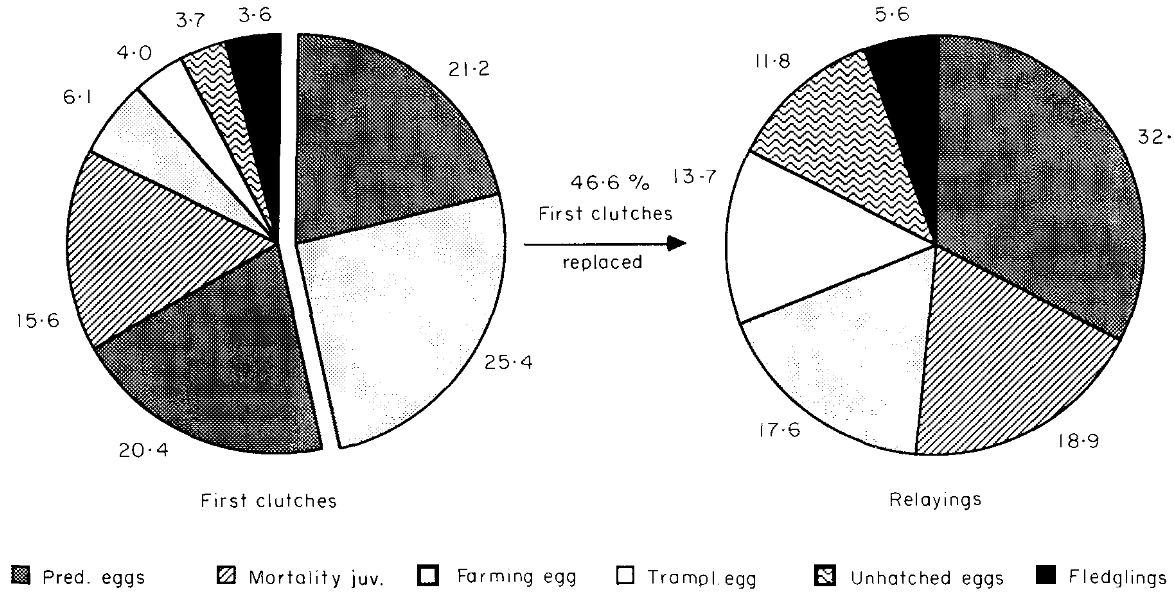

Figure 2. Effects of different factors on the reproductive success of Curlews. The size of the reduction in reproductive success is given as percentage of the potential 3.92 fledglings per pair. Pred. eggs = predation of eggs; mortality juv. = mortality of hatched chicks; farming egg = eggs destroyed by farming practices; trampl. egg = trampling of eggs by cattle; unhatched eggs = eggs that do not hatch in nests that survived until hatching (in relayings this figure also includes a reduction in clutch-size); and fledglings = proportion of eggs that produced fledglings. Data from 56 first clutches and 31 probable relayings.

least to the human eye, they are more difficult to see than on grassland early in the season.

The main cause of nest destruction was predation. Unlike the effect of farming practice, the predation probability did not differ between habitats or time of season, though predation rate was higher at the mixed site than at the arable site. Møller (1989) showed in an experimental study that open nests are more easily preyed upon near forest edges than further out in the fields but, in the present study, Curlew nests placed further away from forest edges than random control sites, did not suffer a higher predation rate than those close to forest edges. This is probably because Curlews are large birds, which have aggressive anti-predator behaviour and often can defend themselves against corvids and other avian predators, whereas Møller mimicked nests of passerines, which cannot defend their nests. Among Curlews, however, there was a significantly lower chick survival among chicks from nests close to forest edges compared to far away and this might explain the preference for nest sites farther away.

Both parents guard their young just after hatching, but the female usually leaves the breeding site after 7–14 days and the male is left alone with the chicks. In 21 monitored pairs the earliest female left her male after 4 days and the latest after 17 days. The adults are very alert just after hatching and are often seen attacking crows and other potential chick predators. When the chicks grow older they are probably not easily preyed upon by crows. At that stage the female leaves the site, and it is probable that the limited food availability in farmland later in the season also makes it advantageous for her to leave early.

As many as 74.7% of the chicks from first broods and 89.8% of the chicks from relaid clutches died before the age of 35 days. The direct causes of chick mortality are unknown, but predation and hay-cutting are known to have killed some Curlew chicks. Survival of chicks differed between habitats and, surprisingly, survival on meadows was lower than on tillage and leys. The most probable explanation for this is a higher predation rate on meadows, since there is usually higher food availability on natural grasslands than on tillage fields (Steen 1983). Mink *Mustela vison* were common in the meadow area and might have been responsible for the low chick survival in this habitat; adult Curlews are less successful in defending their chicks against mammalian predators than against corvids. Weather and chick condition when hatching probably also affected the survival of chicks, as has been discussed for Lapwing *Vanellus vanellus* chicks in farmland (Galbraith 1988).

The decline of the Curlew population and changes in farming policy

The production of fledged young in this study was only 0.25 young per breeding pair, which is lower than the 0.72 fledglings per pair reported from northern Finland (Ylimaunu *et al.* 1987). Their study was made at a site with little influence from agriculture on reproductive success (only 6% of nests destroyed by agriculture), which indicates that Curlews have a higher production of young in undisturbed habitats than on farmland with a large proportion of intensively managed tilled fields.

The area of natural grasslands and sown grasslands in Sweden has decreased markedly during the modernization of farming. The area of leys has decreased from 1.6 million ha in 1945 to 0.9 million ha in 1989 (Statistiska Centralbyrån

1970, 1980, 1990). The decrease of natural grassland has also been substantial; starting in the late 19th century and continuing until today, with less than 10% of the 2 million ha of natural grasslands in 1850 remaining (Larsson 1985). Cattle farming is still relatively common in northern Sweden (southern and northern Norrland), where 61% of the farmland area is ley, compared to only 19% in middle Sweden (plain districts of Svealand, Statistiska Centralbyrån 1990). Curlews are also found in much higher densities in the north of Sweden than in southern Sweden. Census data (Berg & Sjöberg in press) show that Curlew densities are low in southern Sweden (Götaland 0.22 territories/km^2 farmland) and in middle Sweden (Svealand 0.12 pairs km^{-2} farmland). Densities are higher in the north of Sweden. In southern Norrland 0.62 territories/km farmland were found and in northern Norrland densities around 4–6 territories/km farmland have been reported. The low reproductive success of Curlews on modern farmland, compared to natural grasslands and leys, is therefore probably an important factor in the decline of Swedish Curlew populations.

Although Curlew breeding success on modern farmland is poor, nests on fallow fields, the preferred nest habitat in the arable farmland site, were less likely to be destroyed by farming practice than nests on still unsown tillage. Without fallow fields, practically all first clutches in arable farmland would be placed on still unsown tillage and would therefore be destroyed during spring tillage operations. Fallow fields are more common in farmland now than only a few years ago. The total acreage of agricultural land is decreasing in Sweden as a whole as well as in the northern part of the country (Gerell 1988, Sjöberg 1988). In 1975 the area of fallow fields in Sweden was 80 000 ha, after a continuous decrease of fallow area since 1945 (Statistiska Centralbyrån 1970, 1980). However, by 1989 the area of fallow fields in Sweden had increased to 227 000 ha (Statistiska Centralbyrån 1990). Due to overproduction and changed farming policy, farmland is now taken out of production and over 30% of the farmland area in the province of Västmanland will be taken out of production during the next few years. This will benefit the Curlew population in the short term, since reproductive success of Curlews is higher on fallow fields than on tillage, but in a few years the fields will be taken into alternative production, turned into conifer plantations or used for production of short rotation forestry, which will all lead to the same result, i.e. habitats unsuitable for Curlews. If, however, there is an increase in extensive grazing and production of grass for energy purposes, which are also being discussed, this will benefit the Curlew population. It is difficult, however, to predict what will happen to large areas of farmland in Sweden and therefore to the populations of Curlews and several other farmland birds.

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