Breeding success and causes of breeding failure of curlew *Numenius arquata* in Northern Ireland

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Summary

1. The present study investigated breeding success and causes of breeding failure of curlew, a species for which the UK holds internationally important breeding numbers. Studies were undertaken between 1993 and 1995 in two areas of Northern Ireland, where the species' breeding range has recently contracted and breeding numbers are declining. Avian nest predators were abundant in both areas, whereas foxes were abundant on the Antrim study area but generally were absent from the Lough Erne study area, which was mainly islands.

2. Productivity was estimated to be 0·14–0·26 fledglings per pair in Antrim and 0·20–0·47 fledglings per pair on Lough Erne. These figures are lower than most estimates of productivity from other studies of breeding curlew. The differences between the recorded productivity levels and those estimated to be required to maintain a stable population are sufficient to account for the observed decline in Northern Ireland's breeding curlew population.

3. Predation was the main proximate cause of breeding failure, with nest predation being of most importance in reducing productivity. Only 3·6–19·0% of all nests hatched on each study area in each year, with nest predation accounting for 85–97% of failures. Survival of chicks from hatching to 31 days of age was 38·5% in Antrim and 19·1–29·2% on Lough Erne. Predation accounted for 74% of chick mortality.

4. Nest failure rates were not related to the vegetation height around nests nor to clutch laying date on either study area. They differed among the islands and one shoreside site on Lough Erne. Almost all nest predation on Lough Erne was attributable to avian predators, but in Antrim foxes probably accounted for most nest predation. The likelihood of predation on chicks was not related to their hatching date, hatching weight or body condition.

5. The results from this study suggest that predation rates on curlew nests in Northern Ireland may have increased in recent decades. Levels of predator control in Northern Ireland have declined but there have also been considerable changes in land-use that could benefit generalist predator species or increase the vulnerability of curlew nests to predation. It is recommended that large-scale trials of legalized predator control and land-use manipulation should be undertaken to identify appropriate conservation management methods.

Key-words: breeding waders, nesting success, population decline, predation.

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Introduction

Population declines of several wader species, such as lapwing *Vanellus vanellus* L., curlew *Numenius arquata* L. and redshank *Tringa totanus* L., have now been documented in many parts of Europe (Kipp 1985; von Dornberger & Ranftl 1986; Hötker 1991; O'Brien & Smith 1992; Robertson & Berg 1992; Gibbons, Reid & Chapman 1993; Tucker & Heath 1994). Many of these declines have been attributed to land-use changes, usually agricultural improvements and intensification, which have increased greatly in extent in recent decades (Pain & Pienkowski 1997). Such changes may cause declines in breeding wader populations through various mechanisms, including increased mortality of eggs and chicks from machinery or trampling by livestock (Beintema & Müskens 1987; Berg 1992), declines in food availability (Green 1988) and direct loss of breeding habitat.

However, other factors may also be important in causing declines in breeding wader populations, and within the UK there is evidence that the populations of certain generalist predators, particularly corvids and foxes *Vulpes vulpes* L., which depredate wader nests and chicks, have increased in recent decades (Tapper 1992; Gregory & Marchant 1996). Newton (1993) concluded that marked effects of non-introduced predators on breeding numbers appeared unlikely in all but a relatively small proportion of bird populations. Such effects appear to be most likely to occur in species of ground-nesting gamebirds and ducks, which are particularly vulnerable to mammalian predation, both of nests and chicks, and of incubating adults (Duebbert & Kantrud 1974; Duebbert & Lokemoen 1980; Keith & Rusch 1988; Marcström, Kenward & Engren 1988). Some of the most convincing evidence that predators can reduce breeding densities come from a study of grey partridge *Perdix perdix* L. in the UK (Tapper, Potts & Brockless 1996). Few data are currently available on the impact of predation on breeding wader populations, although being ground-nesters there are potential parallels with both gamebirds and ducks. Certainly many studies have documented substantial losses of wader nests and chicks to predators (Hildén 1978; Harris 1967; Pienkowski 1984a; Redmond & Jenni 1986; Beintema & Müskens 1987; Galbraith 1988; Baines 1990; Berg 1992), but in only a few cases have high predation rates been considered as a likely or possible cause of population decline (Mulder & Swaan 1988; Jönsson 1991; Parr 1992, 1993).

The breeding curlew population in the UK is of international importance, probably numbering considerably in excess of 70 000 pairs and representing as much as 30% of the estimated European population (Grant 1997; Hagemeier & Blair 1997). Over the past 20 years this population has undergone a contraction in breeding range, with the province of Northern Ireland being one area in which this contraction is marked (Gibbons, Reid & Chapman 1993). Moreover, repeat surveys on 101 sites distributed across Northern Ireland indicated that between 1986 and 1992 the numbers of breeding curlew on these sites declined by 25%, from an estimated 320 pairs in 1986 (K. Partridge, unpublished data). Further surveys on a sample of these same sites in 1996 indicated a continued decline (Grant 1997). In the present study the survival rates of curlew nests and chicks were measured on two study areas in Northern Ireland. While avian predators were abundant in both study areas, foxes were generally absent from one area comprising mainly islands. The importance of predation as a proximate cause of nest and chick failure is assessed for both areas, and the main predators are identified. Estimates of fledging success are compared to the levels considered necessary for population stability, and the role of predation in the decline of Northern Ireland's breeding curlew population is considered.

Study areas

Research was undertaken in two study areas, namely an area of marginal farmland in Co. Antrim (1993–95), and 13 of the islands, along with one shoreside area, on Upper and Lower Lough Erne in Co. Fermanagh (1994–95) (Fig. 1). The rearing of sheep and beef cattle were the main land-uses on the Antrim study area, ranging from 200 to 400 m a.s.l. in altitude and covering 40 km². Rough and wet grasslands and degraded moorlands, interspersed among agriculturally improved grasslands, provided the main nesting habitats for curlew on this study area. On the semi-natural habitats curlew nesting densities averaged approximately 5–7 pairs km^{-2}. The islands comprising the Lough Erne study area ranged from 5 to 46 ha in area (mean $\pm$ SE = 15 $\pm$ 3 ha), while the one shoreside area covered 63 ha. Most islands were seasonally grazed by cattle, and occasionally sheep, and
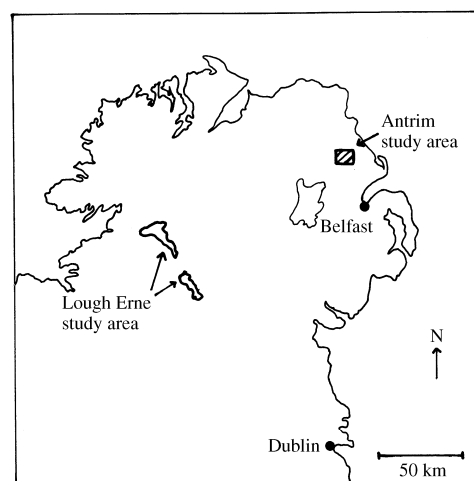
Fig. 1. The location of the two study areas in Northern Ireland.

agriculturally unimproved wet grasslands were the main nesting habitats. Nesting densities of curlew were high, reaching 1 pair per 2–3 ha in some instances.

Potential nest and chick predators included hooded crows *Corvus corone cornix* L., which were abundant in both study areas, ravens *Corvus corax* L. in Antrim and colonies of lesser black-backed gulls *Larus fuscus* L. (with smaller numbers of herring *L. argentatus* Pont. and great black-backed gulls *L. marinus* L.) on Lough Erne. Smaller corvids (e.g. magpies *Pica pica* L.) were abundant in Antrim, but less so on Lough Erne. In terms of mammalian predators, foxes were abundant in Antrim, with stoats *Mustela erminea* L. and possibly badgers *Meles meles* L. also being present. On Lough Erne, mink *Mustela vison* L. were the only mammalian predators likely to occur on the islands, although foxes do occasionally move onto some islands (including one known instance during the study period).

Methods

NESTING SUCCESS

Located nests were marked by pacing the distance on a known compass bearing to a feature (e.g. a rock or fence post). Except on the Antrim study area in 1995, the following measurements were taken on locating each nest; (i) the length (L), maximum breadth (B) and weight (W) of each egg in the clutch (linear measurements taken to the nearest 0·1 mm using vernier callipers, weight measured to the nearest 0·5 g); (ii) the vegetation height at four equidistant points (i.e. north, south, west and east) immediately adjacent to the nest cup; and (iii) measurements of vegetation height at 10 random points within a 1-m² quadrat centred on the nest, and at 10 random points in a 1-m² quadrat located in a random direction, 20 m from the nest. On the Antrim study area in 1995, egg measurements were made only if the clutch was found after the onset of incubation (no handling of eggs occurred otherwise) and measurements of vegetation heights were limited to the four points immediately adjacent to the nest cup. Measurements were restricted in this way to allow tests for possible effects of methods on nest survival (see the Appendix).

Clutches with fewer than four eggs were next visited when it was considered likely that the clutch would be complete. Most completed clutches comprised four eggs (see the Results); the mean interval between the laying of successive eggs in a clutch is approximately 1·5 days (Mulder & Swaan 1992; M.C. Grant, unpublished data). Following clutch completion, nests were generally not visited again until they were estimated to be within 7 days of hatching, except where nests were used in studies to identify nest predators. After this stage visits were made at 2–4 day intervals until hatching, although at 48 nests visits close to hatching

were more frequent than this in attempts to trap one of the adult birds. Expected hatching dates of clutches found during the laying period were predicted by assuming a mean incubation period of 29·5 ($\pm 0·2$ SE) days from laying of the third or fourth egg (M.C. Grant, unpublished data). For nests found after clutch completion, expected hatching dates were estimated with a mean error of approximately 2 days using a regression of days to hatching (D) against an index of egg density for the clutch, i.e. the mean of W/LB^2 (Grant 1996). For nests found after clutch completion, clutch initiation dates were estimated by back dating 33 days from the hatching date (or an appropriately shorter period for smaller clutches). In cases where the nest failed to hatch, back dating was carried out from the predicted hatching date calculated from the equation $D = 0·32((W/LB^2) \times 10^6) - 134·83$ (Grant 1996).

Successful hatching of clutches was confirmed by finding chicks in (or close to) the nest (88% of cases) or from eggs last observed in an advanced stage of chipping, with remains indicative of hatching (e.g. shell membrane) later found in the nest and alarm-calling adults nearby. Predation of clutches was often identified by the disappearance of eggs, but in some cases also by the presence of broken shells close to the nest and by specific methods used to identify nest predators (see below). Losses due to livestock trampling were characterized by the presence of crushed eggs or hoof marks within, or on the edge of, the nest scrape. Nests were classed as replacement clutches if: (i) they were located close to a previously failed clutch (within 250 m in Antrim and 150 m at Lough Erne); (ii) there had been no previous evidence during that season of more than one pair occupying the relevant area; and (iii) likely dates of failure of the first clutch and laying of the presumed replacement were separated by at least 7 days. (Previous studies on individually marked curlew indicated that this was the minimum period between failure and re-laying; M.C. Grant, unpublished data.)

IDENTIFICATION OF NEST PREDATORS

The main method used to determine the relative importance of the different potential predators of curlew nests in 1994 on both study areas, and in 1995 on the Lough Erne study area only, was to place wax-filled hen's eggs in a sample of the nests under study (Major 1991). These were painted to resemble curlew eggs, and were tied to a peg (using a line embedded in the wax) that was buried in the ground. Following predation of the nest, the marks imprinted on the wax egg allowed identification of the predator (at least to the level of bird or mammal). In eight cases a plasticene-filled hen's egg containing a radio-tag was used instead. Following addition of the wax eggs in 1994, one or two additional checks of the manipulated nests were undertaken within 4–8 days. In 1994 the loss

of 45% of the wax eggs placed in nests that were subsequently depredated (due to inadequate securing) meant that 66% of nests at Antrim and 48% at Lough Erne were manipulated in this way. At Lough Erne in 1995 wax eggs were added to 25% of study nests. Adding wax eggs to nests in the Antrim (but not the Lough Erne) study area increased the probability of predation occurring so that this method was abandoned in the Antrim study area in 1995 (see the Appendix).

The main method of obtaining information on the predators of curlew nests in the Antrim study area in 1995 was to determine the timing of the predation event by checking a sample of study nests (23%) at dawn and dusk on every day over four periods of 3–10 consecutive days. Further data on the predators of nests were obtained from shell remains at depredated nests possessing mammalian toothmarks or bird peck marks (Green, Hawell & Johnson 1987). In 1995 it was also recorded whether any remains at all were found in or close to depredated nests (including very small fragments of shell and yolk remains).

BROOD AND CHICK SURVIVAL

Studies of brood and chick survival were undertaken in the Antrim study area in 1993 and 1994, and on the Lough Erne study area in 1994 and 1995.

Chicks were ringed with a numbered metal ring when found in the nest, which was usually within 24–36 h of hatching. Body weight and the lengths of the bill, head plus bill, right wing, and right tarsus plus toe of these chicks were measured (linear measurements taken to the nearest 1·0 mm, and weight to the nearest 0·5 g). During the study 70 of these newly hatched chicks (plus three older chicks from two broods) were fitted with 1·1 g or 1·5 g radio-tags. These chicks were from 40 different broods and represented 46–100% of the broods hatching from study nests in each study area in each year. Within broods, tagging was carried out so as to maintain equal numbers of tagged and untagged chicks where possible, and no more than two chicks were tagged in any brood. Initially tags were mounted by direct gluing onto the chick's back but (due to poor retention) from 1994 tags were glued onto temporary leg rings (i.e. open-ended darvic rings closed with plastic tape) placed above the knee. The total weight of tag plus temporary ring represented 2·7–3·7% of the mean hatching weight of tagged chicks, and 3·4–4·6% of the lightest hatching weight of a tagged chick. The radio-tags used had an operational range of 300–500 m. Operational battery life for tags used in 1993 and half of those used in 1994 was approximately 21 days, while the remainder usually operated for 30 days or more. Where tags with the shorter life span were used, chicks were monitored over a longer period in three instances by replacing the tag before it ceased functioning.

Prior to hatching a total of 27 adult curlew were

trapped on the nest and fitted with 8 g radio-tags, which allowed birds to be relocated at distances of up to 3 km. The tags represented a maximum of 1·3% of the body weight and were attached to the base of the central tail feathers. Trapping of adults was restricted to the late stages of incubation. During the 3 years of study two nests were depredated and one was deserted within a day after the capture of an adult, and these were excluded from calculations of nesting success. In 18 cases tagged adults had broods in which a number of chicks were also tagged.

Curlew chicks usually fledge at 30–40 days of age (Berg 1992; M.C. Grant, unpublished data) so the radio-tagged chicks were monitored until at least 30 days after hatching, unless chick death or tag failure occurred earlier. Monitoring was performed by recapturing chicks every 3 days on average, except for those with back-mounted tags, which were recaptured at 1–2 day intervals to ensure that the tags remained attached. At each recapture the same biometrics were measured as for newly hatched chicks. For broods in which one of the parents was tagged, and either the tagged chicks had died or else no chicks had been tagged at hatching, then the tagged parents were relocated every 3 days to confirm continued survival of at least one chick in the brood. Death of tagged chicks was confirmed either by recovering the tag or carcass or, in cases where one of the parents was also tagged, by being unable to obtain a signal from the chick's tag and by locating the tagged parent and ascertaining that all chicks in the brood had failed on the basis of the parent's behaviour. Several checks were carried out on these adults to ensure that behaviour characteristic of failure occurred consistently. (Adults without chicks lack the vigilant behaviour characteristic of those with chicks and readily fly off when disturbed, whereas those with chicks remain nearby and alarm-call). Where signals from chick radio-tags were 'lost' prior to 31 days of age and broods did not include a tagged adult (or else the tagged adult continued to behave as if with chicks up to 31 days of age), then tag failure was assumed if the timing of 'disappearance' coincided with the expected end of the battery life or irregular signals had been obtained previously from the tag.

Identification of the proximate causes of chick mortality was based upon the locations and conditions of the carcasses or tags when recovered, while radio-tagged chicks that 'disappeared' without prior indication of tag failure were assumed to have been depredated as this was the only likely cause of being unable to receive a signal from such tags.

ANALYSES

Data used in all analyses of daily rates of nest failure and predation from the Antrim study area in 1994 were amended to take account of the apparent effects of adding wax eggs to nests on the predation rates at

this study area (see the Appendix). It was assumed that for each nest where predation occurred by the visit immediately following the addition of a wax egg to the nest, the nest had actually survived up to the midway stage between the visit on which the wax egg was added and the following visit. Data from these nests were then censored at this stage in the subsequent analyses.

Initial estimates of rates of nest failure and predation were calculated using a modification of Mayfield's (1961, 1975) method, which uses a maximum likelihood estimator to allow for possible biases resulting from the visits to nests being at long, irregular intervals (Bart & Robson 1982). However, in subsequent analyses of nest failure rates it was necessary to assume that failure occurred exactly midway between the penultimate visit and the visit on which failure was confirmed. These analyses were performed to investigate whether nest failure rates varied with clutch laying dates, vegetation heights around the nest, and between areas with and without cattle. For the Lough Erne study area, nesting island or site was incorporated as an additional factor. In these analyses survival was modelled as if lifetimes of nests were precisely known and there was censoring, because nests that hatched did not have the chance to fail (Kalbfleisch 1979). The expected probability of a nest surviving *LD* laying days and *ID* days following clutch completion was:

$$E(p) = \exp\left(-(k*ID + k*s*LD)\right)$$

where k is a daily mortality risk statistic for nests following clutch completion, and s is a multiplier that determines how much greater the mortality risk is during laying. Thus, it was possible to test for differences in failure rates between these two stages of the nesting period while incorporating the other effects. The NONLIN module of SYSTAT 5·0 (Wilkinson 1990) was used to calculate maximum likelihood estimates of model parameters, along with the associated deviance for each model. Except for the Antrim study area in 1995, two measures of vegetation height around nests were available for use in analyses (see above). In three of the four cases the two measurements were highly correlated ($r > 0·57$, $P < 0·001$ in both years at Lough Erne and in 1994 at Antrim, but $r = 0·10$, $P > 0·05$ at Antrim in 1993). Thus, to produce the final models the measurement that caused the greatest decrease in the deviance from the null model was selected.

Logistic regression analyses were undertaken to: (i) investigate variation in clutch size and brood size at hatching; (ii) estimate mortality and predation rates of radio-tagged chicks in relation to age; and (iii) determine whether the likelihood of chick predation was related to hatching date, hatching weight and chick body condition.

Analyses of chick mortality rates used whether or not a chick survived or died on each day of the period over which it was monitored as the dependent variable, with chick age being entered as a covariate. Analyses were undertaken for the period from hatching up to 31 days of age, with data from chicks whose tags were assumed to have failed being included up to the age of the last capture. Data from chicks dying from causes other than predation were also treated in this way in order to estimate predation rates. Death was assumed to occur midway between the last capture of the chick and the visit on which death was confirmed. Bootstrap samples (Sokal & Rohlf 1981) were used to calculate 95% confidence intervals for the estimates of chick survival, repeating the process of resampling with replacement 10 000 times in each case. These were taken using the brood as the unit of sampling because chicks from the same brood may not be statistically independent.

Whether chicks survived or were depredated was analysed in relation to hatching date, hatching weight and an index of chick body condition. Data were used only from those chicks that had been monitored since hatching and were either known to have survived to 31 days of age or were classed as having been depredated before reaching this age. Where two chicks from the same brood were radio-tagged and both either survived or were depredated, then only one of these chicks (selected randomly) was used in the analysis. The index of body condition was taken as the difference between actual weight and that predicted by a regression of weight against age. The regression used data from surviving chicks only (with each chick contributing five data points) and encompassed the period from 2 to 18 days after hatching (19 days being the oldest age at which a chick was recorded depredated, while hatching weight was used as an independent variable in the logistic regression). Chick weights were transformed, by taking $\log_e$, due to heteroscedasticity. For each surviving chick the index was calculated as the mean of its residuals, while for depredated chicks the difference between the final recorded weight and that predicted from the regression was used.

In all analyses described above, step-down procedures were used to determine the significant effects. Thus, a model was fitted that included the various explanatory variables (or factors) and then each of these was omitted in turn and the model recalculated excluding that effect. The statistical significance of each variable was tested by treating the difference between the deviance ($-2 \times \log_e$ likelihood) of the models that did and did not include the variable or factor as χ^2 with the appropriate degrees of freedom (i.e. equivalent to the number of parameters being removed from the model). The variable or factor with the lowest significance level was then deleted from the model, and the process repeated until the only remaining variables or factors were those whose removal resulted in a significant (at $P < 0·05$) change in deviance (ΔD). Where first-order interaction terms were incorporated into analyses, the above procedures

were undertaken to test for possible deletion of the interaction terms from the model before being performed on the main effects.

Results

NESTING SUCCESS, CAUSES OF NEST FAILURE AND VARIATION IN FAILURE RATES

Daily failure rates were higher during the laying period of the clutch than during the period from clutch completion to hatching (Table 1). This difference was consistent across years and study areas and was significant in all cases except for the Antrim study area in 1994. The higher failure rates during laying were due to a greater vulnerability to predators at this stage because the daily predation rates showed the same trend and clutch predation accounted for 85–97% of all nest failures at each study area in each year (Table 1). Other causes of nest failure were attributed to trampling by cattle (7% of all failures), destruction by agricultural machinery and flooding of the nest site (together accounting for 2% of all failures). The percentage of nests estimated to survive the entire nesting period ranged from 3·6% to 17·4% on the Antrim study area and was 19·0% and 6·1%, respectively in the 2 years of study at Lough Erne (Table 2).

The assumption that unsuccessful nests failed exactly midway between visits did not appear to be a serious source of bias. Estimates of daily nest failure rates obtained by the method of Bart & Robson (1982) differed little from those that would have been obtained by assuming failure occurred midway between visits (Table 1). Analyses for the Antrim study area indicated that the difference between the laying period and the period following clutch completion was the only significant effect on nest failure rates (Table 3), confirming the findings from the earlier comparisons (Table 1). A similar result was obtained for the Lough Erne study area but it was also apparent that nest failure rates differed among the various islands and the shoreside site in both years (Table 3). Differences between islands persisted when analyses were repeated excluding data from the one shoreside site within the Lough Erne study area, thus demonstrating that this result was not simply a consequence of a difference in failure rates between islands and the shoreside area ($\Delta D = 32\cdot20$, d.f. $= 11$, $P < 0\cdot001$, for 1994, and $\Delta D = 30\cdot56$, d.f. $= 11$, $P < 0\cdot001$, for 1995). On the Lough Erne study area, the risk of nest failure in the 2 years was not significantly correlated between the different islands/site (all islands/site considered, $r_s = 0\cdot01$, $n = 12$, $P > 0\cdot05$, and limiting to those where at least four nests were found in each year, $r_s = 0\cdot54$, $n = 7$, $P > 0\cdot05$).

On both study areas effects of either clutch laying date or vegetation height around the nest on nest failure rates did not occur, irrespective of whether the relationships between these variables and failure rate were expressed as linear, quadratic or exponential functions. Although vegetation height did not influence failure rates, curlew did tend to select nest sites where the vegetation was taller than in surrounding areas, at least on the Lough Erne study area (Table 4).

The tendency for the overall nest failure rates to be higher in Antrim than on Lough Erne in both 1994 and 1995 was not significant, as determined by analyses that incorporated the effects of study area and the difference in failure rate between the laying period and the period following clutch completion. (Following removal of study area from the model, $\Delta D = 0\cdot07$, d.f. $= 1$, $P > 0\cdot05$, for 1994, and $\Delta D = 1\cdot15$, d.f. $= 1$, $P > 0\cdot05$, for 1995.)

CLUTCH SIZE AND BROOD SIZE AT HATCHING

Over 77% of all completed clutches on each study area comprised four eggs, with mean ($\pm$SE) clutch size during the study period being 3·82 ($\pm0\cdot05$) in Antrim and 3·73 ($\pm0\cdot06$) on Lough Erne (there being no differences between study areas in median clutch size, $P > 0\cdot17$ in both 1994 and 1995 based on Mann–Whitney U-tests). Of those clutches that did hatch ($n = 20$ in Antrim and $n = 49$ on Lough Erne), 70% and 53% were known to suffer partial losses prior to hatching at Antrim and Lough Erne, respectively (a difference that was not significant $\chi^2 = 1\cdot0$, d.f. $= 1$, $P > 0\cdot05$). Of the 40 clutches that suffered partial losses, infertility or embryo death occurred in 42·5%, predation in 40·0%, desertion of the last egg(s) to hatch in 17·5% and trampling by livestock in 10%. Thus, successful nests in Antrim produced an average ($\pm$SE) of 2·75 ($\pm0\cdot25$) hatched chicks, while the equivalent figure on Lough Erne was 3·02 ($\pm0\cdot17$). Median brood sizes of successful nests at hatching did not differ between study areas in either 1994 or 1995 ($P > 0\cdot35$ in both years based on Mann–Whitney U-tests).

Logistic regression analyses comparing clutches of four eggs with those with fewer than four eggs indicated that clutch size on Lough Erne varied between sites in both years of study (1994, $\Delta D = 22\cdot38$, d.f. $= 12$, $P < 0\cdot05$, and 1995, $\Delta D = 19\cdot51$, d.f. $= 11$, $P = 0\cdot05$), although there were no significant relationships with laying date at either Lough Erne (1994, $\Delta D = 3\cdot60$, d.f. $= 1$, $P > 0\cdot05$, and 1995, $\Delta D = 2\cdot71$, d.f. $= 1$, $P > 0\cdot05$) or Antrim (in all 3 years, $\Delta D < 2\cdot50$, d.f. $= 1$, $P > 0\cdot05$). Brood size at hatching (i.e. whether four chicks or less) on Lough Erne did not vary significantly with either site (1994, $\Delta D = 5\cdot37$, d.f. $= 7$, $P > 0\cdot05$, and 1995, $\Delta D = 7\cdot45$, d.f. $= 6$, $P > 0\cdot05$) or laying date (1994, $\Delta D = 3\cdot30$, d.f. $= 1$, $P > 0\cdot05$, and 1995, $\Delta D = 0\cdot45$, d.f. $= 1$, $P > 0\cdot05$). Too few nests hatched in Antrim to allow analyses of brood sizes at this study area.

Table 1. Daily rates of nest failure and predation for curlew at two study areas in relation to the stage of the nesting period

Study area	Year	Nesting period	Number of nests studied*	Number of failures due to — Nest predation	Number of failures due to — All causes combined	Number of nest days†	Daily probability of predation (95% CI)‡	Daily probability of failure (95% CI)‡
Antrim	1993	Laying	21	9	11	59	0·133 (0·065–0·244)	0·185 (0·104–0·317)
		Post-clutch completion	43	30	35	549	0·053 (0·036–0·075)	0·065 (0·046–0·090)
	1994	Laying	14	5	5	46	0·104 (0·037–0·212)	0·104 (0·037–0·212)
		Post-clutch completion	29	13	14	324·5	0·039 (0·021–0·064)	0·043 (0·023–0·067)
	1995	Laying	31	13	13	81	0·176 (0·105–0·275)	0·176 (0·105–0·275)
		Post-clutch completion	53	44	46	569	0·078 (0·056–0·104)	0·082 (0·060–0·109)
Lough Erne	1994	Laying	27	14	15	84	0·160 (0·096–0·256)	0·172 (0·105–0·272)
		Post-clutch completion	52	19	24	861	0·024 (0·015–0·036)	0·028 (0·018–0·040)
	1995	Laying	35	21	22	79	0·257 (0·174–0·382)	0·275 (0·191–0·403)
		Post-clutch completion	54	30	33	711·5	0·042 (0·029–0·060)	0·046 (0·032–0·065)

* Three nests that failed within a day after trapping of an adult bird are excluded (see text).

† This is taken as the number of days from locating the nest until hatching of the first chick or, for unsuccessful nests, to midway between the penultimate visit and the visit on which failure was confirmed. Data from nests that failed immediately after the addition of a wax egg in Antrim in 1994 are censored to account for possible bias (see text).

‡ Estimates are calculated by the method of Bart & Robson (1982), see text. Thus, these estimates are not exactly equivalent to the number of nests failed (or depredated) divided by the number of nest days.

Table 2. Estimated percentage survival (with 95% confidence intervals) of curlew nests at two study areas in relation to the stage of the nesting period. The percentage survival in each period is calculated from the estimates of daily failure rates in Table 1 and by assuming a mean laying period of 4·5 days and a mean period of 28·5 days from clutch completion to hatching (see text for justification)

Nesting period	Antrim study area			Lough Erne study area	
	1993	1994	1995	1994	1995
Laying	39·8	61·0	41·8	42·8	23·5
	(18·0–61·0)	(34·2–84·4)	(23·5–60·7)	(24·0–60·7)	(9·8–38·5)
Post-clutch completion	14·7	28·6	8·7	44·5	26·1
	(6·8–26·1)	(13·9–51·5)	(3·7–17·1)	(31·2–59·6)	(14·7–39·6)
Survival to hatching	5·8	17·4	3·6	19·0	6·1

Percentage survival to hatching is calculated as the product of the estimates from the two separate stages of the nesting period.
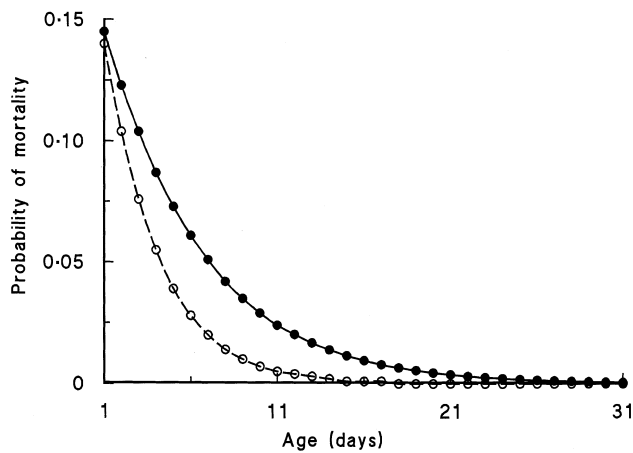

Fig. 2. Daily probability (P) of mortality (●) and of predation (○) of curlew chicks in relation to age on the Antrim study area. $P = (\exp^{(a+b*\text{age})})/(1 + \exp^{(a+b*\text{age})})$, where a (± 1 SE) $+ b$ (± 1 SE) are: (i) for overall mortality, $-1·84$ ($\pm 0·40$) $-0·17$ ($\pm 0·06$); (ii) for predation only, $-1·91$ ($\pm 0·48$) $-0·29$ ($\pm 0·12$). In both cases the incorporation of age to the null model causes a significant decrease in deviance (i.e. $\geqslant 12·96$, $P < 0·001$ in both cases). Data from 22 chicks from 14 broods were used.
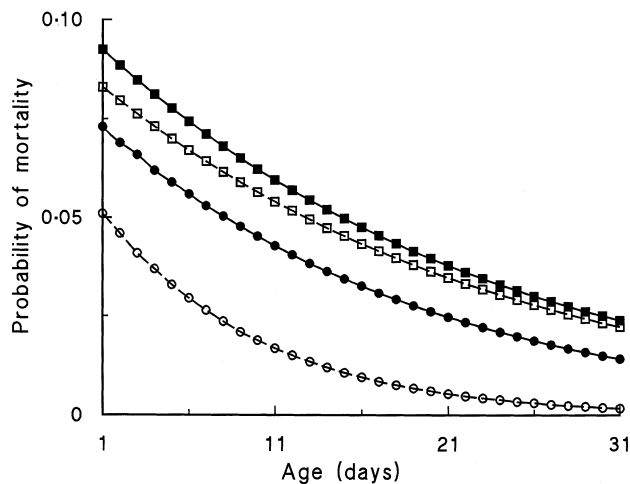

Fig. 3. Daily probability (P) of mortality in 1994 (●) and 1995 (■), and of predation in 1994 (○) and 1995 (□), of curlew chicks in relation to age on the Lough Erne study area. $P = (\exp^{(a+b*\text{age})})/(1 + \exp^{(a+b*\text{age})})$, where a (± 1 SE) $+ b$ (± 1 SE) are: (i) for overall mortality 1994, $-3·01$ ($\pm 0·52$) $-0·09$ ($\pm 0·08$); (ii) for predation 1994, $-2·61$ ($\pm 0·39$) $-0·04$ ($\pm 0·04$); (iii) for overall mortality 1995, $-2·44$ ($\pm 0·34$) $-0·04$ ($\pm 0·03$); (iv) for predation 1995, $-2·32$ ($\pm 0·33$) $-0·04$ ($\pm 0·03$). In no case does the incorporation of age to the null model cause a significant decrease in deviance (i.e. $\leqslant 1·90$, $P > 0·05$ in all cases). Data from 24 chicks from 13 broods and 27 chicks from 17 broods were used in 1994 and 1995, respectively.

Table 3. Changes in the deviance of models of curlew nest failure rates in two study areas, resulting from omission of those variables and factors incorporated in an initial model. The change in deviance given is that associated with the stage at which each particular effect is removed from, or finally retained in, the model using a step-down procedure

Year	Independent variable/factor	Antrim			Lough Erne		
		Order of removal	d.f.	Change in deviance	Order of removal	d.f.	Change in deviance
1993	Clutch laying date	First	1	0·01 NS			
	Cattle in nest field	Second	1	0·01 NS			
	Vegetation height around nest	Third	1	1·88 NS			
	Laying vs. post-clutch completion	Retained	1	9·62 **			
1994	Clutch laying date	First	1	0·01 NS	Third	1	0·87 NS
	Vegetation height around nest	Second	1	1·46 NS	First	1	0·05 NS
	Cattle in nest field†			—	Second	1	0·77 NS
	Laying vs. post-clutch completion	Third	1	3·04 NS	Retained	1	6·19 *
	Nesting island/site			—	Retained	12	41·08 ***
1995	Clutch laying date	First	1	0·10 NS	First	1	0·05 NS
	Cattle in nest field	Second	1	0·16 NS	Third	1	2·23 NS
	Vegetation height around nest	Third	1	0·90 NS	Second	1	0·57 NS
	Laying vs. post-clutch completion	Retained	1	5·10 *	Retained	1	9·04 **
	Nesting island/site			—	Retained	12	35·73 ***

Laying vs. post-clutch completion refers to the difference in failure rate between these two stages of the nesting period. In each case failure rates are higher during laying, with the estimated ratio of failure rates between these two stages of the nesting period being 3·08 and 2·19 for Antrim in 1993 and 1995, respectively, and 2·54 and 2·81 for Lough Erne in 1994 and 1995, respectively.

The range of laying dates was 18 April–30 May, 17 April–29 May and 19 April–5 June in Antrim in 1993, 1994 and 1995, respectively, and 14 April–21 May and 13 April–3 June on Lough Erne in 1994 and 1995, respectively. In Antrim, 44% and 30% of nests were in fields with cattle in 1993 and 1995, respectively, while on Lough Erne 60% and 74% were in 1994 and 1995, respectively.

† The presence or absence of cattle in nesting fields was not recorded at Antrim in 1994.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 4. Mean (±1SE) vegetation heights (mm) in 1-m² quadrats centred on curlew nests and in paired 1-m² quadrats located 20 m from nests in a random direction, at two study areas. Values from each 1-m² quadrat are the average of 10 measurements

Study area	Year	Nest quadrats	Random quadrats	Paired *t*-value
Antrim	1993 (*n* = 55)	157 (±9)	171 (±12)	1·21 NS
	1994 (*n* = 35)	166 (±10)	146 (±10)	1·99 *
Lough Erne	1994 (*n* = 65)	191 (±9)	170 (±9)	2·15 *
	1995 (*n* = 76)	280 (±16)	170 (±12)	6·82 ***

* $P < 0.05$; *** $P < 0.001$.

IMPORTANCE OF DIFFERENT NEST PREDATORS

Examinations of wax eggs from depredated curlew nests indicated that most nest predation on Lough Erne was due to avian predators, whereas foxes appeared to be most important in Antrim (Table 5). (However, data from Antrim may be biased and should be treated with caution; see the Appendix.) Of the 11 nests that were depredated during the series of dawn and dusk checks at Antrim in 1995, eight were lost after the dusk check and before the dawn check, indicating that most predation occurred during the night and was thus likely to be mammalian.

Shell remains found at depredated nests (without wax eggs) on Lough Erne produced similar results to those obtained from the wax eggs, with avian predation recorded at 22 of the 23 nests where shell remains with diagnostic marks were found. Shell remains from depredated nests at Antrim provided evidence of avian predation at 13 of 20 nests where shell remains with diagnostic marks were found, with mammalian toothmarks being present in the remaining cases (at least three of which were attributable to foxes, although further identification was impossible in the other cases). The relatively small number of such remains bearing signs of fox predation at Antrim may have been due to foxes frequently removing eggs from nests, either to be eaten elsewhere or to be cached. In two instances where nests containing a radio-tagged 'egg' were depredated, the radio-tagged egg was found buried 3–4 m from the nest. Also, exam-ination of the remains at all depredated nests in 1995 revealed that in 82% of cases in Antrim (*n* = 56) but only 33% of cases on Lough Erne (*n* = 46) were no remains of any shell or yolk found (χ^2 = 23·8, d.f. = 1, $P < 0.001$). Thus, results from Lough Erne suggested that avian predation was often characterized by at least some breakage of the egg shell in or near the nest, whereas at many depredated nests in Antrim the eggs were presumably removed without damaging the shell.

SURVIVAL OF CHICKS AND BROODS

Of the 73 chicks fitted with radio-tags, 11 were moni-tored to at least 31 days of age and 41 were known to die before reaching this stage. Among the remaining 21, there were three cases where tags dropped off chicks and 13 cases of presumed tag failure before reaching 31 days of age. The remaining five tagged chicks were assumed to have died. Of these, three 'disappeared' within 2 days of hatching (there being no known cases of tags failing so soon) and two were on island sites where no alarm-calling adults, which could not be attributed to other broods, were found following their disappearance. Of the 46 chicks that were classed as having died, 74% were depredated while no other single proximate cause of mortality accounted for more than 7% of failures (Table 6). Avian predators appeared to be considerably more important than mammalian predators on the Lough Erne study area, but data were not available to deter-mine their relative importance in Antrim. Mink were almost certainly responsible for all four cases of known mammalian predation on Lough Erne, while

Table 5. Predators of curlew nests at two study areas, as determined from wax eggs placed in nests that were sub-sequently depredated

	Antrim*	Lough Erne	
Predator	1994	1994	1995†
Avian	2	6	10
Fox	9	0	2
Other mammal	1	0	1

* Data from Antrim may be biased (see the Appendix).
† A fox was known to be present on one island in 1995, where both cases of fox predation occurred.

Table 6. Proximate causes of mortality of radio-tagged cur-lew chicks in two study areas

	Antrim	Lough Erne
Known mammalian predation	2	4
Known avian predation	0	14
All predation	9	25
Tick (*Ixodes* sp.) infestation	0	3
Trampling by livestock	1	2
Other	3	3

it was considered likely that lesser black-backed (or other large) gulls and hooded crows each accounted for at least six of the 14 chicks that were known to be taken by avian predators, based upon the locations in which these tags were found (e.g. in a gull colony or under a crow nest).

Estimates of the proportion of chicks that survived to 31 days of age were obtained from logistic regression models of chick mortality rates which incorporated chick age as a covariate. These estimates were derived separately for both years of study at Lough Erne, but only for the combined data from the two relevant years at Antrim due to the small sample sizes available. In all cases mortality and predation rates of chicks decreased with age, although this effect was not significant at Lough Erne (Figs 2 and 3). However, failure rates of entire broods declined significantly with increasing brood age during the present study ($\Delta D = 5.22$, d.f. $= 1$, $P < 0.05$). Thus, age was retained within the models for Lough Erne from which survival estimates were obtained, as this was considered likely to produce a more realistic estimate of chick survival (mortality rates having been shown to decline with age in most other studies of wader chick survival; Heppleston 1972; Pienkowski 1984b; Galbraith 1988; Baines 1989; Grant 1991; Loegering & Fraser 1995). The percentage survival of chicks from hatching to 31 days of age was estimated as 38·5% (95% CI; 13·6–66·8) at Antrim, and 29·2% (95% CI; 0·0–60·3) and 19·1% (95% CI; 1·7–37·4) at Lough Erne in 1994 and 1995, respectively.

Whether a chick survived to 31 days of age or was depredated during this period was not related to hatching date, chick body condition or hatching weight ($\Delta D < 1.80$, d.f. $= 1$, $P > 0.05$, in all cases). First-order interaction terms between these three variables had no significant effect on whether a chick survived or was depredated ($\Delta D < 0.52$, d.f. $= 1$, $P > 0.05$, for each interaction term). Study area and year effects were not incorporated into this analysis due to the small sample sizes available (i.e. nine chicks in the survived category and 19 in the depredated category).

FLEDGING SUCCESS

Estimates of the number of chicks that fledged from each study area in each year of study were produced by relating the number of chicks estimated to have fledged from nests under study to the number of pairs for which at least one nest was found (Table 7). This is likely to overestimate the actual fledging success per pair because the nests of an unknown (but probably substantial) proportion of those pairs that attempted to breed on the study areas remained unrecorded during the study due to the high failure rates of nests. Evidence that this occurred was obtained by sightings of curlew behaving as if nests had either been initiated or were close to initiation (e.g. attacks on hooded crows flying overhead, frequent scraping or copulation) in locations where on later inspection no nests could be found and, at Lough Erne, by chance location of depredated nests in areas where no active nests were found.

Discussion

Predation was the main proximate cause of both nest and chick failure in this study, with predation of nests being of most importance in reducing productivity as most breeding attempts failed before hatching. Nest predation was relatively high during the laying period, as found in several other wader species and other curlew populations (Beintema & Müskens 1987; Ens 1991; M.C. Grant, unpublished data). Losses at this stage may be offset to some extent if females continue to lay in a second scrape following an initial predation event, and this may have occurred on occasions during the present study (e.g. there was one instance of a recently depredated egg in a scrape found 10 m from an extant but incomplete clutch). However, on most occasions when failure during laying was confirmed there was either no evidence of birds being present on the territory, or else their behaviour provided no evidence of continued nesting. Further, during detailed studies in Orkney there was no evidence of continued laying in 10 cases where the nests of individually marked curlew pairs failed during the laying period (M.C. Grant, unpublished data).

Detailed data on the breeding success of curlew are not available from elsewhere in Northern Ireland but broad-scale surveys in two other important breeding areas have recorded a low proportion of breeding curlew alarm-calling during the probable chick-rearing period, suggesting poor nesting success (M.C. Grant, unpublished data). Additionally, in both of these areas the frequency with which hooded crows and fox scats were sighted did not differ from that recorded during analogous surveys in the Antrim study area (undertaken since completion of the present study), although ravens were sighted more frequently in Antrim (M.C. Grant, unpublished data). Thus, results from the present study may be typical of other curlew breeding areas in Northern Ireland.

Estimates of fledging success in other curlew populations range from 0·07 to 1·4 fledglings per pair, based on data from 17 study populations and using mean values from the different years of study where relevant (von Frisch 1956; Keller 1982; Kipp 1982; Kopp 1982; Opitz 1982; Biologisch Station Zwillbrock 1986; von Dornberger & Ranftl 1986; Ylimaunu *et al.* 1987; Mulder & Swaan 1988; van den Berg 1989; Berg 1992; Boschert & Rupp 1993; Grant 1997; M.C. Grant, unpublished data). In three cases only are the estimates lower than the mean estimated fledging success for the Antrim study area, although they are lower than the 1995 and 1994 estimates of fledging success for Lough Erne in three and 10 cases, respectively.

Table 7. Productivity of curlew at two study areas, as calculated by relating the estimated number of fledglings produced from all nests found to the number of curlew pairs for which at least one nest was found. Data for Lough Erne are shown for all sites (A) and with the one shoreside site excluded (B)

Study area	Year	Number of fledglings from study nests (95% CI)*	Number of pairs studied†	Fledglings per pair (95% CI)
Antrim	1993	7 (2–11)	50	0·14 (0·04–0·22)
	1994	6 (2–10)	23	0·26 (0·09–0·43)
	1995	9 (3–15)	57	0·16 (0·05–0·26)
Lough Erne	1994 A	28 (0–52)	55	0·51 (0·00–0·94)
	1994 B	28 (0–52)	50	0·56 (0·00–1·04)
	1995 A	12 (1–23)	61	0·20 (0·02–0·38)
	1995 B	12 (1–23)	56	0·21 (0·02–0·41)

* Calculated by relating the total number of chicks hatched from study nests to the relevant estimate of chick survival to 31 days of age. The combined estimate of chick survival from 1993 and 1994 at Antrim is used for all 3 years at this study area.
† Accounts for any pairs to be omitted due to nest failure immediately after the addition of a wax egg to the nest at Antrim in 1994, or following trapping of an adult bird (see text).

Although some of these comparisons should be treated cautiously (due to differences in methods and the small sample sizes upon which some estimates are based), they do suggest that fledging success in the present study was relatively low for this species. Few studies provide comparable data on nesting success but this was estimated as 41·2% and 18·5%, respectively, on arable and mixed farmland in Sweden (Berg 1992), 39% on wetland and moorland habitats in Orkney (M.C. Grant, unpublished data), 33% on marginal farmland in northern England (Grant 1997), and 9% in dune habitats in the Netherlands (Mulder & Swaan 1988). Thus, in all but one case nesting success was substantially higher than in the current study, and in the instance of similarly low nesting success the study population was in decline, with clutch predation by foxes considered to be the cause (Mulder & Swaan 1988).

Minimum annual survival rates of breeding adult curlew have been estimated at 82–88%, based upon return rates of marked birds to breeding grounds during four studies, each of 2–6 years duration (Kipp 1982; Ylimaunu *et al.* 1987; Berg 1994; M.C. Grant, unpublished data). Estimates of annual survival rates of adults derived from ringing recoveries are lower, at approximately 75% (Bainbridge & Minton 1978). Based upon ringing recoveries it has been estimated that 47% of fledged curlew survive to 1 year of age (Bainbridge & Minton 1978), although estimates of survival from fledging to 1 year for other wader species are often higher, at 55–65% (Pienkowski 1984b; Jönsson 1991; Peach, Thompson & Coulson 1994). Curlew may begin breeding at 2 years, although 3 is likely to be a more frequent age for this (Glutz von Blotzheim,

Bauer & Bezzel 1977; Evans & Pienkowski 1984). Thus, to maintain a stable population in the absence of immigration it would appear likely that productivity should be in the region of 0·48–0·62 fledglings per pair [based upon (i) all birds begin breeding at 3 years; (ii) survival from fledging to 1 year is 50–65%; (iii) annual survival rate for breeding adults is 88%; and (iv) annual survival rate from 1 year to breeding is also 88%]. This suggests that the production of curlew fledglings on the Antrim study area is consistently too low to maintain a stable population, while on Lough Erne it is too low in some years at least. While this calculation is very approximate, realistic alterations to the assumptions upon which it is based do not affect this conclusion greatly. For example, even if the age of first breeding is assumed to be 2 and juvenile and adult survival rates are increased to 70% and 90%, respectively, then 0·32 fledglings per pair are required to maintain a stable population.

Using the above range of estimates for adult and juvenile survival rates and age at first breeding, then results from the Antrim study area suggest that the population should decline by 25–40% over a 6-year period, while those from Lough Erne suggest a situation ranging from a 2% increase to a 26% decline over 6 years. Thus, it appears likely that the low level of productivity recorded in the Antrim study area is at least sufficient to account for the observed decline of 25% in breeding curlew numbers in Northern Ireland (see the Introduction). For Lough Erne, the recorded level of productivity could be sufficient to account for such a decline.

The findings from the present study, together with the evidence for a decline in Northern Ireland's breed-

ing curlew population, suggest that predation rates on curlew nests in Northern Ireland may have increased in recent decades. This could have arisen via an increase in the populations of the relevant predators, or via changes to the breeding habitat of curlew which have increased the vulnerability of nests to predation.

A possible decline in the overall levels of persecution of predatory species in Northern Ireland is indicated by the recent range expansions of ravens and buzzards *Buteo buteo* L. (Gibbons, Reid & Chapman 1993). Elsewhere in the UK, past and present distributions of these species have probably been limited by persecution (Tapper 1992; Gibbons *et al.* 1995). More specifically, there is evidence that levels of fox control may have declined over the past few decades. Historical information is limited to Co. Antrim, where foxes appeared to be rare during the early parts of this century, possibly due to control by gamekeepers and shepherds (Fairley 1975). However, as game shooting declined in these areas, foxes increasingly became regarded as 'pests', leading to the instigation of a province-wide bounty scheme between 1943 and 1977. Whether or not this scheme effectively controlled fox numbers is questionable, but from 1954 to 1967 7000–9000 bounties were paid out annually (Fairley 1969). On Lower Lough Erne the numbers of breeding lesser black-backed gulls have increased from approximately 80 to 415 pairs between 1970 and 1996 (RSPB, unpublished data).

In recent years considerable land-use changes have also occurred in Northern Ireland. Sheep numbers more than doubled between 1960 and 1995, and over the same period the area of rough grazing decreased by 42% while that of permanent grassland increased by 29% (Department of Agriculture, Northern Ireland, unpublished data). Such changes may increase food supplies for foxes and corvids (by increasing the availability of carrion and soil invertebrates) and so could increase their annual survival rates. They are also likely to have caused curlew breeding habitat to become increasingly fragmented, possibly enabling predators to hunt for nests more efficiently.

Determining the importance of these factors in causing the high levels of nest and chick predation will require large-scale trials of both legalized predator control and land-use manipulations. These would identify the specific management methods required to conserve breeding curlew. Findings from the Antrim study area might suggest that controlling fox numbers alone would be sufficient to reduce predation rates. However, results from Lough Erne demonstrate that avian predators can also cause high losses, while the removal of foxes only may be followed by compensatory predation on nests by corvids (Reynolds & Tapper 1996). Thus, both direct predator control and land-use manipulations will require considerable resources. At present it is difficult to envisage ways in which this could be achieved on a sufficient scale to

impact upon curlew populations throughout Northern Ireland, without fundamental changes in systems of agricultural support and associated environmental measures. Thus, in the short to medium term, the field trials and resulting management methods should be targeted at those areas of Northern Ireland where reasonable concentrations of breeding curlew still remain.

References

Bainbridge, I.P. & Minton, C.D.T. (1978) The migration and mortality of the curlew in Britain and Ireland. *Bird Study*, **25**, 39–50.

Baines, D. (1989) The effects of improvement of upland, marginal grasslands on the breeding success of lapwing (*Vanellus vanellus*) and other waders. *Ibis*, **131**, 497–506.

Baines, D. (1990) The roles of predation, food and agricultural practice in determining the breeding success of the lapwing (*Vanellus vanellus*) on upland grasslands. *Journal of Animal Ecology*, **59**, 915–929.

Bart, J. & Robson, D.S. (1982) Estimating survivorship when the subjects are visited periodically. *Ecology*, **63**, 1078–1090.

Beintema, A.J. & Müskens, G.J.D.M. (1987) Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology*, **24**, 743–758.

Berg, Å. (1992) Factors affecting nest-site choice and reproductive success of curlews *Numenius arquata* on farmland. *Ibis*, **134**, 44–51.

Berg, Å. (1994) Maintenance of populations and causes of population changes of curlews *Numenius arquata* breeding on farmland. *Biological Conservation*, **67**, 233–238.

van den Berg, L.M.J. (1989) De uitbreiding van de wulp als weidevogel. *Limosa*, **62**, 49.

Biologisch Station Zwillbrock (1986) Weidevogels in West-Mhnsterland (BRD). *Limosa*, **59**, 83–89.

Boschert, M. & Rupp, J. (1993) Brutbiologie des großen brachvogels *Numenius arquata* in einem Brutgebiet am shdlichen Oberrhein. *Vogelwelt*, **114**, 199–221.

von Dornberger, W. & Ranftl, H. (1986) Brutbestand des gro8en brachvogels *Numenius arquata*, des rotschenkels, *Tringa totanus* und der uferscnepfe *Limosa limosa* in Nordbayern 1977–1986. *Anzieger der Ornithologischen Gesellschaft in Bayern*, **25**, 189–194.

Duebbert, H.F. & Kantrud, H.A. (1974) Upland duck nesting related to land use and predator reduction. *Journal of Wildlife Management*, **38**, 257–265.

Duebbert, H.F. & Lokemoen, J.T. (1980) High duck nesting success in a predator-reduced environment. *Journal of Wildlife Management*, **44**, 428–437.

Ens, B.J. (1991) Guarding your mate and losing the egg: an oystercatcher's dilemma. *Wader Study Group Bulletin*, **61** (Supplement), 69–70.

Evans, P.R. & Pienkowski, M.W. (1984) Population dynamics of shorebirds. *Shorebirds, Breeding Behaviour and Populations. Behaviour of Marine Animals, 5* (eds J. Burger & B.L. Olla), pp. 125–145. Plenum Press, New York, NY.

Fairley, J.S. (1969) A critical examination of the Northern Ireland fox-bounty figures. *Irish Naturalists' Journal*, **16**, 213–215.

Fairley, J.S. (1975) *An Irish Beast Book. A Natural History of Ireland's Furred Wildlife*. Blackstaff Press, Belfast, UK.

von Frisch, O. (1956) Zur brutbiologie und jugendentwicklung des brachvögels. *Zeitschrift für Tierpsychologie*, **13**, 50–81.

Galbraith, H. (1988) Effects of agriculture on the breeding ecology of lapwings *Vanellus vanellus*. *Journal of Applied Ecology*, **25**, 487–504.

Gibbons, D., Gates, S., Green, R.E., Fuller, R.J. & Fuller, R.M. (1995) Buzzards *Buteo buteo* and ravens *Corvus corax* in the uplands of Britain: limits to distribution and abundance. *Ibis*, **137**, S75–S84.

Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. T and AD Poyser, London, UK.

Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. (1977) *Handbuch der Vögel Mitteleuropas*. Band 7. Akademische-Verlagsgesellschaft, Wiesbaden, Germany.

Grant, M.C. (1991) Nesting densities, productivity and survival of breeding whimbrel *Numenius phaeopus* in Shetland. *Bird Study*, **38**, 160–169.

Grant, M.C. (1996) Predicting the hatching dates of curlew *Numenius arquata* clutches. *Wader Study Group Bulletin*, **80**, 53–54.

Grant, M.C. (1997) Breeding curlew in the UK: RSPB research and implications for conservation. *RSPB Conservation Review*, **11**, 67–73.

Green, R.E. (1988) Effects of environmental factors on the timing and success of breeding of common snipe *Gallinago gallinago* (Aves: Scolopacidae). *Journal of Applied Ecology*, **25**, 79–93.

Green, R.E., Hawell, J. & Johnson, T.H. (1987) Identification of predators of wader eggs from egg remains. *Bird Study*, **34**, 87–91.

Gregory, R.D. & Marchant, J.H. (1996) Population trends of jays, magpies and carrion crows in the United Kingdom. *Bird Study*, **43**, 28–37.

Hagemeier, W. & Blair, M. (1997) *The EBCC Atlas of European Breeding Birds*. T and AD Poyser, London, UK.

Harris, M.P. (1967) The biology of oystercatchers, *Haematopus ostralegus*, on Skokholm Island, south Wales. *Ibis*, **109**, 180–193.

Heppleston, P.B. (1972) The comparative breeding ecology of oystercatchers (*Haematopus ostralegus* L.) in inland coastal habitats. *Journal of Animal Ecology*, **41**, 23–51.

Hildén, O. (1978) Population dynamics of temminck's stint, *Calidris temminckii*. *Oikos*, **30**, 17–28.

Hötker, H. (1991) Waders breeding on wet grasslands in the countries of the European Community – a brief summary of current knowledge on population sizes and population trends. *Wader Study Group Bulletin*, **61** (Supplement), 50–55.

Jönsson, P.E. (1991) Reproduction and survival in a declining population of the southern dunlin *Calidris alpina schinzii*. *Wader Study Group Bulletin*, **61** (Supplement), 56–67.

Kalbfleisch, J.G. (1979) *Probability and Statistical Inference II*. Springer-Verlag, New York, NY.

Keith, L.B. & Rusch, D.H. (1988) Predation's role in the cyclic fluctuations of ruffed grouse. *Proceedings of the International Ornithological Congress*, **19**, 699–732.

Keller, H. (1982) Artenschutzprojekt grossen brachvögel

(*Numenius arquata*) im Donaumoos bei Langenau: erst zwischenbilanz. *Beihefte Veröffentlichungen Naturschutz Landscaftspflege Baden-Württemberg*, **25**, 113–118.

Kipp, M. (1982) Ergebnisse individueller farbberingung beim großen brachvogel und ihre bedeutung für den biotopschutz. *Beihefte Veröffentlichungen Naturschutz Landscaftspflege Baden-Württemberg*, **25**, 87–96.

Kipp, M. (1985) Zur bestandsentwicklung des großen brachvogels (*Numenius arquata*) in Westfalen. *Charadrius*, **21**, 101–113.

Kopp, F. (1982) Die bestandssituation des grossen brachvögels (*Numenius arquata*) in Hessen unter besonderer berücksichtigung des hessischen rieds. *Beihefte Veröffentlichungen Naturschutz Landscaftspflege Baden-Württemberg*, **25**, 61–64.

Loegering, J.P. & Fraser, J.D. (1995) Factors affecting piping plover chick survival in different brood-rearing habitats. *Journal of Wildlife Management*, **59**, 646–655.

Major, R.E. (1991) Identification of nest predators by photography, dummy eggs, and adhesive tape. *Auk*, **108**, 190–195.

Marcström, V., Kenward, R.E. & Engren, E. (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *Journal of Animal Ecology*, **57**, 859–872.

Mayfield, H.F. (1961) Nesting success calculated from exposure. *Wilson Bulletin*, **73**, 255–261.

Mayfield, H.F. (1975) Suggestions for calculating nest success. *Wilson Bulletin*, **87**, 456–466.

Mulder, J.L. & Swaan, A.H. (1988) *De Vos in Het Noordhollands Duinreservaat Deel 5: de Wulpenpopulatie*. Rijkinstituut voor Natuurbeheer, Arnhem, The Netherlands.

Mulder, J.L. & Swaan, A.H. (1992) Body-weight changes of egg-laying curlews *Numenius arquata*, as monitored by an automatic weighing system. *Ardea*, **80**, 273–279.

Newton, I. (1993) Predation and the limitation of bird numbers. *Current Ornithology*, **11**, 143–198.

O'Brien, M. & Smith, K.W. (1992) Changes in the status of waders breeding on wet lowland grasslands in England Wales between 1982 and 1989. *Bird Study*, **89**, 165–176.

Opitz, H. (1982) Bestand und bestandsentwicklung des grossen brachvögels (*Numenius arquata*) in Baden-Württemberg. *Beihefte Veröffentlichungen Naturschutz Landscaftspflege Baden-Württemberg*, **25**, 15–31.

Pain, D.J. & Pienkowski, M.W. (1997) Farming and birds in Europe. *The Common Agricultural Policy and its Implications for Bird Conservation*. Academic Press, London, UK.

Parr, R. (1992) The decline to extinction of a population of golden plover in north-east Scotland. *Ornis Scandanavica*, **23**, 152–158.

Parr, R. (1993) Nest predation and numbers of golden plovers *Pluvialis apricaria* and other moorland waders. *Bird Study*, **40**, 223–231.

Peach, W.J., Thompson, P.S. & Coulson, J.C. (1994) Annual and long-term variation in the survival rates of British lapwings *Vanellus vanellus*. *Journal of Animal Ecology*, **63**, 60–70.

Pienkowski, M.W. (1984a) Breeding biology of ringed plovers, *Charadrius hiaticula*, in Britain and Greenland: nest predation as a possible factor limiting distribution and timing of breeding. *Journal of Zoology, London*, **202**, 83–114.

Pienkowski, M.W. (1984b) Behaviour of young ringed plovers, *Charadrius hiaticula*, and its relationship to growth and survival to reproductive age. *Ibis*, **126**, 133–155.

Redmond, R.L. & Jenni, D.A. (1986) Population ecology of the long-billed curlew (*Numenius arquata*) in western Idaho. *Auk*, **103**, 755–767.

Reynolds, J.C. & Tapper, S.C. (1996) Control of mammalian

predators in game management and conservation. *Mammal Review*, **26**, 127–156.

Robertson, J. & Berg, C. (1992) Status and population changes of farmland birds in southern Sweden. *Ornis Svecica*, **2**, 119–130.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. Freeman, London, UK.

Tapper, S.C. (1992) *Game Heritage. An Ecological Review from Shooting and Gamekeeping Records.* The Game Conservancy, Fordingbridge, UK.

Tapper, S.C., Potts, G.R. & Brockless, M.H. (1996) The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix*. *Journal of Applied Ecology*, **33**, 965–978.

Tucker, G.M. & Heath, M.F. (1994) *Birds in Europe: Their Conservation Status*. Birdlife International, Cambridge, UK.

Wilkinson, L. (1990) *Systat: the System for Statistics*. Systat, Evanston, Illinois.

Ylimaunu, O., Ylimaunu, J., Hemminki, O. & Liehu, H. (1987) Isokuovin pesimäekologiasta ja kannasta Suomessa. *Lintumies*, **22**, 98–103.

Appendix

Given the results from the present study, it is important to consider whether the methods used influenced predation rates and produced any detrimental effects, particularly on nesting success. The design of the study did not permit an experimental approach to identifying whether the breeding success of 'studied' and 'unstudied' populations differed, but several comparisons of the effects of certain of the methods used can be undertaken and these are presented below.

EFFECTS OF ADDING WAX 'EGGS' TO NESTS

In both years of study at Lough Erne, the effects of adding wax eggs to nests on nest failure rates were tested by incorporating whether or not they had been added to a nest into the models of nest failure rates (Table 3). In both years the resulting ΔD of the model was not significant, although the overall failure rate was somewhat lower for those nests that included wax eggs (1994, $\Delta D = 0.02$, d.f. = 1, $P > 0.05$, and 1995, $\Delta D = 3.09$, d.f. = 1, $P > 0.05$).

An analogous comparison for the Antrim study population in 1994 was not valid because wax eggs were added to a large proportion of the nests under study and often after many of the other nests had already failed. Nests to which wax eggs were added in Antrim in 1994 were more likely to be depredated by the visit following the addition of a wax egg than following other visits (45% of 22 occasions following wax egg addition as opposed to 12% of 41 occasions following other visits, $\chi^2 = 7.0$, d.f. = 1, $P < 0.01$). This effect was further investigated by undertaking a logistic regression analysis that considered all study nests at Antrim in 1994 and where the dependent variable was the fate of the nest on each day over the period in which it was monitored (assuming that failure occurred midway between the penultimate visit and the visit on which failure was confirmed). Independent variables and factors entered were: whether or not a wax egg had been added on the previous visit,

whether or not a wax egg was present in the nest, whether or not the eggs in the clutch had been measured on the previous visit, whether it was the laying or post-clutch completion period, and the date. Using a step-down procedure the only significant effect was whether or not a wax egg had been added on the previous visit ($\Delta D = 21.50$, d.f. = 1, $P < 0.001$). The actual presence of a wax egg in the nest did not influence the likelihood of failure ($\Delta D = 0.01$, d.f. = 1, $P > 0.05$), suggesting that the effects of wax egg addition on predation rates were of a short-term nature.

EFFECTS OF DAWN AND DUSK NEST CHECKS AT ANTRIM IN 1995

Incorporation of whether or not a nest had been subjected to dawn and dusk checks into the models of nest failure rates (Table 3) indicated that these checks did not influence the likelihood of nest failure ($\Delta D = 0.01$, d.f. = 1, $P > 0.05$).

EFFECTS OF MEASURING EGGS AT ANTRIM IN 1995

Predation rates of nests in which the eggs were handled and measured after clutch completion were compared with those of nests in which no handling of eggs occurred (most of which were found during the laying period). Limiting comparisons to the post-clutch completion period, the daily predation rates were 0.054 (95% CI; 0.033–0.080) for nests in which the eggs were measured ($n = 26$) and 0.123 (95% CI; 0.074–0.189) for nests in which there was no handling of the eggs ($n = 27$), thus indicating that handling and measuring of eggs did not influence the likelihood of predation.

EFFECTS OF NEST VISITS

Two comparisons were undertaken to test for effects of nest visiting on failure rates. Data were analysed separately for each year in each study area, although no analyses were performed for the Antrim study area in 1994 due to the effects of adding wax eggs. First, failure rates following the initial visit to a nest were compared with those following subsequent visits. Analyses of nest failure rates were undertaken as before (see the Methods) but with the periods following first and subsequent visits to nests treated separately. The same independent variables and factors were entered as in the previous analyses (Table 3), with the addition of whether or not the period followed first or subsequent visits. Incorporating this additional factor had no effect on failure rate ($\Delta D < 1.76$, d.f. = 1, $P > 0.05$ in all cases).

Secondly, for those nests not involved in predator identification studies, daily failure rates during the period following clutch completion when nests were rarely visited were compared with those of nests and periods (i.e. within approximately 7 days of hatching) with frequent visits following clutch completion (see the Methods). Daily failure rates did not differ between these two groups, and for rarely visited and frequently visited, respectively, they were: 0.062 (95% CI; 0.042–0.092) and 0.076 (95% CI; 0.034–0.138) for Antrim 1993; 0.062 (95% CI; 0.041–0.091) and 0.108 (95% CI; 0.070–0.163) for Antrim 1995; 0.034 (95% CI; 0.021–0.056) and 0.021 (95% C.I; 0.011–0.041) for Lough Erne 1994; and 0.036 (95% CI; 0.023–0.056)

and 0·051 (95% CI; 0·028–0·093) for Lough Erne 1995.

EFFECTS OF RADIO-TAGGING CHICKS

Combined data from the present study and a study of curlew in northern England (Grant 1997) indicated no differences in the survival of tagged and untagged chicks, based upon 14 broods in which the survival of both tagged and untagged chicks could be monitored. Analyses were also undertaken that demonstrated no differences in chick growth rates between tagged and untagged chicks. It is intended to publish these results elsewhere.