![British Ecological Society logo]

Nesting Success of Birds Breeding in Dutch Agricultural Grasslands
Author(s): A. J. Beintema and G. J. D. M. Muskens
Source: *Journal of Applied Ecology*, Vol. 24, No. 3 (Dec., 1987), pp. 743-758
Published by: British Ecological Society
Stable URL: https://www.jstor.org/stable/2403978
Accessed: 14-01-2019 11:32 UTC

NESTING SUCCESS OF BIRDS BREEDING IN DUTCH AGRICULTURAL GRASSLANDS

By A. J. BEINTEMA and G. J. D. M. MÜSKENS

Research Institute for Nature Management, Postbus 46, 3956 ZR Leersum, The Netherlands

SUMMARY

(1) Daily survival rates of nests with respect to predation are referred to as *P*-values, trampling survival rates are expressed as 'standardized trampling values', estimated as daily survival rates at an exposure of one grazing animal ha^{-1}.

(2) *P*-values were lower during laying than during incubation. *P*-values in hidden-nesting species are higher than in open-nesting species. *P*-values are not constant, but are highest in the middle of the nesting season. *P*-values differ between regions and years, and are positively correlated with densities of voles, *Microtus* sp. In years following a collapse of vole populations, ground predators switch more to birds' nests.

(3) Standardized trampling values are independent of cattle densities and field size, hence the probability of surviving is a simple function of stock density and days exposure.

(4) A renesting model is presented, to estimate nesting success per pair, taking renesting into account, based on *P*-values and trampling values. The model enables the testing of the effects of different management schemes on nesting success.

INTRODUCTION

About two-thirds of the land area of the Netherlands consists of grasslands, mostly of a moist type. These grasslands, generally used for dairy farming, not only produce milk and butter, but also large quantities of birds, collectively known in the Netherlands as 'meadow birds'. The meadow-bird community is dominated by wader and duck species. The six main species are lapwing *Vanellus vanellus* (L.), black-tailed godwit *Limosa limosa* (L.), redshank *Tringa totanus* (L.), oystercatcher *Haematopus ostralegus* L., ruff *Philomachus pugnax* (L.), and snipe *Gallinago gallinago* (L.), the first four being the most numerous, with breeding populations in Holland of *c.* 110 000, 90 000, 60 000, and 20 000 pairs, respectively (van Dijk 1983). The international importance of the godwit population is particularly spectacular, as it represents 80–90% of all European black-tailed godwits.

The main factor that distinguishes Dutch meadows from other European ones is the high water table, which causes slow spring growth of the vegetation, and late accessibility for livestock and machines, in spite of fertile soils. This enables the birds to hatch their eggs safely in an area rich in food. This situation is rapidly changing with improved drainage and intensified management. However, the international importance of the Dutch meadow-bird areas is now widely recognized, and steps are being taken, privately and by the government, to preserve sufficient areas.

The practical manager of areas rich in meadow birds often notices that a large proportion of eggs fail to hatch, because of predation and agricultural activities, notably

trampling by cattle and mowing. This paper analyses nest loss, and its significance in the population dynamics of meadow-bird species. The results may help in designing efficient management schemes, especially where compromises between the interests of birds and farmers are sought.

METHODS

Data collection

From 1974 to 1983, data have been collected on *c*. 18 000 nests of birds breeding in Dutch grasslands. Nests were found in the course of several research projects, partly at the Research Institute for Nature Management, and partly from other investigators.

Nests were located in three ways: (i) searching fields systematically, (ii) locating nests of flushed birds and (iii) watching birds returning to their nests after disturbance. Choice of method depended on bird population density, height of the vegetation, and whether incomplete clutches were to be included.

Nests were marked with sticks, which were put in a ditch and indicated direction, not distance. When the nest was close to a ditch, the stick was placed in the ditch at the far side (ditches were 6–20 m apart). As the data were from different sources, it was not possible to check for increased predation caused by marking. Workers agreed that, in artificial pastures, with dense patterns of ditches and many obstacles, sticks placed as described did not attract the special attention of predators.

Nests were not marked in grazed fields because, when a grazing cow encounters a stick, it becomes excited, trampling everything within a 10-m radius.

Nests were checked once or twice a week. During checks, nests were observed at some distance, in case predators should follow the trail. With few exceptions, nest losses were not increased on the day after a visit (Bart 1977; Willis 1973). In a few cases where a predator learned to follow the investigators, nests or fields were excluded from analysis.

The contents and outcome of each nest were noted. Recognizing trampling is easy but distinguishing between hatching and predation can be difficult. Typically, a hatched nest contains miniscule shell fragments from the first hole made by the chick. Predated nests may contain larger fragments or remains of spilt yolk. When all the eggs have been removed, the linings of the nest often look torn.

Calculation of nest survival; predation

It has long been recognized that studies in which nesting success is simply expressed as the percentage hatching from a sample of nests found may give seriously (mostly upwardly) biased results (Snow 1955; Mayfield 1961). The main bias comes from the obvious, but often overlooked, fact that nests lost before they could have been found are not included. Accordingly, Mayfield (1961, 1975) developed a useful method of measuring nesting success as daily survival rate, which he defined as the probability, P, that a nest present one day would survive to the next. It is estimated from the formula:

$$P = \frac{A}{A + B}$$

in which A = total number of 'nest days' (the sum of all daily totals of nests present during the observation period), and B = total number of nests lost. The day on which a nest is lost

is not counted as a nest day. Nests were assumed to have been lost half way between the last two checks.

In its original form, Mayfield's method assumed constant survival rates through the nesting stage, and between individuals. Problems arise if this is not the case (Green 1977; Willis 1981), but these can be solved by grouping the data in short periods and subpopulations (Willis 1981). The problem then is the vast quantity of data needed for such subdivisions.

Daily survival rates, with regard to predation, were calculated with Mayfield's formula, and are referred to as 'P-values'. The standard deviation, from which 95% confidence intervals were derived (Johnson 1979), is:

$$S.D. = \frac{B(-B)}{A^3}$$

Trampling by cattle

The calculation of survival rates with respect to trampling is more complex, since the cattle density and possibly the field size are also parameters. To tackle this, in earlier studies (Directie Beheer Landbouwgronden 1980; Beintema *et al.* 1982), complex likelihood functions were used, developed by J. Oude Voshaar and F. J. de Vries (personal communication). But eventually, survival rates were reduced to survival per animal per hectare per day, thus assuming that 10 days' grazing by one animal gives the same result as 1 day's grazing by ten animals. With this assumption (tested in the studies mentioned above, see also 'Trampling losses'), Mayfield's method can be adapted by first converting all data to standard densities of one grazing animal per hectare. The only problem is that statistical comparisons are not easily made, as the standard deviation given by Johnson (1979) is no longer valid (J. B. van Biezen, personal communication). Therefore, van Biezen developed an alternative estimator for trampling survival. Trampling intensity is estimated as:

$$I = \frac{C}{A}$$

in which C is the number of nests lost (due to trampling), and A is total exposure as the product of exposure days and stock density: a day with cattle density of 2 ha^{-1} is counted as 2 days, etc. Days on which observations were terminated were fully counted. Days on which a nest was lost (either by predation or trampling) were counted as 0·5 day (on days with cattle density of 2 ha^{-1} as 1 day, on days with density of 3 ha^{-1} as 1·5 days, etc.). The daily survival rate, standardized at a density of 1 ha^{-1}, is:

$$V = Exp(-I)$$

V is the 'standardized trampling value'; its standard deviation is:

$$S.D. = \frac{Exp(-I) \times \sqrt{C}}{A}$$

The derivation of these formulae is given in the Appendix.

RESULTS

Predation; differences between species

Daily survival rates with respect to predation (*P*-values) were calculated for seventeen species of grassland-dwelling birds, for the laying period and the incubation period separately (Table 1). Survival rates during laying were lower than in the incubation phase ($P < 0.05$). The difference was most significant in the lapwing, black-tailed godwit, oystercatcher, and redshank (no overlap in 95% confidence intervals), reflecting the number of observations available.

Bias may arise from partly predated, abandoned clutches, mistaken for nests in the laying phase. These are likely to be further removed by the predator. However, *P*-values during laying are lowest at the onset of the season, while the probability of occurrence of this error should increase when full clutches are getting more numerous, and incomplete ones scarcer.

Experienced workers were asked to classify the species according to the difficulty of finding their nests (Table 1). This resulted in an arbitrary scale, from 1 (easy) to 7 (difficult). Hidden nests suffered less predation during incubation than open ones ($P < 0.05$, Spearman rank correlation). In spite of conspicuous nesting, avocet and common tern showed high survival rates, probably a result of effective colonial anti-predator behaviour.

Seasonal variation in predation and density dependence

In the four most numerous wader species, *P*-values were calculated for different periods through the breeding season, for the incubation (Fig. 1a, 18 weeks) and laying phases (Fig. 1b, nine 2-week periods). The number of nest days per week reflected the seasonal distribution of the presence of nests.

TABLE 1. Daily survival rates (predation only) for grassland birds, during laying and incubation. P = *P*-value. Hiding score indicates how difficult nests are to find (arbitrary scale)

| Species	Hiding score	Laying phase P	S.D.	Incubation P	S.D.
Lapwing *Vanellus vanellus* (L.)	3	0·928	0·0073	0·987	0·0007
Black-tailed godwit *Limosa limosa* (L.)	4	0·941	0·0060	0·989	0·0007
Redshank *Tringa totanus* (L.)	5	0·955	0·0084	0·993	0·0010
Ruff *Philomachus pugnax* 1(L.)	6	—	—	0·999	0·0011
Snipe *Gallinago gallinago* (L.)	7	1·000	—	0·994	0·0043
Oystercatcher *Haematopus ostralegus* L.	1	0·950	0·0077	0·986	0·0010
Avocet *Recurvirostra avocetta* L.	1	0·958	0·0182	0·995	0·0018
Black-headed gull *Larus ridibundus* L.	2	0·953	0·0227	0·987	0·0030
Common tern *Sterna hirundo* L.	2	0·992	0·0078	0·996	0·0010
Mallard *Anas platyrhynchos* L.	4	0·963	0·0122	0·994	0·0016
Shoveler *Anas clypeata* L.	5	0·998	0·0022	0·996	0·0013
Garganey *Anas querquedula* L.	7	—	—	1·000	—
Tufted duck *Aythya fuligula* (L.)	6	1·000	—	1·000	—
Coot *Fulica atra* L.	2	0·992	0·0084	0·984	0·0040
Moorhen *Gallinula chloropus* (L.)	3	1·000	—	0·994	0·0062
Skylark *Alauda arvensis* L.	6	0·900	0·0949	0·987	0·0058
Meadow pipit *Anthus pratensis* (L.)	6	—	—	0·997	0·0029
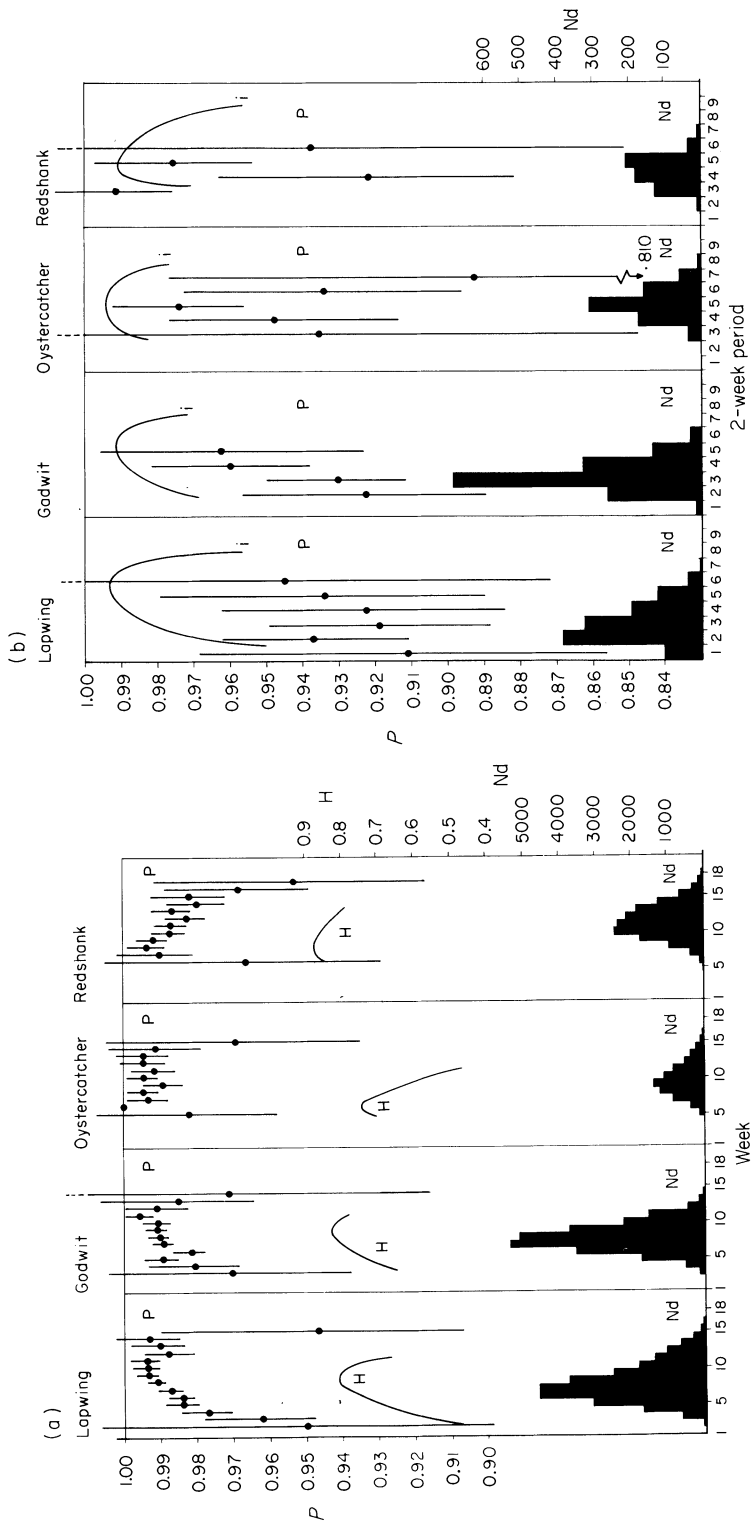
Fig. 1. Daily survival rates of nests and eggs (P-values; predation only) (a) during incubation per week and (b) during the laying phase per 2 weeks. Vertical lines indicate 95% confidence intervals. P = P-value. H = estimated survival over total incubation period (losses during laying not included). i = fitted lines for P-values during incubation. Nd = number of nestdays (a) per week or (b) per 2 weeks.

To illustrate the cumulative effect of *P*-values, Fig. 1a also gives the estimated hatching success *H* as a function of the date of the first day of incubation:

$$H = p_1 \times p_2 \times \ldots \times p_i$$

where p_1 is the *P*-value of the first incubation day and p_i is the *P*-value of the last incubation day, day *i*. When *p* is constant:

$$H = p^i$$

Figure 1 leads to the following observations:

(a) An increase in daily survival rate may be due to the least well-hidden nests being removed first (Miller & Johnson 1978), but the decrease later in the season cannot be explained by such selection, unless late nesters are of such poor quality (or inexperienced) that they do not effectively hide or guard their nests.

(b) An increase in cover with growing vegetation is an alternative explanation for the rapid increase of survival rates in the first weeks. Again, the decrease later in the season cannot be explained in this way.

(c) An inverse relationship may exist between the population density of a prey species, and the probability that an individual will be taken (swamping effect). This should give maximum survival rates during the peak of the season, when nest densities are highest. Species may add to each others' swamping effect; as in the early-nesting lapwing, maximum survival rates are reached later than the peak density (nest days), while in the late-nesting oystercatcher it is just the reverse.

(d) Another explanation for maximum survival rates being synchronized in all species, could be that survival depends on the predators themselves, e.g. because of a limited action radius in aerial predators (gulls and crows) during their own nesting season, or abundance of alternative food sources.

(e) Figure 1b does not allow much detailed analysis, but values in the laying phase follow a similar pattern but are smaller.

TABLE 2. Percentage variance accounted for in different regression models. $Y = P$-value per week during incubation (predation only). Models fitted: 1. $X =$ number of nest days (*N*) per week of a single species, 2. $X = \log(N)$ of the same species, 3. multiple regression with $\log(N)$ of all four species. Contribution of species to 3, tested in 4–7, each with one species omitted from 3. Asterisks in 3 indicate difference from 2, asterisks in 4–7 indicate difference from 3 ($*P < 0.05$, $**P < 0.001$)

Model	1	2	3	4	5	6	7
						Model 3	
	N	Log(*N*)	Log(*N*)	Model 3	Model 3	without	Model 3
	same	same	all	without	without	oyster-	without
Species	species	species	species	lapwing	godwit	catcher	redshank
Lapwing	13·9	47·6	76·0*	—	63·8*	77·7	78·2
Godwit	12·7	46·2	54·8	53·1	—	59·5	57·0
Oystercatcher	28·7	50·7	69·4	73·1	72·6	—	71·7
Redshank	8·2	36·6	95·9**	94·7	72·2**	38·9**	—

Interspecific swamping was examined in more detail by multiple regression between weekly *P*-values (incubation) for each species and the logarithm of the number of nest days for the species in the same week. The results in Table 2 lead to the following observations.

(a) Godwit and oystercatcher do not benefit from swamping by lapwing or redshank.
(b) The lapwing (early nester) benefits from the godwit (early nester), and the redshank (late nester) benefits from the oystercatcher (late nester).
(c) The redshank–oystercatcher and lapwing–godwit relationships are not mutual, which may indicate that benefit is not based just on swamping, but perhaps on active defence by species that show the strongest antipredator behaviour (godwit and oystercatcher).

Differences between years and regions; the vole cycle

Overall seasonal P-values for different years and regions are given in Fig. 2. Similarities in patterns of variation in lapwing and godwit (for which we have most data) suggest that both species are affected in the same way.
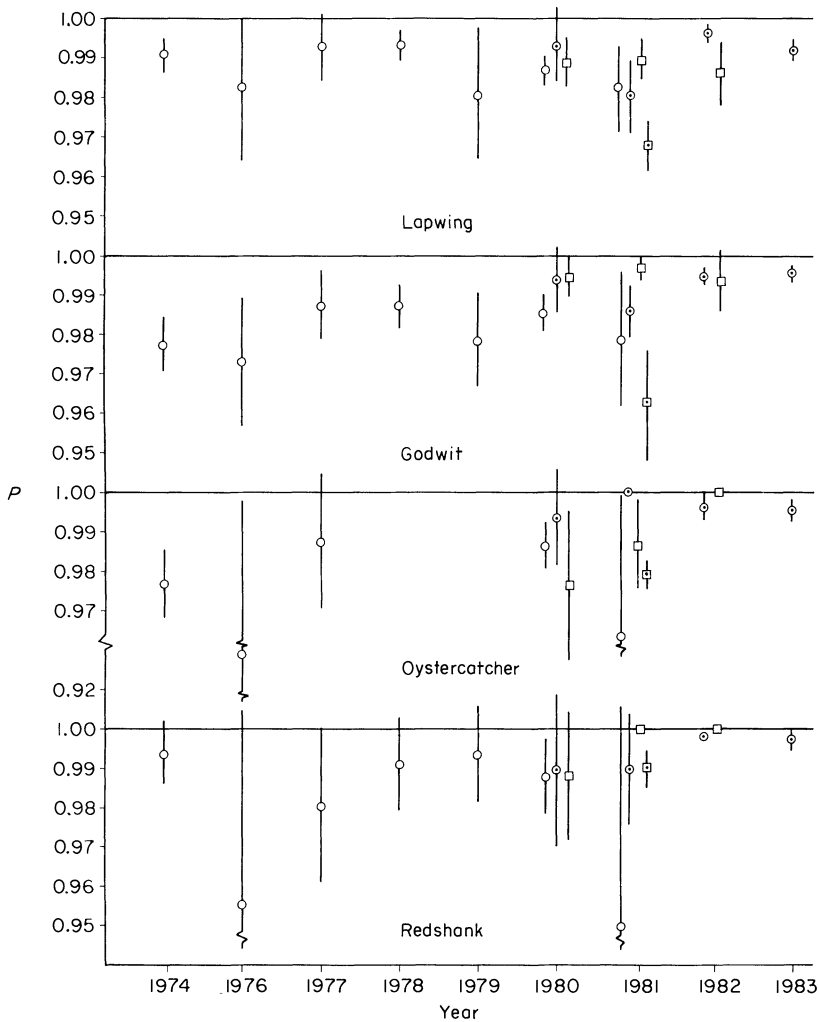

Fig. 2. Annual and regional variation in P-values (whole season). O = Friesland excluding Bandpolder, ⊙ = Noord–Holland, □ = Zuid–Holland, ⊡ = Bandpolder. Vertical lines indicate 95% confidence intervals.

Variations in predation pressure may be linked with numbers of field voles *Microtus arvalis* (Pallas), the preferred food of many predators that also eat wader eggs. In 1981, the authors noted that heavy predation of mustelids on redshank nests, in an area where nesting success had been high in the previous year, coincided with a collapse in vole populations. Similarly, Roselaar (1979) attempted to link annual variations in numbers of curlew sandpipers *Calidris ferruginea* (Pontoppidan) with lemming cycles in Siberia.

Data on regional vole densities were obtained from J. Buker, D. Jonkers, and J. de Jong (personal communication), and assigned to three density levels (March–June). Relationships between *P*-values (Fig. 2) and vole densities are given in Fig. 3. Especially in years when vole densities were low, predators appeared to switch from voles to birds. In fact, predation pressure on birds' nests (as a measure of the difficulty of obtaining voles) was not related to absolute vole densities, but to the amount and direction of change in these densities. Predator switching affected early nesters (lapwing and godwit) most.

Trampling losses

Trampling survival values were calculated for four types of husbandry commonly used in the Netherlands: (i) dairy cattle that graze during the day only, (ii) dairy cattle that stay in the field day and night, (iii) young cattle (day and night), (iv) sheep (day and night).

It has been suggested that animals graze more evenly over small fields, so that nests survive better in large fields. It has also been suggested that trampling per animal is heavier under high densities of cattle than under low. To test this, survival rates per animal per hectare per day, for the four types of livestock mentioned above, were calculated for each bird species, for two classes of cattle density and for three classes of field size (Fig. 4). Differences between classes were not significant (Spearman). One can therefore use one 'standardized trampling value' per type of livestock and per bird species
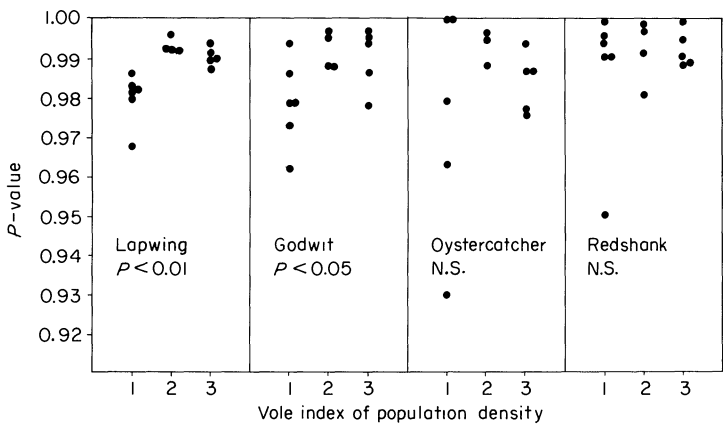

FIG. 3. Relationship between *P*-values (see Fig. 2) and regional vole densities after J. Buker, J. de Jong and D. Jonkers (personal communication) 3 = high density, 1 = low density after crash, 2 = intermediate cases.

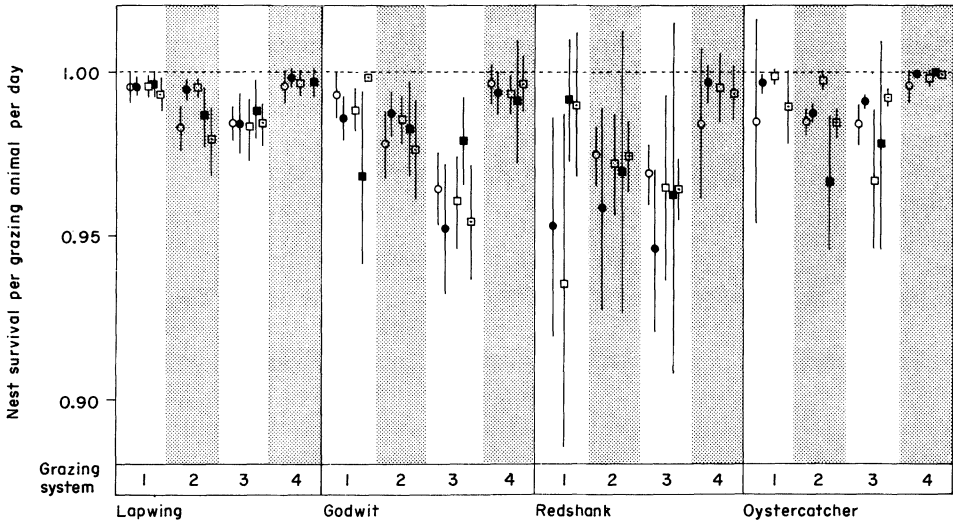|	1974	1976	1977	1978	1979	1980	1981	1982	1983
Friesland	3	1	2	2	1	3	1		
Noord–Holland						3	1	2	2
Zuid–Holland						3	3	1	
Bandpolder							1		

FIG. 4. Trampling values (daily survival rate per animal ha^{-1}) for different conditions under four grazing systems: 1 = dairy cattle during the day only; 2 = dairy cattle day and night; 3 = young cattle day and night; 4 = sheep day and night. $\bigcirc$ = 0–10 animals ha^{-1}, $\bullet$ = > 10 animals ha^{-1}; $\square$ = field 0–2·5 ha, $\blacksquare$ 2·5–5·0 ha, $\boxdot$ = > 5 ha. Vertical lines indicate 95% confidence intervals.

(survival rate per animal per hectare per day). This is convenient, since, once these values are known, survival rates can be predicted for any complex grazing system. Standardized values are given in Table 3. Similar values were found for British cattle (R. Green, personal communication), and for beef cattle in extremely low densities in the U.S.A. with artificial nests (Koerth et al. 1983).

Young cattle were the worst tramplers, for most bird species, especially when trampling was compared with food consumption (Table 3). In terms of food consumption (or

TABLE 3. Basic trampling values and daily survival rates per grazing unit ha^{-1}. One grazing unit = 1 dairy cow = 2 yearlings = 10 sheep. Grazing systems: 1, dairy cattle during the day only; 2, dairy cattle day and night; 3, yearlings day and night; 4, sheep day and night

Species	Grazing system	Standardized trampling value	S.D.	Daily survival rate per grazing unit ha^{-1}
Lapwing	1	0·995	0·0013	0·995
	2	0·990	0·0017	0·990
	3	0·984	0·0024	0·968
	4	0·996	0·0015	0·970
Godwit	1	0·988	0·0027	0·988
	2	0·982	0·0031	0·982
	3	0·960	0·0050	0·922
	4	0·993	0·0026	0·932
Redshank	1	0·972	0·0097	0·972
	2	0·973	0·0045	0·973
	3	0·964	0·0045	0·929
	4	0·993	0·0034	0·932
Oystercatcher	1	0·996	0·0015	0·996
	2	0·986	0·0017	0·986
	3	0·991	0·0011	0·982
	4	0·999	0·0004	0·990

grazing pressure), one adult cow = three 'yearlings' = five sheep. Sheep have a reputation for damaging nests (they even eat eggs), but they did little harm per individual. It was their stocking density that did the damage.

Birds did little to defend their nests against grazers. They often flew off at the last minute, to avoid being stepped on. Only lapwing and oystercatcher actively tried to distract cattle. Table 3 suggests that oystercatchers had some success, especially with young cattle.

Interaction between predation and trampling

It has been suggested (Beintema *et al.* 1982) that losses due to predation are heavier in grazed than in ungrazed fields. This was tested for lapwing, black-tailed godwit, redshank and oystercatcher, for five periods, yielding twenty figures for grazed situations, and twenty for ungrazed ones. In the lapwing, two out of five comparisons gave a better survival in grazed fields, and in the godwit this was the case in four out of five. In oystercatcher and redshank, all ungrazed situations gave better survival values. Nineteen of the twenty matched pairs overlapped their 95% confidence intervals. One can therefore conveniently treat predation and trampling as independent influences.

Various additional losses

Trampling and predation were important causes of nest loss in Dutch pastures (Table 4), In addition, nests were destroyed by a variety of agricultural activities. In terms of daily survival rates, the probability of surviving mowing is zero. Survival rates for other activities, such as fertilizing, can be estimated from the percentage of the land touched by wheels.

Lapwings may abandon the nest when the vegetation becomes too tall. Godwits sometimes lost eggs in very tall, over-fertilized grass. They kept pulling at leaves to maintain the roof over the nest but, in this vegetation, leaves bent over too easily, and piled up on the bottom. Odd accidents occurred, such as nests being overrun by a hare, turned over by a surfacing mole, or fouled by explosion of a rotten egg.

Partial losses were most often due to infertile eggs. When one egg was damaged by cattle, the nest was abandoned. When a predator took one egg, it usually returned to collect the rest. Some chicks died in the shell. These chicks were often malformed. In the exceptionally wet spring of 1983, many godwit chicks died during hatching. Entire clutches were found dead, bills emerging from holes in the eggs.

When both clutch size and partial losses are taken into account, the average number of chicks hatching per successful nest is 3·21 for the lapwing, 3·56 for the godwit, 3·64 for the redshank, and 3·00 for the oystercatcher (Beintema & Müskens 1981). Harris (1969) found a decrease in clutch size in oystercatchers with season. Our data do not show such trends, for any of the species mentioned (Buker *et al.* 1984).

TABLE 4. Frequency of causes of nest loss (as % of total loss); P = predated, T = trampled, M = mechanically destroyed, A = abandoned, U = unknown

	P	T	M	A	U
Lapwing	44·0	22·7	7·1	7·4	18·9
Godwit	40·1	23·7	7·4	9·3	18·8
Redshank	26·3	51·6	10·1	8·4	3·6
Oystercatcher	42·1	33·5	8·9	9·1	6·5

Significance of nest loss and the impact of management

Ideas on the significance of nest loss may be subjective or even depend on vested interest. The Dutch province of Friesland has a long tradition of collecting lapwing eggs for consumption, a practise now restricted by law. People in favour of it may say that it is harmless because lapwings produce replacement clutches, but that predators should be exterminated. Others say that it is a threat to the lapwing, but that predators are harmless because lost clutches are replaced!

Replacement clutches play an important role in the productivity of meadow birds. Lapwings can be induced to lay eight clutches in succession. One cannot interpret nesting success studies, without taking into account replacement clutches. Quantitative information on replacement clutches is difficult to obtain. Information on replacement behaviour of lapwings is given by Klomp (1951), and of the black-tailed godwit by van Balen (1959).

To predict the impact of management on nesting success, a deterministic renesting model was developed (Beintema & Müskens 1981), in which theoretical nests were exposed to daily survival rates based upon *P*-values, modified by management. For each day, the fraction of nests surviving was set equal to the daily survival rate. Lost nests were, with certain restrictions, re-entered in the model on a later day. This model has been improved, and made stochastic. The fate of each nest is decided on each day by comparing the daily survival rate with a random number between 0 and 1, until the nest either hatches, or fails. Also, other parameters, such as the length of the laying period, incubation period, and replacement interval (number of days between loss and first egg of replacement clutch), are not fixed, but may be drawn from a distribution, each time they are needed for calculation. Distributions are based on field observations. Thus, repeated runs yield different outcomes, giving statistical information on the results. An outline of the model is given in Fig. 5. Parameters needed are:

(a) Properties of bird species: laying dates of first clutches, length of laying period, length of incubation period, length of replacement interval, probability of making a replacement clutch as a function of the date of nest loss, daily survival rates (*P*-values) throughout the season, for laying and incubating period separately (Figs 1 and 2), and species-specific standardized trampling values (Table 3).

(b) For each management unit (plot): dates of mowing and fertilizing, grazing dates, cattle densities, etc.

(c) Composite daily survival rates are obtained by multiplying *P*-values with agricultural daily survival rates derived from management schemes.

As a simple example of the use of the renesting model, Fig. 6a gives the relationship between cattle density and estimated nesting success (per pair) under permanent grazing; Fig. 6b gives the relationship between the first mowing date and nesting success (per pair), when activities after mowing inhibit any successful nesting or renesting. Parameters used were derived from earlier studies (Beintema & Müskens 1981), modified by the results presented in this paper.

DISCUSSION

Although predation took a heavy toll (roughly half of all nests were eaten), nesting success was high under natural circumstances, as a result of renesting (Fig. 6a, density 0). Therefore, predation cannot be considered as a major threat to the existence of meadow birds in the Netherlands.
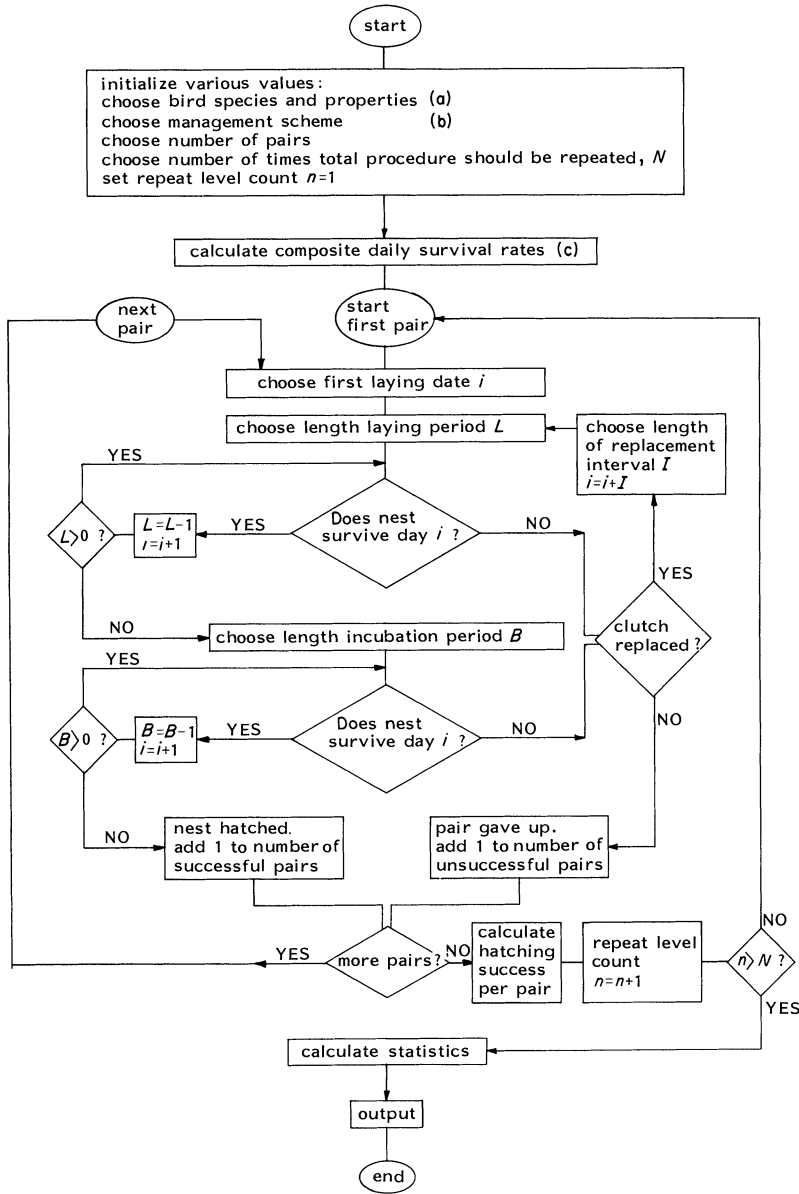
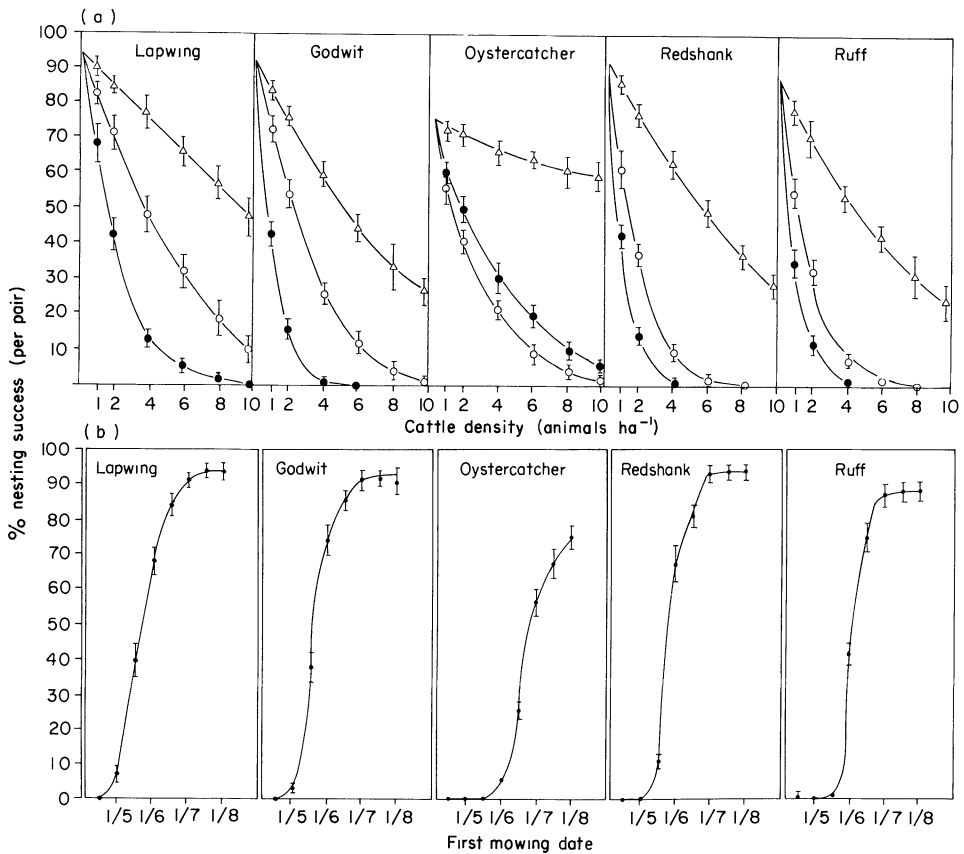FIG. 5. Scheme of renesting model. Letters in parentheses refer to text.

FIG. 6. Hatching success per pair according to renesting model in relation to (a) cattle density under permanent grazing and (b) in relation to first mowing date, when renesting after first mowing is inhibited. O = dairy cattle, ● = yearlings, △ = sheep, all grazing day and night. Vertical lines indicate 95% confidence intervals.

Under agricultural conditions, the impact of management rapidly exceeded the loss due to predation. In particular, the tremendous increase in cattle densities, following the increased fertilization (Beintema, Beintema-Hietbrink & Müskens 1985), had a severe effect on overall nesting success (Fig. 6b). Economically ideal management, as proposed by governmental agricultural agencies, has a devastating effect on nest survival (Beintema & Müskens 1981).

In the evaluation of the impact of nest losses, renesting plays a crucial role. Quantitative information on renesting is scanty, but it is known among farmers and egg collectors that during the first weeks of the breeding season c. 100% of all nests lost will be replaced. This has also been found by Klomp (1951) and van Balen (1959). Later in the season, the probability of renesting decreases, but more research is needed to quantify this; renesting may then be influenced by external factors other than time.

The use of a renesting model enables comparison of different management schemes with respect to their effect on nesting success. The outcome can be used as a relative measure for the pressure, or the intensity, of agricultural management (Beintema 1983).

There are two major points of criticism of the renesting model in its present form. First,

replacement clutches are assumed to occur at the same location as the lost nest, and this is known not to be necessarily true. Second, the probability of replacement is related to season only, whereas in reality it may also be related to management, or the state of drainage. In the Lauwersmeer, Visser (1982) found that in dry situations the nesting season ended earlier than in moist situations, possibly because lost nests were not replaced. An explanation could be that the birds have problems in obtaining sufficient extra food for egg production when the soil fauna retreats to a greater depth.

Even predation pressure may depend on drainage, not only because dry terrain is more easily accessible to ground predators. In the Ganzengouw—an area that was very wet at the start of the nesting season, but which gradually dried out and where soil fauna was almost absent—Visser (1983) found an extremely high predation rate. Halfway through the season the area was practically deserted by the birds (mostly lapwings), indicating that no replacement clutches were produced. An explanation for the high predation rate could be that the birds had to travel far to feed, spending too much time away from the nest.

Finally, initial laying dates may depend on management; intensification of agriculture (improved drainage and fertilization) has induced an advance in laying dates of *c.* 2 weeks in all the species mentioned (Beintema, Beintema-Hietbrink & Müskens 1985). The model leaves freedom of choice of laying dates.

ACKNOWLEDGMENTS

REFERENCES

Balen, H. van (1959). Over de voortplanting van de grutto *Limosa limosa* (L.) (in Dutch; English summary). *Ardea*, **47**, 76–86.

Bart, J. (1977). Impact of human visitations on avian nesting success. *Living Bird*, **16**, 187–192.

Beintema, A. J. (1983). Meadow birds as indicators. *Environmental Monitoring and Assessment*, **3**, 391–398.

Beintema, A. J., Boer, T. F. de, Buker, J. B., Müskens, G. J. D. M., Wal, R. J. van der & Zegers, P. J. (1982). *Verstoring van weidevogellegsels door weidend melkvee* (in Dutch). Directie Beheer Landbouwgronden, Utrecht; Rijksinstituut voor Natuurbeheer, Leersum.

Beintema, A.J. & Müskens, G. J. D. M. (1981). *De invloed van beheer op de produktiviteit van weidevogels* (in Dutch). Report 81/19, Rijksinstituut voor Natuurbeheer, Leersum.

Beintema, A. J., Beintema-Hietbrink, R. J. & Müskens, G. J. D. M. (1985). A shift in the timing of breeding in meadow birds. *Ardea*, **73**, 83–89.

Buker, J. B., Winkelman, J. E., Boer, T. F. de & Beintema, A. J. (1984). *Voortgangsverslag (1982 en 1983) van het weidevogelonderzoek in Waterland* (in Dutch). Directie Beheer Landbouwgronden, Utrecht; Rijksinstituut voor Natuurbeheer, Leersum.

Dijk, G. van (1983). De populatieomvang (broedparen) van enkele weidevogelsoorten in Nederland en de omringende landen (in Dutch). *Het Vogeljaar*, **31**, 117–133.

Green, R. F. (1977). Do more birds produce fewer young? A comment on Mayfield's measure of nest success. *Wilson Bulletin*, **89**, 173–175.

Harris, M. P. (1969) Effect of laying date on chick production in oystercatchers and herring gulls. *British Birds*, **64**, 70–75.

Johnson, D. H. (1979). Estimating nest success: the Mayfield method and an alternative. *Auk*, **96**, 651–661.
Klomp, H. (1951). Over de achteruitgang van de kievit, *Vanellus vanellus* (L.), in Nederland en gegevens over het eilegmechanisme en het eiproductie-vermogen (in Dutch; English summary). *Ardea*, **39**, 143–182.
Koerth, B. H., Webb, W. M., Bryant, F. C. & Guthery, F. S. (1983). Cattle trampling of simulated ground nests under short duration and continuous grazing. *Journal of Range Management*, **36**, 385–386.
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.
Miller, H. W. & Johnson, D. H. (1978). Interpreting the results of nesting studies. *Journal of Wildlife Management*, **42**, 471–476.
Roselaar, C. S. (1979). Fluctuaties in aantallen krombekstrandlopers *Calidris ferruginea* (in Dutch). *Watervogels*, **4**, 202–210.
Snow, D. W. (1955). The breeding of blackbird, songthrush and mistle thrush in Great Britain, Part III. Nesting success. *Bird Study*, **2**, 169–178.
Visser, G. H. (1982). *De broedvogels van het Lauwerszeegebied in 1980* (in Dutch). Doctoraalverslag 100, University of Groningen.
Visser, G. H. (1983). *Opgroeiende kievit-, grutto- en tureluurkuikens* (in Dutch). University of Groningen; Rijksinstituut voor Natuurbeheer, Leersum.
Willis, E. O. (1973). Survival rates for visited and unvisited nests of bicolored antbirds. *Auk*, **90**, 263–267.
Willis, E. O. (1981). Precautions in calculating nest success. *Ibis*, **123**, 204–207.

APPENDIX

By H. A. Van Biezen

Estimation of probabilities of predation and trampling of nests and their standard deviations

(1) A 'nest day' is defined as 1 day of one nest during the observations. Thus, 3 days observation of two nests yields 6 nest days.

(2) The probability p that a day for one nest is a day of predation ($= 1$ minus the probability that this day is a day of survival in relation to predation) can be estimated by the formula

$$p = \frac{B}{A}$$

where A is the total number of observed nest days (nest days of nests where predation is observed, nest days of nests where trampling is observed, and nest days of nests where no predation or trampling has been observed) and B is the number of observed predations. It is important to include nest days of nests where no predation has been observed, because not including these days results in overestimation of the probability of predation.

(3) The formula for daily survival rate and its standard deviation given by Mayfield (1961, 1975) and Johnson (1979), based on the above, suggest that the days of predation follow a binomial distribution, A being the total number of samples and B being the number of 'successes', so that p is an estimator for the probability of a 'success' or of a nest day being a predation day.

(4) It is possible to estimate the probability of predation per day in another way, which is only interesting in the context of the more complex way in which the probability of trampling must be estimated: the 'intensity' of predation I can be estimated by the formula

$$I = \frac{B}{0 \cdot 5B + 0 \cdot 5C + D}$$

where C is the number of observed tramplings and D is the number of nest days without predation or trampling (so $A = B + C + D$). This estimator corrects for the fact that the moment of trampling or predation during the day is not known exactly. The mean time of most predation and trampling should be around the middle of the day, so in this estimator days of predation or trampling are counted as half days in the denominator. Note that there is a difference between the probability of predation per day and the 'intensity' of predation; however, this difference is small when both values are small. The probability of non-predation per day (the survival rate P in relation to predation) can be estimated by using the formula

$$P = Exp(-I)$$

So, the estimator for the probability of predation is $1 - Exp(-I)$.

(5) In an analogous way, it is possible to estimate the 'intensity' of trampling for cow density 1 by the formula

$$I = \frac{C}{0 \cdot 5b + 0 \cdot 5c + d}$$

where c is the sum of the products of the trampling days and the cow densities on those days, b is the sum of the products of predation days and the cow densities on those days and d is the analogous sum for the non-predation and non-trampling days. The probability of non-trampling per day for cow density 1 (the survival rate V in relation to trampling for cow density 1) can be estimated by using the formula

$$V = Exp(-I)$$

(6) The standard deviation of the estimator of the probability of non-trampling per day for cow density 1 can be estimated as

$$\text{S.D.} = \frac{Exp(-I)\sqrt{C}}{A}$$

This formula rests on the assumption that durations of trampling at a constant cow density have an exponential distribution as probability distribution. Further, this formula rests on a first-order Taylor series approximation and the supposition that, on average, the deviation from half-day duration for days of predation or trampling is negligible.