BREEDING SEASONS OF SOME BRITISH WADERS

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SUMMARY

1)   The detectability of breeding waders is known to be affected by the stage of the breeding cycle, many species becoming particularly demonstrative near to the hatching time and when with young. Such an effect can potentially bias the results of the Nature Conservancy Council surveys of breeding upland waders unless the timing of breeding cycle events is known.

2)   This report summarizes the findings of an analysis of the British Trust for Ornithology's nest record cards for eight species of waders. The research was requested by the Nature Conservancy Council to assist in the evaluation of its field survey work in upland areas and documents dates of egg laying, dates of hatching, and breeding success in relation to altitude, habitat, and regions of Britain.

3)   For the Lapwing the main period for egg-laying is 22 March – 10 May, occasionally with a late peak in June. The main hatching period is 21 April – 9 June. A regional analysis showed that a smaller proportion of young hatch early in the season the more northerly the region, with a pronounced peak of hatching in Scotland between 1-20 May.

4)   In the Golden Plover the main period of egg-laying is 21 April – 10 May and of hatching is 31 May – 9 June.

5)   In the Snipe the main period of egg-laying is 11-20 April, with secondary peaks between 1-10 May and 21 – 30 May. The majority of newly hatched Snipe are found between 11-30 May.

6)   For Curlew the main period of egg-laying is 21 April – 20 May and of hatching 21 May – 20 June.

7)   In the Common Sandpiper the main period of egg-laying is 11 – 20 May and for hatching 31 May – 19 June.

8) For Redshank the main period of egg-laying is 21 April -
10 May but the peak of laying in Scotland is 20 days later
than in northern England. For hatching the main period is
11 May - 9 June but the peak of hatching is later in Scotland
(and also in eastern England) than in north England.

9) The Greenshank data were too few to draw any firm conclusions
The few records show the period for egg laying extends from
late April to late May and for hatching from late May to the
end of June.

10) In the Dunlin the main periods of egg-laying are 11-20 May
and 31 May - 9 June. For young hatching the main periods are
10-19 June and 30 June - 9 July.

11) Egg survival was calculated using Mayfield's method of
estimating nest success. Generally speaking, egg survival
was higher in Scotland and in moorland habitats. Eggs of
Curlew and Dunlin were more successful at high altitudes and of
Lapwing at low altitudes. Egg survival decreased with laying
date in Lapwing, Curlew, Redshank and Common Sandpiper but
increased in late nests of Golden Plover and Snipe. These
trends introduce a seasonal bias in census efficiency into
upland wader survey work.

INTRODUCTION

The Nest Record Scheme is a long-standing (since 1939) enquiry of the British Trust for Ornithology and is currently organised under contract to the Nature Conservancy Council. Nest record cards are completed by amateur birdwatchers for each nest found and provide information on nest sites, breeding habitats and altitudes of nests as well as details of nest contents on each nest visit. Some nests are visited once only but others, with more visits, provide details of egg laying dates, clutch sizes, dates of young hatching, number of young hatching and nest success. The collection of cards is biassed towards the more densely populated areas of Britain and towards the earlier months of the spring and summer when enthusiasm for nest-finding is greatest and the growth of vegetation less making nests easier to find (see Mayer-Gross 1970 for further information).

There is much interest at the current time in monitoring and **assessing** breeding wader populations and the objectives of this report are to provide useful background information on the breeding of those wader species of special relevance to the NCC, with particular reference to the effects of timing of the breeding cycle on census efficiency. Many species are known to be much more conspicuous at certain points in the breeding cycle than others. Barash (1975) points out that in altricial species the distraction display increases progressively in conspicuousness as the egg-nestling unit grows older, being at its peak when the young have recently left the nest. In contrast, the parents of precocial species often reach their maximum conspicuousness around the time of

hatching. In addition the mobility of chicks between nesting and feeding habitats may affect their conspicuousness and that of their parents: for example, Redfern (1982) found that Lapwing chicks hatched in areas of blanket-bog moved into areas of adjacent pasture soon after hatching. It is, therefore, important to know the distribution of first egg laying dates and first hatching dates of the species being censussed in order to interpret results. The distribution of hatching dates for a species will normally mirror the distribution of egg laying dates, allowing for a standard incubation and hatching period, but the hatching date distribution will further lag behind the laying dates if a significant proportion of egg-losses is incurred; some measure of breeding success is therefore desirable to check for this.

The present report was prepared at the request of the Nature Conservancy Council and analyses the nest record cards for eight species of wader commonly found breeding on moorland habitats in Britain: Lapwing <u>Vanellus vanellus</u>, Golden Plover <u>Pluvialis apricaria</u>, Snipe <u>Gallinago gallinago</u>, Curlew <u>Numenius arquata</u>, Common Sandpiper <u>Actitis hypoleucos</u>, Redshank <u>Tringa totanus</u>, Greenshank <u>T. nebularia</u> and Dunlin <u>Calidris alpina</u>.

Moorland covers an altitude range from sea-level to the highest peaks of Britain (Fuller 1982) and can be found from southwest England to the outlying islands of Orkney and Shetland. For these reasons the data, where sample sizes allow, have been analysed by region and altitude as both factors may influence climate and thus have an effect on the breeding seasons of the species concerned. Spring is usually later and colder northwards, thus affecting vegetation growth and the activity of soil-dwelling

invertebrates; this may in turn affect the availability of
suitable nest sites and of food. For the Meadow Pipit
Anthus pratensis Coulson (1956) found breeding to be earlier in
south than north Britain and later as altitude increased
(approximately one day later for every 130 feet (39m) rise in
altitude). Differences in habitat may also affect the timing
of breeding due to differences in the availability of food.
Finally, variation in the timing of breeding may be affected
by year to year differences in spring weather (Perrins 1979).

METHODS

This paper is based on analysis of all nest record cards contributed up to and including 1981 for the seven species listed in Table 1. In the case of Lapwing, for which the annual intake of cards varied between 127 and 845, a sample of 100 cards per annum for the years 1962-81 was used. The sample was selected at random from nests which had been visited at least three times, except that a minimum of ten cards from Scotland was included.

Each nest record card was analysed using a standard BTO computer program devised for the purpose. Using a species specific parameters file containing estimated data on incubation period, fledging period, maximum clutch size, and their allowable limits, etc. the program, in this analysis, sets upper and lower limits for date of first egg laid and date of first young hatched. For example, in the case of a card with a single visit when the nest contained three eggs the upper and lower limits would be set very wide as this visit could relate to a nest where the clutch has been completed recently or to a nest where the eggs are just about to hatch. If the same card has a second visit showing an increase in the number of eggs the limits would be reset so that the upper and lower now overlap showing that an accurate first egg date is recorded. Each visit on a card is treated thus, with the upper and lower limits for the variables modified each time. With all visits taken into account the final estimate of egg date may have been determined precisely (upper and lower date limits overlap) or with some uncertainty. For the present analysis date estimates were accepted wherever the degree of uncertainty was not more than ten days, the central value being taken as the laying or hatching date.

Mortality rates for eggs were obtained using the method developed by Mayfield (1961, 1975). This method of calculating breeding success makes use of the fragmentary information found on many nest record cards and allows for the fact that the number of eggs lost varies both with the number of eggs in the sample and with the number of days 'exposure' to failure. Mayfield's method has been examined by Johnson (1979) who concluded that although Mayfield's assumption that failure occurs at the midpoint between the visit on which failure was recorded and the previous visit is biassed, the method yields very similar results to more sophisticated procedures. Therefore, instead of assigning failure to the midpoint between the last visit to the intact nest and the visit on which failure was recorded, as Mayfield suggests, the present analysis follows O'Connor and Morgan (1982) and computes the limiting mortality rates on assuming that failures occurred just after the last visit prior to the discovery of the failure/on and assuming that failure occurred just before the visit recording it. The mean of these two limits was used as the best estimate of mortality.

For each species laying dates and hatching dates were analysed with respect to a) the regions of Scotland, north England, Wales, west England, east England and south England as defined by Batten and Marchant (1976); b) three altitude classes of 0-152m, 153-304m, and over 304m; and c) two habitat classes, respectively "moorland" and "other" habitats. The altitude classes correspond to 500 feet intervals, with most moorland in Britain occurring above 300m (Fuller 1982).

In the case of waders it is not possible to use data from nest record cards to establish fledging periods as the young are highly mobile, often leaving the nest within a few hours of hatching. Hence it is often impossible to attribute broods to a particular nest with any certainty.

Results

Tables 2-33 present for each species the computed first egg date and first hatching date distributions, on the basis of ten-day periods.

Lapwing

The Lapwing was the earliest breeder of the species considered, with clutches started in the period 11-21 March in five of the 20 years analysed (Table 2). The peak of laying was usually between 21 March and 20 April, though with some annual variation. Occasionally a late peak of laying activity was recorded in early or mid-May, probably reflecting repeat nesting attempts following earlier failures such as Jackson and Jackson (1975) found for a population in the New Forest, Hampshire. The later clutches were started in the period 20-29 June. Combining data for all years the main period of egg laying lasted from 22 March to 10 May (Table 3, Figure 1). There was no clear regional trend in the timing of egg laying although the peak period in Scotland was slightly later and more contracted than for other regions (Table 3). Table 4 shows the distribution of first egg dates with altitude: no significant difference was found although a greater proportion of clutches were started later, in May and June, at higher altitudes ($X^2_6 = 15.98$ N.S.)

Table 5 shows the annual distribution of first hatching dates. In general these will be similar to the corresponding distributions of egg dates after allowance for incubation, except where egg loss is highly seasonal. A small proportion of young hatched as early as 11-20 April in six of the 20 years but the majority of young Lapwings appeared between 21 April and 9 June, with a few as late as 10-19 July. Table 5 shows that the peak period for young

hatching was usually 21 April - 10 May in 'early' years (such as 1971-72) and 1-20 May (or even 30 May) in 'late' years (such as 1977). Table 6 and Figure 2 show a regional trend in the distribution of Lapwing hatching dates, with a smaller proportion of young appearing in the early part of the season the more northern the region (X^2_{12} on all regions = 32.90 p<0.01). A very pronounced peak in the period 1-20 May is apparent for nests in Scotland, with very few young hatching late in the season (after 9 June).

Golden Plover

Only 48 nest record cards yielded first egg dates for Golden Plover. The egg laying season extends from the period 1-10 April to 10-19 June (Figure 3), with 44 per cent of clutches started between 21 April and 10 May (Table 7). All but four records were from Scotland and northern England and no difference was apparent between these two regions, although the sample sizes were small. No altitudinal differences in timing of breeding were detected (Table 8).

Newly-hatched Golden Plover chicks were recorded from 1-10 May to 10-19 July. The peak period was between 31 May and 9 June (Table 9 and Figure 3). These data are in broad agreement with Ratcliffe (1976).

No regional or altitudinal differences were apparent in Golden Plover hatching dates (Tables 9 and 10).

Figure 3 shows a small, late peak both for egg laying dates and for hatching dates for Golden Plover, consistent with Parr's (1979) finding that some Golden Plovers are prevented from breeding earlier by lack of access to a suitable breeding area and will move into breeding ranges vacated by a previous successful pair.

Snipe

First egg dates were recorded from 82 Snipe nest record cards covering the period 22-31 March to 20-29 June. Most clutches were started between 11-20 April with secondary peaks occurring between 1-10 May and 21-30 May (Table 11, Figure 4). There were insufficient data to draw any conclusions about regional (Table 11) or altitudinal (Table 12) differences in laying dates.

The earliest newly-hatched Snipe were found between 11-20 April and the latest between 20-29 July (Table 13, Figure 4). The peak period was from 11 May to 9 June in Scotland and 1-30 May in northern England ($X^2_3 = 23.31$ $p < 0.001$). There were insufficient data to draw any conclusions about altitudinal (Table 14) or habitat (Table 15) differences in hatching dates.

Although the season is extended and with several peaks of activity in the case of egg-laying dates, Snipe are not thought to be double-brooded (Mason and Macdonald 1976). Tuck (1972), studying a marked population, found that late-nesting individuals were first-time breeders.

Curlew

First egg dates were calculable from 145 Curlew nest record cards. The earliest and the latest periods recording egg laying were 1-10 April and 31 May- 9 June respectively (Table 16, Figure 5). A distinct peak of egg laying activity was apparent between 21-30 April. A x^2 examination of regional variation in laying dates showed no significant difference (Table 16) but altitudinal variation was almost significantly different, with the peak of laying at low altitudes (0-152m) slightly earlier than that at higher altitudes (Table 17, Figure 6). No difference was apparent between moorland nesting Curlews and those in other habitats (Table 18).

The distribution of 301 Curlew first hatching dates is given in Table 19 and Figure 5. The pattern reflects that for egg laying described above after allowing for the 29 day incubation period (Witherby et al 1940). No significant differences were found when regional, altitudinal and habitat variation was examined (Tables 19 to 21).

Common Sandpiper

A total of 150 nest record cards gave information on first egg dates for the Common Sandpiper. The earliest and latest dates were in the periods 11-20 April and 10-19 June respectively (Table 22 Figure 7). Common Sandpipers are single-brooded and the timing of egg laying shows a distinct peak between 11 and 20 May (when over 40 per cent of clutches were started). No regional or altitudinal differences were apparent (Tables 22 and 23).

The hatching dates reflect the laying dates, allowing for the 22 day incubation period. Again, no regional or altitudinal differences were found (Tables 24 and 25).

Redshank

The distribution of the 251 first egg dates for Redshank is shown in Table 26 and Figure 8. The egg laying season for this speci is extended, from the end of March until mid-June, with the peak period between 21 April and 10 May. A regional analysis shows significant differences (X^2_9 = 23.05 p<0.01), with most of the variation accounted for by the difference between Scotland and the north of England (X^2_3 = 20.3 p<0.001). The peak of laying in Scotlar is about 20 days later than in the north of England (Table 26, Figure 9). Most Redshank nests were recorded from between sea-level and 152m (Table 27), thus falling almost entirely within only one of the altitude classes used for the present report.

Table 28 shows the distribution of Redshank first hatching dates in the various regions of Britain. The overall distribution closely parallels the egg laying dates allowing for the 23 day incubation period (Witherby et al). The regional difference noted above was again apparent (X^2_9 = 28.31 p<0.001), with the difference between Scotland and northern England very marked (X^2_3= 20.79 p<0.001) but a difference between northern England and eastern England is also apparent (X^2_3 = 14.31 p<0.01): surprisingly, a higher proportion of hatching dates occurred before 20 May in northern than in eastern England.

Greenshank

The nests of the Greenshank are both difficult to find and often in remote country and very few observers have managed to record details of this species for the nest record scheme. A total of 85 Greenshank cards have been submitted: of these only seven gave egg laying dates and only 12 yielded hatching dates (Table 30, Figure 10).

All the records are from Scotland and show a spread in laying dates from late April to late May and in hatching dates from late May to the end of June. For a detailed study on this elusive species see Nethersole-Thompson and Nethersole-Thompson (1979).

Dunlin

The distribution of the 68 Dunlin first egg dates available is shown in Table 31 and Figure 11. Dunlins commence breeding quite late compared to most other species described in this report, the peak of laying occurring between 11-20 May with a secondary peak as late as 31 May - 9 June. All but one first egg dates were from Scotland or northern England (Table 31). Too few cards were obtained from above 152m to warrant analysing altitudinal variations (Table 32).

Newly-hatched young were found from 21-30 May until late July; the distribution of the 69 records is shown in Table 33, with hatching slightly later in Scotland than in northern England ($X^2_1 = 7.26$ p$<$0.01). The sample size was too small to examine altitudinal trends (Table 34).

Egg Survival to Hatching

Earlier in this report it was noted that many waders reach their maximum conspicuousness at hatching time. The preceding section has established the distributions of egg laying dates and hatching dates, the latter necessarily being a lagged mirror of the former except for any effects of differential survival or of bias. A bias in the estimated distributions of laying and hatching dates might, however, arise when observer coverage is biassed towards the early part of the season. The following section, therefore, looks at survival of eggs using an unbiassed method developed by Mayfield (1961, 1975). (See methods section for further details).

Regional variation

Table 35 shows the proportion of eggs surviving to hatching for seven species of wader in six regions of Britain with confidence intervals of one standard error either side of the mean figure. In the case of Lapwing, Golden Plover, Snipe, Common Sandpiper and Redshank, the survival rate was high in Scotland and in the case of Redshank and Dunlin the survival rate was high in Wales also. The very high survival rate for Golden Plover in west England, Curlew in east England and the very low rate for Golden Plover in Wales may be artificial and due to small sample sizes as they differ so very markedly from the other figures.

Altitudinal variation

Table 36 shows egg survival in relation to altitude for seven species of wader in three standard altitude classes of 0-152m, 153-304m and over 304m, with confidence intervals of one standard error either side of the mean figure.

The Lapwing shows a progressively lower survival of eggs as altitude increases in contrast to Curlew, Redshank and Dunlin which show better survival as altitude increases.

Habitat variation

Table 37 shows egg survival in moorland and other habitats for seven species of wader with confidence intervals of one standard error either side of the mean figure. The results show higher survival in moorland than other habitats for Lapwing, Snipe, Curlew, Common Sandpiper, Redshank and Dunlin and no difference in the case of Golden Plover.

An explanation for these differences in egg survival may lie, at least in part, in there being fewer predators in Scotland, at higher altitudes and in moorland habitats. Predation is likely to be a major mortality factor affecting egg survival in ground-nesting waders (Ricklefs 1969).

To check this the nest record cards for the seven species of wader were divided into those recording and not recording predation when the nest contained eggs. Table 40 shows the proportion failing through predation according to region and habitat. The absolute predation rates thus estimated are biassed since it is easier to record predation failure (which can occur and be recorded at any stage of the laying and incubation period) than egg success (which can be recorded only after incubation is complete). A differential bias by

region or habitat is less likely, though it could arise if
observer coverage differed in the different regions or habitats.
In practice the differences in Table 40 are sufficiently marked
that they corroborate the earlier suggestion that predation is
low in Scotland and particularly in moorland habitats.

Seasonal variation

Table 38 shows the percentage survival of eggs for seven
species of wader when the first egg dates fell a) before May
b) during May and c) after May; confidence intervals of one
standard error either side of the mean are also shown. The results
for Lapwing, Curlew, Redshank and Common Sandpiper are similar in
that eggs from nests started late in the season (after May) had a
much lower success rate than those laid in April and May. In Snipe
and Golden Plover the later nests were more successful.

For the three species with relatively large sample sizes -
Lapwing, Redshank and Curlew - Table 39 shows percentage egg
survival to hatching by ten-day periods throughout the egg-laying
season; confidence intervals of one standard error either side of
the mean are also shown. Lapwing eggs laid very early (before day
80) were very successful, thereafter the level oscillated between
43 per cent - 51 per cent until day 160 after which success was
considerably lower. The Redshank pattern varied between 51 per cent
and 64 per cent throughout the season with one very low figure
towards the end of the season (35 per cent between day 151-160).
The season for Curlew is noticeably shorter than the other two
species, perhaps associated with the large amount of energy required
to produce over 300g of eggs, more than any other British wader
(Lack 1968). Curlew show good egg survival early in the season,
moderate survival in the middle and very poor survival at the end.

Conclusions

The seven main species of wader considered in this report (excluding Greenshank for which data is too sparse to draw any firm conclusions) vary considerably in the timing of the main periods of egg-laying but fall into three broad groups: (a) the early breeders (Lapwing, Snipe) with peak egg-laying activity in mid April; (b) a middle group (consisting of Redshank, Golden Plover and Curlew) with peak egg-laying activity in late April to early May; and (c) the late breeders (Common Sandpiper, Dunlin) with peak egg-laying in mid-May.

A similar pattern is observed with respect to the hatching dates after allowing for the incubation period and hatching period for each species: the main period for Lapwing and Snipe hatching is in early and mid May; for Redshank, Golden Plover and Curlew in late May and early June; and for Common Sandpiper and Dunlin young are prevalent in early and mid June. Thus, ideally any census should take into account these main periods of laying and hatching activity and compensate for differences in species conspicuousness at different stages of the breeding cycle.

An examination of regional, altitudinal and habitat (moorland against other habitats) variation in timing of egg-laying and young hatching revealed significant differences in four species. A smaller proportion of young Lapwings hatch early in the season the more northerly the region, the peak of Redshank egg-laying and hatching is later in Scotland than in northern England and Snipe and Dunlin hatch later in Scotland than in northern England.

Generally speaking, egg survival was higher in Scotland and in moorland habitats. Egg survival for Curlew, Redshank and Dunlin was greater at high altitudes but for Lapwing it was greater at low

altitudes. Egg survival decreased with laying/date in Lapwing, Curlew, Redshank and Common Sandpiper but increased in late nests of Golden Plover and Snipe.

These trends in survival rates of eggs, particularly that with respect to laying date, has a significant implication for the detectability of a species during census work: a differential proportion of late-nesting pairs will not rear any young and will therefore be less conspicuous to the census worker, thus altering census efficiency seasonally.

Acknowledgements

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Table 1. Nest Record Card totals of seven species of wader.

Species	Coverage	Highest Annual Total	Grand Total
Golden Plover _Pluvialis apricaria_	1943-81	45	383
Snipe _Gallinago gallinago_	1939-81	57	934
Curlew _Numenius arquata_	1945-81	86	1477
Common Sandpiper _Actitis hypoleucos_	1941-81	46	774
Redshank _Tringa totanus_	1943-81	119	1456
Greenshank _Tringa nebularia_	1959-81	10	85
Dunlin _Calidris alpina_	1947-81	62	316

TABLE 2.

Annual variation in distribution of Lapwing first egg dates.

Year	March		April			May			June			N
	12-21	22-31	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	
1962	-	4	11	7	2	3	1	2	1	-	-	31
1963	-	2	2	3	-	4	-	-	2	-	-	13
1964	-	2	4	9	3	3	1	-	-	2	-	24
1965	-	-	4	1	-	6	2	1	1	-	-	15
1966	-	7	8	5	5	6	-	1	-	-	2	34
1967	-	9	7	10	-	1	-	-	-	-	-	27
1968	-	9	8	8	3	2	2	1	-	-	-	33
1969	-	1	13	6	2	4	1	2	2	-	-	31
1970	-	2	17	10	2	5	3	2	-	-	-	41
1971	-	12	9	7	2	2	1	-	1	-	-	34
1972	-	3	8	1	6	4	7	2	2	1	-	34
1973	-	2	11	7	4	4	3	4	-	-	-	35
1974	1	2	7	1	1	3	-	-	-	-	-	15
1975	1	6	3	7	5	1	3	1	1	-	-	28
1976	-	2	7	7	3	9	3	2	-	-	-	33
1977	2	2	5	3	3	3	-	1	1	-	-	20
1978	1	4	8	9	2	2	3	2	1	-	-	32
1979	-	1	5	9	3	3	-	1	-	-	-	22
1980	-	6	10	3	6	7	1	1	-	-	-	34
1981	1	10	9	4	1	11	2	1	1	-	-	40

576

TABLE 3.

Distribution of Lapwing first egg dates in different regions.

Region	March		April			May			June			N
	12-21	22-31	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	
Scotland	-	7	28	16	5	8	2	1	1	-	-	6₿
North England	4	46	82	70	31	49	18	19	10	1	2	33₂
Wales	-	7	4	7	2	3	1	-	-	-	-	2₿
West England	-	11	8	8	5	7	6	-	--	...	-	4₂
East England	-	9	20	11	7	11	4	1	1	1	-	6₿
South England	2	6	14	5	3	5	2	3	1	1	-	4₂
Total	6	86	156	117	53	83	33	24	13	3	2	576
%	1.0	14.9	27.1	20.3	9.2	14.4	5.8	4.2	2.2	0.5	0.3	

TABLE 4.

Distribution of Lapwing first egg dates in relation to altitude.

Altitude(m)	March		April			May			June		N
	12-21	22-31	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	
0 - 152 m	2	31	87	38	26	35	14	10	2	1	246
153-304 m	2	33	45	42	13	29	7	6	6	-	183
305+ m	1	11	10	16	7	13	8	6	4	1	77

Note: After joining adjacent columns and amalgamating those
from 11 May onwards $X^2 = 15.98$ (6 df) $p < 0.02$

TABLE 5.

Annual variation in distribution of Lapwing first hatching dates.

Year	April			May			June			July	N
	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19	
1962	-	2	16	8	3	4	4	1	2	-	40
1963	-	6	9	4	-	4	-	-	1	-	24
1964	-	3	13	15	5	5	4	1	1	-	47
1965	-	5	11	10	6	1	4	-	2	-	39
1966	2	7	15	5	11	8	1	-	1	2	52
1967	1	12	15	13	6	2	2	1	-	-	52
1968	-	10	12	11	2	2	2	1	-	-	40
1969	-	-	25	11	5	5	4	3	1	-	54
1970	-	3	15	17	7	4	2	3	-	-	51
1971	-	9	12	6	2	2	-	-	1	-	32
1972	-	11	13	2	4	5	3	1	2	1	45
1973	-	3	11	6	6	3	4	2	1	-	36
1974	-	10	12	4	4	5	4	1	-	-	40
1975	2	8	6	16	10	4	3	1	2	-	52
1976	-	1	8	10	8	10	5	3	-	-	45
1977	3	5	13	7	7	3	3	1	2	-	44
1978	3	8	12	9	3	5	5	3	-	-	48
1979	-	4	6	10	8	1	2	4	-	-	35
1980	-	5	13	3	8	6	2	3	-	-	40
1981	1	6	8	5	3	12	2	2	2	-	41

TABLE 6.

Distribution of Lapwing first hatching dates by region.

Region	April			May			June			July		N
	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19	
Scotland	-	-	8	47	30	11	12	4	1	1	-	114
North England	-	7	58	126	80	58	47	23	22	14	3	438
Wales	-	-	10	8	10	6	-	3	2	-	-	39
West England	-	-	8	14	14	9	10	8	1	1	-	65
East England	-	2	16	31	22	15	17	7	2	1	-	113
South England	-	3	18	19	16	9	5	11	3	1	-	85
Total	-	12	118	245	172	108	91	56	31	18	3	854
%	-	1.4	13.9	28.7	20.1	12.7	10.7	6.5	3.6	2.1	0.3	

Note: After combining the data for Wales and west England, combining adjacent columns and amalgamating those from 10 June onwards $X^2 = 32.90$ (12 df) $p < 0.01$.

TABLE 7.

Distribution of Golden Plover first egg dates by region.

Region	April			May			June		N
	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	
Scotland	-	2	4	2	2	1	-	-	11
North England	1	2	8	6	3	3	6	4	33
Other	-	1	-	1	1	1	-	-	4
Total	1	5	12	9	6	5	6	4	48
%	2.1	10.4	25.0	18.8	12.5	10.4	12.5	8.3	

Distribution of Golden Plover first egg dates in relation to altitude.

Altitude (m)	April			May		June			N
	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	
0 - 304 m	1	2	3	3	2	1	–	–	12
305+ m	–	3	8	6	3	4	6	3	33

TABLE 9.

Distribution of Golden Plover first hatching dates by region.

Region	May			June			July			N
	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19		
Scotland	–	6	4	7	5	1	2	1	26
North England	2	7	10	11	6	4	3	7	. 50
Other	–	2	1	3	2	2	–	–	10
Total	2	15	15	21	13	7	5	8	86
%	2.3	17.4	17.4	24.4	15.1	8.1	5.8	9.3	

TABLE 10.

Distribution of Golden Plover first hatching dates in relation to altitude.

Altitude (m)	May			June			July		N
	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19	
0 - 304 m	–	8	5	10	3	2	2	1	31
305+ m	2	5	8	11	10	4	3	6	49

TABLE 11.

Distribution of Snipe first egg dates by region.

Region	March		April		May			June			N
	22-31	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	
Scotland	-	-	2	-	3	1	2	3	1	1	1]
North England	2	3	12	4	6	5	5	1	2	1	4]
Wales	-	-	2	-	-	-	-	-	-	-	2
West England	-	1	-	3	-	-	2	-	-	-	6
East England	-	1	3	.-	4	1	4	-	1	1	15
South England	-	-	1	3	1	-	-	-	-	-	5
Total	2	5	20	10	14	7	13	4	4	3	82
%	2.4	6.1	24.4	12.2	17.1	8.5	15.9	4.9	4.9	3.7	

TABLE 12.

Distribution of Snipe first egg dates in relation to altitude.

Altitude (m)	March		April		May			June			N
	22-31	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	
0-152 m	-	-	4	3	6	3	3	2	2	2	25
153+ m	2	3	6	4	2	4	4	-	1	-	26

TABLE 13.

Distribution of Snipe first hatching dates by region.

Region	April		May			June			July			
	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19	20-29	
Scotland	–	–	2	5	7	9	3	5	7	3	–	4
North England	1	5	20	25	17	5	7	5	2	1	–	8
Wales	–	1	–	–	3	1	1	–	–	–	1	
West England	–	–	–	–	2	2	–	–	1	–	–	
East England	1	1	5	5	7	5	2	1	–	–	–	2
South England	–	2	1	4	3	3	2	1	1	–	–	1
Total	2	9	28	39	39	25	15	12	11	4	1	18
%	1.1	4.9	15.1	21.1	21.1	13.5	8.1	6.5	5.9	2.2	0.5	

Note: After joining columns up to the end of May and after May and excluding the rows Wales and west England $X^2 = 23.31$ (3 df) $p < 0.001$.

TABLE 14.

Distribution of Snipe first hatching dates in relation to altitude.

Altitude (m)	April		May			June	July					
	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19	20-29	
0 – 152 m	–	3	10	13	11	10	7	4	7	2	1	68
153+ m	1	2	5	9	10	4	2	4	2	2	–	41

TABLE 15.

Distribution of Snipe first hatching dates in moorland and in other habitats.

Habitat	April		May			June			July			N
	11-20	21-30	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19	20-29	
Moorland	1	2	1	7	9	6	1	2	2	1	-	32
Other habitats	1	7	27	32	30	19	14	10	9	3	1	153

TABLE 16.

Distribution of Curlew first egg dates by region.

Region	April			May			June	N
	1-10	11-20	21-30	1-10	11-20	21-30	31-9	
Scotland	-	2	9	6	4	2	1	24
North England	-	4	25	24	15	11	5	84
Wales	-	3	5	4	4	-	-	16
West England	-	-	2	-	2	1	1	6
East England	1	-	5	2	1	-	-	9
South	-	1	3	-	2	-	-	6
Total	1	10	49	36	28	14	7	145
%	0.7	6.9	33.8	24.8	19.3	9.7	4.8	

Note: After dividing the data into two columns, a) April and b) after April, and three rows, Scotland, north England and other regions combined $X^2 = 4.27$ (2 df) N.S.

Distribution of Curlew first egg dates in relation to altitude.

Altitude (m)	April			May			June	N
	1-10	11-20	21-30	1-10	11-20	21-30	31-9	
0-152 m	1	3	20	11	11	6	1	53
153-304 m	-	1	6	7	9	3	3	29
305 + m	-	-	4	7	3	4	2	20

Note: After dividing the data into two columns, a) April and
b) after April, and two rows, 0-152m and over 152m
$X^2 = 5.89$ (1 df) p between 0.05 and 0.1

TABLE 18.

Distribution of Curlew first egg dates in moorland and in other habitats

Habitat	April			May			June	N
	1-10	11-20	21-30	1-10	11-20	21-30	31-9	
Moorland	-	3	8	8	3	5	1	28
Other habitats	1	8	42	28	25	9	6	119

TABLE 19.

Distribution of Curlew first hatching dates by region.

Region	April		May				June			N
	11-20	21-30	1-10	11-20	21-30	31-9	10-20	21-29	30-9	
Scotland	1	-	-	1	24	25	15	6	3	75
North England	-	-	-	8	46	67	22	11	5	159
Wales	-	-	-	2	10	11	6	3	-	32
West England	-	-	-	1	3	4	2	2	1	13
East England	-	-	-	2	5	1	3	-	-	11
South England	-	-	-	-	6	1	1	3		11
Total	1	-	-	14	94	109	49	25	9	301
%	0.3	-	-	4.7	31.2	36.2	16.3	8.3	3.0	

Distribution of Curlew first hatching dates in relation to altitude.

Altitude (m)	May		June			July	N
	11-20	21-30	31-9	10-20	21-29	30-9	
0 - 152 m	5	26	49	13	11	5	109
153 - 304 m	1	14	22	8	4	1	50
305 + m	3	12	16	5	2	2	40

TABLE 21.

Distribution of Curlew first hatching dates in moorland and in other habitats.

Habitat	April		May			June				N
	11-20	21-30	1-10	11-20	21-30	31-9	10-20	21-29	30-9	
Moorland				2	39	31	10	6	4	92
Other habitats	1	-	-	12	57	82	40	19	5	216

TABLE 22.

Distribution of Common Sandpiper first egg dates by region.

Region	April		May			June		N
	11-20	21-30	1-10	11-20	21-30	31-9	10-19	
Scotland	-	-	12	26	16	9	4	67
North England	1	-	11	30	10	5	2	59
Wales	-	-	-	6	2	1	3	12
West England	-	-	-	3	5	2	2	12
Total	1	-	23	65	33	17	11	150
%	0.7	0.0	15.3	43.3	22.0	11.3	7.3	

Distribution of Common Sandpiper first egg dates in relation to alti[tude]

Altitude (m)	May			June		
	21-30	1-10	11-20	21-30	31-9	10-19
0-152 m	9	25	11	6	3	
153+ m	10	16	11	6	5	

TABLE 24.

Distribution of Common Sandpiper first hatching dates by region.

Region	May			June			July		N
	1-10	11-20	21-30	31-9	10-19	20-29	30-9	10-19	
Scotland	-	-	1	29	27	13	5	2	77
North England	1	-	4	20	30	10	5	1	71
Wales	-	-	1	4	6	1	2	1	15
West England	-	-	-	2	4	4	5	1	·16
Total	1	-	6	55	67	28	17	5	179
%	0.6	-	3.4	30.7	37.4	15.6	9.5	2.8	

TABLE 25.

Distribution of Common Sandpiper first hatching dates in relation to altitude.

Altitude (m)	May	June				July	N
	21-30	31-9	10-19	20-29	30-9	10-19	
0 - 152 m	2	19	27	14	3	4	69
153+ m	4	26	16	9	7	1	63

TABLE 26.
Distribution of Redshank first egg dates by region.

Region	March		April		May			June		N
	22-31	1-10	11-20	21-30	1-10	11-20	21-30	31-9	10-19	
Scotland	-	1	1	10	14	2	-	1	-	29
North England	-	-	20	17	10	8	13	3	2	73
Wales	-	-	1	2	1	1	5	1	-	11
West England	-	-	1	-	2	-	1	-	-	4
East England	1	3	12	32	20	12	9	3	-	92
South England	-	1	7	11	10	5	4	4	-	42
Total	1	5	42	72	57	28	32	12	2	251
%	0.4	2.0	16.7	28.7	22.7	11.2	12.7	4.8	0.8	

Note: After dividing the data into four columns, a) up to 20 April,
b) 21-30 April, c) 1-10 May and d) after 10 May and four rows
(by excluding Wales and West England) $X^2 = 23.05$ (9 df) $p < 0.01$.

Using the same columns and the rows for Scotland and north
England $X^2 = 20.3$ (3 df) $p < 0.001$.

TABLE 27.

Distribution of Redshank first egg dates in relation to altitude.

Altitude (m)	March		April		May		June		N
	22-31	1-10	11-20	21-30	1-10	11-20	21-30	31-9	
0 - 152 m	1	5	17	43	29	16	17	7	135
153+ m	-	-	4	6	2	-	2	-	14

TABLE 28.

Distribution of Redshank first hatching dates by region.

Region	April 21-30	May 1-10	11-20	21-30	June 31-9	10-19	20-23	July 30-9	10-19	N
Scotland	1	2	3	17	14	3	–	–	–	40
North England	–	5	30	29	11	17	7	2	3	104
Wales	–	–	–	–	2	2	6	–	–	10
West England	–	–	1	–	4	1	2	–	–	8
East England	–	3	15	33	30	14	13	4	1	113
South England	–	5	11	15	10	6	5	4	–	56
Total	1	15	60	94	71	43	33	10	4	331
%	0.3	4.5	18.1	28.4	21.5	13.0	10.0	3.0	1.2	

Note: After dividing the data into four columns a) up to 20 May,
b) 21-30 May, c) 31 May – 9 June and d) after 9 June and
four rows (by excluding Wales and west England)
$X^2 = 28.31$ (9 df) p< 0.001.

Using the same columns and the rows for Scotland and north
England $X^2 = 20.79$ (3 df) p< 0.001.

Using the same columns and the rows for north England and
east England $X^2 = 14.31$ (3 df) p<0.01.

TABLE 29.

Distribution of Redshank first hatching dates in relation to altitude.

Altitude (m)	April 21-30	May 1-10	11-20	21-30	June 31-9	10-19	20-23	July 30-9	10-19	N
0 – 152m	1	13	22	55	37	18	21	8	2	177
153+ m	–	1	7	8	3	6	1	–	–	26

TABLE 33.

Distribution of Dunlin first hatching dates by region.

Region	May		June			July		N
	21-30	31-9	10-19	20-29	30-9	10-19	20-29	
Scotland	1	13	16	7	12	1	1	51
North England	4	6	6	-	-	1	-	17
Wales	1	-	-	-	-	-	-	1
Total	6	19	22	7	12	2	1	69
%	8.7	27.5	31.9	10.1	17.4	2.9	1.4	

Note: After dividing the data into two columns, before and after
19 June and using the rows for Scotland and north England
only $X^2 = 7.26$ (1 df) $p < 0.01$.

TABLE 34.

Distribution of Dunlin first hatching dates in relation to altitude.

Altitude (m)	May		June			July		N
	21-30	31-9	10-19	20-29	30-9	10-19	20-29	
0-152m	-	9	13	3	2	1	1	29
153 - 304 m	1	1	1	-	-	-	-	3
305 + m	4	4	7	1	-	1	-	17

Table 35. Regional variation in egg survival to hatching in various species. Figures given are percentages of eggs laid that survive a standard incubation period and hatch. See text for details. (STD and STU = one standard error down and one standard error up from the mean respectively).

REGION	LAPWING			GOLDEN PLOVER			SNIPE			CURLEW		
	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU
SCOTLAND	46.1	47.9	49.8	37.0	42.3	48.3	32.2	34.8	37.7	35.5	37.8	40.2
N. ENGLAND	33.3	34.1	34.8	37.7	40.5	43.6	35.1	36.7	38.3	27.3	28.5	29.7
WALES	37.5	40.8	44.3	8.4	12.2	17.6	18.0	22.2	27.4	36.6	39.8	43.2
W. ENGLAND	28.8	30.5	32.4	74.8	82.9	92.0	22.0	25.8	30.2	19.2	24.0	30.1
E. ENGLAND	37.0	38.6	40.4	-	-	-	32.7	35.1	37.7	50.0	55.0	60.5
S. ENGLAND	43.0	44.9	47.0	-	-	-	27.7	31.1	34.9	25.8	30.8	35.8

REGION	COMMON SANDPIPER			REDSHANK			DUNLIN		
	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU
SCOTLAND	42.6	45.0	47.6	44.4	47.6	50.9	22.4	25.8	29.7
N. ENGLAND	34.8	37.0	39.3	20.8	22.1	23.5	27.4	32.2	37.7
WALES	20.8	25.8	31.8	47.4	52.5	58.1	35.1	51.5	75.0
W. ENGLAND	42.4	48.0	54.4	19.4	23.1	27.5	-	-	-
E. ENGLAND	-	-	-	25.2	26.4	27.6	-	-	-
S. ENGLAND	-	-	-	33.3	35.6	38.1	-	-	-

Table 36. Variation in egg survival to hatching in various species in relation to altitude. Figures given are percentages of eggs laid that survive a standard incubation period and hatch. See text for details. (STD and STU = one standard error down and one standard error up from the mean respectively).

ALTITUDE	LAPWING			GOLDEN PLOVER			SNIPE			CURLEW		
	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU
0 - 152m	38.5	39.4	40.3	27.2	35.8	47.1	34.1	35.9	37.8	27.4	28.9	30.5
153 - 304m	33.7	34.7	35.8	37.5	42.4	47.9	28.3	30.5	32.9	25.1	27.0	28.9
OVER 304m	23.5	24.9	26.5	36.2	39.0	41.9	36.4	39.9	43.7	32.3	35.2	38.2

ALTITUDE	COMMON SANDPIPER			REDSHANK			DUNLIN		
	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU
0-152m	37.8	40.2	42.7	25.7	26.8	27.8	21.0	24.9	29.5
153-304m	28.9	31.2	33.7	39.3	44.8	51.1	37.9	50.1	66.0
OVER 304m	35.1	40.5	46.6	26.7	31.8	37.8	37.9	44.1	51.4

Table 38. Seasonal variation in egg survival to hatching in various species. Figures given are percentages of eggs laid that survive a standard incubation period and hatch. See text for details. (STD and STU = one standard error down and one standard error up from the mean respectively).

DATE OF FIRST EGG LAID	LAPWING			GOLDEN PLOVER			SNIPE			CURLEW		
	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU
BEFORE MAY	45.3	46.6	47.9	63.1	69.7	76.9	44.7	48.6	52.8	42.2	45.5	49.0
MAY	44.3	46.6	49.0	50.3	56.2	62.8	45.7	49.8	54.3	35.1	38.0	41.2
AFTER MAY	33.7	39.3	45.8	79.8	86.6	94.0	55.3	62.4	70.4	7.3	12.5	20.9

DATE OF FIRST EGG LAID	REDSHANK			COMMON SANDPIPER			DUNLIN		
	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU
BEFORE MAY	54.2	56.5	59.0	-	-	-	33.4	49.4	72.6
MAY	56.9	59.5	62.2	61.0	64.0	67.1	47.5	54.0	61.3
AFTER MAY	31.6	38.4	46.4	26.6	31.5	37.2	41.2	50.1	60.8

Table 39. Seasonal variation in egg survival to hatching in various species in ten day periods. Figures given are percentages of eggs laid that survive a standard incubation period and hatch. See text for details. (STD and STU = one standard error down and one standard error up from the mean respectively).

Date (day 1 = Jan. 1st) of first egg laid	LAPWING			REDSHANK			CURLEW		
	STD	MEAN	STU	STD	MEAN	STU	STD	MEAN	STU
0-80	55.8	63.6	72.6	-	-	-	-	-	-
81-90	43.0	45.6	43.3	44.8	62.5	86.9	-	-	-
91-100	44.6	46.6	48.7	51.4	62.0	74.5	-	-	-
101-110	41.2	43.7	46.3	47.6	51.5	55.9	56.5	62.8	69.8
111-120	47.8	51.2	54.8	55.9	58.8	62.0	34.1	37.7	41.6
121-130	45.4	48.3	51.3	60.4	64.3	68.5	37.3	41.7	46.6
131-140	34.5	39.0	43.9	52.7	58.0	63.9	42.1	47.1	52.8
141-150	45.4	51.2	57.6	49.0	53.5	58.4	4.9	7.4	11.2
151-160	38.4	45.2	53.1	28.0	35.1	44.0	7.3	12.5	20.9
161--	16.7	24.8	36.5	38.5	54.2	75.8	-	-	-

Table 40. Regional and habitat variation in the proportion of nest record cards giving predation as the cause of failure in various species. Figures given are percentages of nests predated at the egg stage with sample sizes of cards.

a) Regional

	Lapwing		Golden Plover		Snipe		Curlew		Redshank		Common Sandpiper		Dunlin		All Species	
	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N
Scotland	8.3	254	2.3	130	3.7	272	7.4	443	5.6	180	2.6	429	9.6	208	5.6	1916
N. England	19.9	1081	4.2	213	16.1	378	12.0	711	22.5	417	5.9	273	10.2	49	15.5	3122
Wales	8.3	72	8.7	23	8.1	62	6.2	178	1.4	73	4.4	45	-	-	5.9	459
W. England	13.3	180	2.4	41	9.2	65	5.0	80	6.3	48	4.7	43	11.1	9	8.8	466
E. England	9.5	273	-	-	6.5	168	7.8	51	15.7	498	-	-	-	-	12.0	991
S. England	5.8	224	-	-	5.4	74	11.1	45	10.6	246	-	-	-	-	8.1	591

b) Habitat

	Lapwing		Golden Plover		Snipe		Curlew		Redshank		Common Sandpiper		Dunlin		All Species	
Moorland	7.5	53	4.1	340	4.9	132	4.4	547	3.9	51	3.8	26	1.2	84	4.3	1283
Other	14.6	2053	1.5	188	10.4	849	12.3	376	15.0	1416	3.9	772	13.3	188	10.8	5423
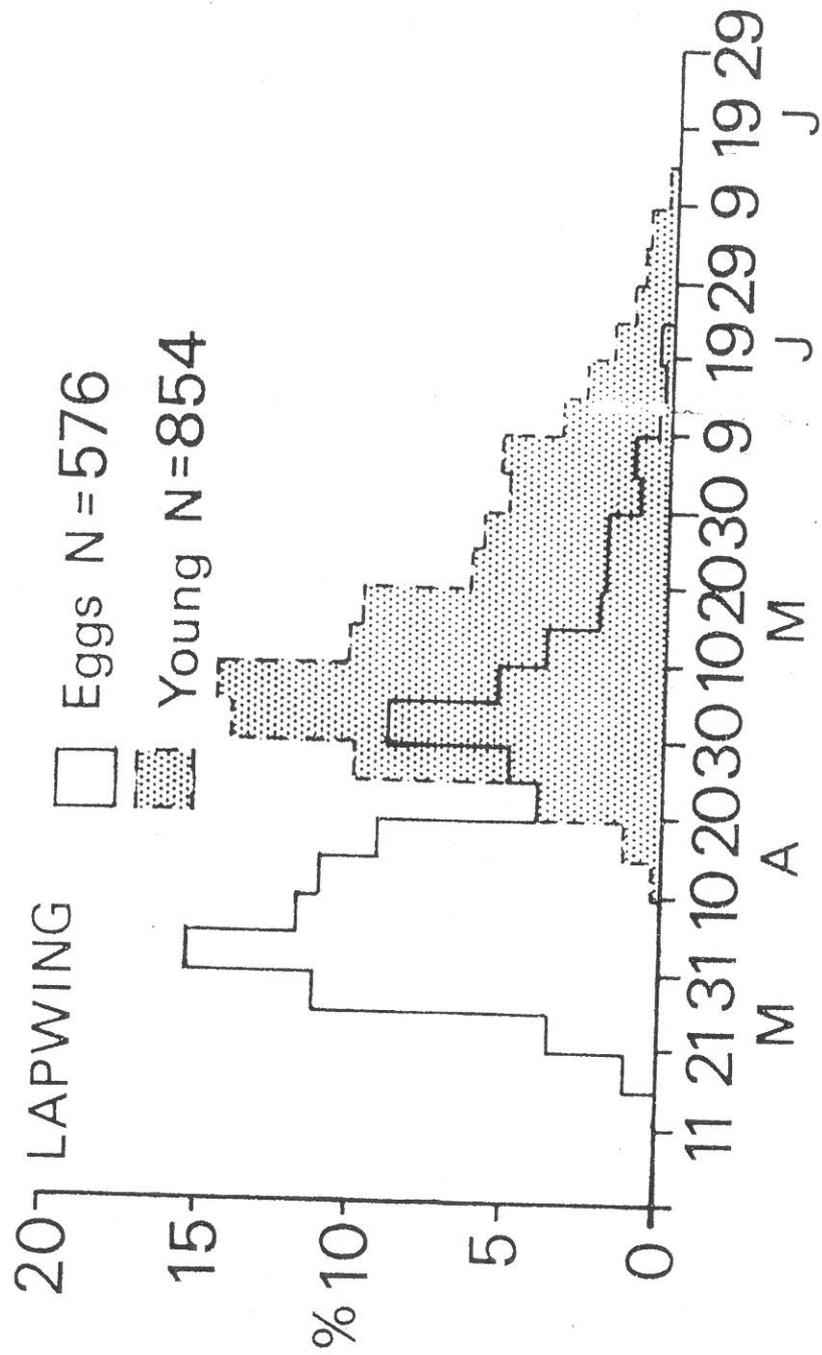
Figure 1. Distribution of Lapwing first egg dates and first hatching dates.
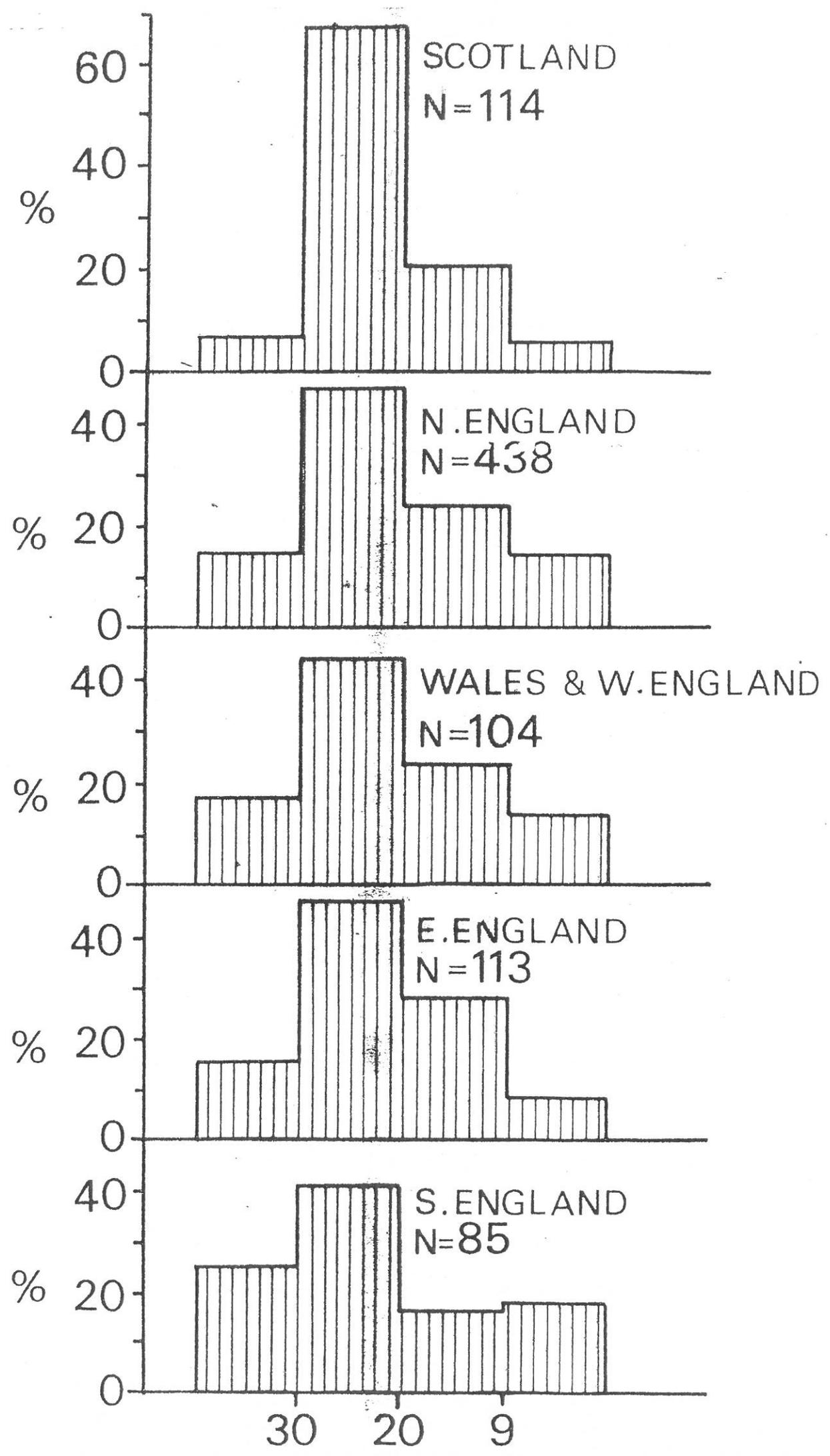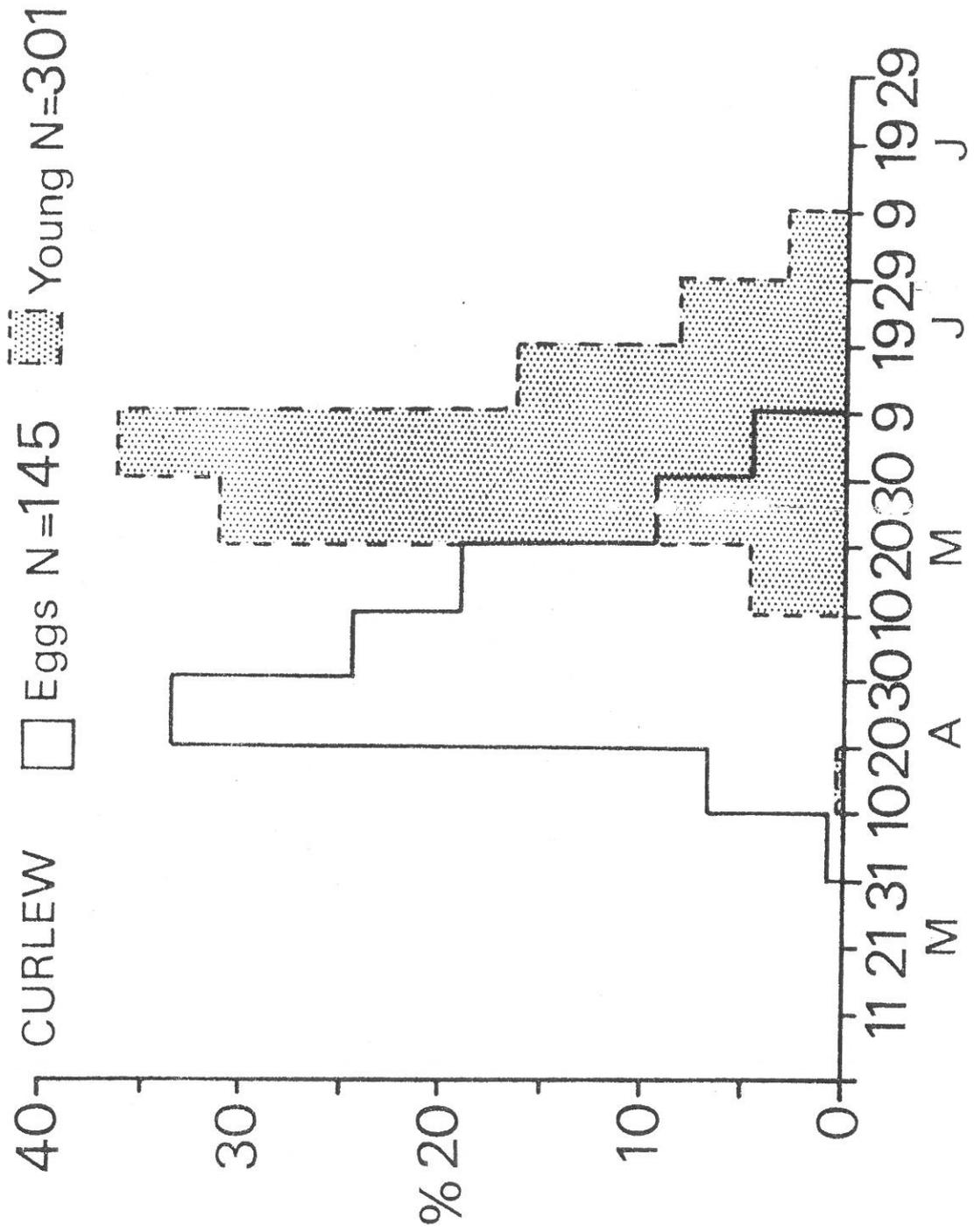
Figure 5. Distribution of Curlew first egg dates and first hatching dates.

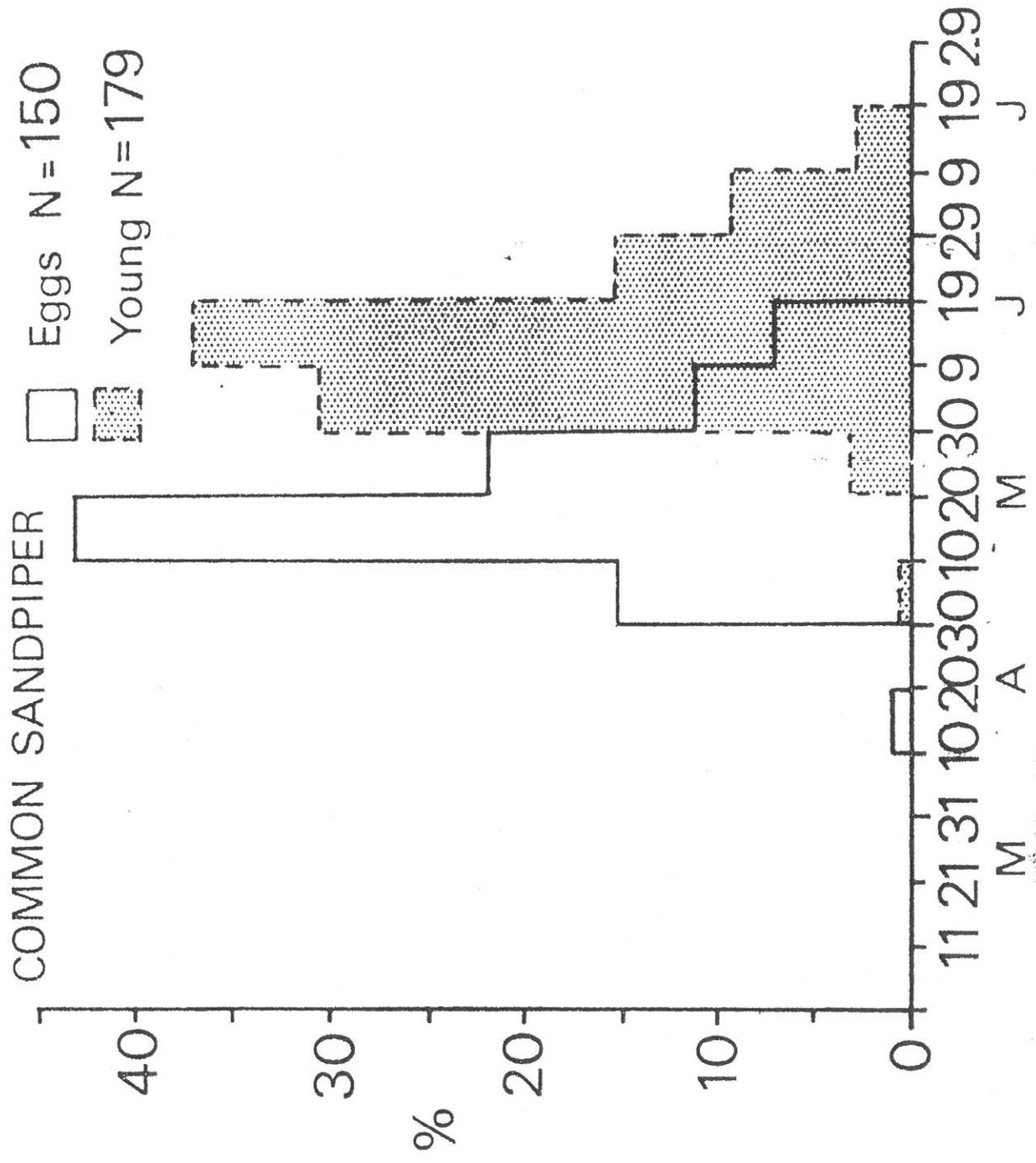Figure 6. Distribution of Curlew first egg dates in relation to altitude.

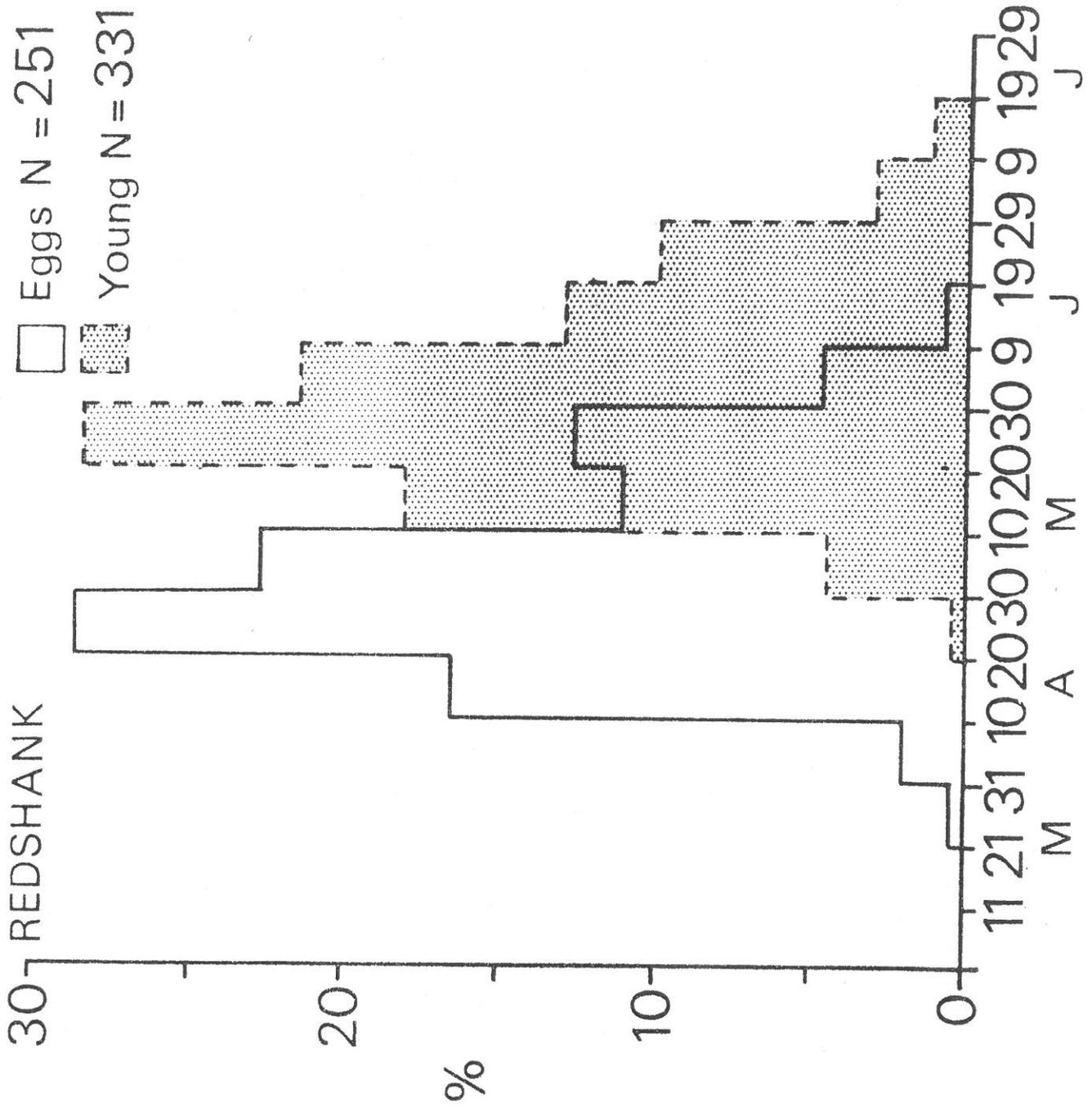Figure 7. Distribution of Common Sandpiper first egg dates and first

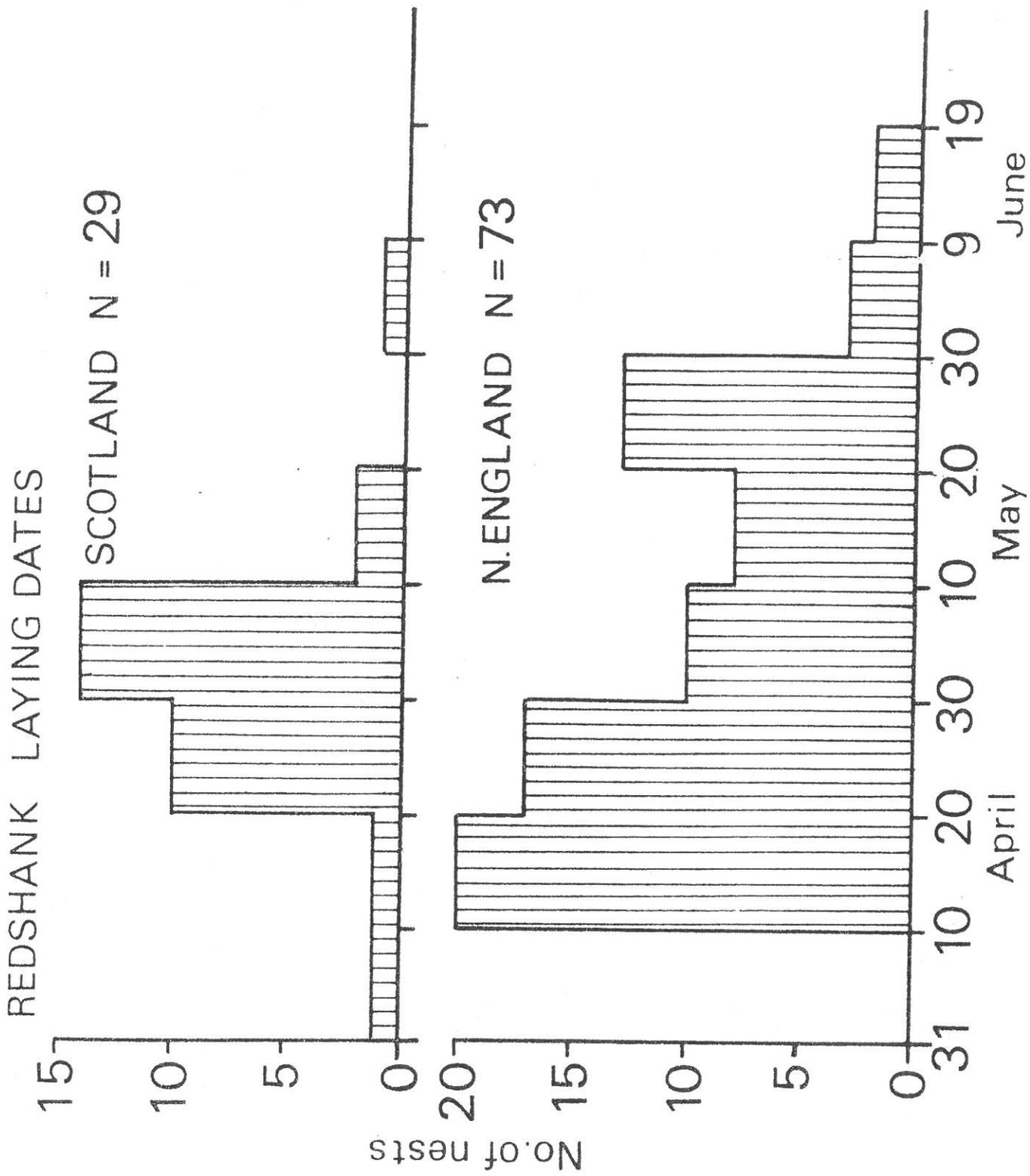Figure 8. Distribution of Redshank first egg dates and first hatching dates.

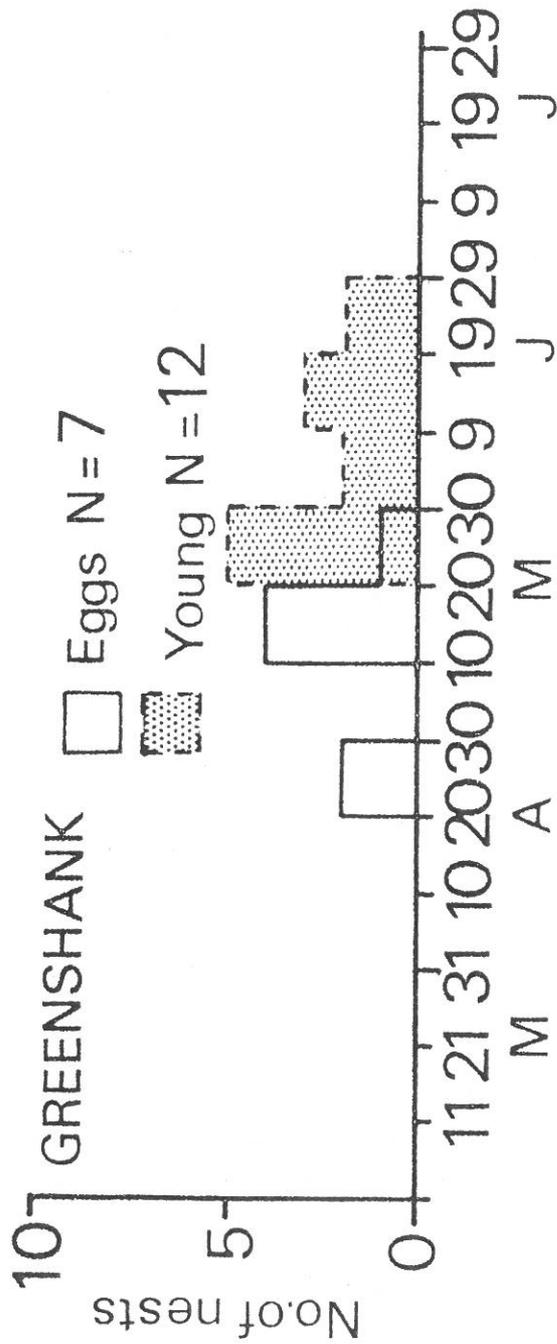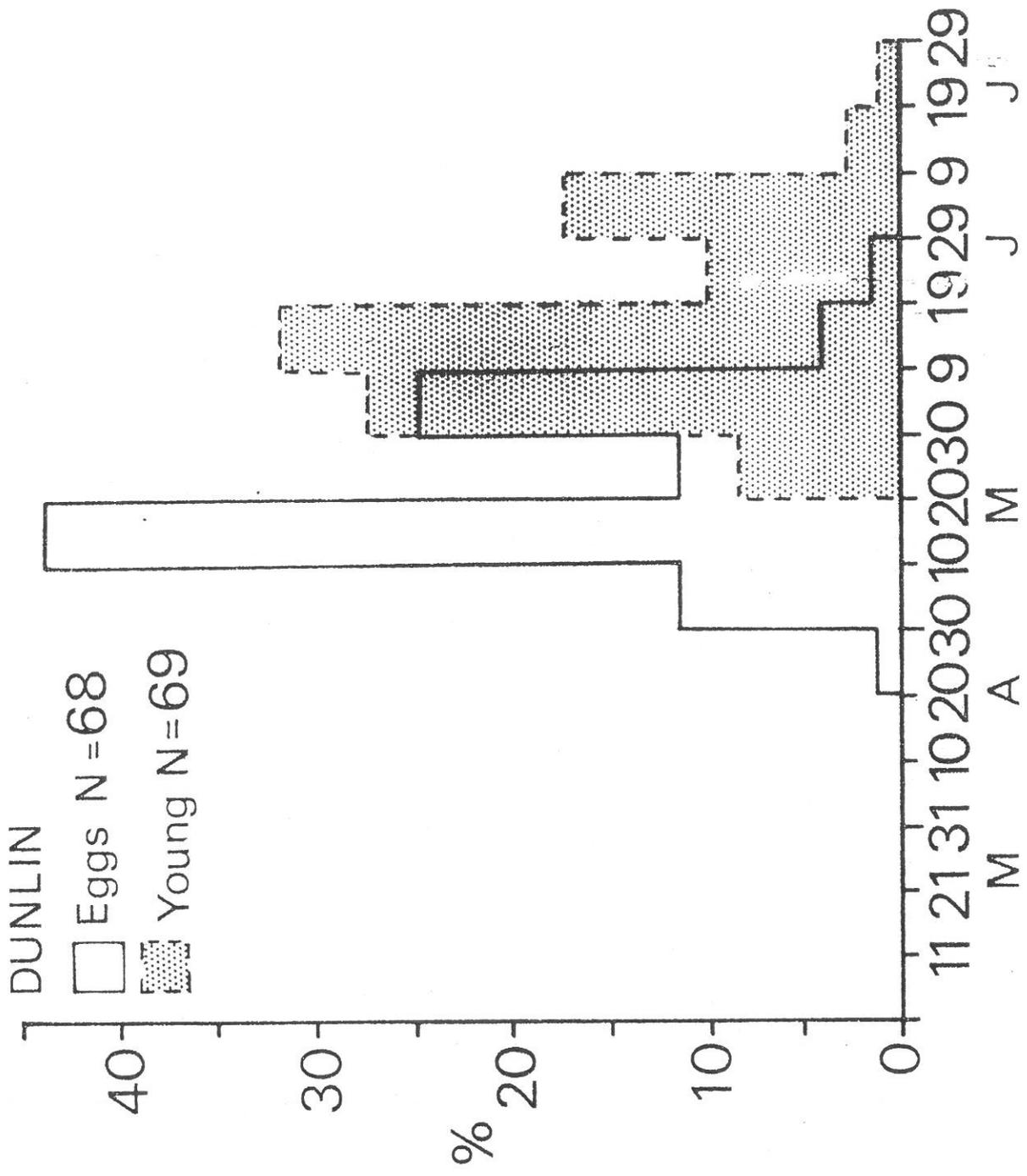Figure 9. Distribution of Redshank first egg dates by region.

Figure 10. Distribution of Greenshank first egg dates and first hatching dates.

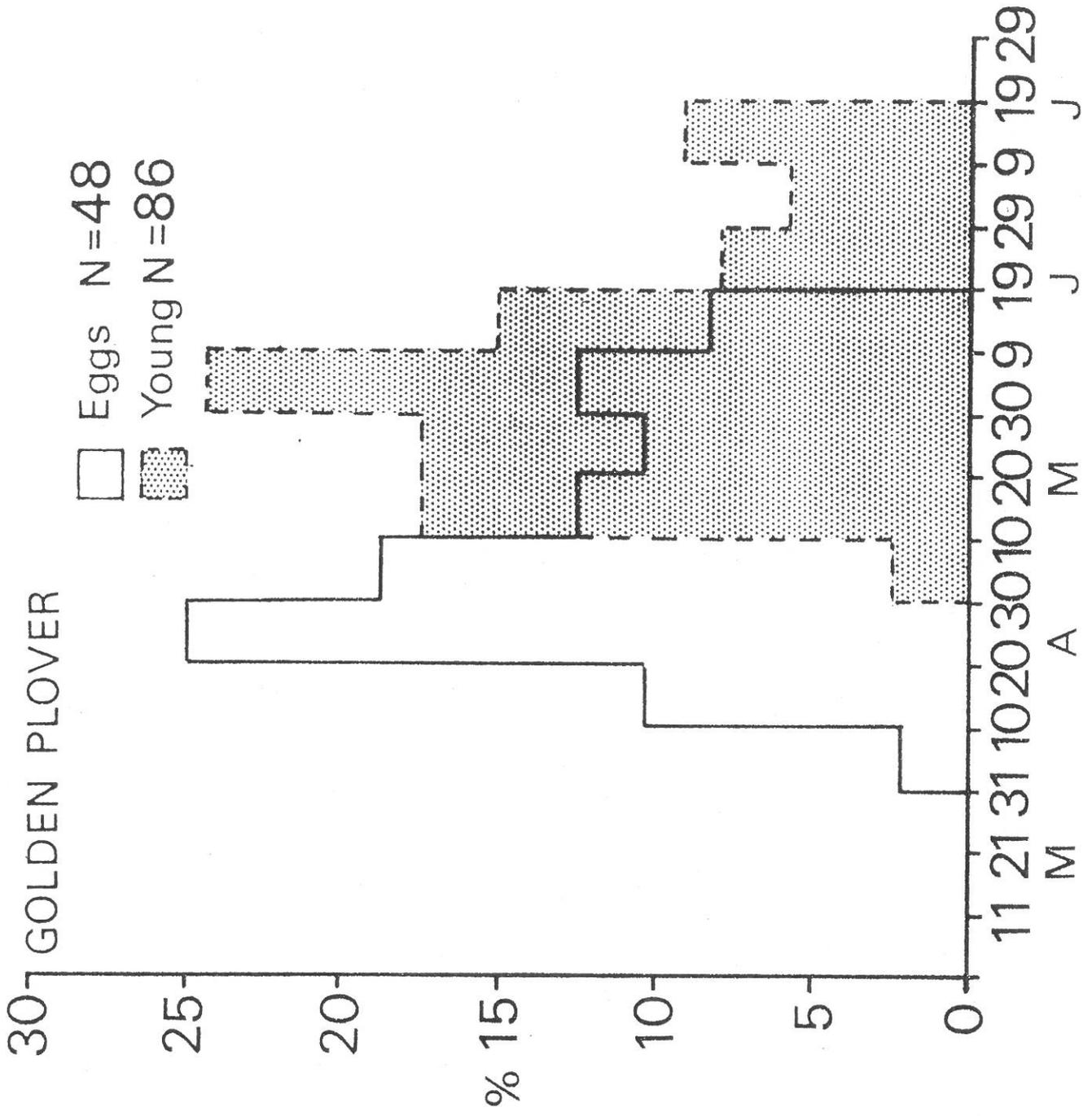Figure 11. Distribution of Dunlin first egg dates and first hatching dates.

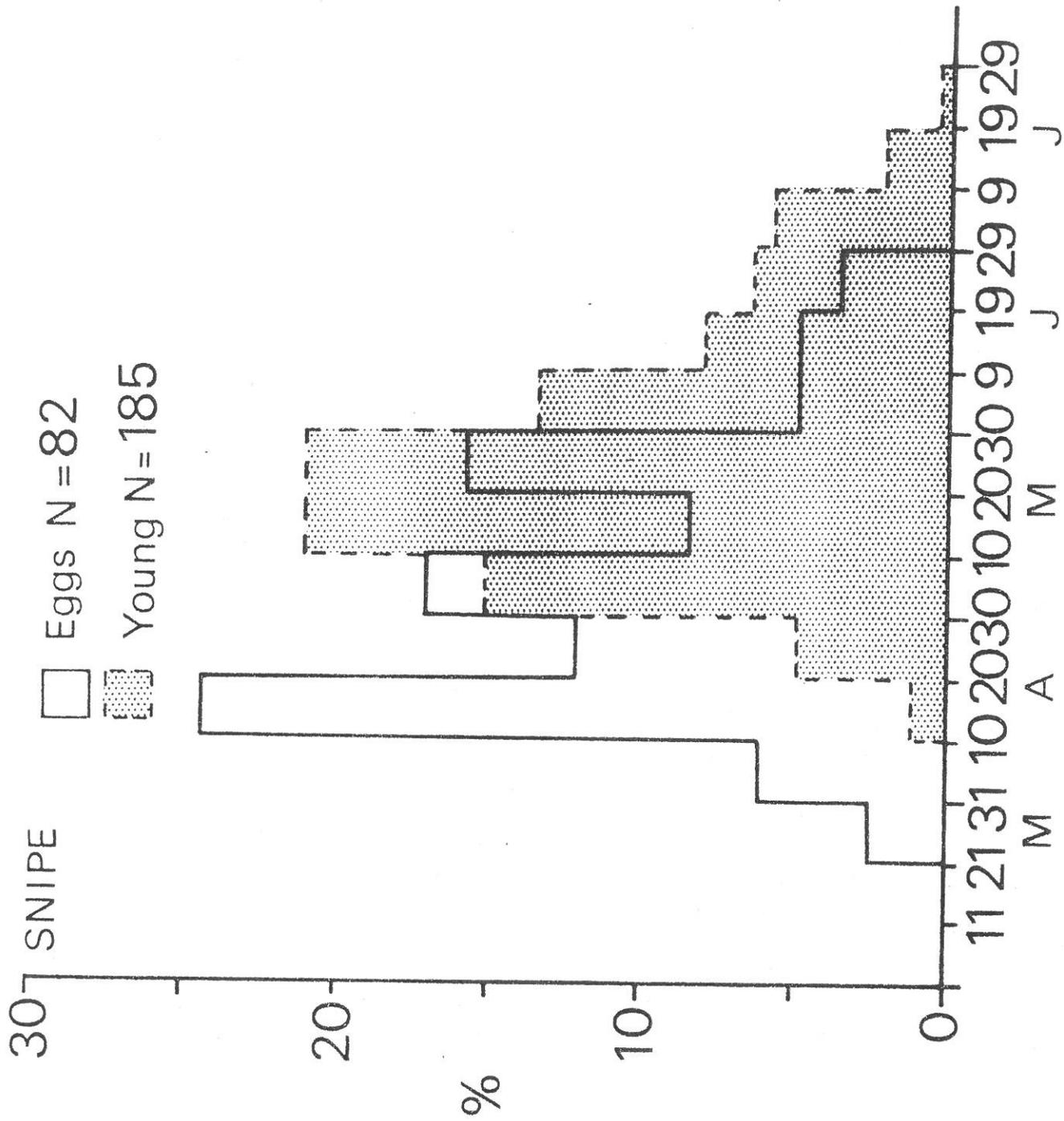Figure 3. Distribution of Golden·Plover first egg dates and first

Figure 4. Distribution of Snipe first egg dates and first hatching dates.