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TRENDS IN THE BREEDING PERFORMANCE OF GOLDEN PLOVER IN BRITAIN

by

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Comments: This report provides an analysis of Nest Record Cards in order to investigate any historical changes in nesting success of Golden Plover *Pluvialis apricaria* across different locations and habitats in Britain.

The species is of particular interest because of its inclusion in Annex one of the EEC Directive on the conservation of Wild Birds (79/409/EEC). Britain has an obligation to ensure the survival of Golden Plover as both a breeding and a wintering species. The range of habitats used by the species throughout the year is such that population decline in the species can be attributed to changes in land-use in the uplands and the lowlands. The most important of these changes that have had a direct effect on the extent of habitat available to breeding Golden Plovers have been afforestation of moorland in both upland and lowland areas, reclamation of moorland for agricultural expansion, over-grazing, reseeding and grassland improvement. The character and productivity of upland habitats has been altered to varying extents due to changes in land-use such as afforestation, increased grazing and a decline in traditional moorland management.

The results of the analysis of these nest record data show that individuals bred later and laid smaller clutches on grass- dominated moorland than did those on heather-dominated moorland and bog. Breeding in all habitats is delayed by cold and rain, both accounting for up to half the variation in timing of breeding. The variation in productivity and timing of breeding between moorland habitats is thought to be related to the difference in productivity of feeding areas.

The productivity of Golden Plovers nesting on heather moorland and on bogs has not changed significantly over the years for which data are available. However, there has been a marked decrease in the productivity of pairs nesting on grass moor, especially in NE England and Wales. This may be attributable to increase in stocking densities of sheep over the period.

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SUMMARY

1. 669 Nest Record Cards of the British Trust for Ornithology's Nest Record Scheme were analysed to investigate changes in nesting success of Golden Plovers by year, region and habitat.

2. Birds nesting on grass moorland bred on average 11 d later than those on heather moorland and bog.

3. Rain and low minimum daily temperatures in April and May delayed breeding in both habitats, accounting for 13-49% of the variance in timing of breeding. Altitude did not effect timing of breeding significantly, although there were relatively few records from very high altitudes (>600 m a.s.l.).

4. Clutches of Golden Plovers nesting on grass moorland were slightly smaller than those on heather moorland and bog. This could be due to early partial egg losses or to a real difference in the numbers of eggs laid.

5. Nest failure rates have not changed over the years for birds nesting on heather moorland and bog, but have increased significantly in NW England & Wales on grass moorland during 1982- 89 compared with earlier years. The most likely reason for this change is the increased stocking rates of sheep over the period.

RECOMMENDATIONS

1. A comprehensive field study on Golden Plovers should be undertaken to investigate breeding ecology and productivity in the three major U.K. habitats: upland grass, upland heather and blanket bog.

2. Particular attention in this comparative study should be paid to:

   a. The feeding ecology of adults and chicks in relation to their food supplies.

   b. The breeding productivity of populations in relation to their food supplies.

   c. The relationship between sheep stocking rates and nest losses.

   d. The importance of nest predation by crows and other avian predators.

3. The aims of such a study would be to predict whether Golden Plover populations would be sustainable in the U.K. if there is a continued loss of the apparently preferred bog and heather moor habitats, necessitating a switch to a greater proportion breeding on grass moors.

1. INTRODUCTION

The Golden Plover (*Pluvialis apricaria*), along with the Red Grouse (*Lagopus lagopus*), is a useful avian indicator species of 'upland' habitats in Britain (Fuller 1982). It is a bird of flat, gently sloping heather or grass moorland or bog (Ratcliffe 1976, 1990, Nethersole-Thompson & Nethersole-Thompson 1986). The British and Irish breeding populations are considered distinct and relatively isolated from the populations of Scandinavian birds that visit in winter (Ratcliffe 1990).

Concern has been expressed that the Golden Plover population in Britain has declined (Ratcliffe 1976, 1990). Sharrock (1976) estimated its population to be 30,000 pairs, but Marchant *et al.* (1990) suggests only 23,000 pairs. Indeed, there is evidence for a general decline of its southern populations throughout the western Palearctic (Cramp & Simmons 1983). It is listed on the European Communities Council Directive of April 1979 on the Conservation of Wild birds as requiring special protection and monitoring (NCC 1988). In all countries, the evidence for population decline is largely anecdotal and properly designed monitoring programmes need to be initiated.

There are a variety of possible reasons why Golden Plovers may have declined in Britain. These include habitat loss due to (a) afforestation, (b) agricultural improvement, but (c) loss or degradation of grouse moors is considered to be the most important factor (Ratcliffe 1976, 1990; Stroud *et al.* 1987; Parr 1990; Marchant *et al.* 1990). Other factors include: increasing populations of predators such as the Peregrine (*Falco peregrinus*); increasing populations of egg predators, particularly carrion Crows (*Corvus corone*) (Parr 1989, Ratcliffe 1990); increasing disturbance from recreational walkers on moorland (Yalden & Yalden 1989); and a general decline in productivity of the Western Highland and Islands of Scotland due to prolonged nutrient take- off by livestock (Ratcliffe 1976, 1990).

There have been very few detailed studies of Golden Plovers in Britain (see below), but they can provide evidence and reasons for local population declines only. A more general analysis of British population trends is currently underway by G.Boobyer of the Joint Nature Conservation Committee. This study was commissioned by the Joint Nature Conservation Committee to investigate a country-wide dataset, the BTO's Nest Record Cards, covering 1943-1989. An earlier analysis by Morgan (1982) covered the species briefly as part of a comparative study of breeding British waders. 669 nest records are examined below to explore variations in Golden Plover breeding performance over the years and to compare nesting success among major regions and habitats.

1.1 The Golden Plover

A brief summary of the Golden Plover's breeding biology in Britain is outlined below, based on the work of Ratcliffe (1976, 1990), Parr (1979, 1980), Nethersole-Thompson & Nethersole- Thompson (1986).

Flocks of Golden Plovers return to low-lying pastures near their breeding grounds in mid-February. Territory establishment takes place on adjacent, higher altitude moorland breeding grounds during March and the majority of

egg laying occurs in April and May. Pairs do not use their territories for feeding until their eggs hatch, but they fly up to 5 km to feed on pasture or, in more remote areas, to flush bog and spring complexes. Incubation is shared between the sexes, but is usually by the male in day-time and by the female at night. When the young hatch out, the brood may be divided between the parents. They leave the nest at 1-2 days and are led away to feed up to 1 km from the nest. The chicks take 4-5 weeks to fledge and then join the flock on the adjacent pastureland. Territorial defence ceases at hatching and non-breeding birds from the flock on adjacent pasture may take over such territories for their own nesting attempts. About 50% of birds that lose their nests try to re-nest, but second broods are unknown.

Golden Plover nests are among the hardest to find of British waders (Campbell & Ferguson-Lees 1972, Ratcliffe 1976) which explains why relatively few (669) have been recorded on BTO Nest Record Cards compared with Lapwing (16,585) or Ringed Plover (6,112). It is usually not possible to monitor accurately the progress of nidifugous chicks once they have left the nest, so the analyses below concentrate on the egg stage of the breeding cycle.

2. METHODS

Contributors to the British Trust for Ornithology's Nest Record Scheme complete Nest Record Cards (NRCs) to provide (a) details of a nest's location and (b) a record of its contents on each visit made by the observer. The information is computerised and estimates of certain variables, such as laying date, are calculated for each record by using reasonable values of a species' breeding parameters (Baillie 1988). These parameters include, for example, egg-laying interval and minimum and maximum incubation periods and are culled from the literature. Details of the 58 parameters are available from the BTO.

Estimates of three dates are used in this study: the first egg date (FED), last egg date (LED) and first hatch date (FHD). For each nest record, the earliest and latest possible FED, LED and FHD were calculated and, when these were less than 10 days apart, the midpoints were used in the analyses below. Although these are all measures of the timing of breeding, sample sizes differ between the three dates because cards differ in the amount of information they present. Given the paucity of Golden Plover NRCs, it was useful to compare the results obtained from the three dates to gain the maximal amount of information.

The records were divided according to regions used by the U.K. Meteorological Office. Amalgamation of closely allied regions was necessary to avoid the sample of NRCs from being too finely subdivided. The three regions used were: (a) West Scotland, (b) East Scotland/NE England/Midlands and (c) NW England /Wales (see Fig. 1, Table 2). Data for each region was provided from 7, 9 and 5 weather stations respectively (the stations were suitably spaced to provide representative records for each area; see Fig. 1). Weather data for each region were averaged over all stations and monthly means calculated for minimum daily temperature, snow- days (days with snow lying at 09.00 hrs) and rain-days (days with >0.2 mm rainfall) for each year from 1959-89.

The cards were split into three periods containing approximately equal numbers of cards: 1943-73, 1974-81, 1982-89 (any finer sub-division would have severely limited sample sizes and hence the value of the statistical tests performed).

Two main habitats were considered: Upland Heather Moor and Bog (HEATHER-BOG), and Upland Grass (GRASS) (including the few records for rough grazing and pasture which were from relatively high altitude sites near moorland). Unspecified Moor is also discussed occasionally, and included the records for wet heath, unspecified heath and rock.

Statistical analyses were undertaken using SAS programs (SAS 1985). The distribution of First Egg Dates (FEDs) was normalized by transformation to the reciprocal (Kolmogorov-Smirnov, $D=0.076$, $n=127$, $p=0.071$). The reciprocals of Last Egg Dates (LEDs) and First Hatch Dates (FHDs) were significantly different from normal ($D=0.091$, $n=180$; $D=0.083$, $n=190$ respectively), but normal probability plots were nearly straight, suggesting that analysis of variance could be used on these transformed data with caution.

3. RESULTS

3.1 General information and natural history

The oldest NRCs date from 1943 but annual intakes only surpassed 20 after the early 1970s. The numbers of NRCs received for each decade are shown in Table 1.

The geographical distribution covered by NRCs broadly reflects that of the Golden Plover in Britain (Table 2, Sharrock 1976), although there are disproportionately few from Scotland and none from the small population in South-West England.

The most frequently recorded habitats on NRCs were Upland Heather Moor (27.8%), Upland Grass Moor (18.5%), Unspecified Moor (38.7%) and Bog (11.8%). Small numbers (<1%) of NRCs were recorded from woodland (n=2), Bracken (1), wet heath (1), unspecified heath (5), open-montane (2), rock area (4), pasture (1) and rough grazing (4).

The altitudinal distribution of NRCs ranged from 6 m to 991 m a.s.l. with a median of 411 m a.s.l. Altitude was recorded for 605 nests and the majority fell between 300-600 m a.s.l. (Table 3).

Two unusual natural history observations were recorded on the cards and are noted here for general interest. One concerned a Golden Plover nest with 2 eggs that also contained a Lapwing egg, an unusual but not unique record of interspecific clutch mixing among waders (Larson 1978, Breiehagen 1983). The other concerned a Golden Plover nest positioned only 1.5 m from the nest containing 9 eggs of a Red Grouse. The outcomes of all these nests were unknown.

3.2 Laying and Hatching Dates

The frequency distributions of FED, LED and FHD are shown in Fig 2. There is a small secondary peak in June that could represent relays after failure (Ratcliffe 1976, Nethersole-Thompson & Nethersole-Thompson 1986) or sequential breeding of different pairs on the same territory (Parr 1979). Summary statistics for FED, LED, and FHD are presented in Table 4a.

3.2.1 Altitude

FED, LED, and FHD were not significantly different between the altitude classes given in Table 3 (Kruskal- Wallis tests, $p>0.2$) and Pearson correlations on reciprocal- transformed data with altitude were also not significant. The lack of relationship between FED, LED or FHD with altitude was confirmed when nests on HEATHER-BOG and GRASS were considered separately, with or without nests in West Scotland (which occur at significantly lower altitudes than those in other areas).

3.2.2 Habitat, Region and Years

Three-way ANOVA on reciprocal- transformed data were highly significant: FED, $F_{14,84}=2.35$, $p=0.010$; LED, $F_{14,108}=2.46$, $p=0.005$; FHD, $F_{14,117}=3.17$, $p=0.0004$. However, the significance of the individual components and their interactions were not significant (only one was just significant at $p=0.049$), indicating that the three independent variables were highly correlated with each other, violating the assumptions of ANOVA (Sokal & Rohlf 1969). Indeed, contingency table analysis of the three variables showed a close association between the NW England/Wales Region with GRASS and the 1974-81 period, as well as one between the W Scotland and E Scotland/NE England/Midlands Regions with HEATHER-BOG and the 1982-89 period (X^2 tests, $P<0.003$; Table 4b). To disentangle this complex situation, while maintaining sufficient sample sizes in each classification, a series of one-way ANOVAs was undertaken on subsets of the data and Tukey's Standardized Range Tests identified the significant pairwise comparisons (Table 5).

Golden Plovers nesting on HEATHER-BOG bred at around the same time of year in all regions and periods (mean FEDs = 22-25 April). The results from W Scotland and E Scotland/NE England/Midlands regions suggested that birds nesting on GRASS laid later than those on HEATHER-BOG (by an average of 11 days). (This difference was not apparent in the NW England/Wales region, but sample sizes were small and further work is needed to confirm or deny this suggestion.)

Among birds nesting on GRASS, those in the NW England/Wales region hatched their eggs about 11 days later than those in E Scotland/NE England and about 20 days later in 1974-81 than in 1982-89. Since these results were not paralleled in laying dates, their importance is difficult to interpret.

3.2.3 Weather

The effect of the weather in April and May on the timing of breeding was investigated by multiple regression on reciprocal-transformed FED, LED and FHD for individual nests. The weather variables included in the analyses were mean minimum temperature (TMIN), rain-days (RAIND) or snow-days (SNOWD) for each month and the combination was sought that explained the highest proportion of the variance (highest R^2) while producing a significant overall regression at the $P<0.05$ level. Given that breeding dates in W Scotland and E Scotland/NE England/Midlands regions were shown to be highly correlated, these regions were combined below to investigate the effect of weather on the timing of breeding.

The most important factor that appeared to delay breeding in both habitats was rain: in April for GRASS nests and in May for

HEATHER-BOG nests (Table 6). In the Scotland/NE England/Midlands region, low temperatures in April and May also contributed to delayed breeding. The weather factors explained an important part of the variance in the timing of breeding: R^2 values ranged from 13-49%.

3.3 Clutch size variation

The vast majority (96%) of 490 completed clutches were of 4 eggs, but there were 18 of 3 eggs and 3 of 2 eggs. It is possible that clutches of 2 and 3 eggs had suffered partial losses before observations began (Shrubb 1990). Two additional nests contained unusually large clutches, one of 5 and another of 7 eggs, the latter was almost certainly the product of two females. Mean clutch size (excluding the latter two nests) was 3.95. Regression of clutch size with First Egg Date was significant (Clutch= 4.31-(0.00372547xFED), $F_{1,109}$=4.20, p=0.043), suggesting a slight seasonal decline.

Clutch sizes did not differ between regions and periods. Clutches from GRASS were slightly smaller (mean=3.90, n=100) than those on HEATHER-BOG (Mean=3.96, n=202, Kruskal-Wallis p=0.044). The difference is slightly greater than that expected from the difference in laying date of 11 days between the two habitats. (From the regression equation above, average GRASS clutches would be predicted to be 0.041 smaller than HEATHER-BOG).

3.4 Nest losses

3.4.1 Causes of loss

Very few records reported the causes of nest destruction or losses of eggs. Egg predation by Carrion Crows was suspected in five instances, by a gull (species unknown) once and by a stoat once. Trampling by livestock, either sheep or unknown, was recorded on five occasions and fire was blamed for the loss of one nest. Two nests were deserted possibly due to disturbance from walkers: one "after a very hot and crowded weekend" on Danby Beacon, N.Yorks., and another, which was close by a general pathway to the summit of Pendle Hill, Lancs.

3.4.2 Hatching success

Hatching was recorded at 33% of 669 Golden Plover nests, and failure before hatching at 6% (39) of nests. Unfortunately, hatching success or failure was unknown for the vast majority of nests (61%), but if these were not biassed toward success or failure then, of those nests followed to an outcome (n=260), 15% failed and 85% were successful. This success rate is considerably higher than that recorded elsewhere for Golden Plovers (Ratcliffe 1976, Campbell 1978) and is higher than that expected from Mayfield analyses of NRC data (see

below). Therefore the recording of nests through to hatching was biassed toward those found near the end of the incubation period and too few were followed through from egg-laying.

3.4.3 Nest-failure rates

Nest failure rates were calculated using Mayfield's (1961, 1975) method and standard errors calculated after Johnson (1979). There were too few nests in individual years for the calculation of annual nest failure rates, so they were calculated over the periods used in the rest of the analysis (Table 7). (Means were considered to be significantly different if they did not lie within 2x the standard error of each other).

Over all nests, the mean daily nest failure rate was lower in 1982-89 than the peak in 1974-81. Nests on HEATHER-BOG paralleled this general trend. Nests on GRASS showed no change from the early years to the 1970s, but their failure rate then trebled in 1982-89.

It was possible to split the data into geographical regions, but samples became very small in some cases and the following results should be treated with caution. When the two regions NW England/Wales and Scotland/NE England were considered separately, the failure rate on HEATHER-BOG had changed very little over the years. (Although the failure rate in NW England/Wales was very high in 1974-81, the standard error was also relatively large). However the failure rate on GRASS in NW England/Wales increased by an order of magnitude in the 1980s.

In Scotland/NE England, the failure rate on GRASS was not significantly different from that on HEATHER-BOG over 1974-81 or in 1982-89. In NW England/Wales the failure rate on GRASS increased from equality to six times that on HEATHER-BOG in 1982-89.

When these daily nest failure rates were translated into the proportions of nests failing over 30 days incubation (Table 7), between 22-38% of nests failed before hatching. The failure rate of GRASS nests in the 1980s was double that in the 1970s and treble that of nests on HEATHER-BOG in the 1980s. These differences were caused by GRASS nests in NW England/Wales, of which 96% failed before hatching, compared with 28-41% elsewhere or in previous years.

4. DISCUSSION

Ratcliffe (1976, 1990) proposed that although Golden Plovers occur widely on acidic grasslands, they prefer to nest on heather moors and blanket bogs. The highest densities of breeding pairs occur on upland limestone grassland, a relatively rare and highly localized habitat in Britain, but the next highest densities occur on recently burnt heather moors. Long heather and tall tussocky grass is avoided by Golden Plovers as it limits the ability to detect predators and provides a difficult terrain for young chicks to move through (Ratcliffe 1976). They prefer areas of recently burned heather (Campbell 1978) and therefore benefit from management of heather moors for grouse. The control of nest predators on grouse moors, especially crows, may also increase the chance of Golden Plovers nesting successfully (Parr 1989, Ratcliffe 1990).

The analyses of Nest Record data sheds light on the reasons for these habitat preferences. Golden Plovers nesting on grass moorland tend to lay between one and two weeks later than those on heather moorland or bog in the same region and they have a smaller average clutch size. This could be due to two factors or a combination of them: Firstly, Golden Plovers suffer from a higher rate of nest losses on grassland than heather moor and bog, and the later laying dates may be a result of a higher proportion of relays after failure. Secondly, grassland may be a less productive habitat generally than heather moor and bog. Egg- laying is energetically costly to Golden Plovers: they have one of the largest eggs of the Charadriidae at 16.2% of the female's weight (Lack 1968) and a clutch of four eggs can weigh up to 73% of the female's weight (compared to 46% for the Lapwing) (Nethersole-Thompson & Nethersole-Thompson 1986). Prior to egg- laying, females spend 60-90% of their time feeding, which compares with c. 20% at later stages of the nesting cycle (Byrkjedal 1985). The delay in laying shown by Golden Plovers on grassland may be due to poorer food supplies, also explaining why they occur at lower densities than on heather and bog. Golden Plovers nesting on heather fly to highly productive improved grassland to feed (Ratcliffe 1976, Parr 1980), but it may be the case that birds nesting on grassland actually use their territories for feeding prior to egg-laying. The productivity of upland grass is less than that of improved pasture and this may be reflected in the longer time to attain the condition required for egg-laying. Thomas (1986) investigated the productivity of Golden Plovers in the South Pennines, to compare birds on limestone grassland with those on blanket bog; the results were inconclusive because of the study's short duration and small samples of birds. Comparative studies of Golden Plovers nesting on grass and heather moors are needed to test these hypotheses.

The influence of weather on the timing of breeding showed that rain and cold temperatures around the time of laying can delay its onset. Contrary to Parr's (1980) findings, there was no effect of snow cover on laying date. However, his may have been a local manifestation of more general effect of precipitation on laying. Surprisingly, there was no influence of altitude on laying dates, even when the low altitude nests from the North of Scotland and the Scottish Islands were removed. Ratcliffe (1976) and Nethersole-Thompson & Nethersole-Thompson (1986) suggested that birds at higher altitudes tend to lay later, but the effect of weather acting equally on birds at medium and high altitudes may have masked this effect or there may not

have been enough data from really high altitudes (>600 m a.s.l.). Byrkjedal (1978) found a great delay in nesting by birds nesting at 1300 m a.s.l. in Norway compared with those at 300 m a.s.l., but the influence of snow cover seemed paramount at those greatly elevated levels.

The nesting success of Golden Plovers on grassland in the NW England/Wales region apparently fell dramatically in the 1980s compared with earlier years. There was not a corresponding decrease for those birds nesting on heather moors and bogs. Although the dataset is very limited, this result is unlikely to have been the effect of (a) increased recreational pressure because similar effects would have been expected on heather moors or (b) increased corvid predation because populations of crows have levelled off in the 1980s after big increases in the previous two decades (Marchant *et al.* 1990). Instead, the fall in nesting success in this region may be due to increased stocking rates of sheep on upland grass in response to the Hill Livestock Compensatory Allowances (Mowle & Bell 1988). Nesting Lapwings have suffered increasingly from trampling and desertion due to sheep on upland areas (Shrubb 1990) and there is no reason to suspect that Golden Plovers should not be affected similarly. Partial nest losses due to sheep may be a cause for the lower mean clutch size recorded from grassland areas, as Shrubb (1990) has observed for Lapwings.

Information from MAFF (1979-88) and DAFS (1979-88) show large differences between regions in sheep stocking rates (Table 8). Not only are sheep at much higher densities in NW England/Wales than in Scotland/NE England/Midlands (1.6-2.8 times higher), but that numbers have been rising faster too. These changes are apparent whether the large area of Highland Region is included or not.

One of the main threats to Golden Plover populations is due to afforestation of moorland and bog (Thompson *et al.* 1988, Ratcliffe 1990, Parr 1990). Stroud et al.'s (1987) analysis of habitat preferences of Golden Plovers and foresters in the Flow Country of Sutherland and Caithness suggested that forestry has already caused the loss of 19% of the Golden Plovers in that area and would cause more in the future. It is not just the loss of the area covered by plantations that affects Golden Plovers because there is evidence that they avoid moorland blocks that are enclosed by forestry (Thompson *et al.* 1988) and that nesting densities are lower on moor that is closely adjacent to plantations compared with distant moor (Parr 1990), although this latter effect could be due to vegetational or landscape differences (Avery 1989). If forestry tends to occur preferentially on heather moors and bog, if grouse moors continue to be lost (Ratcliffe & Thompson 1988) and if heather moor continues to be transformed into grassland by grazing, then Golden Plovers may have to depend increasingly on the less productive grass moors. If these areas are subject to increasing stocking rates and the remaining heather moors are subject to more recreational disturbance, then the lowered nesting success and productivity of Golden Plover populations in Britain may affect their viability.

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7. TABLES

Table 1: Totals of Nest Record Cards received by the BTO for 10-year periods.

Years	n	% of Total
1940-49	8	1.2%
1950-59	56	8.4%
1960-69	83	12.4%
1970-79	229	34.2%
1980-89	293	43.8%

Table 2: The regional distribution of Golden Plover Nest Record Cards.

		n	%
West Scotland			
	Central	2	0.3
	Dumfries & Galloway	4	0.6
	Highland	81	12.1
	Orkney	10	1.5
	Strathclyde	16	2.4
	Shetland	47	7.0
	Western Isles	10	1.5
	Region unrecorded	1	0.1
	TOTAL	171	25.6
East Scotland, NE England & Midlands			
	Borders	4	0.6
	Cheshire	3	0.4
	Derbyshire	61	9.1
	Durham	74	11.1
	Grampian	14	2.1
	Greater Manchester	10	1.5
	Lothian	3	0.4
	Northumberland	38	5.7
	North Yorkshire	104	15.5
	Staffordshire	2	0.3
	South Yorkshire	6	0.9
	Tayside	22	3.3
	West Yorkshire	21	3.1
	TOTAL	362	54.1
NW England & Wales			
	Clwyd	37	5.5
	Cumbria	65	9.7
	Dyfed	1	0.1
	Lancashire	23	3.4
	Powys	10	1.5
	TOTAL	136	20.3

Table 3: Altitudinal distribution of Golden Plover Nest Records.

Altitude (m a.s.l.)	n	%
0-99	54	8.0
100-199	61	9.2
200-299	50	7.4
300-399	118	17.7
400-499	119	17.8
500-599	146	21.8
600+	57	8.5

Table 4a: Summary Statistics for laying and hatching dates (1 March = day 60).

	First Egg Date	Last Egg Date	First Hatch Date
Range	29 Mar-19 Jun	5 Apr-25 Jun	23 Apr-24 Jul
Median	26 Apr	2 May	31 May
Mode	28 Apr	5 May	16 May
Mean*	117.75 (28 Apr)	123.14 (3 May)	151.84 (1 Jun)
Mean +/- 2xS.E.*	114.91-120.73 (25 Apr-1 May)	120.92-125.45 (1 May-5 May)	146.60-154.14 (27 May-3 Jun)
n	127	180	190

*Back-transformed from distributions of 1/FED, 1/LED and 1/FHD.

Table 4b: Numbers of NRCs recorded in each REGION/HABITAT/YEAR category

(i)	W Scotland	E Scotland/ NE England/ Midlands	NW England/ Wales
HEATHER-BOG	65	163	37
GRASS	16	53	60
(ii)			
	1943-73	23	4524
	1974-81	22	5944
	1982-89	36	11229

Table 5: Comparison of Habitat, Region and Period with respect to FED, LED and FHD, using one-way ANOVAs on reciprocal-transformed data; significant pairwise comparisons were identified using Tukey's Studentized Range Test.

		F.E.D.			L.E.D.			F.H.D.		
	Factor	F	n	p	F	n	p	F	n	p
(a)	HEATHER-BOG Only									
	Region	1.38	51	n.s.	1.92	65	n.s.	1.81	67	n.s.
	Period	0.82	51	n.s.	0.71	65	n.s.	0.79	67	n.s.
(b)	GRASS Only									
	Region	0.68	33	n.s.	0.83	43	n.s.	3.23	50	0.0486*
	Period	0.52	33	n.s.	3.49	43	0.0401*	8.83	50	0.0006*
(c)	NW England/Wales Only									
	Habitat	2.51	29	n.s.	1.84	35	n.s.	1.57	37	n.s.
	Period	0.23	29	n.s.	1.04	35	n.s.	1.48	37	n.s.
(d)	Scotland/NE England/Midlands Only									
	Habitat	4.62	55	0.0362*	2.98	73	n.s.	0.05	80	n.s.
	Region	1.29	55	n.s.	2.07	73	n.s.	3.17	80	n.s.
	Period	2.24	55	n.s.	3.91	73	0.0245*	5.84	80	0.0043*
(e)	as (d) but without 1982-89 period									
	Habitat	3.35	23	0.0813*	3.79	35	0.0600*	3.80	37	0.0592*
	Region	0.04	23	n.s.	0.30	35	n.s.	0.33	37	n.s.
	Period	0.13	23	n.s.	1.05	35	n.s.	1.03	37	n.s.

* Tukey's tests showed that all significant results for Habitat, Region and Period were due to higher values for GRASS than HEATHER-BOG, for NW England/Wales than NE England/Midlands, and for 1974-81 than 1982-89; except for Period differences between LEDs in GRASS only, when there were no significant Tukey tests.

Table 6: The relationships between April and May weather and FED, LED and FHD (analysed by multiple regression on reciprocal transformed data).

	Weather variables (significance)		Overall Significance	p	R^2
(a)	HEATHER-BOG: Scotland/NE England/Midlands				
FED	$RAIND_{May}$	(0.008)	$F_{3,38} = 4.52$	0.009	0.28
	$1/TMIN_{May}$	(0.038)			
	$1/TMIN_{April}$	(0.046)			
LED	$RAIND_{May}$		$F_{1,49} = 6.99$	0.011	0.13
FHD	$RAIND_{May}$		$F_{1,9} = 3.07$	0.008	0.14
(b)	GRASS: Scotland/NE England/Midlands				
FED		-	$F_{1,11} = 2.00$	n.s.	
LED		-	$F_{1,17} = 2.29$	n.s.	
FHD	$RAIND_{April}$	(0.021)	$F_{3,22} = 5.72$	0.006	0.49
	$1/TMIN_{April}$	(0.004)			
	$1/TMIN_{May}$	(0.001)			
(c)	GRASS: NW England/Wales				
FED	$RAIND_{April}$		$F_{1,22} = 5.90$	0.025	0.23
LED	$RAIND_{April}$		$F_{1,25} = 7.09$	0.014	0.24
FHD	$RAIND_{April}$		$F_{1,27} = 7.00$	0.014	0.22

Table 7a: Daily failure rates of Golden Plover nests during incubation. Figures given are: Mean (S.E.)

		1943-73	n	1974-81	n	1982-89	n
(i)	Britain						
	ALL	0.0098 (0.0035)	67	0.0158 (0.0037)	81	0.0081 (0.0023)	112
	GRASS	0.0118 (0.0114)	8	0.0123 (0.0205)	38	0.0328 (0.0124)	21
	HEATHER-BOG	0.0075 (0.0052)	22	0.0164 (0.0164)	21	0.0076 (0.0027)	67
(ii)	Scotland/NE England/Midlands						
	GRASS	0.0375 (0.0328)	3	0.0087 (0.0086)	8	0.0109 (0.0087)	12
	HEATHER-BOG	0.0096 (0.0067)	18	0.0066 (0.0064)	12	0.0053 (0.0025)	56
(iii)	NW England/Wales						
	GRASS	0.0000 (0.0000)	5	0.0130 (0.0045)	30	0.1004 (0.0375)	9
	HEATHER-BOG	0.0000 (0.0000)	4	0.0744 (0.0340)	9	0.0174 (0.0099)	11

Table 7b: Average proportion of nests that fail over 30 days incubation, calculated from the daily failure rates in Table 7a.

(i) Britain

ALL	26%	38%	*	22%	
GRASS	30%	31%	*	63%	*
HEATHER-BOG	20%	39%		20%	

(ii) Scotland/NE England/Midlands

GRASS	68%	23%	28%	
HEATHER-BOG	25%	18%	15%	
				*

(iii) NW England/Wales

GRASS	0%	32%	*	96%	
HEATHER-BOG	0%	90%		41%	*

* Differences (connected by lines) were considered significant when the mean daily failure rates did not lie within two standard errors of each other.

Table 8: Sheep numbers in the 8 major counties for Golden Plover NRCs. (Data from MAFF (1979-88) and DAFS (1979-88).

(a)

	Mean no. Sheep 1978-81	1982-87	Increase
NW England/ Wales*	2,771,876	3,264,210	17.8%
Scotland/NE England/ Midlands*			
+ Highlands	4,903,413	5,551,615	13.2%
- Highlands	3,754,425	4,312,778	14.9%

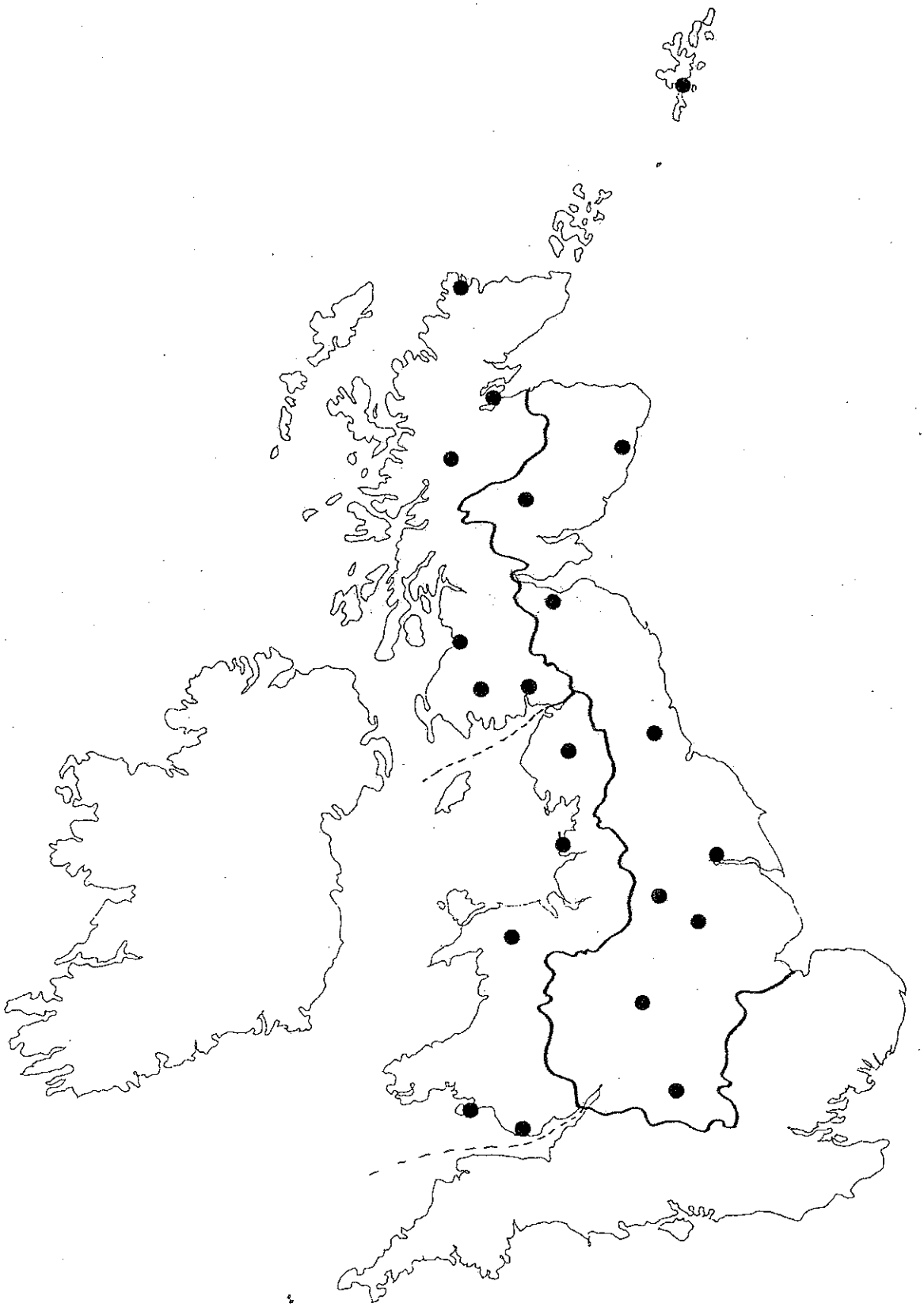
(b)

	County Area* (km^2)	Sheep Density (km^{-2}) 1978-81	1982-87
NW England/ Wales*	9,361	296	349
Scotland/NE England/ Midlands*			
+ Highlands	44,968	109	123
- Highlands	19,844	189	217

* The counties used were those contributing at least 5% of Golden Plover NRCs (see Table 2). County areas were obtained from Mason (1977); sheep densities will be underestimated, but this bias is unlikely to affect the conclusions greatly because the percentage cover of grass and rough grazings is approximately equal in the different areas.

8. FIGURES

Figure 1: Map of the regions used in the analysis of Golden Plover Nest Record Cards and of the locations of weather stations that supplied weather data.



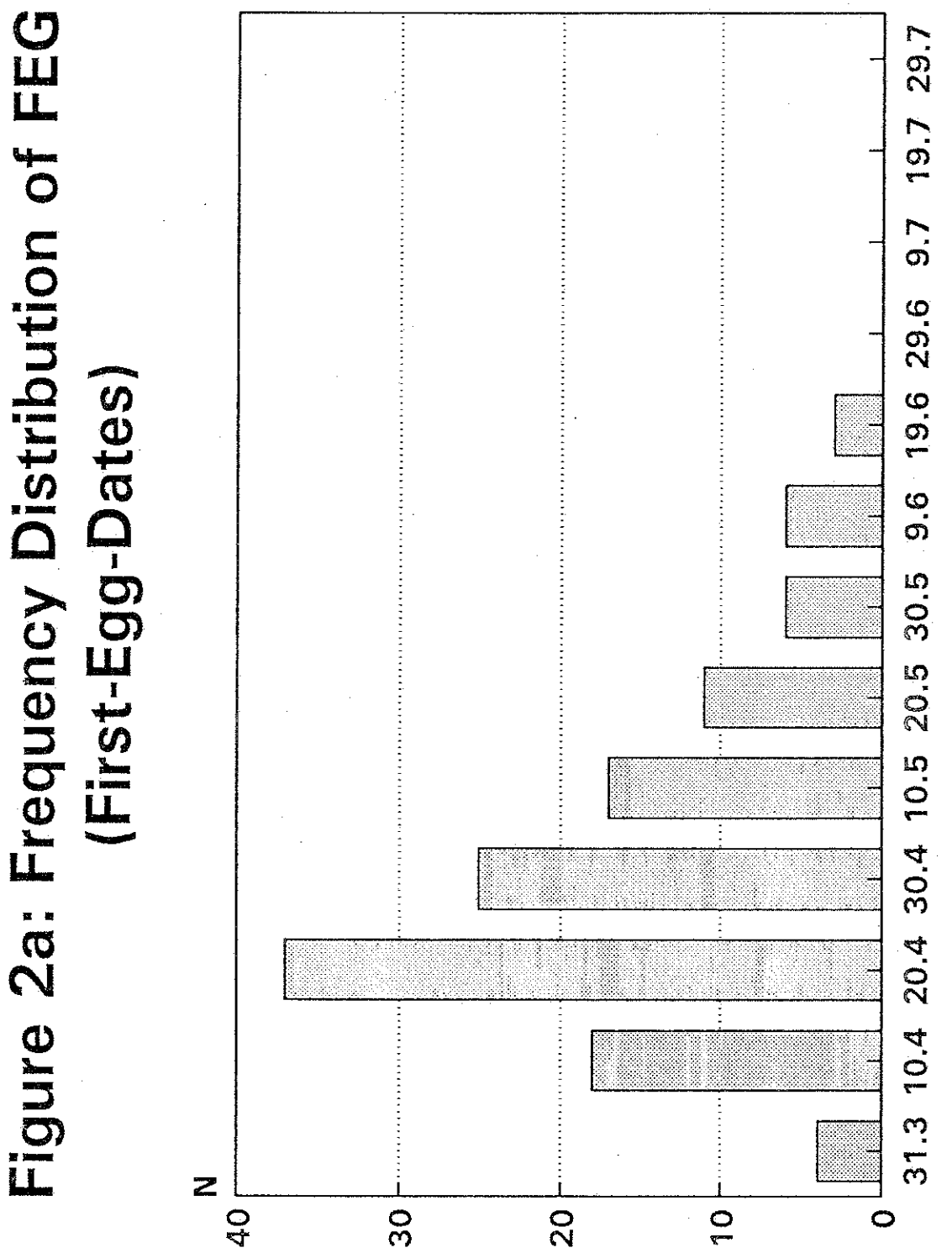


Figure 2a: Frequency Distribution of FEG
(First-Egg-Dates)
N
40
30
20
10
0
31.3 10.4 20.4 30.4 10.5 20.5 30.5 9.6 19.6 29.6 9.7 19.7 29.7
Date (Day.Month)

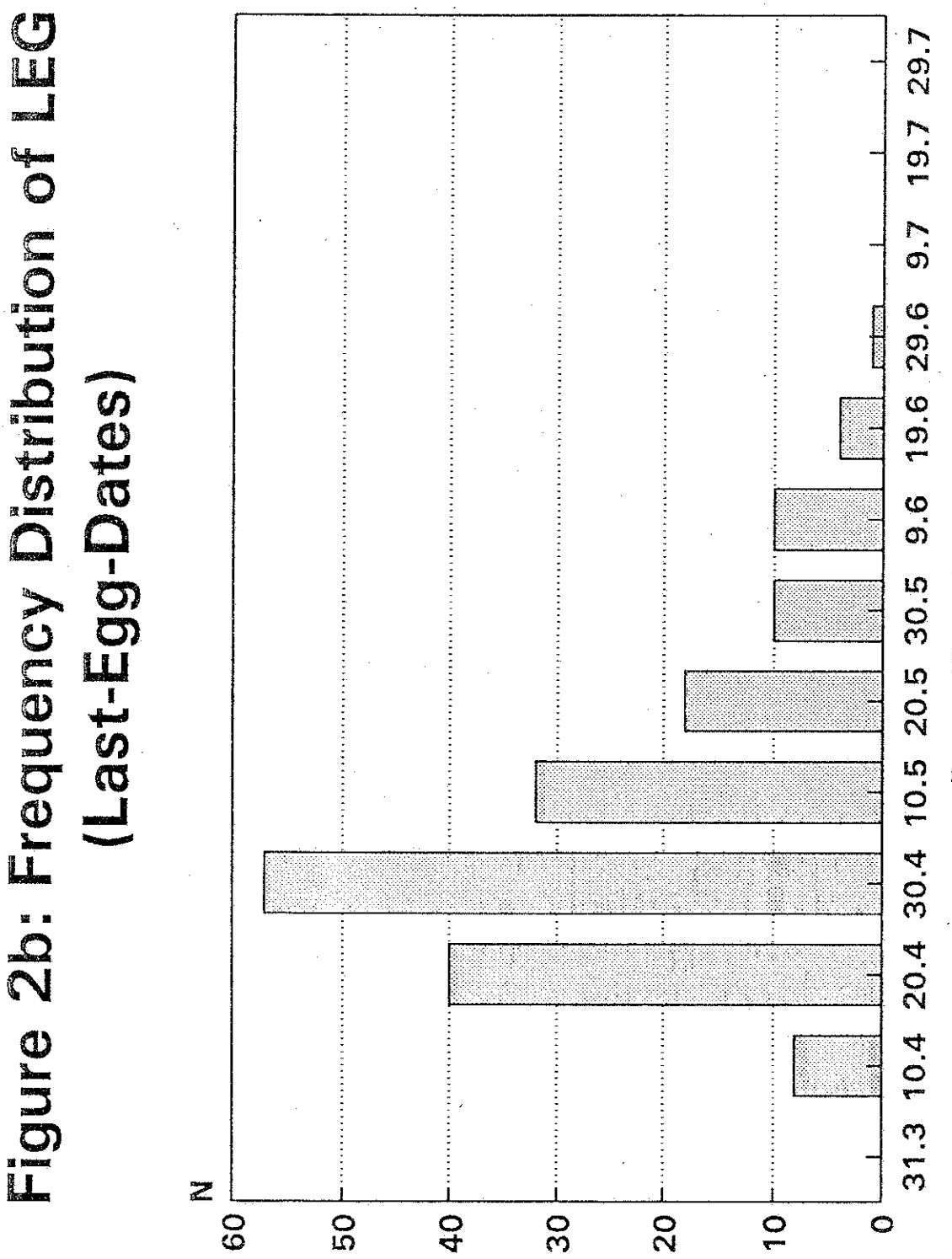


Figure 2b: Frequency Distribution of LEG
(Last-Egg-Dates)
N
60
50
40
30
20
10
0
31.3 10.4 20.4 30.4 10.5 20.5 30.5 9.6 19.6 29.6 9.7 19.7 29.7
Date (Day.Month)

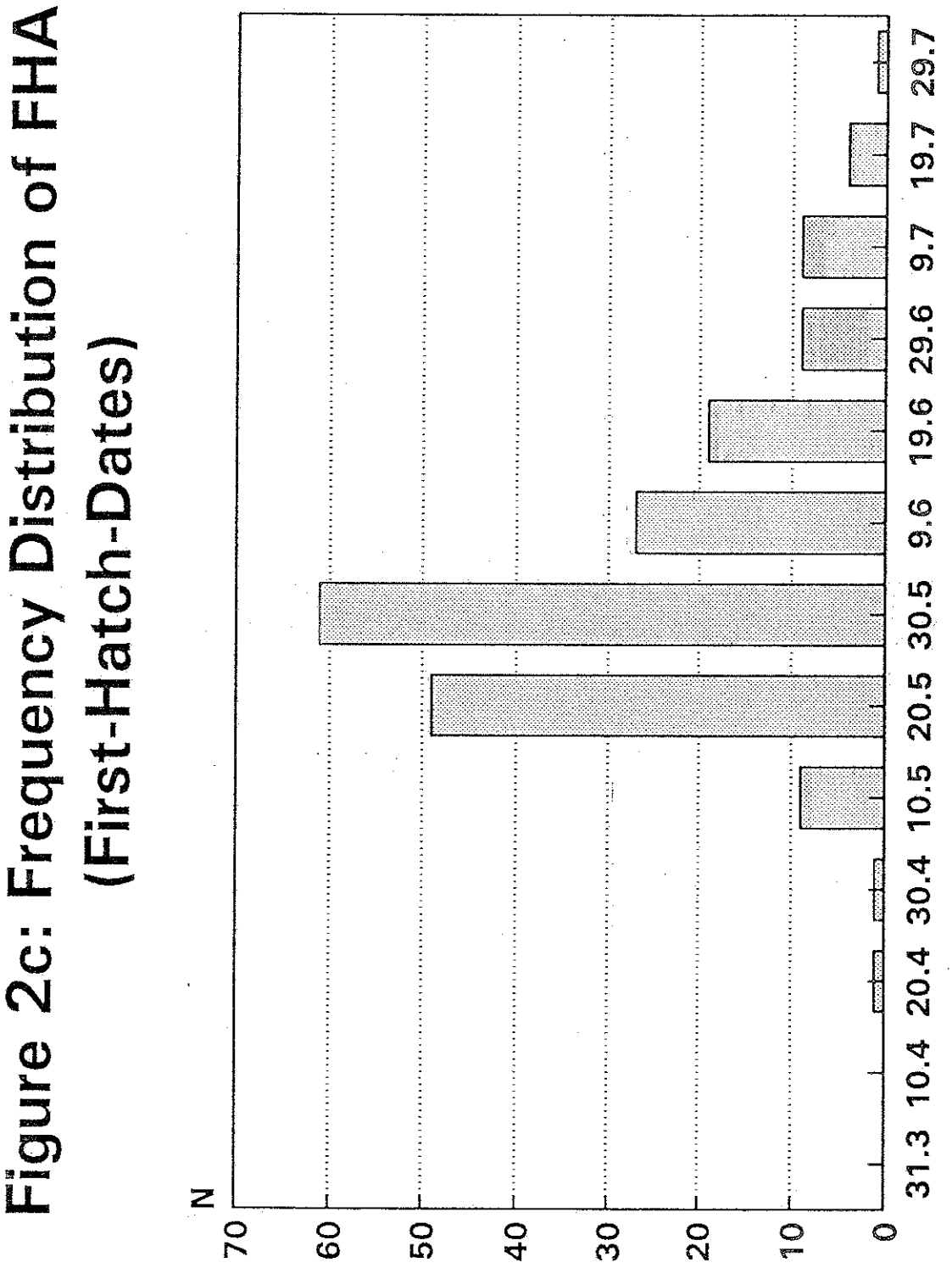


Figure 2c: Frequency Distribution of FHA
(First-Hatch-Dates)
N
70
60
50
40
30
20
10
0
31.3 10.4 20.4 30.4 10.5 20.5 30.5 9.6 19.6 29.6 9.7 19.7 29.7
Date (Day.Month)