

Breeding biology and population dynamics of Ringed plovers *Charadrius hiaticula* in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding

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(With 5 figures in the text)

The nesting of Ringed plovers was investigated in 1974 at Mestersvig, north-east Greenland, and in 1974–76 at Lindisfarne, north-east England. Difficulties in the use of Nest Record Cards for this species (to obtain information from more sites) are discussed.

Territory sizes tended to be smaller, and more feeding took place within territories, at Lindisfarne than at Mestersvig. Clutch sizes were similar in different areas. Incubation (mean period about 25 days) was shared fairly equally by the two sexes. Longer incubation shifts at Mestersvig and some areas at Lindisfarne than at other Lindisfarne sites were associated with greater distances between nests and feeding areas. Most egg losses were probably due to predation, and were fewer in the Arctic than in Britain, where nesting success varied greatly in different areas and years, and in relation to timing within a season. Up to five nestings per pair per year were made at Lindisfarne, but only one at Mestersvig.

The timing of breeding is discussed, and it is concluded that the date of start of egg-laying in north-east Greenland is determined by the timing of snow clearance, while that at Lindisfarne is related to the decreasing probability of egg-predation later in the season. Because of the high nest losses, the production of young at many temperate sites, including parts of Lindisfarne, was probably inadequate for the population to be self-supporting. The reasons for the large seasonal, annual and geographical differences are discussed. It is concluded that increasing predation probably determines the southern nesting limits of Ringed plovers, but that this limit may be modified by varying degrees of different types of natural and artificial protection, and extent of habitat suitable for egg camouflage. Increased human usage of nesting beaches probably has an adverse effect on nesting success, but because of the complexity of the number of inter-related factors affecting the latter, without field experiments it is difficult to predict how this could best be offset by protection measures.

Contents										Page
Introduction	85
Study areas	85
Scoresby Land	85
Northumberland	86
Methods	86
Results	88
Territorial establishment and egg-laying	88
Incubation	92
Nesting success and failure and relayings	95
Population dynamics	100
Discussion	101
Timing of breeding	101
Possible reasons for differences in breeding success between areas and years	104
Southern limits of distribution and some implications for conservation	106
Summary	109
References	110

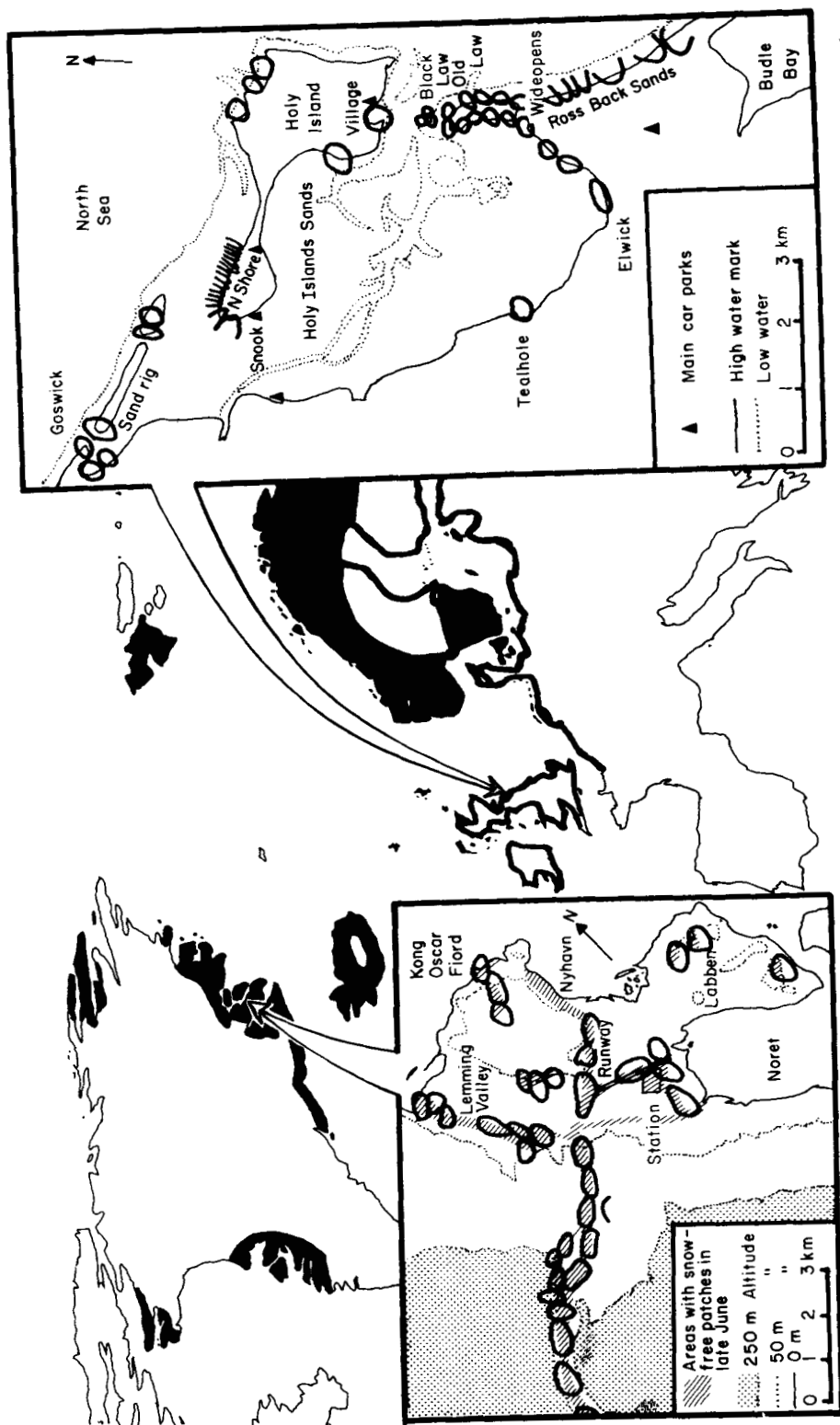


FIG. 1. The western part of the breeding distribution of Ringed plovers according to Voous (1960). Inset are main study sites, showing by bold lines Ringed plover territories in 1974.

Introduction

Studies on the factors limiting breeding distributions and determining timing of breeding have tended to concentrate on questions of food supply. The importance of such factors is well established for some passerine populations (e.g. Perrins, 1970), and the tendency for predators to be limited by their food supply rather than *vice versa* is well entrenched in the ecological literature (e.g. Lack, 1954). In the present study, the effects of various factors on the breeding of Ringed plovers *Charadrius hiaticula* were investigated, and the situations in high arctic and temperate areas, towards the two extremes of the wide breeding range of this species (Fig. 1) were compared. A study of population dynamics of populations in southern breeding areas was of additional interest because of suggestions of a decrease, since the 1940s, in the numbers and range of Ringed plovers breeding in Britain, possibly due to increased human disturbance on their coastal nesting habitats (see Parslow, 1967; Prater, 1976).

The Ringed plover is the commonest wader species in parts of Greenland (e.g. Salomonsen, 1950; Larson, 1960; Meltote, 1975; Green, 1978), as is its replacement, the Semipalmated plover *C. semipalmatus* (sometimes considered to be conspecific—see Smith, 1969), in some areas of the Canadian Arctic archipelago (Sutton & Parmelee, 1955).

In the northern parts of the breeding range, Ringed plovers nest both inland and near the coast, on barren land such as stony ground and river gravels. At lower latitudes, such habitats are generally restricted to the coast and, in Britain, the species is mainly a coastal nester.

Aspects of the breeding of Ringed plovers and the other small European plovers have been described by Laven (1940), Edwards, Hosking & Smith (1947), Mason (1947), Simmons (1953, 1955, 1956), Sluiters (1954), Rittinghaus (1956), Walters (1957) and Glutz *et al.* (1975). However, studies on the Arctic breeding grounds, which form most of their range, are lacking. Furthermore, no intensive study of the species in Britain has been published since concern was expressed about the possible decline.

This paper presents information on the nesting of Ringed plovers at the Lindisfarne National Nature Reserve, Northumberland, in the southern part of the breeding range, and compares this with the situation in Scoresby Land, north-east Greenland, well to the north (Fig. 1). Using also information on the later stages of the breeding season and subsequent survival of young (Pienkowski, *In press b*), the timing of breeding, population dynamics and breeding distribution are discussed.

Study areas

Scoresby Land

Observations were made near Statens Luftfartvaesen Mestersvig, Scoresby Land, north-east Greenland (72° 14' N, 23° 55' W), from 25 June 1974, at which time the birds were taking up territory and laying, to 16 August, shortly after the first young had fledged. The 1974 season was exceptionally late. Some less detailed information from other valleys in Scoresby Land (where times of breeding differed—Green, Greenwood & Lloyd, 1977) are also incorporated.

The detailed study area around Mestersvig station (Fig. 1) was mainly “river-bed” shingle and sparse tundra heath (i.e. 30–60% cover by vascular plants; organic crust of lichen covering ground between heath plants; some disturbances by frost heaving—Green, Pienkowski

et al., 1978; Green, 1978). During the study period, snow cover progressively decreased from greater than 90% on 25 June to about 60% on 6 July, and to less than 10% by late July. Generally, a damp zone existed in the latest areas from which snow had melted, and also in small pools and streams. The shore of the small inlet, Noret, was ice-covered until mid-July. After then, melt run-off and slight tidal movement gave rise to a damp zone there also. Certain other areas visited in north-east Greenland had more vegetation cover, but Ringed plovers tended to occupy the more barren areas (see Green, 1978; Ferns, 1978).

Northumberland

Studies at Lindisfarne National Nature Reserve (55° 40' N, 1° 50' W) and adjacent parts of the Northumberland coast (Fig. 1) took place in 1974 (until mid-June), 1975 and 1976.

At Lindisfarne, Ringed plovers nested on the shore, in sand dunes, gravel flats or occasionally on fields immediately adjacent to the shore. Most nests were close to intertidal areas, where much of the feeding took place, although some of the birds nesting on sea beaches (e.g. Ross Back Sands) moved to the sheltered sand- and mud-flats to feed (see Pienkowski, *In press c*).

Methods

Bird distribution, territories and feeding locations were mapped using observations of bird behaviour, made with a tripod-mounted 15–60×60 telescope and 11×50 binoculars. Nests were found by searching suitable habitat in the territories or watching, from a concealed or distant viewpoint, the birds' returns. The fates of nests were determined by regular checks; searches were made for indications of causes of loss in unsuccessful cases. It is possible that tracks and activities of observers increased the predation rate on nests at Mestersvig (cf. Willis, 1973; Picozzi, 1975). At Lindisfarne, it is unlikely that this had an effect, as observer activity formed only a small proportion of human activity in the area. To check on this, in 1976, a number of nests were inspected for much of the time only from a distance (by telescope) rather than by close approach. The rate of predation on these nests did not differ from that on nests inspected closely.

Because of the difficulties in detecting nests on the date of laying of the first egg (and the consequent over-estimation of survival rates), nesting success was calculated by Mayfield's (1961, 1975) "exposure" method. This uses the field data to estimate the probability of a clutch being lost, by dividing the number of unsuccessful nests by the number of nest-days of observation. The estimated survival rate of a nest, from the laying of the first egg to hatching, is the daily chance of survival raised to the power d , where d is the number of days in this period. The method assumes that the chance of loss does not vary systematically through the laying and incubation period: checks on my data indicate this to be approximately true, apart from seasonal effects considered later. The only situations in which observations were detailed enough to allow approximate estimates of nest survival, from laying of the first egg to hatching, by the "conventional" method were at the North Shore of Holy Island Snook in 1975 and 1976: they were 24% and 3%, respectively (based on samples of nests of 29 and 30). These compare with 13% and 1% calculated by Mayfield's method. As expected, the conventional estimates are higher because, even in the detailed study areas, some nests were not found until after the clutches had been lost (e.g. signs of recently damaged eggs and scrape in a territory where a nest had been suspected but not found). In other areas, because of less complete coverage and consequent biases in the conventional method, Mayfield's method is the only practicable one. Therefore, this is used throughout this paper for data gathered in the present study. Hensler & Nichols (1981) showed that Mayfield's estimator of nest survival is the maximum likelihood estimator, and derived estimators of variance and significance tests.

The Nest Record Cards of the British Trust for Ornithology (BTO) were also examined, in an attempt to investigate egg production and nesting success of Ringed plovers in other sites. Unfortunately, serious difficulties in their use became apparent. First, a large number of single-visit cards had to be ignored, because they could not be used in estimating hatching success, nor even clutch size. Second, many cards covered periods at unknown stages of incubation; their use, even for calculating mean clutch size, was dubious because of the uncertainty of previous losses of one or more eggs. Third, coverage through the breeding season was very uneven, becoming non-existent at many sites later in the season. This was apparent from notes and dates of checks on some of the cards themselves, and is reflected in the early end to the season indicated by these data (see Fig. 2). Fourth (and most serious), in a very large number of cases, the outcome of the nest was unknown, making estimates of survival rate by any method impossible. Disregard of such cases—which were typically a majority of cards for any

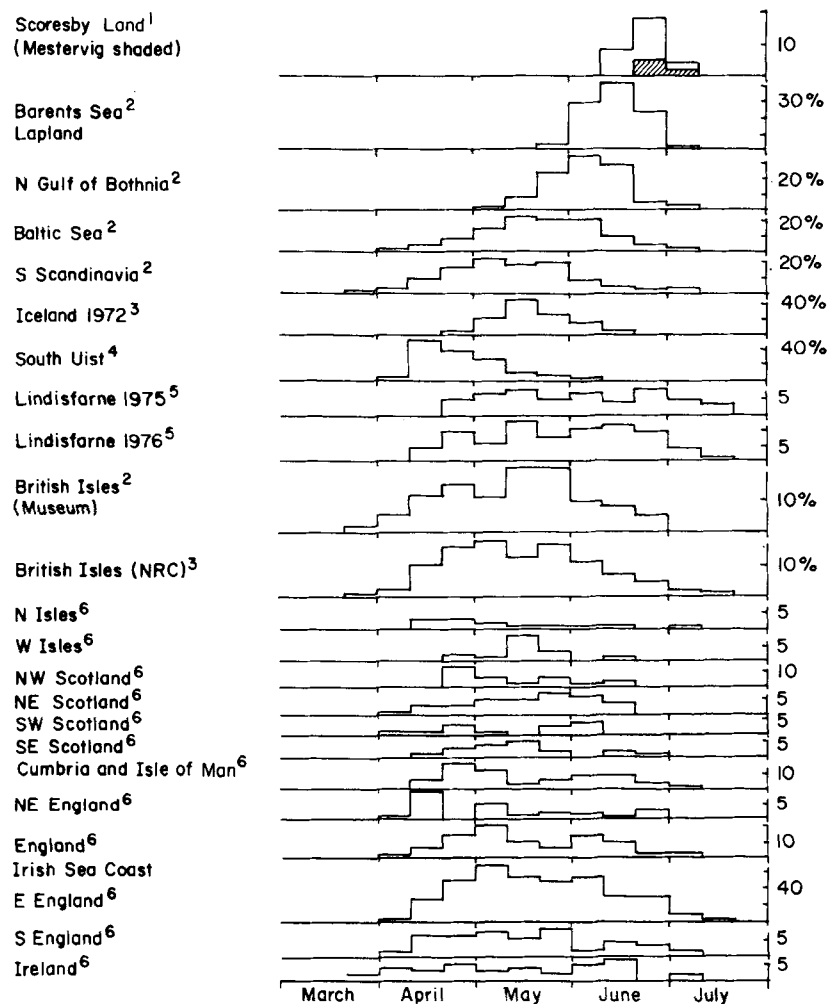


FIG. 2. Distribution of dates of laying the first egg of Ringed plover clutches in various areas. Sources: ¹Green, Greenwood & Lloyd (1977) & present study; ²Väisänen (1977); ³Prater (1974); ⁴Wilson (1978); ⁵Present study; ⁶BTO Nest Record Cards.

region or year—could have introduced large and unknown biases. It is not clear how Prater (1974) dealt with such cards, as the method of analysis that he used, developed by D. I. Sales, has not yet been published. The present author investigated the possibility of restricting analysis to cards from certain sites, such as bird observatories and nature reserves, but it soon became clear that some biases applied here also. Thus, although nest record cards, as gathered by the current system, may be valuable for examining the breeding biology of, e.g. summer-visiting songbirds with a restricted breeding season and nidicolous young, their use for species with a protracted season and, particularly, nidifugous chicks seems to be very limited. In this paper, they are used, with some provisos, in describing the timing of the nesting season, but not for analysis of nesting success. Instead, some information from other areas was obtained by correspondence with individual field workers who are acknowledged in the text.

Incubation schedules were monitored by watches, at the nest, from a hide placed nearby. In Greenland, these watches usually covered 24 h periods, the period 2400–0600 h and 1200–1800 h generally being covered by myself and 0600–1200 h and 1800–2400 h by another observer, generally D. I. North. Time of day is given as GMT (which is used locally, although solar midnight occurs at 0136 h). At this time of year, the sun did not drop below the horizon, although it was lower in the sky (and in some situations was hidden by hills) around midnight. Consequently “nights” tended to be considerably cooler than “days”. At Lindisfarne, only one observer was normally available, and watches covered either all, or most of, the daylight period. Although at this latitude in summer the short nights are not very dark, it was not usually possible to see the incubating bird throughout the night. Times were recorded as British Summer (or Standard) Time, solar midnight occurring at about 0108 h. Thus times in the two areas are roughly comparable.

During each observation period, note was kept of weather conditions, including air temperature at ground level, wind force and direction, and rainfall. In Greenland, these were supplemented by records at the meteorological station, which was within the study area. In both study areas, as many birds as possible were marked with combinations of colour rings, unique to each individual.

Results

Territorial establishment and egg-laying

Numerous Ringed plovers were making stiff-winged (“butterfly”) song flights, over the areas clear of snow, when the expedition arrived at Mestersvig on 25 June. These areas were the only ones where territories were established (Fig. 1). In other localities, notably parts of the Nyhavn and Labben hills, pairs established territories on snow-free patches of tundra, but later deserted them, possibly when further snow clearance failed to reveal unvegetated areas, which Ringed plovers always used for nesting. These pairs may later have established territories in more suitable areas. However, this seems unlikely, as no territories were established late in the regularly censused area. Furthermore, it is unlikely that sufficient time for incubation and growth of young would remain for birds beginning to lay after early July. Many areas offering, after snow melt, apparently suitable nesting sites remained unutilized because snow clearance came too late (although some were used for rearing the young—see Pienkowski, *In press b, c*). In some gravel areas, particularly in “Lemming Valley”, fairly dense aggregations of pairs appeared to be trying to establish territories as the snow began to clear, in late June and early July. By mid-July, many of these defended areas were deserted; the remaining territories apparently enlarged. The average size of 30 defended territories at Mestersvig was about 20 ha. However, the pairs were generally widely spaced and disputes infrequent once territories had been established, so that boundaries were very diffuse.

During the period of territory establishment at Mestersvig, birds appeared to feed both on their defended territories and in neutral areas. These undefended areas included a strip of marsh land and extensive melt water pools in the low ground beside the road between Mestersvig and Nyhavn. Such areas apparently did not provide suitable nesting sites for Ringed plovers, and the birds did not attempt to defend them. The birds fed on both wet and dry areas, but did not often wade in pools. As with other waders, the wet areas left by retreating snow cover were favoured feeding habitats. Foraging was almost entirely by the typical plover "run-stop-peck" method (see e.g. Pienkowski, 1981*a, b*, 1983), prey usually being taken from the surface of the vegetation or the substrate; shallow probing was infrequent. Prey comprised a variety of invertebrates, particularly dipteran larvae and—as soon as they were available—adults, some larger larvae, and spiders (Pienkowski, *In press c*).

In all areas, the birds nested on bare ground in shallow scrapes, unlined or sparsely lined with small stones, etc. At Mestersvig, egg laying followed soon after snow clearance and territory establishment (Figs 2, 3). The laying dates of the first eggs of seven nests in the Mestersvig area were estimated to be between 22 June and 1 July, with both earlier and slightly later dates being recorded in other areas in Scoresby Land in the same year (Fig. 2). Eggs were laid at approximately 1 day intervals, the clutch size at Mestersvig being four (11 cases) or three eggs (two cases) and, in all areas in Scoresby Land, four (19 cases) or three (three cases), mean 3.86 (Green, Greenwood & Lloyd, 1977, 1978; present study).

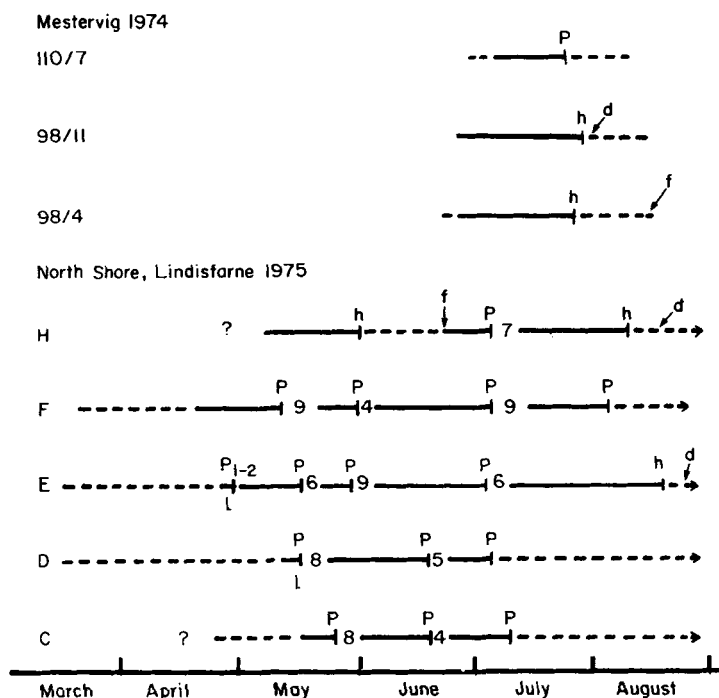


FIG. 3. Example nesting histories. --- Birds on territory without nest; — nest in existence. Numbers indicate days between loss and start of replacement clutches. P = eggs taken by predator; l = clutch not yet complete when lost; h = eggs hatch; d = chicks die; f = chicks fledge.

At Lindisfarne, territory establishment was a much more gradual process. Some birds stayed at Lindisfarne throughout the year, whereas others dispersed or migrated relatively short distances and returned from February onwards (Pienkowski, 1980, In press *b*). Such birds typically joined the winter feeding flock on the intertidal flats. They gradually spent increasing proportions of the day (both feeding and roosting) on territories from February onwards. Most took up permanent residence in March or April (see Fig. 3).

Because birds nesting on the North Shore at Lindisfarne (Fig. 1) fed mainly on territory or, to a lesser extent, at accessible nearby communal feeding areas, it was possible to assess the amount of time spent feeding. For example, values for females on the North Shore on two days in late April, before commencing nesting, were 49% and 61% of the daylight hours spent feeding. There was probably almost no feeding at night at this season (Pienkowski, 1982). Many casual observations also indicated that much of the available feeding time was not used, and that the above values were fairly typical. Later in the season, during incubation, the maximum possible feeding time averaged 50% (because incubation was shared fairly equally between the sexes—see below), but non-incubating birds were seen to spend much of their time resting, preening, bathing, etc.

Territories were established around much of the shore of the Reserve (Fig. 1). The main exceptions were steep rocky shores, or sites where mudflats and *Spartina* marshes reached the high water mark, leaving no gravel or sand area above the intertidal. Some areas, notably the North Shore of Holy Island Snook, Tealhole and around Guile Point, seemed to hold territories of approximately constant size and position in each year. In these areas returning birds often took up the same territory as in previous years (Pienkowski, In press *b*). In other areas, *viz.* parts of Goswick, the Sand Rig, part of Old Law and Ross Back Sands, the locations of territories varied more between years, possibly because these beaches were more subject to changes in configuration by winter storms, and by wind-blown sand at all times of year. These were also the areas where less feeding was generally done on territory (see below). Birds returning to these in successive years tended to return to the same general area, rather than to a particular territory (Pienkowski, In press *b*). In extreme cases, e.g. part of the Elwick shore, over-winter changes in surface substrate appeared to make areas suitable for nesting in some years, with high shores and some gravel expanses, but unsuitable in others, when shore level was lower or gravel covered.

In all years at Lindisfarne, one or two pairs began to establish territories on the eastern end of the North Shore, but abandoned these without nesting by mid-May. This appeared to be associated with the increasing use of this shore by humans at this time of year.

Territory sizes at Lindisfarne varied greatly, but were generally far smaller than in Greenland. On the North Shore, territories as small as about 0.3 ha were well defined (sometimes even by footprints left by opposing males walking parallel up and down the shore). At Ross and Goswick, more diffuse territories of over 10 ha were common. In the terneries at Black Law (in the Lindisfarne Reserve) and at Aberlady Bay (East Lothian, 80 km north-west), they were probably even smaller than on the North Shore. At Lindisfarne, territorial activity was maintained throughout the breeding season, presumably a result of the small, tightly packed territories and the frequently repeated nesting attempts (see below). Territory sizes previously reported for Ringed plovers also range widely in different areas, from about 0.06 ha in a closely packed group nesting in a tern colony in Co. Dublin, Ireland (Mason, 1947), to other large territories in Greenland (e.g. Meltofte, 1979).

Laying dates of first eggs spread over several months (Fig. 2). The possible bi- or tri-

modality at Lindisfarne is known not to be due to renesting after a successful brood, as there was only one case of this in each year. It arises instead from a certain degree of synchrony in the dates of predation of clutches, leading to some synchrony in laying of replacement clutches (see also below). Prater (1974) used the bimodality in the distribution of first-egg dates of BTO Nest Record Cards as evidence for double brooding.

Reanalysis of the Nest Record Cards (Fig. 2) indicates that the wide spread of first-egg dates occurs throughout the British Isles (early dates are probably fairly reliable, but the end of season data probably not—see Methods). As found by Prater (1974), there are some indications that the earliest start to the season occurs in Ireland, generally followed by Irish Sea coasts and much of England, with the latest in northern Scotland (but this may be due to lack of observer coverage before the tourist season there; however, inland breeding birds in central Scotland generally do not start nesting until May or June—J. Mitchell, pers. comm.). At more northerly sites, laying commences progressively later, as found by Väisänen (1977) whose results are also summarized in Fig. 2. First laying dates in Iceland and southern Scandinavia were somewhat later than the British Isles, and considerably earlier than northern Scandinavia and Greenland. (The data for the end of the season in Iceland is incomplete, because of a change in work-pattern of the observers there.) Laying dates on the Taimyr Peninsula (Krechmar, 1966) appear to be fairly similar to those in north-east Greenland.

Some information on laying intervals was obtained on the North Shore of Holy Island. However, this was limited, because the frequency of nest visits was deliberately restricted to minimize the chance of attracting predators. Seventeen estimated intervals between egg-laying ranged from one to three days and averaged about 1.5 days. Prater (1974) estimated slightly longer mean intervals of 1.74, 1.66 and 1.99 for the three inter-egg intervals, respectively.

The mean clutch size (3.84, Table I) was similar to the 3.86 found both in Greenland and in north Finland (Väisänen, 1969), and marginally higher than the 3.79 from British Nest Record Cards (Prater, 1974), which may be biased by early losses of eggs and inclusion of incomplete clutches. One apparent case of a complete clutch of two eggs at Lindisfarne may possibly have been a case of very early loss of one or more eggs. One case of five eggs was observed, but the laying frequency and birds responsible were not observed. This clutch was incubated for at least 40 days without hatching (the mean incubation period was 23.5 days—see below).

TABLE I
Sizes of complete clutches of Ringed plovers at Lindisfarne

	No. of eggs/completed clutch				Mean clutch size
	2*	3**	4	5	
North Shore					
1974		2	12		3.86
1975		5	22		3.81
1976	1	1	15		3.82
Ross Back Sands & Old Law 1976		5	23	1	3.86
All	1	13	72	1	3.84

*It is possible that this clutch had lost some eggs before discovery.

**There was some tendency for 3-egg clutches to occur more as later replacement clutches (Pienkowski, unpublished).

Incubation

Both sexes incubated, generally sharing the time fairly equally (Table II), although there was some variation. Some of this may have been an artifact of observations usually limited to 24 h or less, if there was a bias in the time of day that these were made. Various authors (e.g. Walters, 1957, for Kentish plover *Charadrius alexandrinus*) have suggested that, in some species, there may be a regular diurnal pattern in the schedule of incubation of the two sexes. Although this appeared to be so for Ringed plovers on some days, there seemed to be no consistent pattern within or between pairs. A possible regularity at times may have resulted simply from the long incubation shifts in some sites (Pienkowski, 1980; and see below). There was no evidence that one sex alone incubated at night, although the sex of the Lindisfarne birds could not be determined in darkness. The percentage of time during which the nest was attended by neither parent tended to be greater early and late in incubation than during mid-incubation.

TABLE II
Summary of observations of incubation schedules of Ringed plovers

Nest	Date	Stage of incubation	Observation period (h)	% Of incubation time by:			Mean shift durations (min.)*	
				♂	♀	Neither	♂	♀
Mestersvig 1974								
Tunnelev	2-3 July	Early	23.8	24	41	35	66 (5)	83 (5)
S end runway	5-6 July	Early	24.7	48	47	5	209 (3)	166 (4)
S end runway	25-26 July	Late‡	35.7	31	49	20	59 (11)	60 (12)
S end runway	28 July	Late‡	12.1	33	60	7	58 (4)	51 (4)
N end runway	11-12 July	Mid	21.3	52	44	4	66 (6)	78 (6)
Radio hut	17 July	Mid	24.0	60	38	2	380 (2)	178 (3)
All		Early	48.5	36	44	20	102 (8)	112 (9)
All		Mid	45.3	56	41	3	102 (8)	102 (9)
All		Late	47.8	31	52	17	58 (15)	59 (16)
All		Whole period	141.6	41	46	13	78 (31)	79 (34)
Lindisfarne 1975								
E Old Law	19 May	Early	11.9	47	46	7	112 (2)	174 (2)
Tealhole	22 May	Early	16.2	65	30	5	76 (7)	34 (7)
Tealhole	4 June	Mid	16.1	55	44	1	47 (9)	48 (8)
North Shore D	1 June	Early	14.4	53	41	6	44 (8)	48 (7)
North Shore D	9 June	Mid	11.2	38	62	0	76 (3)	81 (4)
North Shore B	1 June	Early	6.0	57	39	4	33 (4)	60 (2)
North Shore L	1 June	Early	9.5	85	9	6	110 (3)	24 (2)
Snook End	6 June	Early	13.1	33	63	4	49 (5)	78 (5)
Elwick	14 June	Early	14.0	43	56	1	31 (11)	33 (12)
North Shore T/F	19 June	Mid	11.9	41	56	3	44 (4)	63 (4)
All		Early	85.1	53	42	5	49 (40)	45 (37)
All		Mid	39.2	46	53	1	50 (16)	59 (16)
All		Whole period	124.3	51	45	4	49 (56)	49 (53)

*Means calculated after logarithmic transformation, to normalize distributions. Sample sizes given in parentheses. 2-Way analysis of variance of log(shift duration) by sex and study area gives: sex $F_{1,170}=0.001$, $P=0.97$; area $F_{1,170}=12.7$, $P<0.001$; interaction $F_{1,170}=0.028$, $P=0.87$. 2-Way analysis of variance of log(shift duration) by sex and incubation stage, for Mestersvig data only, gives: sex $F_{1,59}=0.01$, $P=0.92$; Stage $F_{2,59}=2.84$, $P=0.066$; interaction $F_{2,59}=0.016$, $P=0.58$.

‡All four eggs chipping on 25-26 July; young hatching on 28 July, and values given concern the period until the first chick left the nest.

Incubation shifts (i.e. the period, between reliefs, for which an individual was in attendance at the nest, including brief interruptions) were very variable in duration, but there was no significant difference between the sexes (Table II). Mean incubation shifts were significantly longer in Greenland than at Lindisfarne. Most birds watched at the latter site had feeding areas near the nest. An exception was at the sea-beach at Old Law, where incubation shifts were generally longer than on the other nests watched at Lindisfarne. On the basis of more casual observations, incidental to other activities such as catching, the longer shifts are thought to have been typical of this area and of Ross Back Sands. In common with the situation at Mestersvig, Ringed plovers nesting on the sea-beaches of Old Law and Ross Back Sands generally moved some distance to feed, rather than doing so on territory. Longer feeding periods are probably more efficient as distance to feeding grounds increases (cf. Brown, 1975; Brooke, 1978). Variations with stage of incubation were difficult to assess, particularly at Lindisfarne, because of the high probability that any given nest under observation would not survive long. At Mestersvig, there was some indication of a decrease in duration of each shift as activity increased around hatching time.

During incubation at Mestersvig, most feeding took place well away from the nest, apart from brief periods during change-overs of incubating birds and during disturbances. Colour-ringed birds were seen feeding over 3 km from their territory. This may have been a result of the local variations in prey availability, the large day-to-day changes in this, and the differences in temporal patterns of such changes between sites (see Greenwood, 1974, 1978). Observed prey included various invertebrates, with spiders and adult Diptera most important. Adult and larval Lepidoptera were also observed as prey (Pienkowski, *In press c*). As indicated above, at Lindisfarne the extent of feeding within the territory varied somewhat. On the North Shore, most feeding took place on territory. Some additional feeding, at times in flocks, took place on flats away from defended territories (Fig. 1). Birds from Ross Back Sands and the seaward beach of Old Law appeared to obtain most of their food on the intertidal flats on Budle Bay or west of Old Law, away from the territory. Later in the season, however, family parties obtained most of their food in the area of the territory, at least initially. Some of the birds nesting on the sea-beach later took their broods to the flats of Budle Bay or through Wideopens. At Mestersvig, family parties left the area of the nest soon after the young hatched, and moved to better feeding areas (Pienkowski, *In press c*).

Generally, the clutch was incubated for more than 90% of each day, but possibly less in the first days of incubation and just before hatching (Table II).

One incubation was abnormal in that the male took almost no part in it. This was the fifth nesting attempt by pair E on the North Shore in 1975, the first four having been unsuccessful (see Fig. 3). Up to and including the fourth nest, which was lost to predation at around the expected date of hatching at the end of June, both birds shared incubation normally. The male had started wing-moult by early July. (The starting of wing-moult by incubating birds in July is fairly common at Lindisfarne.) The birds displayed and made preliminary scrapes normally in the first few days of July, and the first egg of the fifth clutch was found on 9 July. By 13 July there were three eggs and incubation had started, probably on that day. Observations during incubation are summarized in Table III. The incubation period was abnormally long: 35 days to the hatching of the first young; and the hatching was prolonged and asynchronous. The female was unable to tend both eggs and young which had left the nest scrape. Detailed observations had to be stopped shortly after hatching and the young did not survive until the next check about a week later.

TABLE III

Incubation of the fifth nest of pair E. North Shore, 1975

Date	Observation period	% Time incubation by female*	% Time no incubation	Duration (min) of incubation sessions:		Notes
				Mean	S.D. (n)	
13 July	1005–1556	74%	26%	22.3	16.3 (12)	Male continued territorial behaviour and occasionally ran towards nest as if to incubate but stopped short. Male had dropped first 2–3 inner primary feathers and replacements were well grown
20 July	1040–2150	54%	41%	51.6	61.4 (7)	Male behaved as above additionally incubating once for 36 min at most. Female off nest for one long period in afternoon as well as several shorter ones
27 July	1049–2151	77%	23%	20.3	34.7 (25)	Male still defended territory but did not show any signs of incubation or approaches to nest. Female left nest frequently to feed, chase intruders or to avoid people
3 August	1012–1902	71%	29%	15.1	12.9 (25)	Female had dropped first 1–2 inner primary feathers at start of moult. Male still defended territory
4 August to 17 August only female seen incubating during frequent checks.						
12 August first egg "starred"						
13 August all eggs "starred"						
14–17 August slow progress toward hatching by chicks						
17 August	1243–1813	78%	22%	18.4	15.1 (14)	Male still present but showing little territorial activity and for a time associated with flock of non-breeding birds which spent some time nearby. One egg hatched late on 17 August
18 August	Male still present but showed no interest in brooding chick even when this attempted to brood with him. Female brooded young but only occasionally spent brief times on nest. Second young hatched later that day; third not at all despite being well advanced in hatching					

*These estimates are probably too low for the total proportion of the day spent incubating as the female spent more time off the nest feeding, etc. during the day than late in the evening, and presumably even less at night.

The percentage of time the eggs were incubated by this female alone (probably about 80%) was rather similar to that of some Arctic wader species in which normally only one adult incubates. In contrast, incubation by two parents typically involves the eggs being covered for greater than 90% of the time (Norton, 1972; Pienkowski & Green, 1976). Frequent feeding excursions from the nest, as shown in the case described above, were also typical of incubation by a single parent and probably lead to increased conspicuousness of the nest to predators (see Pienkowski & Green, 1976; *contra* Pitelka, Holmes & MacLean, 1974). Clearly, in the Ringed plover, neither the parents nor the eggs are adapted to single-adult incubation, which in this case resulted from the male's desertion, presumably because of a

change in hormonal condition towards the end of the breeding season. The female did not appear the following year and had presumably died in the interval. The male occupied the same territory in 1976.

One incubation period in Greenland was measured as 25–26 days. At Lindisfarne, four incubation periods were measured as 23 days and four as 24 days (mean 23.5), plus the one exceptional case of 35 days (making the overall mean 24.8). The mean incubation period is similar to the 22–25 days reported by Bent (1929), 24 of Witherby *et al.* (1940) and 24.0 of Prater (1974). After allowing for the laying period and for the asynchrony of hatching, this gives a total period in the nest of about 29 days, and this figure is used below.

The birds left the nest to perform distraction displays if people, and probably other ground predators, approached. The reaction to potential aerial predators (notably Long-tailed skuas *Stercorarius longicaudus*, Raven *Corvus corax* and Glaucous gulls *Larus hyperboreus* at Mestersvig; Carrion crows *Corvus corone*, Kestrels *Falco tinnunculus* and various gulls at Lindisfarne) varied. Usually the birds sat still, relying on camouflage, although occasionally the predators were mobbed, especially in higher-density nesting areas. Generally, the reaction to predators, and the intensity and development of distraction displays, increased markedly just before the eggs hatched, to a level typical of that of birds with young. The frequencies of disturbance from the nest by humans (which tended to be the most frequent cause observed) varied greatly between sites. At Mestersvig, the 6-hourly changes of observer and occasional movements by the observer were often the only human disturbances occurring. This was also true on some occasions at Old Law, Elwick and Tealhole, but at the Snook disturbance was much more intense especially at weekends and holidays when ten disturbances per hour during daylight were common.

Birds at both Mestersvig and Lindisfarne also occasionally left the nest to chase intruders, usually of the same species. Both sexes were involved in agonistic and anti-predator behaviour. There were some indications that males were more involved in agonistic exchanges when both birds were available to do this, but this was more obvious both earlier, during territory establishment, and later, when with young.

Nesting success and failure and relayings

The nesting successes of Ringed plovers in the present study and in other detailed studies are summarized in Table IV, which shows marked differences between sites, and at the same site in different years. These differences are, in the main, statistically significant. For example, in 1976 mean nest survival per day at Ross Back Sands and Old Law was 0.96 and, at Holy Island Snook, 0.86. Variances, estimated by the method of Hensler & Nichols (1981), were 0.0000734 and 0.0004806, respectively. The difference was highly significant ($t=4.249$, $P<0.001$). Further analyses (Tables V, VI) demonstrate a seasonal difference in nesting success at Lindisfarne with early nests generally more likely to fail. Similar effects were also shown at some other sites.

Predators were the suspected cause of all nest losses at Mestersvig, Arctic fox *Alopex lagopus* definitely being the agent in one case. Other potential predators were Stoat *Mustela erminea*, Long-tailed skua, Glaucous gull and Raven. One case of a Musk ox *Ovibus moschatus* kicking an egg from a scrape and causing it to crack was suspected in one Greenland study area, and Musk oxen did appear to be a potential danger to eggs at Mestersvig early in the season, as both species made use of the few areas clear of snow. Arctic

TABLE IV

Estimated percentages of nests surviving to hatching, calculated by Mayfield's method, in the present and other detailed studies

Location	Year	Nest-days	Losses	Survival per nest day ($\pm 95\%$ confidence limits*)	Survival through laying and incubation
Mestersvig ¹	1974	182	6	0.9670 (± 0.0255)	38%
Lindisfarne ¹	1975	393	25	0.9364 (± 0.0234)	15%
including Holy Island Snook		370	25	0.9324 (± 0.0248)	13%
Lindisfarne ¹	1976	788	57	0.9277 (± 0.0175)	11%
including Ross Back Sands		212	11	0.9481 (± 0.0291)	21%
Old Law		311.5	9	0.9711 (± 0.0183)	43%
Holy Island Snook		250.5	35	0.8623 (± 0.0400)	1.4%
Farne Islands, Northumberland ²	1975	194	7	0.9639 (± 0.0258)	34%
St Cyrus, Fife ³	1974	70.5	32	0.9585 (± 0.0386)	29%
St Cyrus, Fife ³	1975	394	50	0.8731 (± 0.0396)	2.0%
Uists, Outer Hebrides ⁴	1973	374	10	0.9733 (± 0.0161)	46%
		Clutches found	Clutches hatching	Nest survival	
Danmarks Havn, NE Green- land ⁵	1975	9	7	78%	
Home Bay, Baffin Island ⁶	?	117	100	85%	

*Confidence limits calculated following Hensler & Nichols (1981).

Sources: ¹Present study; ²Messrs Heywood, Watts, Thompson & Chester (pers. comm. & Nest Record Cards); ³N. K. Atkinson, pers. comm.; ⁴J. R. Wilson, pers. comm.; ⁵from Meltofte (1979); ⁶from Smith (1969). Although the Mayfield method cannot be used on the data available for 5 and 6, nests were found during laying or early incubation and any over-estimation of survival is likely to be small.

TABLE V

Estimated percentages of nests surviving to hatching in relation to area and season at Lindisfarne NNR

	Up to mid-May	Mid-May to mid-June	Mid-June onward	Total	No. of nest-days used	No. of nests used
1975						
Snook	3.4%	40%	6.4%	13%	370	34
Total	3.4%	45%	6.4%	15%	393	35
1976						
Ross Back Sands	3.6%	31%	31%	21%	212	15
Old Law	33%	20%	70%	43%	311.5	19
Snook	0.2%	2.4%	1.9%	1.4%	250.5	36
Others	—	0.2%	3.3%	1.1%	14	6
Total	2.8%	8.7%	22%	11%	788	76

TABLE VI

Comparison of nest survival at the detailed study areas in Lindisfarne NNR in 1975 and 1976 in relation to season (based on 110 nests)

Period	Days without loss	Loss days	Total	Losses/day	Variance
Up to mid-May (a)	177.5	23	200.5	0.1147	0.0005065
Mid-May to mid-June (b)	407	25	432	0.0579	0.0001252
Mid-June onwards (c)	514.5	34	548.5	0.0620	0.0001060

Comparison of daily probability of survival: a vs b, $t=2.26$, $P<0.05$; a vs c, $t=2.13$, $P<0.05$; b vs c, $t=0.27$, n.s.

hares *Lepus arcticus* were suspected of damaging a clutch at Danmarkshavn (Meltøfte, 1979). As discussed by Pienkowski (In press b), rates of predation on wader eggs and young at Mestersvig were probably higher than is typical for NE Greenland, because of the higher density of predators around the station, where they were sustained by scavenging from tips, etc. The values from Danmarkshavn and Baffinland (Table IV) may be more typical, and Jehl (1971) also found higher hatching success (176 eggs hatched/219 eggs found—80%) in Semipalmated plovers at Churchill, Manitoba in 1964–67.

Causes of loss of whole clutches at Lindisfarne and St Cyrus are summarized in Table VII. A few cases of flooding by spring tides (probably all those occurring being detected) were recorded in all situations; covering by blown sand may have been slightly more frequent than the identified cases indicate. A fairly wide range of predators was responsible for most losses, and there are signs that the causes of losses varied from place to place and year to year: note, for example, the difference between years at the Snook in the extent of predation by corvids. Observations of behaviour of Crows, of fox *Vulpes vulpes* tracks, etc. suggest that relatively few individuals of both species may have been involved, and that changes in their behaviour could have had marked effects on nest survival. During the period of most detailed coverage, 1976 at the Snook, the estimated mean probability of any one nest being lost on any one day was 0.14. However, days with several or no nest losses were significantly more frequent, and days of single losses less so, than expected if nest losses were independent events (Table VIII). This suggests that a small number of predators was making occasional visits and finding several clutches on each occasion. There were indications of a similar pattern at St Cyrus. As also pointed out with reference to nest losses of Golden plovers *Pluvialis apricaria* (Ratcliffe, 1976), predation may be of major importance to the numbers or breeding success of the prey but form only a small part of the predator's diet.

In one case at St Cyrus and one at Lindisfarne (after the main study years) an adult bird was taken at the nest, probably by a fox and a dog, respectively. Usually Ringed plovers leave the nest to lure potential mammalian predators away while the latter are still distant, so that losses of adults at the nest are probably infrequent. However, an important element of Ringed plover defence appears to be the unpredictability of its behaviour (Meltøfte, 1976, 1977, 1979; Green, 1978; present study) and sitting tight on the nest, more typical of some

TABLE VII

Causes of losses of whole clutches of Ringed plover eggs at Lindisfarne NNR and St Cyrus NNR

Cause of loss	Snook and Goswick		Ross Back Sands and Old Law		St Cyrus*	
	1975	1976	1975	1976	1974	1975
Flooding by spring tide	2	1	1	2	1	2
Covering by blown sand			1			
Taken by:						
Dog	3	1			1	
Dog or fox		3				
Fox	2	6	1	1		3
Rat <i>Rattus norvegicus</i>						2
Weasel <i>Mustela nivalis</i> or Rat		1				
Stoat					4	
Great black-backed gull <i>Larus marinus</i>					3	
Crow	1	5		2	16	35
Unknown predator	8	2			3	7
Man (taken or broken accidentally)		2	1		3	1
Disappearance; cause unknown	10	15	1	15		
Failure to hatch				1‡		
Desertion	1**				1	1

*N. K. Atkinson (pers. comm.); **probably disturbed by man; ‡5-egg clutch (see text); ||including one taken by either Crow or Jackdaw *Corvus monedula*.

other wader species relying on camouflage, may be one extreme of this. This variable strategy may also be true of Golden plovers (see Ratcliffe, 1976).

At Mestersvig there were no partial losses of clutches, and no cases of eggs failing to hatch. At Lindisfarne six of 121 (5%) eggs of successfully incubated clutches were lost before hatching. Prater (1974) obtained the same proportion from Nest Record Cards. In all cases at Lindisfarne, the eggs were thought to have been removed by humans; one such "predation" was witnessed and others probably deterred by the presence of observer or hide. Of the 115 eggs of successful clutches, nine (8%) failed to hatch. These eggs included losses at various stages including some fully developed young where the failure appeared to be due to an insufficient degree of synchrony between hatching times of eggs in the clutch. Prater (1974) estimated 6% from British Nest Record Cards and Meltøfte (1979) found the same value at Danmarkshavn, Greenland. Some values for other species are 5% for Dotterel *Charadrius morinellus* (Pulliainen, 1970), 4% for Golden plover (Ratcliffe, 1976), 6% for Upland sandpiper *Bartramia longicauda* (Higgins & Kirsch, 1975), and 15% for Temminck's stint *Calidris temminckii* (Hildén, 1978).

At Mestersvig no unsuccessful nests were replaced, probably because insufficient time for incubation and rearing remained. It is possible that there was sufficient time for replacement clutches in some other areas, such as Ørsted Dal and Karupelv (see Green, Greenwood & Lloyd, 1977). At Danmarkshavn in 1975 several pairs probably renested after desertion during a late snow storm in mid-June around the time of laying (Meltøfte, 1979).

TABLE VIII

Comparison of the numbers of Ringed plover nests lost per day at Holy Island Snook, Lindisfarne NNR, in 1976 with the expected pattern if nest losses were independent events

No. of active nests on any day	Number of days on which nest losses were:								Total days	Total active nest-days
	0	1	2	3	4	5	6	7		
1	15 (13.76)	1 (2.24)							16	16
2	28 (22.93)	3 (7.46)	0 (0.61)						31	62
3	14 (13.99)	7 (6.83)	1 (1.11)	0 (0.06)					22	66
4	5 (4.38)	1 (2.85)	1 (0.70)	1 (0.08)	1 (0.003)				8	32
5	1 (0.94)	0 (0.77)	1 (0.25)	0 (0.04)	0 (0.003)	0 (0.001)			2	10
6	4 (2.43)	0 (2.37)	1 (0.96)	0 (0.21)	0 (0.03)	0 (0.002)	1 (0.00005)		6	36
7	2 (1.39)	0 (1.59)	1 (0.77)	0 (0.21)	1 (0.03)	0 (0.003)	0 (0.0002)	0 (0.00004)	4	28
Total days	69 (59.82)	12 (24.11)	5	1	1	0	1	0	Total = 250	
(5.07)										
Total nest losses	0	12	10	3	4	0	6	0→Total = 35		

Probability of nest being lost in 1 day = $35/250 = 0.14$.

Expected values, assuming nest-losses were independent events given in parentheses.

The observed values differed significantly from this ($\chi^2 = 9.18$, $P < 0.005$), due to clumping of nest losses on some days.

At Lindisfarne, the long season and high predation rate of chicks led to numerous renestings, the birds being able to relay, in a new scrape, within a few days of the loss (e.g. Fig. 3). Only two cases of "genuine" repeat clutches (i.e. following the hatching of young, rather than replacing depredated clutches) were recorded, these being on the North Shore in 1975 and Old Law in 1976. The North Shore pair hatched their first brood (from a first clutch) on 1 June and relaid around the time these fledged (and were still in the area of the territory) in late June. This clutch was, however, lost in early July and replaced by a third in mid-July. The young from this hatched on 8 August but did not survive until fledging. The Old Law pair hatched their first clutch on 28 May. The newly fledged young were still in the territory when the second full clutch was found on 27 June, after the start of incubation. This hatched about 15 July and the young fledged in early August.

The numbers of nesting attempts in each year by each pair in the detailed study area are shown in Table IX. The higher mean number in 1976 reflects the higher loss rate in that year. No nest was found in one territory in either 1975 or 1976 (the same territory in both years) despite intensive searching and watching of the birds. Numerous "display" and "trial" scrapes were made and it seems possible that the birds were incapable of producing eggs. The birds concerned were not colour-ringed, so it is not known if they were the same individuals in both years, although this seems likely.

TABLE IX

*Numbers of nesting attempts on the North Shore
per pair per season*

No. of attempts	1975*	1976*	Both years
0	1	1	2
1	1	0	1
2	7	1	8
3	3	4	7
4	0	4	4
5	1	0	1
Mean	2.2	3.0	2.6

*Different sample sizes in the two years reflect different extents of detailed coverage.

The means for the two years do not differ significantly.

TABLE X

Summary of data on production and survival of young Ringed plovers

	Mestersvig	Lindisfarne	
Mean no. of clutches per pair per year	1	2.6	(Table IX)
Mean no. of eggs laid/clutch	3.86	3.84	(Table I)
Probability of clutch surviving to hatching	(0.38*)	s	(See Tables IV & V)
		(Very variable)	
Probability of eggs surviving in successful clutches	1	0.95	(Text)
Probability of incubated egg in successful clutch hatching	1	0.92	(Text)
Probability of hatched young fledging	0.5*	0.45	(Pienkowski, In press <i>b</i> : table 13)
Probability of fledged young surviving to 1-year-old	n.d.	0.57	(Pienkowski, In press <i>b</i> : table 6)

*Probably atypically low for Scoresby Land.

Population dynamics

If a breeding population of animals is to be maintained without continual net immigration, the production of young surviving until reproductive age must not be exceeded by the mortality of the breeding adults.

The annual mortality of nesting adults (regardless of age) at Lindisfarne was 20% (Pienkowski, In press, *b*). Thus each pair need to produce, on average, 0.4 surviving young per year. The figures, relevant to production of young and their survival are summarized in Table X. At least some young birds are capable of breeding at one-year-old but only some

do so, probably because of territoriality (Table 10 in Pienkowski, In press *b*). Therefore, the product of items 1 to 7 in Table X gives the mean number of potential recruits per pair per year: 2.24s at Lindisfarne. (Because of the number of components and their methods of calculation no confidence limits can be attached to this value.) For this value to exceed 0.4, $s > 0.4/2.24$, i.e. 0.179. It is clear from Table IV that production of Ringed plovers was only marginally sufficient to replace losses in several study areas. Furthermore, it was totally inadequate in some years in some situations, notably Holy Island Snook in 1976 (and several years since then—Table XI and unpublished data) and St Cyrus in 1975.

Figures at Mestersvåg are inadequate for the equivalent calculation to be made. However, using the Lindisfarne survival rates of adults and juveniles and the probable underestimates for chick survival, clutch survival of 0.36 is required for population stability. The acknowledged under-estimate of 0.38 exceeds this, and other, probably more typical, Arctic estimates greatly so (Table IV).

TABLE XI

Summary of Ringed plover nesting success at Lindisfarne NNR in 1977

Place	No. of clutches attempted	No. of clutches hatched	Success (%)
North Shore	19	1	2
Rest of Holy Island	16	5	31
Ross Back Sands	15	5	33
Old Law	31	18	58
All other areas of NNR	8	1	12.5
Totals	89	30	34

Source: P. A. Snell (pers. comm.). Data not available for Mayfield method, so that percentage success values are probably overestimates.

Discussion

Time of breeding

In some species of birds, the breeding season is timed either so that the young are being raised when food is most plentiful or, if food is in short supply early in the season, eggs are laid as soon as sufficient food is available to the female to allow their production (e.g. Lack, 1954, 1966, 1968; Perrins, 1970; Källander, 1974; Slagsvold, 1975; Dunn, 1976). Högstedt (1974) has presented evidence that this applies to at least one wader, the Lapwing *Vanellus vanellus* in southern Sweden, where the birds spend longer on territory before egg-laying if the density of available earthworms, their main prey, is low.

Many breeding waders, including Ringed plovers, utilize the very high summer productivity of prey species, notably Diptera, in both Arctic and temperate breeding grounds, to allow production and growth of their young (e.g. Holmes, 1966*a, b*; Holmes & Pitelka, 1968;

Nettleship, 1973, 1974; Pienkowski, *In press b, c*). However, while an abundant available food source is clearly a prerequisite, changes in abundance do not necessarily determine the time of breeding. In the present study, in Greenland, the timing of snow clearance from nesting areas appeared to be the relevant factor, as evidenced by the observations at Mestersvig, the differences in date of nesting in other valleys with different timings of snow melt and the lack of a marked seasonal peak in prey availability. These results are discussed more fully by Green, Greenwood & Lloyd (1977) who also consider the differences between north-east Greenland and some other high Arctic areas. The possible effects of timing of snow clearance, acting through availability of food or of nesting sites, are difficult to separate. However, evidence from Norway suggests that the important feature may be the availability of large snow-free areas, in which nest-finding by predators is difficult (Byrkjedal, 1980; and see below).

At Lindisfarne, there is no such obvious determinant of the timing of breeding as snow-clearance. The long delay there between territory establishment and the commencement of laying is, at first sight, anomalous. Settled snow is fairly rare there even in mid-winter and nest sites are available throughout the season. It is unlikely that food for the laying female is critical, because both before and during incubation much potential feeding time is not utilized; available prey appears to be abundant throughout the season (Pienkowski, 1980); and the birds appeared to have no difficulty in obtaining most or all of their food from their small territories, whereas Greenlandic birds foraged outside their larger territories. Also, throughout the season, egg production appeared not to be difficult, as relaying after the loss of a clutch commonly began within as little as four days (or, in the case of one nest lost to predation during laying, one or two days), and the replacement clutches apparently took no longer to produce (Fig. 3). Up to five clutches (mean 2.6) were produced by a female in a season (Table IX). Although there was a slight tendency for an increase in frequency of three-egg clutches later in the season (Pienkowski, unpublished), the frequency remained low and there is no reason to suppose that a proximate factor (food shortage) was responsible. The reduced time taken to lay smaller clutches may have benefits later in the season when an earlier hatching of young by one or two days may be an appreciable benefit as probability of survival of young falls towards the end of the season (Pienkowski, *In press b*). Additionally, the shortened nest exposure time reduces the risk of predation, but the magnitude of this benefit, alone, is inadequate to compensate for the loss of 25% of the clutch. (Many passerines lay smaller clutches later in the season, the principal reason for this, put forward by Lack (1966), being the reduction in suitable food available for feeding the young later in the season. Such a cause is unlikely, however, in the case of Ringed plovers, for reasons discussed by Pienkowski (*In press b*).

An alternative to the food-for-egg-formation argument is that by delaying laying, the birds are "insuring" against the risk of food shortage during incubation, and a consequent need to desert (Brooke, 1978). This seems unlikely to apply to Ringed plovers because, apart from the reasons outlined above, desertion for any reason is rare (Table VII), and probably due to human interference when it does occur. Furthermore, nests of Ringed plovers stand a high probability of loss for other reasons (Table III, VII). Also, incubation shifts do not become shorter later in incubation (Table II) as would be expected by Brooke (1978) if food was initially difficult (or time consuming or involved long journeys) to obtain but later became easier to collect.

Timing of production of young to coincide with prey abundance also seems a difficult

hypothesis to apply to Ringed plovers. Although there are indications of an increase in availability of flies in April and early May, sandhoppers were already very numerous by then and intertidal prey were also available (Pienkowski, 1980, 1982, In press *a*). Also, the increase in fly abundance occurred well before the hatching of the first young. Indeed, if production of young is delayed to match increased fly availability, an earlier start would be expected, because of the decreased probability of survival of young later in the season (Pienkowski, In press *b*). Moreover, throughout the season the chicks appeared to have surplus feeding time, their rates of weight gain showed no sign of dependence on food availability, and losses were due to other causes (Pienkowski, In press *b*).

It also seems unlikely that the risk of severe weather early in the season delays nesting, as the conditions in the northern parts of the breeding range in June and July are considerably less clement than at Lindisfarne in April. The only conditions which caused prolonged brooding and cessation of feeding by the young were heavy rain on one day and fairly frequent low overnight temperatures in Greenland in August, and a single occasion of a freak snowfall on 1 June 1975 at Lindisfarne. Although severe weather has led to some desertions in Greenland (Melfo, 1979), moderately cold, wet or windy weather in summer at Lindisfarne did not appear to depress hatching success. Indeed, one could argue that it might have a beneficial effect, since tourists were deterred by it (see below).

A feature that does appear to account for the delay in commencement of nesting at Lindisfarne is the high risk of nest predation early in the season. This factor alone is probably sufficient to account for the late start to the breeding season, as the probability of a clutch surviving to hatching before mid-May at Lindisfarne was only about 3% (Table V).

The reason for the seasonal variation in incidence of predation is less clear. As indicated above, generalizations on this aspect are particularly difficult, because a large proportion of the losses may be due to the actions of a small number of individual predators, to which eggs of Ringed plovers are a minor food source. Therefore, small changes in the behaviour of these individuals may have marked effects on plover nesting success. Thus, the increase in alternative foods such as other birds' eggs and young Rabbits *Oryctolagus cuniculus* may decrease the predation pressure on Ringed plover nests. Also, as the predators themselves breed, the spread of their activities may become more restricted. It is also possible that Ringed plovers may gain protection later in the season from other bird species nesting in the vicinity (notably terns which do not arrive till later), and this is explored later.

A breeding situation with some similarities to that of Ringed plovers in both Greenland and Britain occurs in Golden plover *Pluvialis apricaria* in southern Norway where, by observations and field experiments, Byrkjedal (1980) found decreasing egg predation later in the season. He attributed this to the high vulnerability of nests situated on small, snow-free, patches of ground.

Annual variability in hatching success may be common amongst waders, Purdue (1976*b*) reporting 29–100% in Snowy (= Kentish) plover in the Great Salt Plains of Oklahoma, Harris (1967) 44–82% for Oystercatchers *Haematopus ostralegus* at Skokholm, Wales, and Soikkeli (1967, 1970) 30–97% for Dunlin *Calidris alpina* in Finland (note that some studies used different methods for calculating nesting success). Hildén (1978) found that the number of Temminck's stints hatched per adult in west Finland varied between 0.63 and 2.37.

The end of the nesting season of Ringed plovers may be determined by the need for adult birds to divert energy to other activities, such as moult at Lindisfarne or preparation for migration in Greenland.

This is evidenced by the incidence of a few desertions by one or other of the pair late in the season (and possibly by the failure to return next summer of a female left late in the season to incubate alone, discussed earlier). The decreasing pre-fledging survival of chicks hatched late in the summer (Pienkowski, In press *b*) may be a consequence of lack of adult attentiveness then, but may also have other causes which would lead the adults to reduce their investment in chick-rearing then.

Possible reasons for differences in breeding success between areas and years

Apart from the erratic differences due to the behaviour of individual predators referred to above, several possible factors may give rise to the differences in Table IV. These include distribution of predators, conspicuousness and accessibility of nests to predation, intra- or inter-specific interference and protection, human interference and conservation measures.

The birds at the northern end of Old Law appeared to gain some warning of the approach of predators (or observers) from the adjacent ternery; and the terns also appeared, incidentally to the defence of their own nests, to afford effective protection against aerial predators, which were mobbed. The observer at St Cyrus (N. K. Atkinson, pers. comm.) came independently to the same conclusion in accounting for the marked difference in nesting success in the two years there: "the main difference between 1974 and 1975 was the latter's late 'spring', which included gale-force north-easterly winds in late May, snow showers on June 1st [see above], and generally cold temperatures till mid-June. Apart from this, and possibly due to it, the Arctic terns [*Sterna paradisaea*] (c. 65–70 pairs in 1974) did not really get going, and these definitely help the Ringed plovers by keeping Crows out. Normally, the heaviest predation occurs from mid-April to late May, before the terns have started nesting, and later in July if they do not have a successful year".

Protection from aerial predators by terns probably occurs also on the offshore Farne Islands (Northumberland), where the Ringed plovers probably benefit also from the absence of ground predators and the control of human visitors by wardens (see Table IV). The benefit of nesting in proximity to terns at Lindisfarne and the Farne Islands was noted previously by Bolam (1912). At Aberlady Bay, East Lothian, nests in the ternery are more successful than those outside, probably due both to protection by terns and by the exclusion of humans from the ternery (pers. obs.). There are several anecdotal reports of Ringed plovers benefitting from nesting in colonies of terns or Black-headed gulls *Larus ridibundus*; on Scolt Head, Norfolk, nesting in a ternery afforded protection from Carrion crows and Rooks *Corvus frugilegus* (Turner, 1928). At this site, some birds increased their chances of avoiding predation by nesting under branches of *Suaeda*. Similar behaviour was noted at Lindisfarne, where some birds on the North Shore occasionally nested under tree branches washed up on the shore, and some at Ross Back Sands commonly nested among marram grass. Walters (1957) reported that Kentish plovers in the Netherlands often nest and find protection in colonies of Common terns *Sterna hirundo* and Avocets *Recurvirostra avosetta*. Fuchs (1977) described a situation in Scotland where Sandwich terns *Sterna sandvicensis* gained protection by breeding in colonies of other terns and Black-headed Gulls and apparently adjusted their time of breeding according to that of the "protecting" species. There have been numerous other reports of various species gaining protection by nesting in such colonies (e.g. Bergman, 1946, 1957; Ahlen & Andersson, 1970; Bengtson, 1972).

The effect of human disturbance may be the reason for the differences in nest survival in the three main areas at Lindisfarne (Table IV). This difference was maintained in 1977 (Table XI) and probably in other years since (less systematic observations). The North Shore lies near the road to the tourist centre of Holy Island village and there are numerous access points to the beach and dunes (Fig. 1, Table XII). Access was unrestricted and generally unsupervised. Well over a hundred tourists were commonly recorded at the eastern end of the North Shore (east of the territories maintained through the summer, shown in Fig. 1, but coinciding with the area where territories were abandoned early in the season). Many of these tourists walked around the Snook. At Ross Back Sands, where a walk of about 1.2 km is required from car park to nearest beach, rarely more than 50 people visited the area in a day; most stayed near the footpath access and only about a tenth walked around Old Law.

TABLE XII
Percentage of nests surviving to hatching in different areas at Lindisfarne in relation to human disturbance

	Nest survival (%)		Distance from car park (km)	Number of human visitors per day
	1976	1977*		
Old Law	43	58	3.0-4.5	c. 5
Ross Back Sands	21	33	1.0-2.5	< 50
Snook	1.4	2	0-0.7	Up to > 100

*Survival rates probably slightly overestimated in all areas in 1977.

Some direct deleterious effects of people were noted: five clutches of eggs were stepped on in 1977 (P. A. Snell, pers. comm.); single, or occasionally two, eggs were probably taken from clutches in each year (Table VII; and P. A. Snell, pers. comm.); dogs took several clutches (Table VII); and direct disturbance probably caused desertion of the eastern North Shore territories (see above; cf. Hölzinger, 1975). However, indirect effects of people and their dogs were probably more serious. Incubating birds normally left their nests when people or dogs approached, though a few birds developed considerable tolerance of people as the summer progressed. The more often the birds left the nests, the greater the opportunity for Carrion crows to detect their movements to and from the nest. Some Crows appeared to use vantage points to watch for movements of disturbed birds. (Ringed plovers often remain crouched on the nest and rely on camouflage in response to the presence of aerial predators, in contrast to their early departure at the approach of ground predators. At Lindisfarne most aerial predators are active in daylight and ground predators nocturnal, but the presence of human potential "ground predators" and the reaction to them potentially gives a considerable advantage to aerial predators.) In addition, increased bird movements to and from the nest led to more obvious trails of footprints in sandy areas. These and increased scent trails (possibly of the birds themselves but also well-meaning bird-watchers, and dogs) may have assisted Foxes, Weasels, etc. to locate clutches at night. A comparable interaction between human disturbance of incubating Black oystercatchers *Haematopus moquini* in South Africa and egg predation by gulls has been suggested by Summers & Cooper (1977), and reported for Dunlins and gulls in Scotland (Hobson, 1972).

The effect of mutual interference on nesting is difficult to assess. Various studies have argued that increasing density leads on the one hand to an increase in predation (Tinbergen, 1952; Hinde, 1956; Lack, 1966; Tinbergen, Impeken & Franck, 1967) but, on the other, to increases in mutual alertness and protection within and between species (e.g. Hagen, 1947; Kruuk, 1964; Lack, 1968; Kvaerne, 1973; Goransson, Karlsson *et al.*, 1975; Slagsvold, 1980). Both such effects may apply to Ringed plovers; predators appeared to exploit the proximity of nests on the North Shore to visit the area periodically and take many clutches. Conversely, however, adjacent pairs all performed distraction displays towards, or mobbed, potential predators (as also reported by Mason (1947) and Simmons (1956), undoubtedly causing confusion to them. No obvious pattern of predation rates in relation to density were apparent at Lindisfarne. Rates were highest at the North Shore and lowest at Old Law, both these being areas of high bird density and small territories. Intermediate predation rates were found at the larger, lower density territories on Ross Back Sands.

The reason for the large variation in size of territories is unclear, partly because of the doubts which surround the function of territories in this species. Food supply for adults seem unlikely to be implicated, because of the variation in the extent to which the territory was used for food gathering, at least before the young hatch. Safeguarding of food supply or a feeding area for family parties seems a more feasible function of a territory, but again this argument is weakened in that the territory may be deserted by the family. However, such desertion seemed more frequent in larger and less productive territories: for example, it was more common at Ross Back Sands than North Shore, and was typical in Greenland. Also compatible with the observed variation in nesting density is the suggestion that territories serve to space out nests according to the conspicuousness of nests in relation to nesting habitat. Thus, the highest densities occurred at the Snook and Old Law where the substrate was gravel on which nests are best camouflaged; and lower densities were found on the sandy beaches of Goswick and Ross Back Sands where the nests themselves were more obvious but were difficult to find mainly because of the expanse of sand or the marram cover. The lowest densities occurred in Greenland where, at the time of laying and during the early part of incubation, the possible nest sites were restricted to small clear areas, aiding searches by predators (cf. Byrkjedal, 1980). Simmons (1956) argued that the main function of territory in the three small plovers is in spacing out of pairs and nests, but it is difficult to exclude totally the element of feeding of small young. Harris (1970) argued that territories were required for feeding young Oystercatchers at Skokholm, but this wader species is exceptional in that the adults feed the young. Holmes (1970) argued that territory sizes of Dunlin in Alaska are adjusted to allow enough food for adults early in the season, but his paper does not adequately consider the effects of predation. For the same species in Finland, Soikkeli (1967) argued that the function of territory is to aid pair formation, but if this is the case, it is not clear why territory size should vary so markedly.

Southern limits of distribution and some implications for conservation

Variations in nest survival rate on a wide geographical scale may also be related to predation intensity, and to the extent of available habitat in which to hide a nest. Generally, densities and number of species of potential predators, and the efficiency of predation due to increasing overall prey density, increase at lower latitudes (e.g. Larson, 1960; Voous, 1960; Connell, 1971; Fretwell, 1972; Dorst, 1974; Maiorana, 1976). The study by Jarvinen &

Väisänen (1978), of species diversity of waders in relation to latitude, stressed the importance of increased habitat diversity in increasing species diversity, but commented that predation did not appear to be implicated in the increasing number of species northwards (within Fennoscandia). However, they appeared to consider increasing predation only as a factor which might reduce competition and thereby enhance species diversity, and not the reverse effect that increasing predation might limit the range of individual species and hence the number of species represented. Huffaker (1971) and Krebs (1972) cite numerous cases of predators affecting the distributions of prey species.

The extent of bare ground also decreases at lower latitudes, being restricted in western Europe almost to the shoreline. The increasing predation and decrease in extent of bare ground would tend to increase the probability of nest predation and limit the southern extent of the breeding distribution. However, two closely related species breed further south in Europe and North Africa than Ringed plover. The Little ringed plover *Charadrius dubius* is an inland breeding species, typically found breeding on salt flats (Fig. 4). Its recent spread across Europe and its dependence on man-made, often transient, barren habitats, such as gravel pits and newly reclaimed land, have been well documented (e.g. Parrinder, 1964; Parslow, 1967). The Kentish or Snowy plover is, in the western Palaearctic, largely a coastal species, like the Ringed plover. It differs in being adapted to sand and clay, rather than gravel and stony, substrates by virtue of its body colouring, egg markings, egg covering behaviour (Meinertzhagen, 1954; Simmons, 1956; Hall, 1960; Dybbro, 1970; Maclean 1974) and nest concealment (Bent, 1929; Rittinghaus, 1961). It may also have particular adaptations to warmer conditions, such as egg cooling (Purdue, 1976a; cf. Begg & MacLean, 1976), resistance to water shortage and high salinity (Purdue, 1976b; Purdue & Haines, 1977; cf. Maclean, 1976), and possibly different temperature tolerances for biochemical activity (see Chappell, 1980).

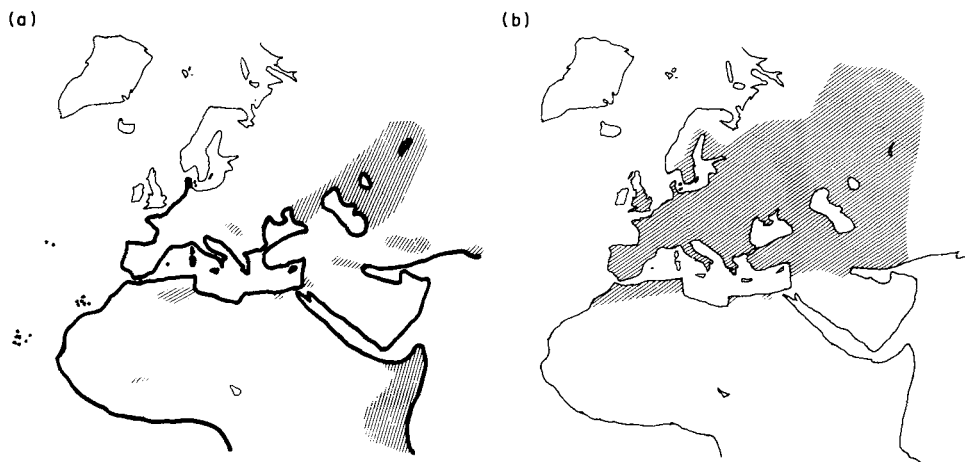


FIG. 4. Breeding distributions of (a) Kentish plovers and (b) Little ringed plovers, according to Voous (1960). Coastal breeding areas indicated by heavy line and inland areas by shading.

There appears to be a latitudinal gradient in the distribution of gravel and sand on coasts (Fig. 5) and this seems to be matched closely by the breeding distributions of the two coastal species (Figs 1, 4). Dybbro (1970) noted that, in Denmark near their northern limit, Kentish plovers nested only in markedly sandy biotopes, and that the breeding population had declined due to increased human activity in these areas. In the Netherlands, where the three small plover species may breed alongside each other, they hold mutually exclusive territories, and there may be some dominance relationship between species which could affect distribution (Sluiters, 1954). The species may compete by the possible increase in nest predation with increasing density as, although all species will be affected, the probability of a nest being lost will be influenced by the match between, e.g. camouflage and habitat (cf. Fretwell, 1972).



FIG. 5. Predominant substrate types at top of depositing shores. — Boulder, gravel, sand and gravel; sand, clay, mud; - - - no data. Sources: Anon. (1974), INQUA (1967-75), Pienkowski (1975, pers. obs.), N. C. Davidson, P. J. Dugan & P. R. Evans (pers. comm.).

Another factor often suggested as contributing to the southern limit of shorebird breeding distributions is the presumed restriction of feeding time for young caused by the shorter daylight period further south. However, the feeding of Ringed plover chicks is less affected by nocturnal darkness at Lindisfarne than by "nocturnal" low temperatures at Mestersvig (Pienkowski, *In press b, c*). It is possible, however, that increased darkness period could have an influence via predation rate, as most losses of chicks at Lindisfarne occurred at night (Pienkowski, *In press b*).

At the limits of a distribution, it is likely that breeding production will approximate to, or be less than, mortality. In the case of the Ringed plover, there are indications that, in much of Britain, the species is only self-supporting at sites where it receives some form of natural or artificial protection (Table IV): namely, off-shore islands protected from ground predators; tern colonies which provide defence against aerial predators; or nature reserves

which can provide protection against some predators and/or people. These requirements may also apply to other species nesting in fairly open situations, and may be relevant to the southern limit of Turnstones *Arenaria interpres* on islands in the Baltic (Voous, 1960; Larson, 1960) and Long-tailed duck *Clangula hyemalis* in the Arctic (Larson, 1960). Colonial birds demonstrate this dependence on protected sites throughout much of their range, e.g. cliff and island-nesting seabirds. Even in the Arctic, terns may have to wait until sea-ice melts before their nesting islands are safe from ground predators (Lack, 1933; Bertram, Lack & Roberts, 1934; Bird & Bird, 1940; Larson, 1960; Meltofte, 1975). Many other species, including the waders Turnstone and Grey phalarope *Phalaropus fulicarius*, appear to depend on island nesting sites for protection from predators in parts of their range (Larson, 1960). The same author also argued that the breeding range of many Arctic shorebirds and other species is limited by the intensity of predation by the Arctic fox, against which protective adaptations vary between species, so that the limits of prey distributions vary also.

For the Ringed plover in western Europe, usage of beaches by people and their dogs creates an additional adverse factor and this may be enough to change a positive net production to a negative one. If conservation of breeding populations of the species is required, it may prove necessary to eliminate public access to certain areas and/or compensate for the effect of humans and dogs by reducing "natural" predation, e.g. by reduction or exclusion of some predators (see, e.g. Forster, 1975). A comparable situation appears to exist in breeding Black oystercatchers in South Africa (Summers & Cooper, 1977).

Because of the possible interactions between the large number of factors probably influencing breeding success, further investigation of these, and examination of prospective conservative measures, would require field experiments, such as by restricting the access of humans or of various predators.

Summary

The nesting of Ringed plovers was investigated in 1974 at Mestersvig, NE Greenland, and in 1974–76 at Lindisfarne, north-east England. The use of Nest Record Cards completed by birdwatchers was investigated in order to obtain information from other areas, but these were found unsatisfactory for most analyses. However, some information supplied by individual workers at several other sites is incorporated.

Territory size was much larger at Mestersvig than Lindisfarne, where it varied considerably. A smaller proportion of feeding took place on territory at Mestersvig than at Lindisfarne, where again there was variation in relation to local geography. It is proposed that territory size is adjusted mainly to reduce the conspicuousness of the nest in relation to its surroundings, but the possibility that feeding conditions are also involved cannot be excluded. Clutch sizes were similar in the two areas. Incubation (mean period about 25 days) was shared fairly equally by the two sexes. Longer incubation shifts at Mestersvig and some areas at Lindisfarne than at other Lindisfarne sites were associated with greater distances between nests and feeding areas. Most egg losses were probably due to predation, and were fewer in the Arctic than in Britain, where nesting success varied greatly in different areas and years, and in relation to timing within a season. Up to five nestings per pair per year were made at Lindisfarne, but only one at Mestersvig.

The timing of breeding is discussed, and it is concluded that the date of start of egg-laying in north-east Greenland is determined by the time of snow clearance, while that at Lindisfarne is related to the decreasing probability of egg-predation later in the season. Because of the high nest losses, the production of young at many temperate sites, including parts of Lindisfarne, was probably inadequate for the population to be self-supporting, and the reasons for the large seasonal, annual and geographical differences are discussed. It is concluded that increasing predation probably determines the southern nesting limits of Ringed plovers, but that this limit may be modified by varying degrees of different types of natural and artificial protection, and extent of habitat suitable for egg camouflage. Increased human usage of nesting beaches probably has an adverse effect on nesting success but, because of the complexity of the number of inter-related factors affecting the latter, without field experiments it is difficult to predict how this could best be offset by protection measures.

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