Some aspects of the ecology of the ringed plover(charadrius hlaticula) during the breeding season.

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Some Aspects of the Ecology of the Ringed Plover (*Charadrius hiaticula*) during the Breeding Season.

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(M.Sc. thesis 1979)

CONTENTS

ABSTRACT

The Ringed Plover *Charadrius hiaticula* was studied during a period of fieldwork in 1979. Data from this and other studies are used in consideration of certain aspects of the ecology of the species during the breeding season. There were two main areas of study, the mainland (Ross Back Sands, Old Law and Budle Bay) and the island (Lindisfarne).

Territories were taken up earlier on the mainland.

There was a fall in the number of territories occupied in 1979, compared to previous years.

There is good evidence for site tenacity, with many pairs occupying the same or an adjacent territory year after year.

The minimum length of territory occupancy ranged from 15 to more than 94 days.

The first egg of 1979 was laid on 2 May.

The clutches were of 3 or 4 eggs.

The peak of laying and the amount of laying per pair varies from year to year.

The final clutch of 1979 was recorded on 18 July.

The interval between territory uptake and the laying of the first egg was longer, the earlier the territory was established.

85% of eggs noted were predated in 1979.

The major agent of egg predation was crows.

The period of hatching lasts from May to August.

The incubation period is usually from 22 to 26 days.

The fledging success of 1979 was between 5.8 and 12.57% of eggs laid.

The birds spend most of their time feeding on the drier areas of the beach.

Invertebrate samples showed much greater potential prey on wet mud areas than on drier sand or muddy-sand areas.

Females feed faster than males.

INTRODUCTION

For six years from 1973 to 1979 the population of Ringed Plovers (Charadrius hiaticula) has been studied at Lindisfarne National Nature Reserve in Northumberland. During this time a colour-marked population has been built up by ringing chicks each year.

AIMS OF THE STUDY

The study area can be split into two sections, the mainland sites and the island sites. Observations from previous years have shown that there is a considerable difference between the breeding success on the mainland and on the island; the pairs on the mainland, particularly Old Law, being more successful in producing offspring. The aims of the 1979 study were to follow the course of the breeding season of the Ringed Plovers on the reserve selecting some of the major aspects of breeding biology for analysis. Using these data, and those of previous years, an attempt is made to account for the variation in breeding success between areas.

The aspects of breeding biology studies were:

1) Number of breeding birds in each area
2) Territoriality
   a) dates of uptake and breakdown
   b) territory size (or nest spacing)
3) Laying of eggs
   a) dates of laying
   b) position of nest scrapes on the beach
4) Hatching of chicks
   a) incubation period
   b) dates of hatching
   c) hatching success
5) Fledging success

Due to 1979 being a disastrous breeding year for the plovers, data on chicks and fledging are very limited.

In addition to the investigation into the breeding biology, aspects of the feeding behaviour were studied around the mainland area of Old Law. Feeding rates were measured and explanations of differences in rates were attempted using data from invertebrate samples.

STUDY AREA

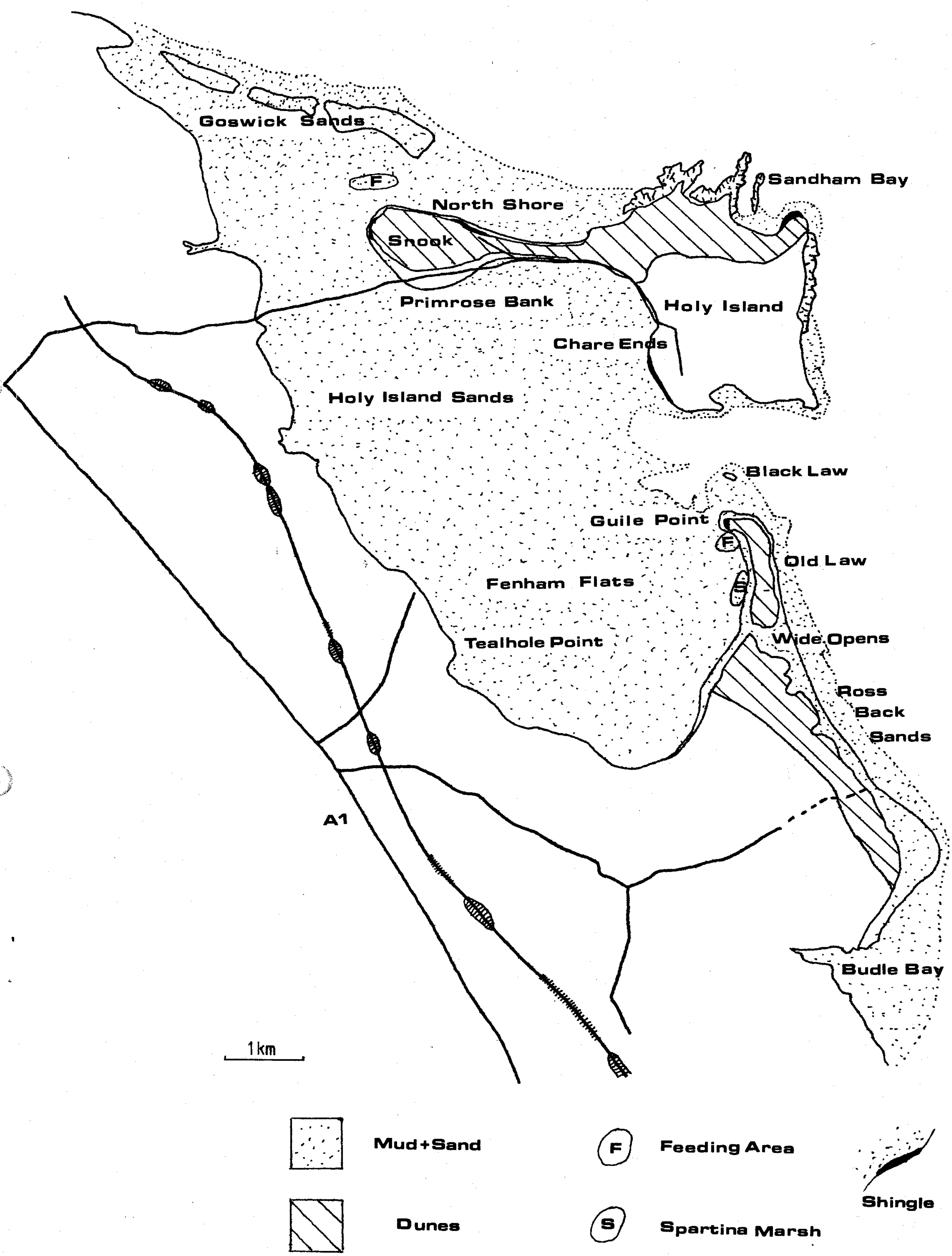
Lindisfarne National Nature Reserve is situated in North Northumberland, and consists of about 8000 acres, most of which is tidal mud flats, sandy beaches and dune areas. The major nesting areas of the Ringed Plover consist of both island and mainland sites. On Holy Island the sites are 1) the North Shore of the Snook, 2) Sandham Bay, 3) Chare Ends, 4) Primrose Bank. Mainland sites are 1) Ross Back Sands, 2) Old Law, 3) Budle Bay, 4) Teal Hole Point, 5) Goswick Sands. A small island between Holy Island and the mainland of Old Law, Black Law, an important Tern nesting site, is also commonly used by at least two pairs of Plover (see Fig. 1).

The North Shore is a piece of coastline about 1½ miles long on the north-west of the island. It contains both sandy and shingle beach backed by marram covered dunes. At low tide about half a mile of sand flats to the north of the beach is exposed. Approximately a quarter of a mile north of Snook point is an important feeding area. At certain conditions of tide and wind a layer of surface water remains over the sand, which attracts both Ringed Plovers and flocks of Dunlin. Along parts of the shore are breaks in the dunes and low-lying areas of shingle slacks appear between them. Some of these are favourite nesting sites of birds. Towards the eastern end of the North Shore is a patch of shingle known as

Fig. 1

The Study Area

FIG. 1 STUDY AREA



Jack Matheson's Bank. This usually holds the highest density of plovers during the breeding season and is enclosed by the Nature Conservancy Wardens during the season in order to protect the nests from human interference. Most holiday-makers visiting the North Shore unfortunately congregate at the western end producing human 'pressure' which can disrupt the normal cycle of the breeding birds.

Sandham Bay is a sandy beach with rocks on either side, and is probably the most heavily visited beach by holiday-makers. It is about a half mile of sand backed by dune cliffs on the north-eastern corner of the island. Despite the considerable use by people, most of whom come during the peak holiday season during June and July, birds still attempt to breed there. At low tide about a hundred yards of sand are exposed and the tide often throws up large quantities of seaweed on which the birds often feed.

Chare Ends is the site on the southern side of the island where the old causeway used to cross. It has only a small patch of shingle beach, but in the past birds have attempted to nest on the cultivated farmland immediately behind it.

The whole of the south side of the island, at low tide, looks out over many acres of mud known as Fenham Flats. This area is used as feeding ground for many waders and geese during the winter. Primrose Bank is a grassy area jutting out into the mud on the south-west corner of the island. On its seaward perimeter are patches of Spartina marsh, but the birds tend to avoid these and usually frequent the westerly side of the Bank. At its broadest the Bank is about 500 yards wide and is backed by the tarmac road of the causeway.

Budle Bay, Ross Back Sands and Old Law are all adjacent and comprise the main plover nesting area on the reserve. Budle Bay is mainly mud flats, dissected by Elwich Burn, but the most important area, and the only part studied in 1979 is the north-west stretch which comprises a grassy bank similar in many respects to Primrose Bank on the island. At low tide the bank looks out over several acres of mud flats within the bay. At the extreme north east corner is a sand spit which juts out into the bay at low tide and is often frequented by large numbers of roosting waders. Here, the coast turns a sharp corner and joins the main sea beach of Ross Back Sands. This is a stretch of about two miles of sandy beach used extensively by holiday-makers. However, people tend to congregate around the footpath entrance, the only access to the beach about a third of the way up, and rarely stray far in either direction. The beach is backed by extensive marram-covered dunes which in turn back onto rough dune pasture used for grazing by both cattle and sheep. Low tide exposes about a hundred yards of sand. At its northern end, Ross Back Sands extends as a large sand spit reaching out towards the south-east corner of Holy Island. The northern end of Ross Back Sands is marked by an extensive open patch of sand completely crossing the spit, known as the Wide Opens, this area is covered by sea only by the highest Spring tides. Beyond this is the main area of the spit known as Old Law. Its eastern side is sand sea-beach similar to Ross, backed by dunes or dune-cliffs. There are inlets into the dunes, some sandy, one large one of shingle, sometimes used as nesting sites. At its northern tip, Guile Point, are two large towers, the Pinnacles, used as a navigational aid. The north west corner of Old Law is probably the single most important breeding site of the whole reserve. It is a patch of shingle beach, backed by dunes facing into a fairly small amount of mud flats at low tide. However, just south of this the coast turns two right-angles producing an elbow bend which looks out over a large expanse of sand flats used extensively as a feeding area. Further south the beach backs a large area of very fertile Spartina marsh, not used extensively by plovers, but at its seaward edge at low tide there are usually many waders. Most of the beach on the west side is sandy, backed by dunes or dune-cliffs and looking out across Fenham Flats.

Two less important mainland nesting sites were visited in 1979. Teal Hole Point is a small area of stony, muddy beach backed by farmland, looking out across Fenham Flats, sometimes used as a nesting site. Further north are Goswick Sands, a vast expanse of sands marking the beginning of a large sand bar stretching out across the north side of the island. Terns often nest at one point on the bar. Plovers, in the past have been known to attempt nesting on the bar but are usually washed off by high Spring tides.

The reserve, as a whole, is a relatively important breeding area for Ringed Plover, in the past supporting about 50 or 60 pairs, approximately 3% of the British breeding population. However, this number now appears to have dropped with only about 40 pairs being seen to attempt breeding in 1979. This may, however, be a temporary reduction after the hard winter of 1978-79.

METHODS

Field work was carried out from 24 April to 27 July 1979. Most of the work was direct observation using binoculars (7 x 40) or Swift Spotting Scope (x15, - x 60). The major sites on the island, the North Shore, Sandham Bay, Primrose Bank and Chare Ends, and on the mainland, Ross Back Sands and Old Law, were visited at least once every three days. The more peripheral sites were visited only occasionally, about once a week for Budle Bank and once a month for Teal Hole Point and Godwick.

The position of each bird seen was noted. It was then sexed and checked for leg rings, from a distance of between 50-100m using the telescope. Sexing the birds was fairly easy if both birds of a pair were present, but on its own, one bird was more difficult. The male has a black collar, and bold black and white markings in the head. The dark markings of the female are usually much browner.

If birds often appeared in the same position in an area, a territory was suspected. This was usually confirmed behaviourally by the birds, most obviously by display flying or aggressive territorial defence, but also more subtly by moving away from an area at the approach of an observer, and returning to it quite quickly once the observer has passed.

As the season progressed it became necessary to locate nest scrapes within the territory. Some of these were on open beach and very obvious. Others were not so. During favourable weather conditions (fairly dry and with little wind) the movement of birds within a territory was well defined by their footprints in the sand. This made detection of a scrape relatively easy, as the footprints would often converge on it. Obviously this method was of no use on shingle beach or grassy areas. Here, the only method, if a bird was seen moving away from an area, and a scrape was suspected, was to hide and watch the bird return to the scrape. This was only useful once incubation had begun, as prior to this the birds do not spend a great deal of time at the scrape. Therefore, this method usually only revealed full clutches. When scrapes with eggs were found, they were photographed and catalogued and checked at each visit to assess their progress.

The presence of chicks in an area was usually fairly obvious due to the considerable behavioural change in the parents at the approach of an intruder. They showed signs of considerable agitation, and often the female would attempt to distract the intruder by means of a broken wing display. Capturing the chicks was a very difficult procedure and for one person, often unsuccessful. When caught they were weighed and colour-ringed and the stage of development of feathers was checked using the procedure proposed by Snow.

Adult feeding behaviour was studied through the breeding season. This involved intensive watches of individual birds and the recording of each feeding movement onto a tape recorder. The recordings were later transcribed and the watches divided into minute intervals to give information on feeding rates.

In order to aid interpretation of the feeding data, a set of invertebrate samples were taken on 26 July. Three areas were sampled about three hours before high tide in the afternoon. The areas were:

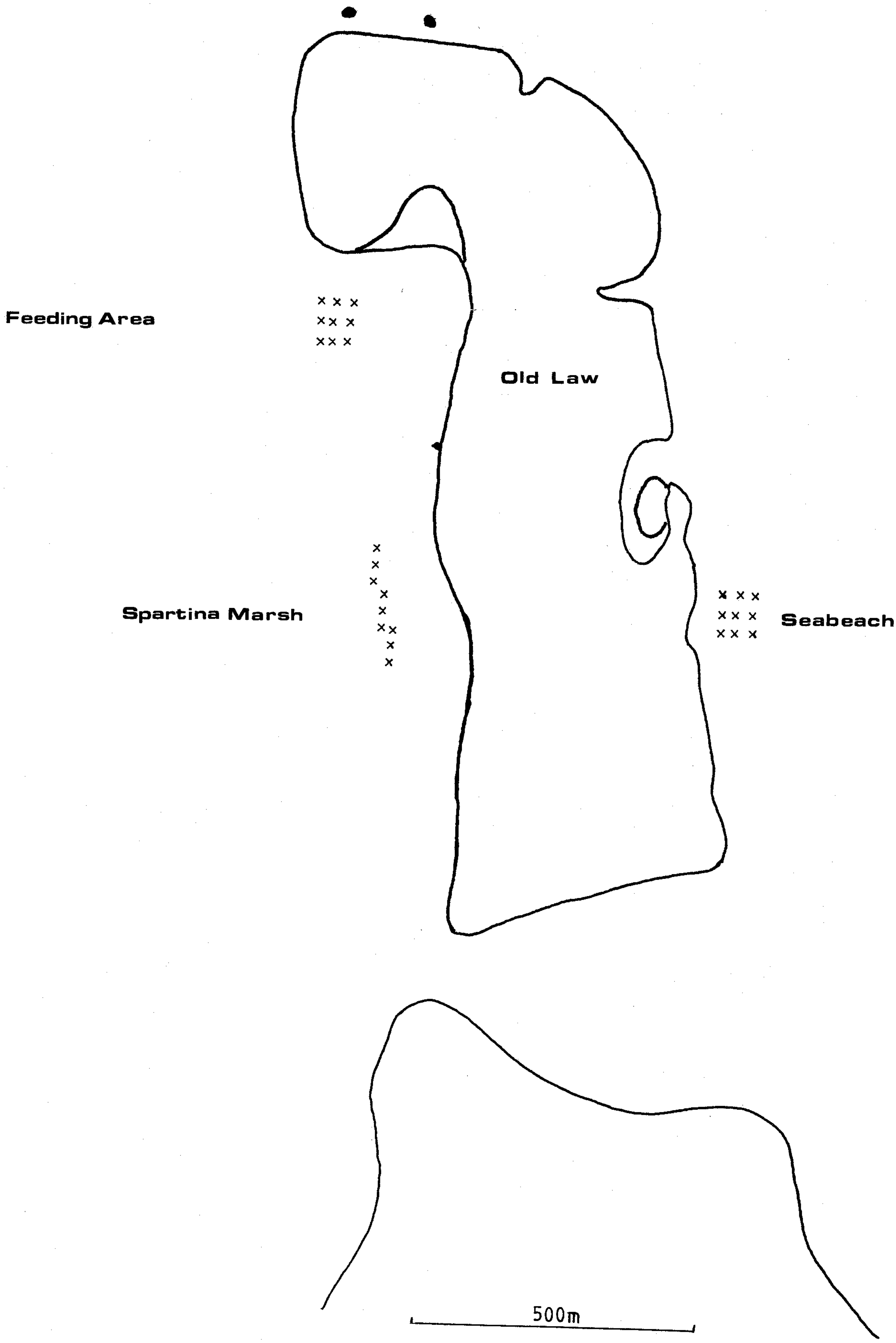
1) The seabeach about halfway along east Old Law.
2) The feeding area, north-west Old Law.
3) The mud bordering the Spartina marsh, west Old Law.
   (see Fig. 2).

Two samples were taken from each of nine points at each area. The points were selected by use of a square grid, points being 25m apart, the starting point for the production of the grid being random. Cores of 10cm diameter and 10cm depth were collected. They were then sieved in situ using a grid size of 11.8 meshes per cm., and the sievings collected in tubes, labelled and returned to the laboratory for analysis.

Fig. 2

The three sites of the invertebrate samples around the shores of Old Law. The feeding area + seabeach samples were taken using a grid of points 25m apart. The spartina marsh samples were taken from the mud, adjacent to the marsh. Each point is separated from the nest by 25m.

FIG. 2 INVERTEBRATE SAMPLE SITES



RESULTS

(A) BREEDING BIOLOGY

(1) Territoriality

During winter birds congregate to form feeding flocks. Very little is known about the wintering area of Lindisfarne birds. Some appear to stay within the area, others not so much migrate as disperse (Pienkowski, pers. com.). In early spring the feeding flocks begin to break down and the birds spread out to take up territories. Uptake is a fairly gradual process with the birds spending more and more time defending a particular area which eventually becomes the territory. Table 1 gives a list of approximate dates of territory uptake for Ross, Budle and Old Law and Holy Island comparing them with the age of the bird if known. The table shows the first date that a bird was seen in an area, if after several more visits that area was accepted as a territory. Many territories had been established before the beginning of field work on 24 April. Some birds begin territory uptake as early as February (Pienkowski, pers. com.). It appeared that a greater percentage of the mainland total (58.3% of 23) were occupied than on the island (21% of 19). This is significantly different ($\chi^2_{1\ d.f.} = 10.85$, $p < 0.001$). A further 12.5% of mainland territories were established in the following week, just before the end of April; 52.6% of the island's territories were established between 26 April and 8 May. This would seem to show that uptake on the mainland was earlier than on the island. However, Pienkowski noted the opposite from 1974 to 1976. He found that the earliest territories to be taken up were those on the North Shore of Holy Island itself. The 1979 data may be biased by the fact that North Shore birds tend to spend a great deal of time off the territory feeding on the sands towards Goswick and therefore were not recorded on territories

Table 1

The approximate dates of territory uptake and breakdown.

The uptake dates can at best be accurate only to within 3 days and may be even more inaccurate due to the gradual nature of territory uptake. In some cases breakdown is quite abrupt but in others it is more gradual and the same problems of accuracy apply here. The length of time in possession of a territory is, therefore, only a minimum value. The area in which the territory lies, is given, as are the age and sex of one of the birds, if known. (No pair had both birds ringed). UR means that both birds of the pair were unringed.

* Those territories were still present at the end of field work.

Table 1 a) Ross, Old Law and Budle

Age(yrs)	Sex	Taken up by	Breakdown	Area	Minimum length(days)
4	♀	24 April	20 July	Ross	87
UR		28 April	7 June	Ross	40
2	♀	24 April	27 July*	Old Law	94
UR		12 May	27 July*	Old Law	76
UR		24 April	27 July*	Old Law	94
UR		24 April	27 July*	Old Law	94
6?	♂	12 May	27 July*	Old Law	76
UR		24 April	11 June	Old Law	48
UR		24 April	27 July*	Old Law	94
UR		24 April	27 July*	Old Law	94
4	♂	24 April	27 July*	Old Law	94
4	♀	24 April	27 July*	Old Law	94
1	♀	28 May	27 July*	Old Law	94
3	♂	28 April	20 July	Old Law	83
UR		28 April	12 July	Old Law	75
6?	♂	28 April	27 July*	Old Law	90
2	♀	24 April	20 July	Old Law	87
UR		1 June	27 June	Old Law	27
UR		4 June	21 June	Old Law	17
UR		24 April	27 June	Old Law	64
3	♂	24 April	20 July	Old Law	87
4	♂	27 May	1 July	Budle	35
1	♀	27 May	11 June	Budle	15

Table 1 (contd.) b) Holy Island

Age (yrs)	Sex	Taken up by	Breakdown	Area	Minimum Length (days)
4	♀	26 April	21 May	North Shore	27
UR		6 May	11 July	North Shore	66
UR		14 May	23 July *	North Shore	70
5	♀	26 April	16 July	North Shore	83
2	♂	11 May	23 July *	North Shore	73
3	♂	11 May	16 July	North Shore	66
4	♂	8 May	11 July	North Shore	65
UR		6 May	23 July *	North Shore	88
UR		6 May	23 July *	North Shore	88
UR		6 May	23 July *	North Shore	88
UR		6 May	23 July *	North Shore	88
6?	♂	29 April	21 July *	North Shore	84
UR		7 May	16 July	Primrose Bank	70
1	♂	7 May	16 July	Primrose Bank	70
UR		7 May	23 July *	Primrose Bank	77
1	♀	26 April	23 July *	Sandham	88
UR		26 April	23 June	Sandham	28
UR		26 April	8 June	Sandham	44
UR		30 May	23 July *		54

during my visits. By the first week in May about 70% of the territories were established. The rest were established by the end of May.

The changes in the number of territories in each of the areas of the reserve, between 1974-1976 and 1979 are given in Table 2.

There has been a considerable fall in the number of territories taken up. This decline may, however, be due to low over-wintering survival during the severe winter of 1978-1979. Territory positions for 1979 are shown in figs. 3-6. Because only a few marked birds were present, only a limited amount of data are available on the effect of age on territory uptake. Of 4 first year birds breeding, only one was present in a territory by the end of April. Of 13 older marked birds breeding, 9 were present in a territory by the end of April. These results are significantly different ($\chi^2_{1\ d.f.} = 14.03$, $p < 0.001$), but obviously much more information is needed before a valid result can be obtained.

The territory itself is usually a strip of land perpendicular to the beach stretching from the dunes behind the beach to the water's edge. Consequently, with such a large tidal movement in the area, some territories increased considerably in length with the state of the tide. However, as the distance from the high water mark increased, the amount of territorial defence appeared to decrease, hence the length of territories at low tide could not be measured as there was no definite end point.

No direct data on the breadth of territories were gained. In crowded areas, for example north-west Old Law or the enclosure on the North Shore, boundary disputes showed that territories were touching, so that breeding density gave some idea of size. On the north-west shore

Table 2 Changes in the numbers of territories in each area of the reserve between 1974 - 76 and 1979.

	1974 - 76	1979
Goswick	4	0
Sand Rigg	3	2
North Shore	17 - 18	11
Chare Ends	1	1?
Holy Island Harbour	1	0
Sandham Bay	2	4
Primrose Bank	3	4
Teal Hole Point	1	0
Budle Bank	3	2
Old Law	15	19
Ross Back Sands	6	2
Total	56-57	42

Figs. 3 - 6 Territories

x An area accepted as a Ringed Plover territory for a period of time during the 1979 breeding season. The colour combinations of any ringed territory holders are given. UR means that both of the pair of birds are unringed.

Fig. 3. Old Law and Ross Back Sands on the mainland.

Fig. 4. The North Shore and Primrose Bank on the island.

Fig. 5. Sandham Bay on the island.

Fig. 6. Budle Bay on the mainland.

FIG. 3 TERRITORIES

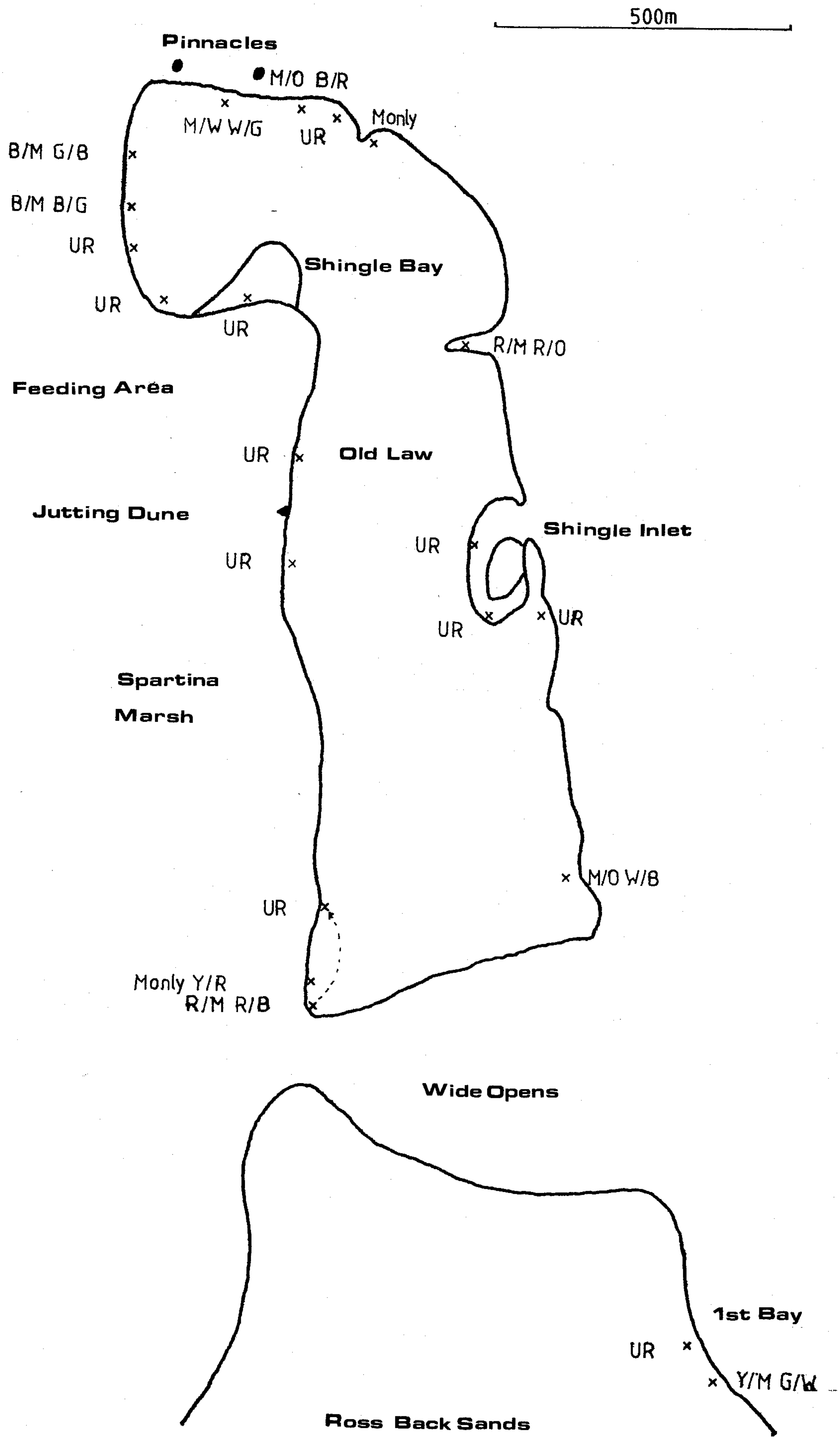


FIG. 4 TERRITORIES

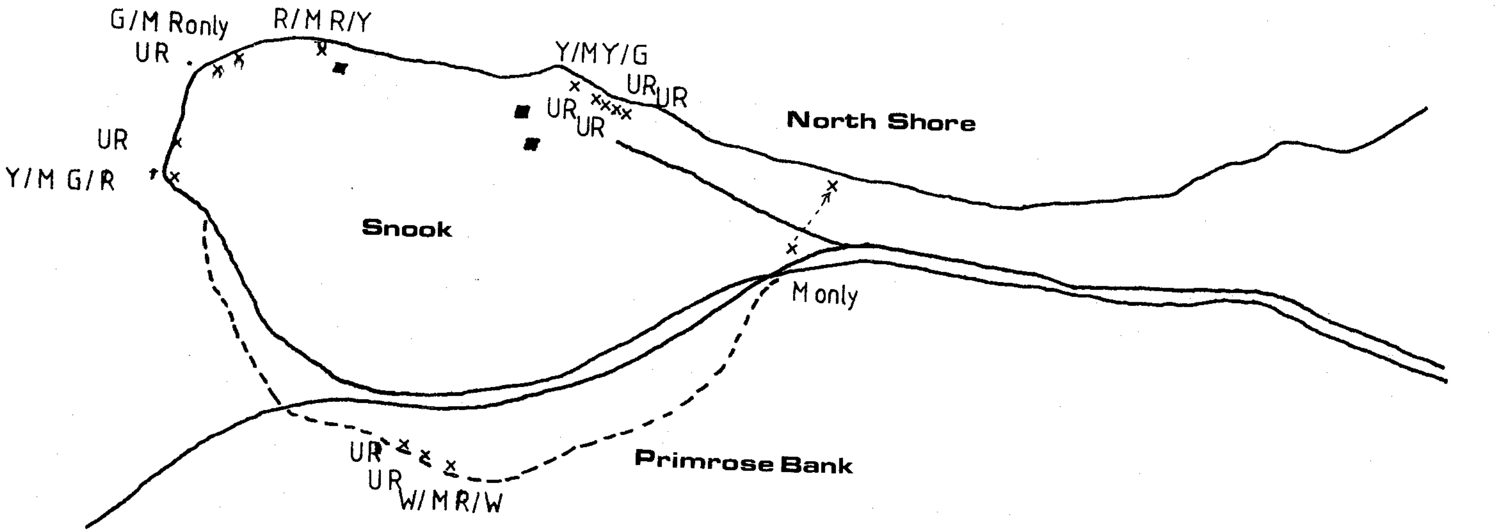


FIG. 5 TERRITORIES

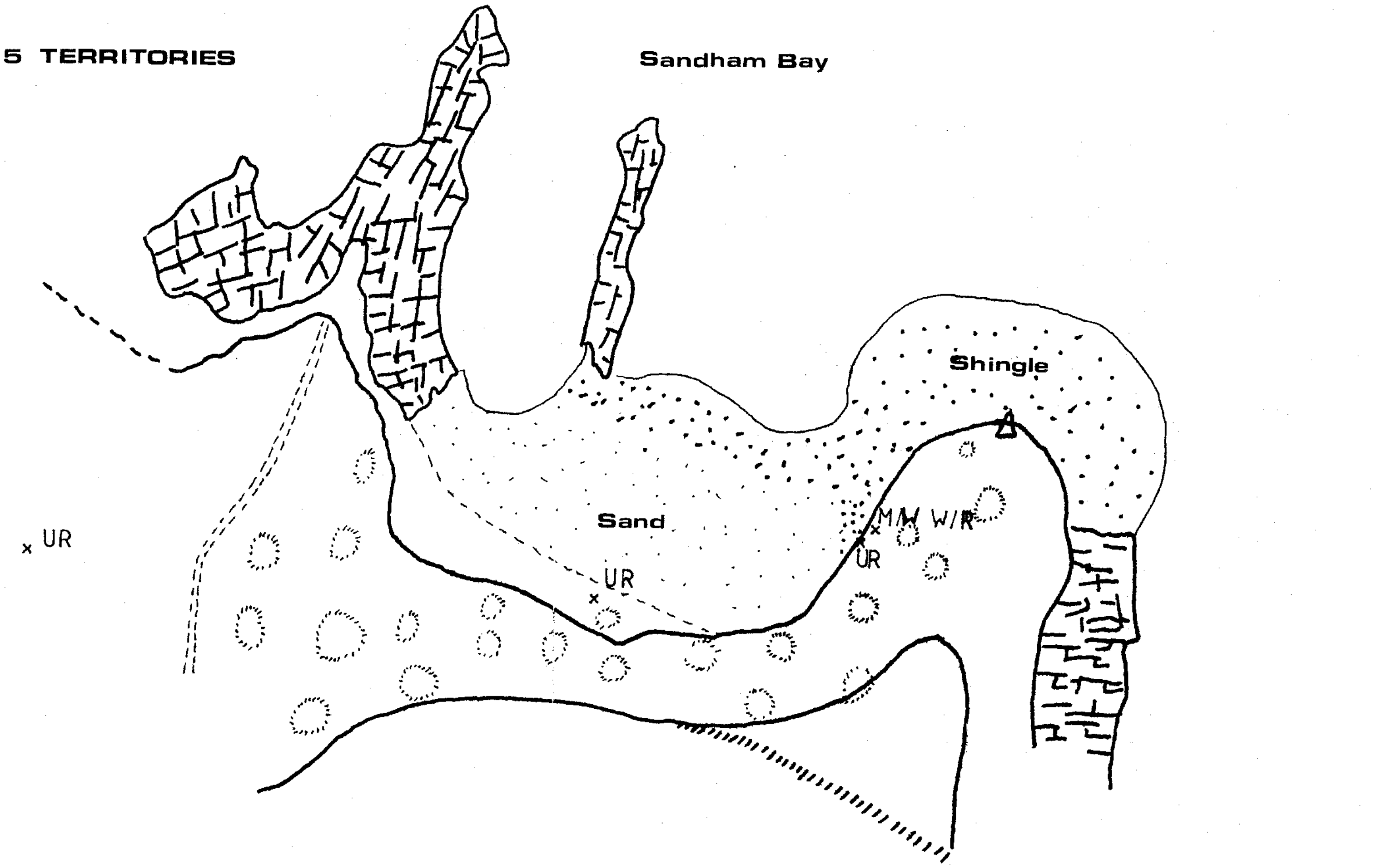
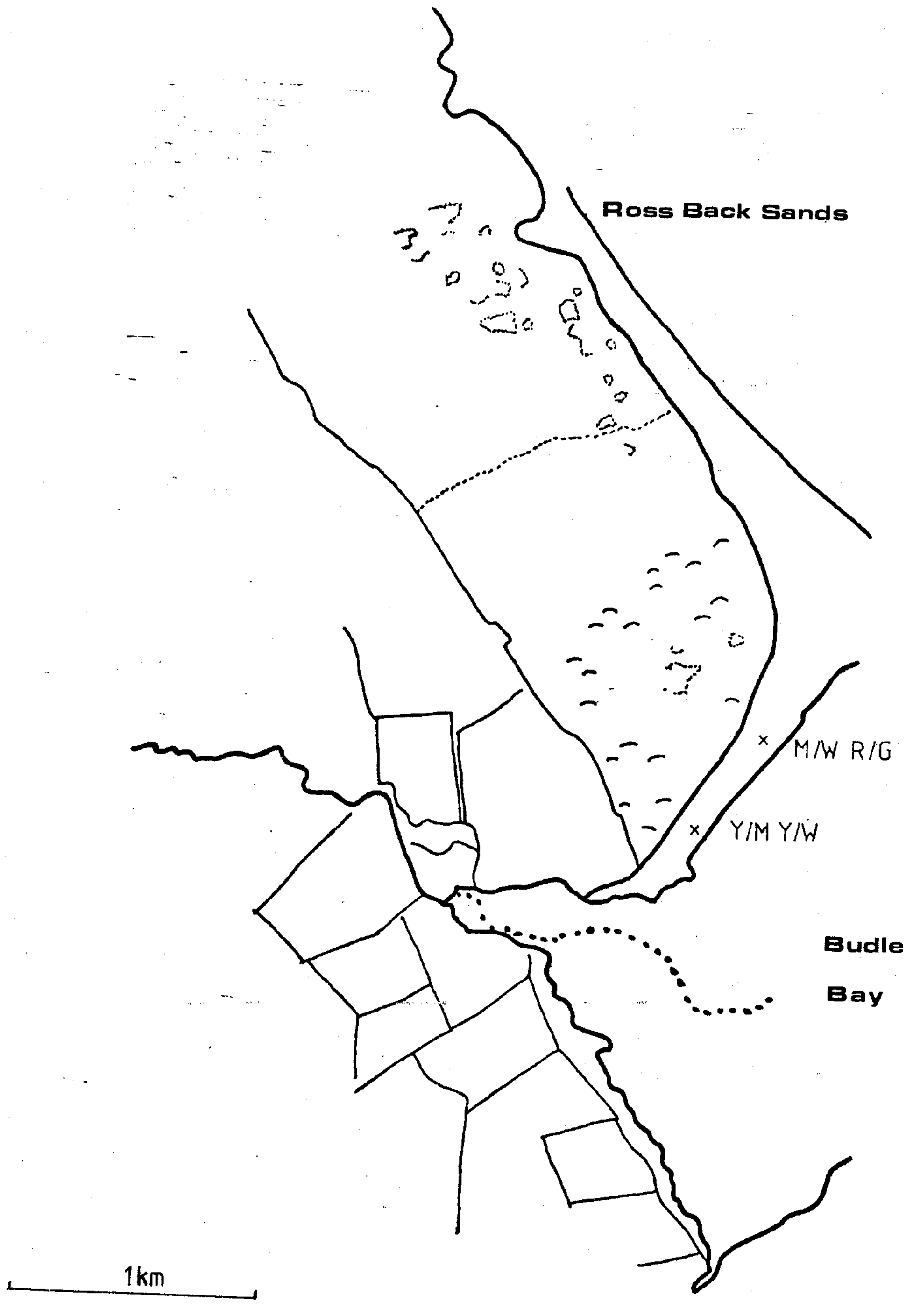


FIG.6 TERRITORIES



of Old Law there were 4 pairs in 300 metres. This gives a territory width of about 75 metres. In less densely populated areas, territory size could not be estimated.

Some territories did not conform to the usual format. They lay away from the beach, in shingle slacks on the North Shore, or in the shingle inlet on east Old Law or on the large patch of bare ground west of Sandham. No territorial behaviour was ever seen at any of these territories so that their size and shape remain unknowns.

Though the amount of information is small there is some evidence of site tenacity in the Ringed Plover. Of 16 cases where the birth site is known and the bird seen in following years, there are 4 cases of birds returning to take up territories in the same area as their site of hatching. This suggests that birds may return to the site of their birth when prospecting for territories.

There are 28 cases of birds having known breeding sites for more than one year (see Appendix 1). Of these, there are 17 cases of birds returning to the same territory (or an adjacent one) as the previous year, 3 cases of birds moving to adjacent areas and 8 cases of birds moving to different areas. This is good evidence for site tenacity, which one might expect to find in a breeding system where birds return to the same region each year. Prior knowledge of a site may well be advantageous to the birds.

Territory breakdown appears to be very variable. Sometimes a bird is seen less and less on its territory, other times the territory owners appear to leave overnight. This, and the timing of breakdown appear to depend almost entirely on the success or failure of clutches during the season. Some birds left after their first failure early in the season, though most remained to relay. Birds on the north-west shore of Old Law still remained in their territories at the end of July, even though they had had two or three unsuccessful breeding attempts.

Territory uptake to territory breakdown could be used as a definition of breeding season. Unfortunately, it is difficult to put a single date on either of these with any certainty. The known minimum length of territory occupancy in 1979 ranges from 15 to more than 94 days (see Table 1).

Of 29 marked birds seen during the 1979 season, 8 did not take up territories within the reserve, though there were free areas which had in previous years been used for territories. For most of these birds the number of sightings is small and it is possible that they attempted to breed outside the reserve.

(2) Laying

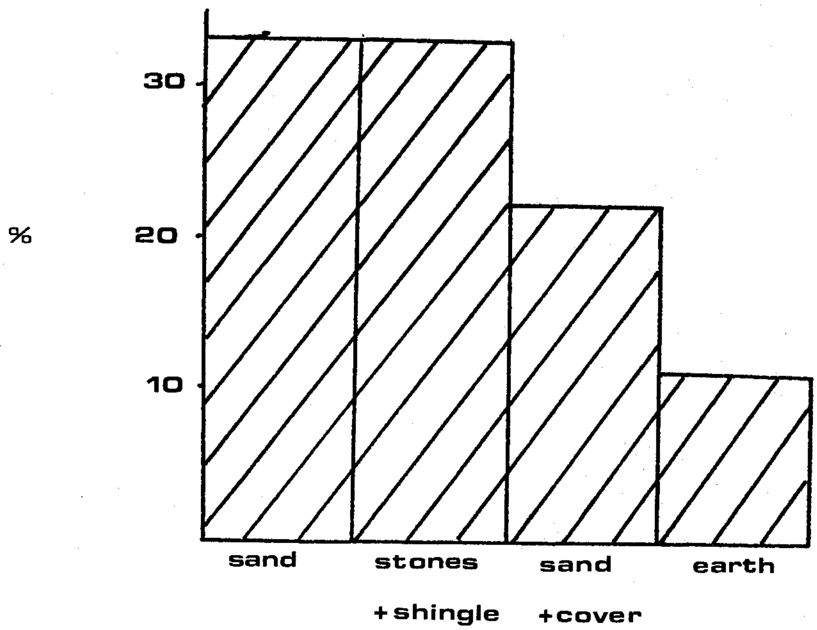
The scrapes used for nesting are formed by the male as part of the courtship display. In shingle areas they are often decorated with fragments of shell which probably help break up the outline of the eggs. The male usually makes several scrapes so that the females has a choice of laying sites. The position of the scrape, making use of available substrate, differed between areas. Some were produced openly on sand, some under cover of marram leaves, or sometimes built in dune banks on ledges under marram roots. Scrapes on shingle tended to be open. Table 3 and fig. 7 show the different uses of position and materials for the different areas.

Two eggs were found on the first day of field work (24 April) on Old Law. However, they were obviously adandoned being cold and sanded over, possibly from the previous year.

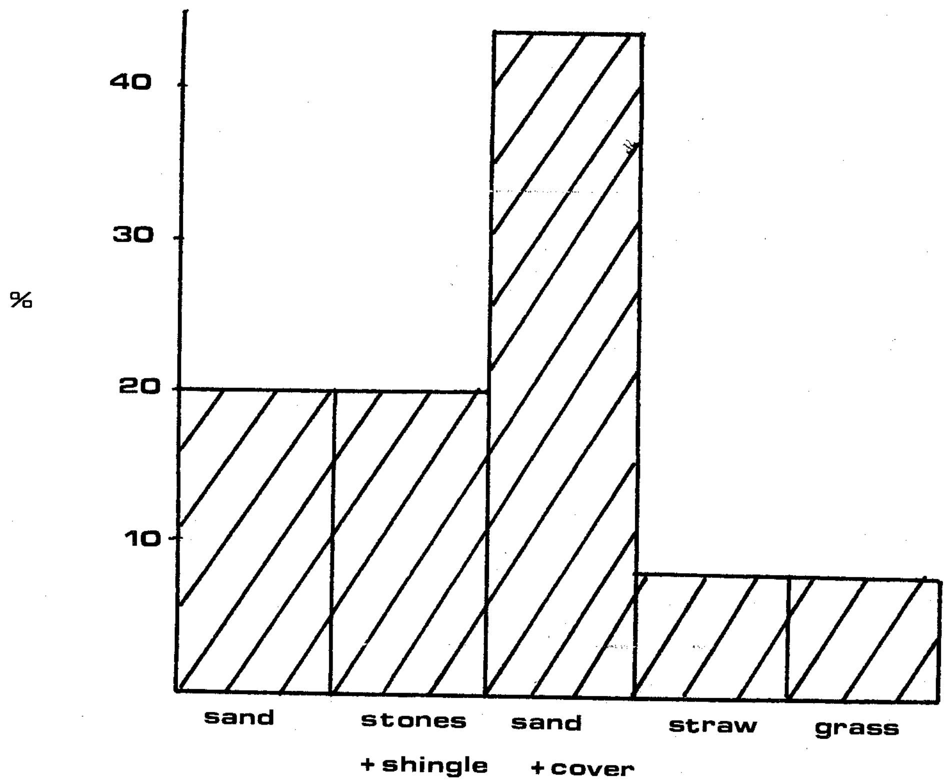
Table 3. The substrate in which the scrape was built, and any additional materials used. The mainland and island areas are compared both by actual numbers of scrapes and percentages.

	Sand	Stones & Shingle	Straw	Sand & cover	earth	turf
Holy Island	6	6	-	4	2	-
	33%	33%	-	22%	11%	-
Ross, Budle and Old Law	5	5	2	11	-	2
	20%	20%	8%	40%	-	8%

FIG. 7 NEST SCRAPE MATERIALS



HOLY ISLAND



ROSS, BUDLE + OLD LAW

The first egg of 1979 was laid on 2 May on west Old Law. The first egg on the island was laid on the North Shore on 6 May. However, laying did not begin in earnest until the middle of May. Table 4 and figs. 8 and 9 show the total eggs present and the total eggs laid, both on the island and the mainland throughout the season. Fig. 9 shows a bimodality caused by predation. The second peak is a consequence of replacement clutches. Figs. 10-13 show the position of all clutches laid. In order to compare laying times with previous years, the number of clutches started in each third of a month are shown in table 5 and fig. 14. Data are given for the years 1975, 1977 and 1979. In each year there is a peak of laying in May. In 1975 it comes in the second third of the month, in 1977 there is a very high peak in the first third of the month and in 1979 the peak is during the last third of the month. In 1975 and 1977 there are two further small peaks and in 1979, one further large one. None of the peaks coincide in any of the years, so that the factors determining the majority of laying must vary from year to year. The amount of laying per pair also differs. In 1977, 81 clutches were laid by 54 pairs, an average of 1.50 per pair. In 1979 53 clutches were laid by 42 pairs, an average of 1.26 per pair. The peak number of eggs present on both the island and the mainland coincide quite closely in 1979 being 30 May on the island and 2 June on the mainland (see Table 4 and fig. 9).

Within an individual clutch the laying of successive eggs appears to vary between one and two days. The average is probably quite close to 1.5 (Pienkowski, pers. com.).

The Ringed Plover is apparently adapted to a low breeding success rate in that it has the ability to lay several replacement clutches. Up to four replacements have been known, but a maximum of two replacements were noted in 1979. The length of time between losing a clutch and the

Table 4. Number of Ringed Plover eggs at Lindisfarne in 1979. The 'present' column gives the number of eggs present in the areas at the times of observations. The 'total' column gives an accumulated total number of eggs laid. The data are accurate to within three days.

Date	Ross, Budle & Old Law Present	Ross, Budle & Old Law Total	Holy Island Present	Holy Island Total	Combined Present	Combined Total
April 24		2				2
May 1	1	3			1	3
6			2	2	3	5
10	1	5			3	7
11	4	8	5	7	9	15
12	5	9			10	16
13	4	9			9	16
14			6	9	10	18
15	13	18			19	27
16	8	18			14	27
21			9	16	17	34
22	16	29			25	45
25			14	21	30	50
26	19	32			33	53
27	21	34			35	55
28			14	23	35	57
30			17	30	38	64
31	29	42			46	72
June 1	40	53			57	83
2	42	55	16	30	58	85
6	41	58			57	88
7	34	66			50	96

Table 4 (contd.)

	Ross, Budle & Old Law		Holy Island		Combined	
Date	Present	Total	Present	Total	Present	Total
June 8			12	30	46	96
9			10	30	44	96
10	30	66			40	96
11	14	66			24	96
12	14	70			24	100
13			17	37	31	107
21	14	74			37	111
23			5	37	19	111
25			3	37	17	111
26			9	43	23	117
27	21	86			30	129
28	19	86			28	129
29	19	88			28	131
30	30		13	47	32	135
July 1	25	96			38	143
9			10	47	35	143
11			8	51	33	137
12	17	99			25	150
18	11	99	12	55	23	154

Table 5. The Number of clutches started during each third of a month.

Period	1975	1977	1979
21 - 30 April (3)	5	2	1
1 - 10 May (1)	7	21	4
11 - 20 May (2)	8	12	9
21 - 31 May (3)	5	5	13
1 - 10 June (1)	7	9	6
11 - 20 June (2)	4	12	3
21 - 30 June (3)	9	7	12
1 - 10 July (1)	5	11	2
11 - 20 July (2)	4	2	3
Total Number of Clutches	54 *	81	53
Number of Pairs of Birds	57	54	54
Average Number of clutches Per Pair	-	1.50	1.46

* This number is only those clutches for which the date of the first egg was known and is nowhere near the total number of clutches laid.

Fig. 8

The accumulative total of the number of eggs laid during the season both for Holy Island, Ross, Budle and Old Law and a combined total of them both.

Fig. 9

The number of eggs present through the season on Holy Island, Ross, Budle and Old Law, and a combined total of both. The key is as in fig. 8.

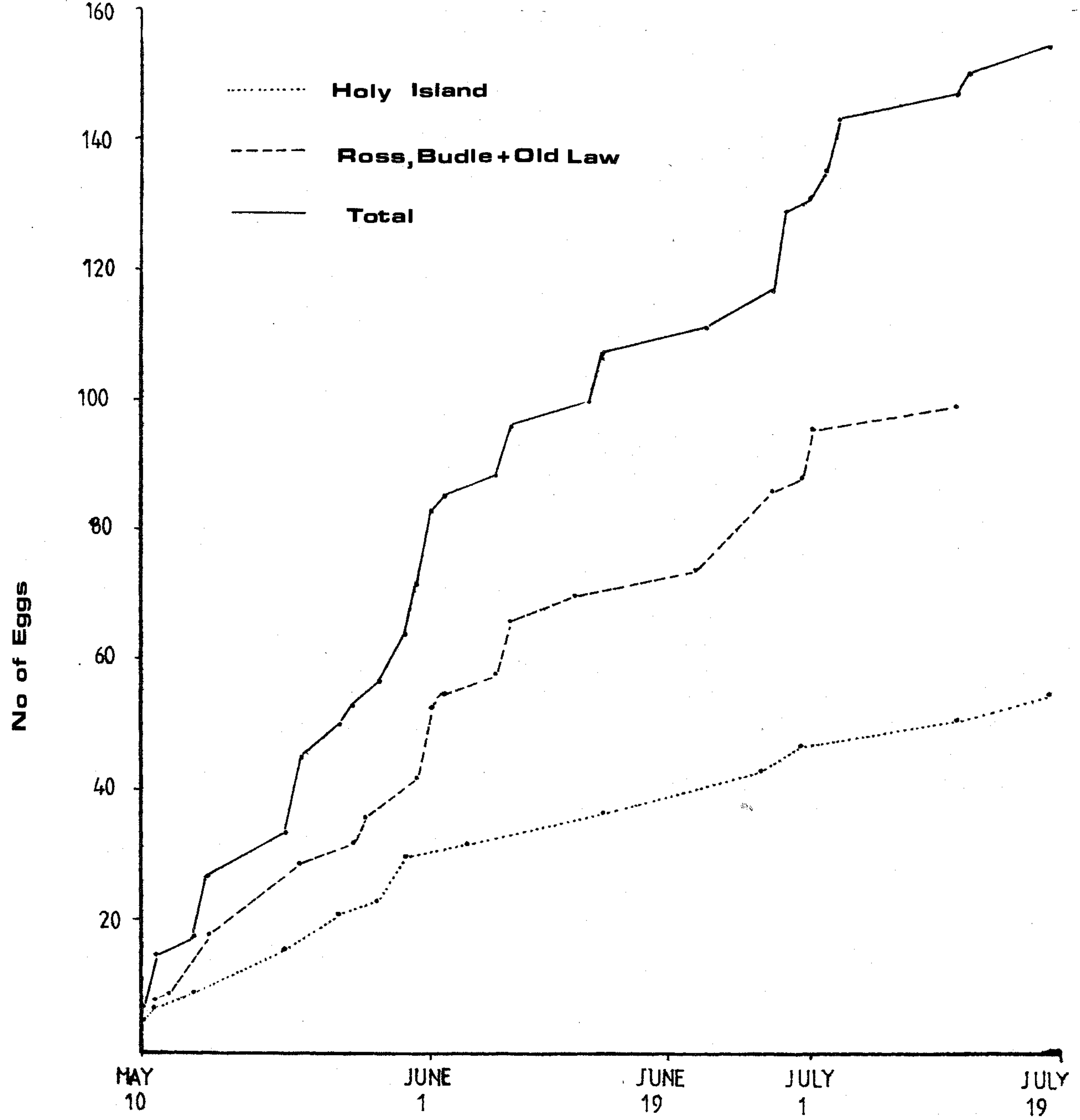
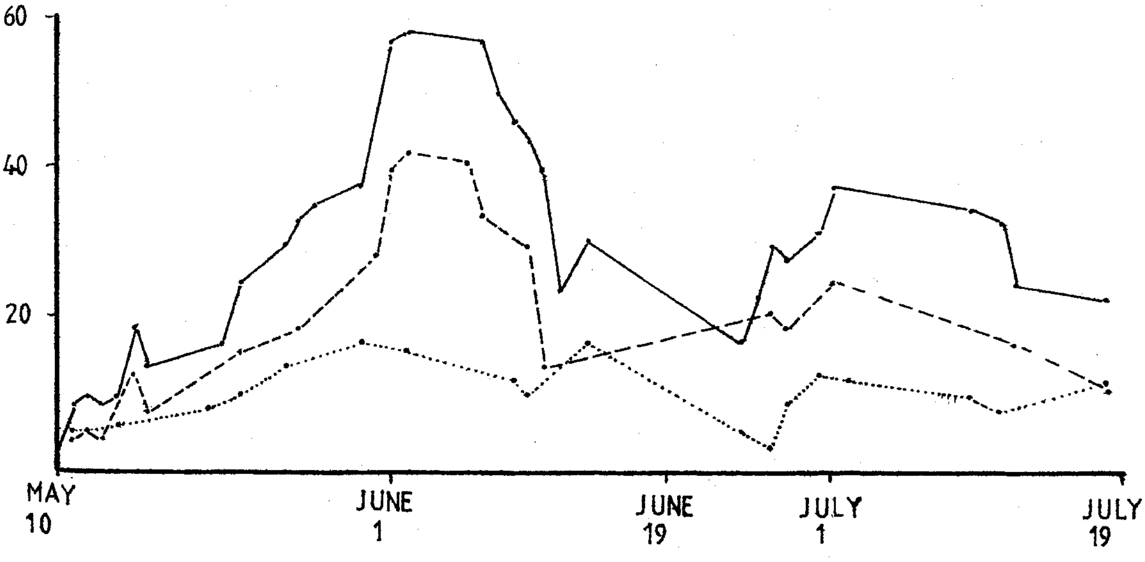


FIG. 9 NO. OF EGGS PRESENT



Figs. 10 - 13

x The positions of all clutches laid during the season.

(x) Clutches succeeding in hatching at least one chick.

Fig. 10. Old Law and Ross Back Sands

Fig. 11 The North Shore and Primrose Bank

Fig. 12 Budle Bay

Fig. 13 Sandham Bay

FIG.10 CLUTCHES

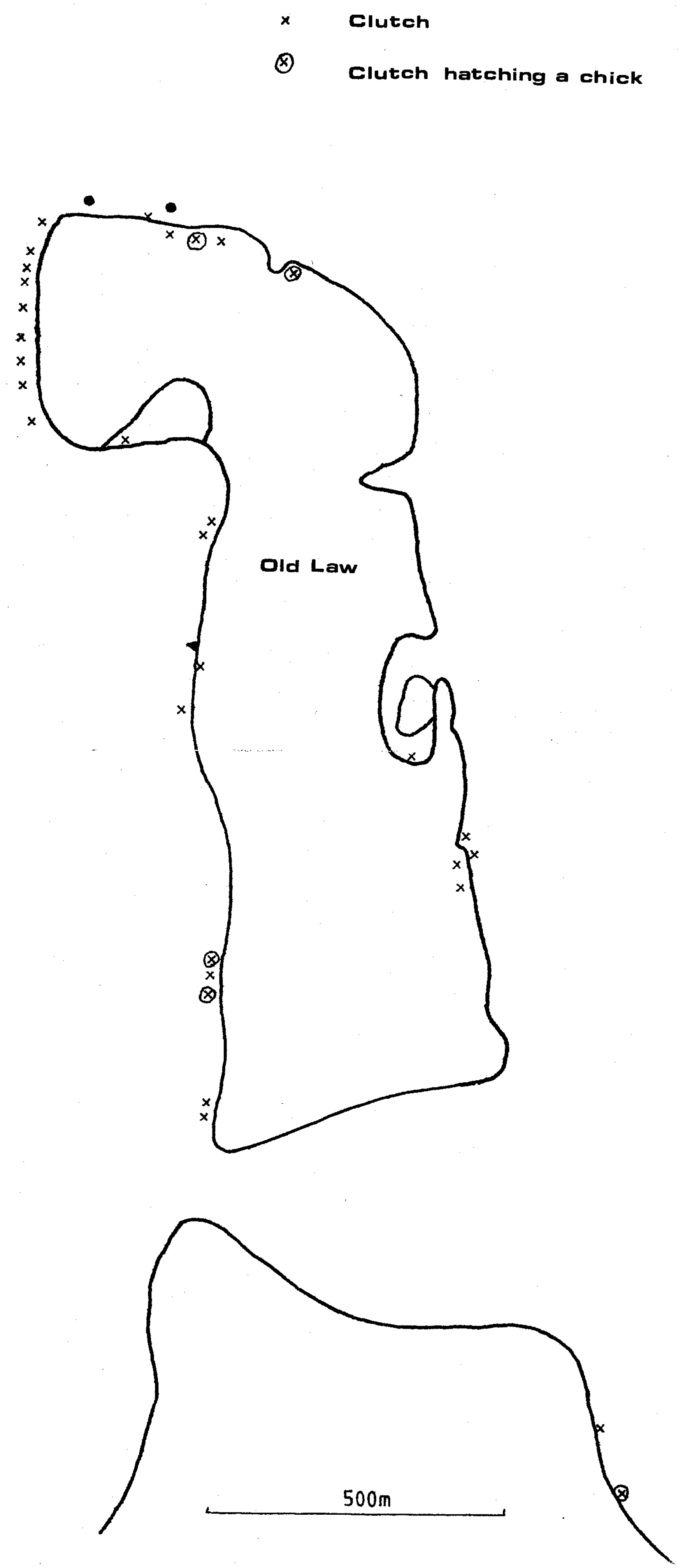


FIG.11 CLUTCHES

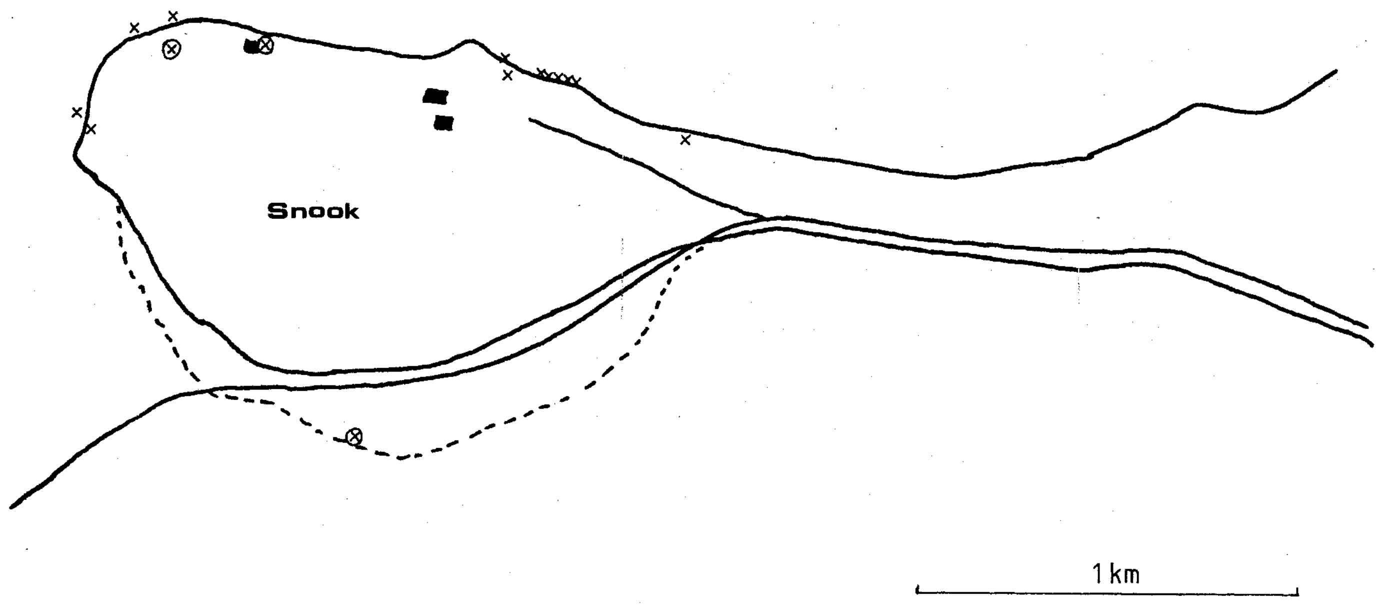


Fig. 7 Nest Scrape Materials.

The histograms show the percentage of nest scrapes made on a particular substrate, and using additional material or not. The results are given both for Holy Island and for Ross, Budle and Old Law on the mainland.

FIG. 12 CLUTCHES

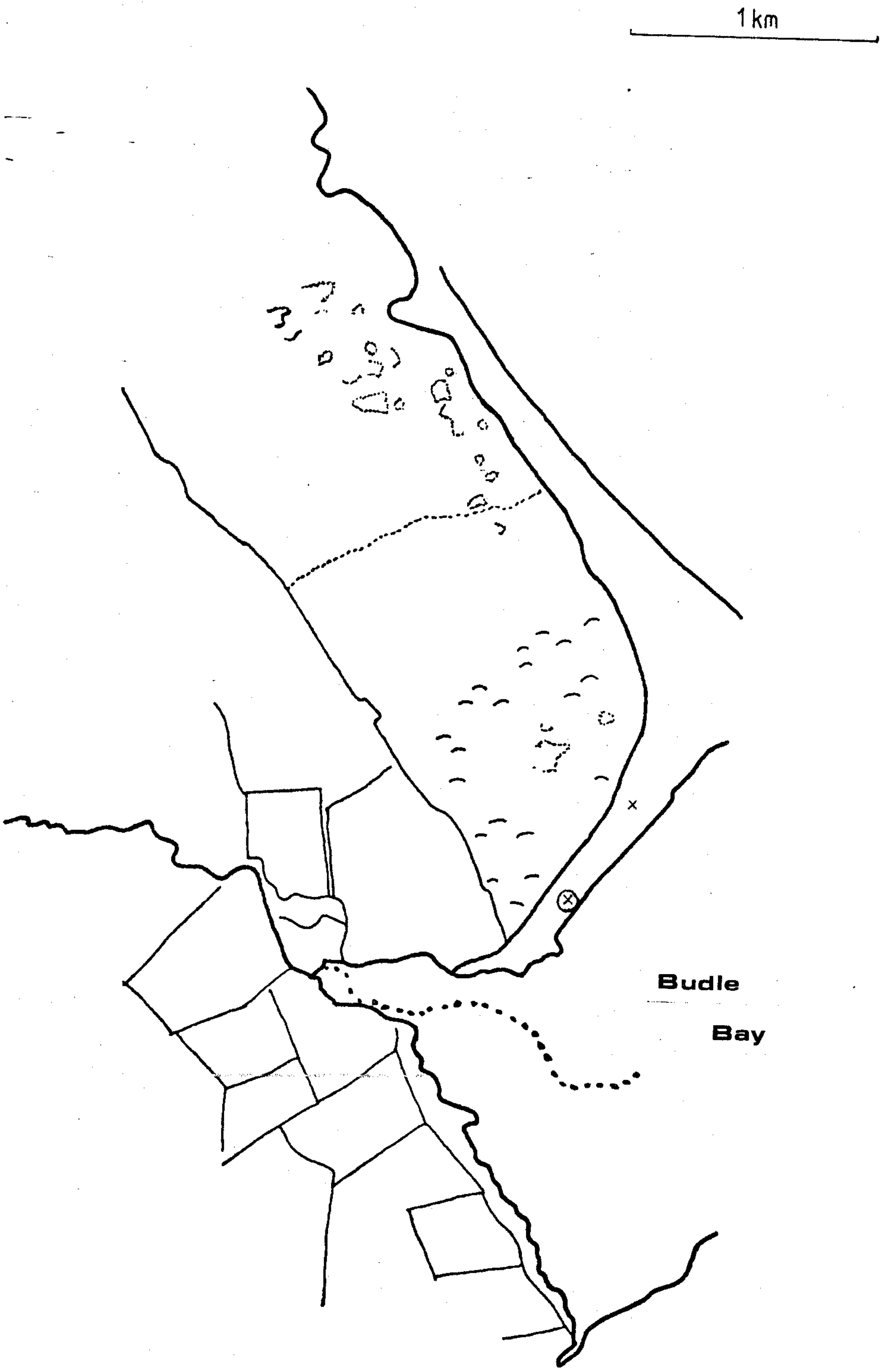


FIG. 13 CLUTCHES

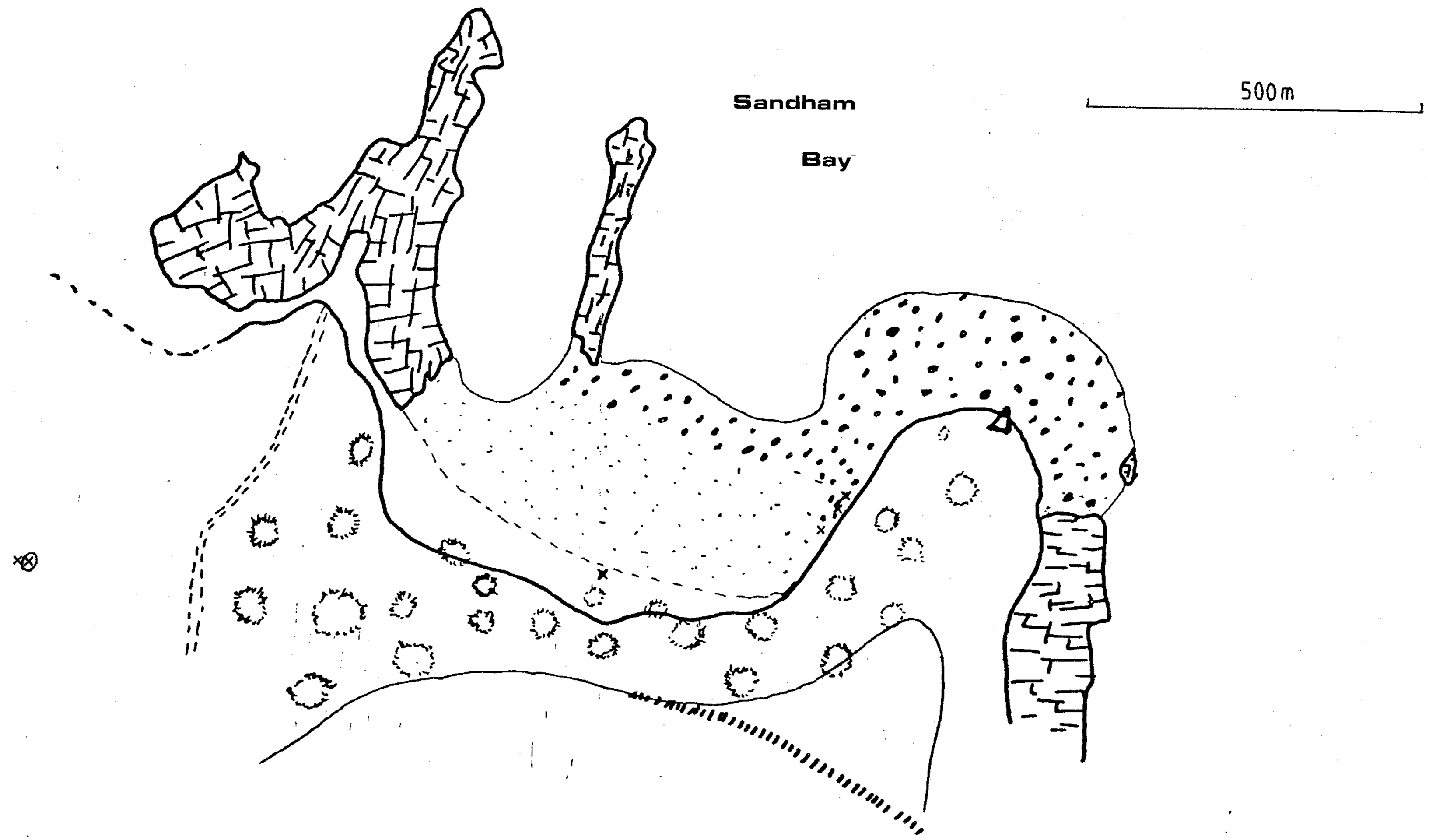
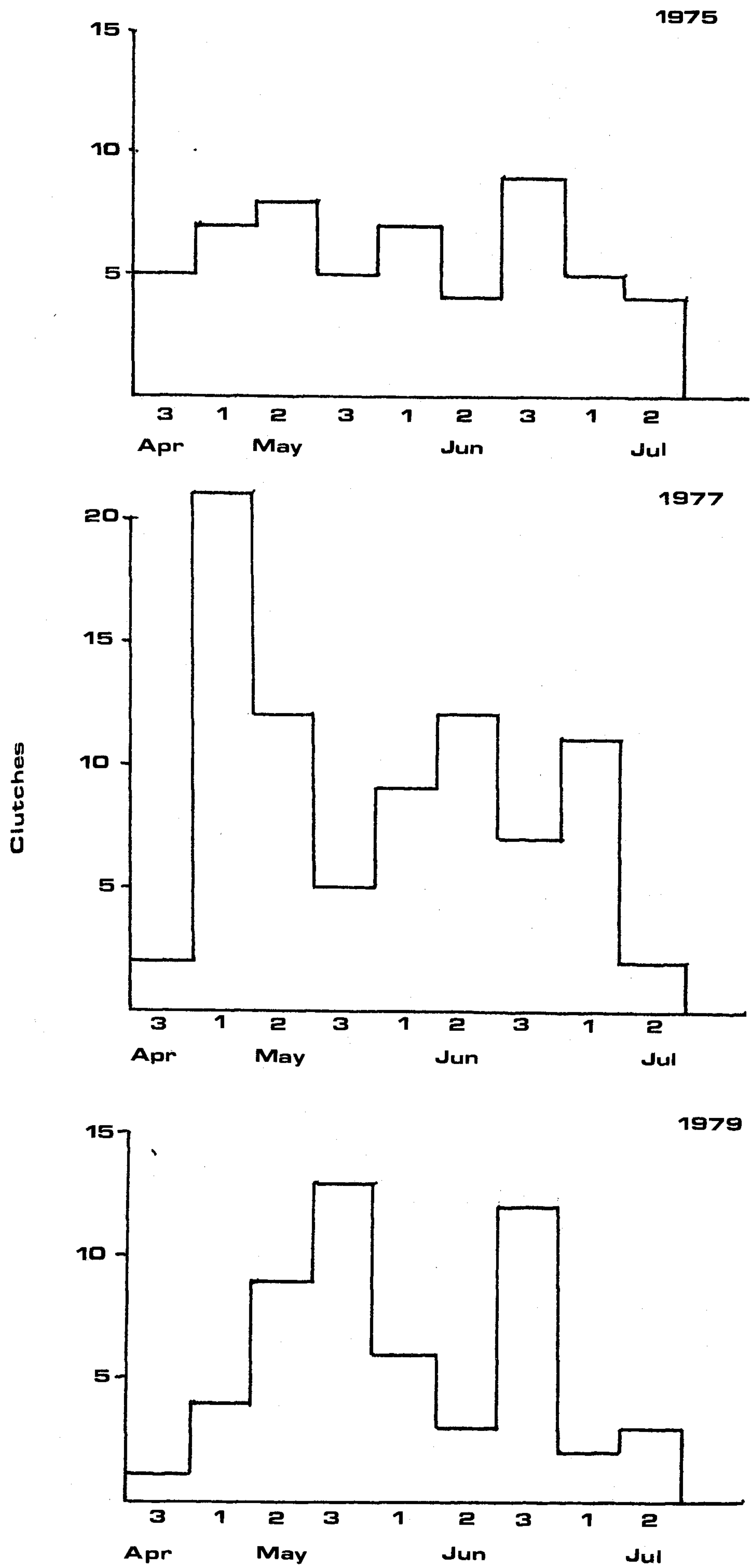


Fig. 14

The number of clutches started on the whole of the reserve, during each third of a month throughout the season, for the years 1975, 1977 and 1979.

April 3	=	21 April to 30 April
May 1	=	1 May to 10 May
May 2	=	11 May to 20 May
May 3	=	21 May to 31 May
June 1	=	1 June to 10 June
June 2	=	11 June to 20 June
June 3	=	21 June to 30 June
July 1	=	1 July to 10 July
July 2	=	11 July to 20 July

FIG. 14 CLUTCHES STARTED



replacement being laid varied from 7 to 43 days (see Table 6). There is no significant change in the interval during the season which is not surprising as biologically it is the time spent for the gonads to return to activity again. The interval in 1977 ranged from 5 to 17 days. The longer intervals in 1979 bay be a bias caused by heavy predation with clutches being laid and taken without being seen, or may have involved a change of the pair in a territory, the change being rapid and unnoticed. Observations in 1979 led to the belief that some birds become more 'prudent' in their nest positioning with replacement clutches. Having laid a first clutch in the open on a beach, a replacement was laid further towards the back of the beach under cover usually of marram. Having nested twice on open beach and been unsuccessful a pair on north-west Old Law moved their nest site to the rear of the beach amongst marram. On the North Shore, having attempted to nest once on open beach a pair moved into one of the shingle slacks beind the beach and were successful in hatching a brood. Eight cases of this type were observed in 1979. Only one case of a pair moving from a hidden site to an open one was observed. This pair had a territory on west Old Law backing onto dune cliffs. Their first attempt at laying was on a ledge under marram roots ten feet up on the cliff face. Their second attempt was laid on open beach. This may have been due to the lack of another suitable 'covered' site. The distance between successive nests was never very great. Only one pair of birds were observed to change their territorial position and relay. They moved about 300m along the beach.

Ringed Plover clutches are usually four eggs, sometimes three, and very rarely five (Prater, 1974). Variation in clutch size during the season was investigated. The season was split into quarters and the average clutch size for each quarter calculated (see Table 7). There

<u>Table 6</u> The time spent between loss of eggs and relaying at different stages of the season on 1979. The data that eggs are lost is accurate to within three days. The relaying date is the date of the first egg laid.

	DATE EGGS LOST	DATE EGGS RELAID	NO. OF DAYS BETWEEN LOSS AND RELAYING
Fortnight 2	11.5	25.5	14
	16.5	6.6	21
	16.5	7.6	22
	16.5	27.6	43
	21.5	13.6	23
	22.5	1.6	10
Fortnight 3	2.6	22.6	20
	4.6	27.6	23
Fortnight 4	7.6	12.7	36
	11.6	27.6	16
	11.6	27.6	16
	11.6	1.7	21
	11.6	21.6	10
	16.6	23.6	7

Average length of interval per fortnight:

Fortnight 2 - 22.17 $\pm$ 4.66 days

Fortnight 3 - 21.5 $\pm$ 1.5 days

Fortnight 4 - 17.67 $\pm$ 4.18 days

Table 7 Clutch size over the season in 1979

Date of laying of first egg	Clutch Size	Average
2 May	NC	n = 3
6 May	NC, NC	$\bar{x}$ = 3.33
11 May	NC, 4	S.D. = 0.58
15 May	3, 3, NC	
21 May	4, 4, 4,	
22 May	4, 4,	
25 May	NC	
26 May	3	n = 14
30 May	4, NC	$\bar{x}$ = 3.86
31 May	4	S.D. = 0.36
1 June	4, 4, 4,	
6 June	3	
7 June	4, NC	
13 June	4	
21 June	NC, 3	n = 7
23 June	4	$\bar{x}$ = 3.83
27 June	4, NC, NC, NC	S.D. = 0.41
30 June	4	
1 July	4, 4	
11 July	4	
12 July	NC	n = 2
18 July	4	$\bar{x}$ = 4

NC = Not completed. This means that the clutch was taken at the one or two egg stage

Not all clutches are included. 18 had insufficient data to be sure of their size.

would appear to be no significant change during the season, with average clutch sizes varying from 3.33 to 4.0. The predation rate in 1979 was such that most clutches were not completed and consequently the amount of information available is quite small.

Observations in 1979 suggested that the interval between territory uptake and the laying of the first egg was longer, the earlier the territory was established. Table 8 shows the data. Territories taken up in April showed a mean interval of 25.1 days. Those taken up in May and June showed a mean interval of 2.9 days. Many of the birds taking up territories later had already laid when they were first seen, suggesting that they had taken up territory and laid almost straight away. It must be remembered that territory uptake dates may suffer from inaccuracy due to the fact that it is a gradual process, and I may have visited an area whilst birds were away feeding.

Egg predation was very high in 1979. 154 eggs were known to have been laid. Some clutches were almost certainly not found. Of the known eggs, 85% were predated. On the mainland there was direct evidence of crows being the major agents of predation. Footprints were found around several sandy scrapes where eggs were taken. There were two particularly disastrous periods concerning heavy predation. On 7 June, 15 eggs were taken and 11 June, 14. On the island there was evidence of crows taking at least one clutch. Most of the other clutches disappeared without any clues. In 1977 the main predation on the island was caused by foxes. Some tracks were found around the North Shore in 1979 but they never coincided with eggs having been taken. On several occasions one or two eggs only disappeared from a clutch. This was almost certainly human interference and often led to the desertion of the clutch. On one occasion on Old Law, a gull was known to have taken a clutch as its footprints led to the scrape.

Table 8 Comparison of territory take up dates with date of laying of the first egg. Both dates are only accurate to within 3 days.* If the date of the first egg was not known it was estimated by allowing 1.5 days for each egg laid.

TERRITORY TAKE UP	FIRST LAYING DATE	INTERVAL (DAYS)
24 April	22 May	28
24 April	10 May	16
24 April	27 June ?	64 ?
24 April	2 May	8
24 April	1 June	37
24 April	23 May	29
24 April	18 May	24
24 April	14 May	20
26 April	21 May	25
26 April	21 May	25
28 April	22 May	24
28 April	17 June ?	50 ?
28 April	7 June	40
6 May	6 May	0
8 May	8 May	0
6 May	14 May	8
11 May	11 May	0
12 May	12 May	0
12 May	26 May	14
14 May	30 June ?	47 ?
26 May	30 May	4
27 May	27 May	0
4 June	4 June	0

Table 8 (contd)

Mean Interval

For April territories	n = 11	= 25.1 days	S.D. = 8.9
For later territories	n = 9	= 2.9 days	S.D. = 5.0

Where the two dates are the same, this means that when the birds were first seen they had already laid.

Date questioned in the table are rather long intervals where a previous clutch is suspected but was not seen. These data are not included in the calculations.

* The territory take up dates are subject to inaccuracy from the possibility of birds being away from the territory for a period of observation. Also, some territories were taken up on an unknown date before field work began on 24 April.

The position of the nest did not appear to be related to the risk of predation. The egg colouration is such that they are well camouflaged on shingle substrates. However, on one occasion three adjacent clutches were taken from a shingle area, though a fourth was missed. Some eggs laid in the open managed to hatch whilst, quite often what appeared to be the best hidden nests, were predated.

It is interesting that crow predation should have been so large in 1979, for though many were seen on Ross Links, very few were seen around the shoreline of Old Law, leading to the hypothesis that the majority of predation was due to just one or two birds. It is possible that these few birds have learnt how to locate Ringed Plover nests by watching the birds or following their footprints.

Termination of laying appears to vary between birds. Some birds gave up after their first attempt failed and did not lay a replacement clutch, others had three attempts in 1979. The date of the loss of a clutch is obviously an important factor, but some birds did not relay after losing a clutch in early June whilst others were still laying in mid-July. The final clutch to be recorded was found on 18 July on the North Shore.

(3) Hatching and Fledging.

The amount of information gathered on hatching and fledging in 1979 is rather small, due to the Plovers having a disastrous year. Only nine broods were seen on the reserve, but one or two more were seen as juveniles. These were probably from areas not studied such as Black Law or areas where nests could not be found, such as Primrose Bank.

Incubation was seen to start soon after the fourth egg was laid. The whole incubation period varied from clutch to clutch, being mainly

22-26 days, though a case of successful hatching after 34 days has been noted. Both birds take turns to incubate the eggs, but the length of incubation stints was not measured.

The period of hatching appears to vary only slightly from year to year. Table 9 gives first and last hatching dates for the years 1975, 1976, 1977 and 1979. Hatching usually begins during the last week in May. This would require eggs to be laid around the first week in May. In 1979, the bulk of laying did not begin until the second week in May, and hence the first hatching date is a week later than usual. The last hatching dates are more variable, occurring some time in August. It would appear that chicks are required to fledge by the first or second week of September, to avoid excess strain on the parents.

Table 10 gives the number of chicks hatching in each area over the years. Ross, Budle and Old Law comprise the most important area. Table 11 gives the hatching success for three main areas of the reserve for 1976, 1977 and 1979. The Old Law figures show the catastrophic effects of predation by crows. The table highlights the fact that Old Law appears to be a far more successful breeding area than Holy Island. Overall the results show that 1979 was a bad year because of :-

1) A fall in the number of birds breeding
2) A fall in the number of eggs laid on Holy Island
3) A large fall in the hatching success on Old Law.

There would appear to be quite a high mortality of chicks during the first few days after hatching. Often, though four eggs were present in a scrape, and all hatch, the number of chicks on first sighting was down to two or three. Only once in 1979 was a full brood of four chicks seen.

Table 9. Hatching dates of the first and last clutches on the reserve for five years of study.

	First	Last
1974	30 May	-
1975	23 May	20 August
1976	28 May	1 August
1977	30 May	13 August
1979	6 June	18 July *

* Field work ended on 27 July, when there were still three clutches remaining on the reserve, which may have hatched.

Table 10 The number of chicks hatching in each area of the reserve.

	Snook + Island	Goswick	Ross, Budle + Old Law	Tealhole Point
1975	20	2	26*	3
1976	7	11	42	0
1977	19	No data	78	No data
1979	8	0	13	0

* Very low estimate, probably nowhere near the full total

Table 11. The percentage of eggs hatching in different areas of the reserve.

	Holy Island	Ross Back Sands	Old Law
1976	1.2% (7)	20%	42%
1977	16.7% (19)	33%	53%
1979	14.5% (8)	50% (4)	12.1% (8)

The numbers of eggs that hatched are given in parentheses.

1977 was a relatively good year as far as breeding of the Plovers was concerned. The number of clutches started each week are compared with the success of hatching in fig. 15. There was high hatching success in nests started early in the season, which fell off rapidly, showing little difference for the rest of the season. Growth rates of chicks were followed. It was obvious that growth rates were influenced by weather. Over the first five days after hatching, a large variation in growth rates was noted, due to the changing conditions. The day after hatching there was a slight decrease in weight probably due to poor feeding efficiency. This was followed by a weight increase of about a gram per day (see fig. 16).

Only one ringed chick was seen to fledge in 1979. Altogether nine juveniles were seen during the season. Assuming that they were all from the reserve, this represents a fledging success rate of 5.8% of eggs. However, some birds often leave the area on fledging. It was likely that at least another six chicks would have survived, as when caught they were past the critical period of about the first two and a half weeks. It is also possible that a further five chicks fledged, as their fate is unknown. This makes a total of twenty chicks fledging which is a success rate of 12.57% of eggs.

2) Feeding

Feeding behaviour was studied throughout the breeding season at four main sites, three on west Old Law and one on Ross Back Sands. The three sites on Old Law were as follows:

1) The feeding area of north-west Old Law, a sandy area used extensively by Plovers.
2) The area around the Spartina marsh on west Old Law, being mainly mud.

Fig. 15

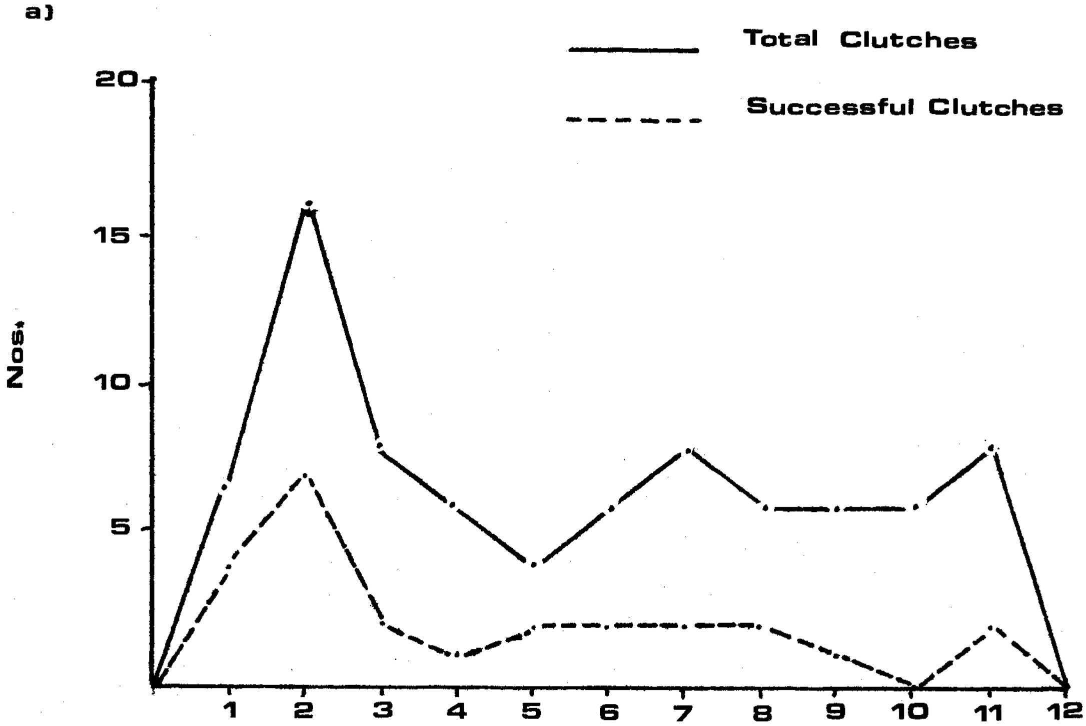
The hatching success throughout the season for 1977.

a) The total number of clutches laid in each week of the season compared with the number of clutches succeeding in hatching at least one chick.

b) The % of clutches each week that succeeded in hatching at least one chick.

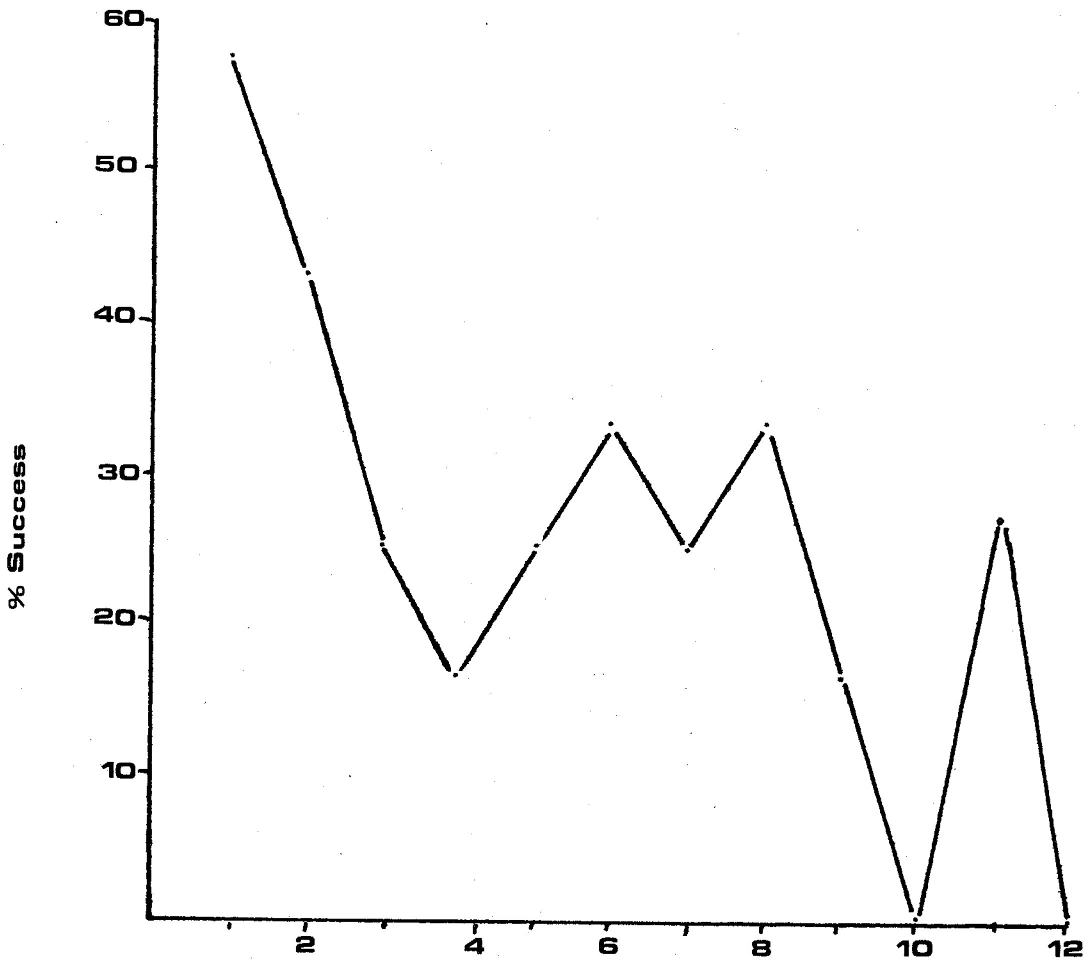
FIG. 15 HATCHING SUCCESS 1977

a)



Weeks of Season

b)

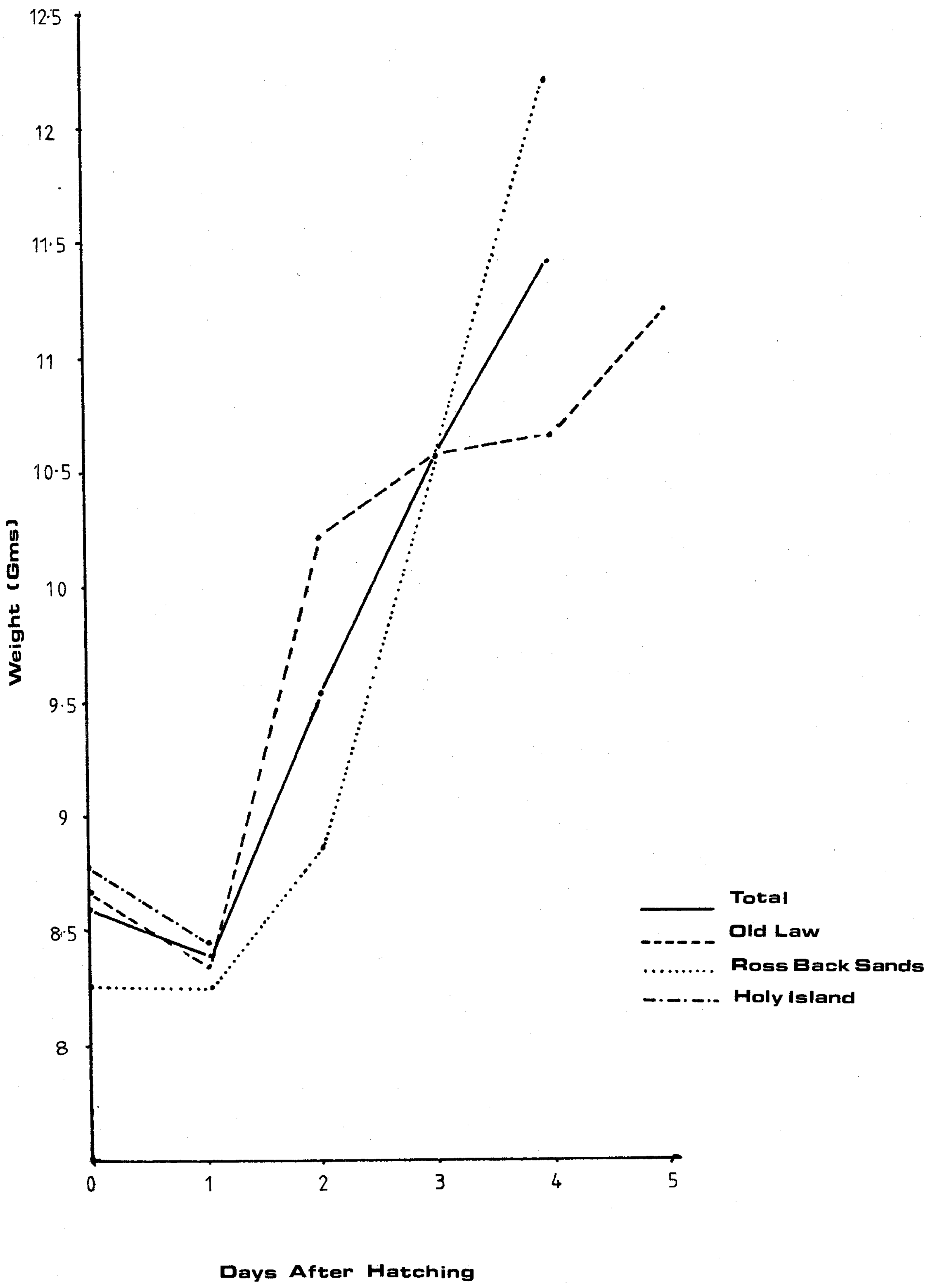


Weeks of Season

Fig. 16 Mean Chick Weights

The mean weights of at least 2 chicks for each of the days following hatching for each of three areas of the reserve and a combined mean of them all.

FIG 16. MEAN CHICK WEIGHTS



3) The south-west point of Old Law, having patches of sand and mud and designated muddy-sand.

The separation of the three substrates was purely by inspection, no measurement of particle size was carried out.

The Ross site, first bay south of the Wide Opens was a sandy sea-beach. The feeding data are thus divided into four sections designated mud, sand, mud/sand and sea-beach.

The Ringed Plover is a very active bird and this is reflected in its feeding behaviour. Pearson and Parker (1973) analysed feeding sequences of non-breeding birds consisting of feeding movements which they called probes, steps and pauses. Their results show that the main features of the feeding behaviour was pauses followed by probes (5.4%) or steps (27.8%) and probes followed by pauses (11.2%) or stepping sequences (12.1%). They established a mean number of steps per minute of 60 ± 3.9. This was much higher than similar measurements made for other members of its family (Pluvialis apricaria, Squatarola squatarola and Vanellus vanellus) and was more comparable with the measurements made on the smaller Scolopacids (e.g. Calidris alpina, C. maritima and Crocethia alba) though their pattern of foraging is totally different.

The present study focuses on the feeding movements themselves. It consists of 35 watches of individual birds feeding. Each watch was begun after seeing five successive feeding movements to make sure that the bird is actually feeding, and was terminated when the bird stopped feeding or in the case of some of the longer watches when it was felt that continuation of the watch would be unprofitable. The feeding movements were split into three categories.

1) Touch - where a bird pecked at the surface of the substrate.
2) Probe - where the bird inserted all of its bill into the substrate with a definite downward 'probing' motion. (Not to be confused with the probes of Pearson and Parker, used for all feeding movements).
3) Catch - where the bird was observed to take a large prey item, usually a worm. The catch could often be seen in the bill using a telescope, but the bird also usually made a separate swallowing motion, unlike in categories 1 and 2.

The feeding areas fell into two categories 1) within a bird's territory, 2) outside the bird's territory. Where the birds fed depended on the position of their territory and whether it had a feeding area or not. Feeding on the west of Old Law had both birds feeding within their territories, and outside. The Ross data were based purely upon watches of a bird feeding within its territory.

Both west Old Law and north of the west end of the Snook had specialised feeding areas where birds would congregate at low tide.

The beach can be compartmentalised into five zones (after Recher, 1966). The waters edge is represented by zone C. Above the waters edge, zone A contains areas lacking a film of water and zone B contains areas retaining a surface film of water on the substrate. Beyond the waters edge zone D contains areas within a third of a metre of the waters edge and zone E, areas beyond that. Each of the 35 watches carried out was categorised into the zones in which they occurred. Where more than one zone was used, the one where the bird spent most of its time was recorded. The results are shown in fig. 17. Recher carrier out work in C.h. semiplamatus at two sites in the U.S.A. His results are given for comparison. The birds tend to spend most of their time feeding on the

Fig. 17 Feeding Position

The percentage of observations of birds feeding in a particular area for a) Lindisfarne in 1979 b) California in 1965 and c) New Jersey in 1965.

a) is for C.h. hiaticula

b) and c) are for C.h. semipalmatus (after Recher, 1966)

A Areas of beach lacking a film of surface water

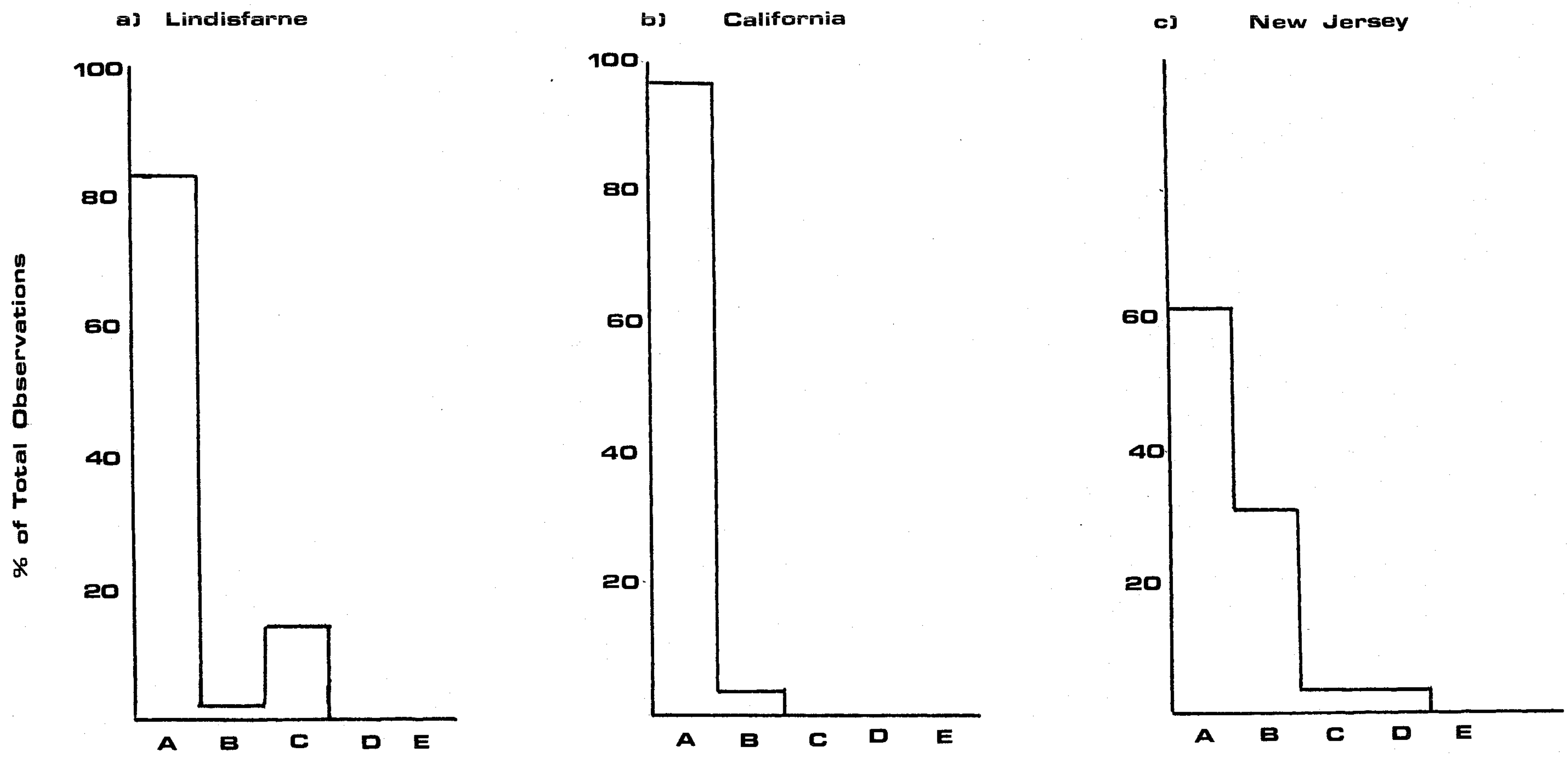
B Areas of beach retaining a film of surface water

C Areas within 1/2 m of the waters edge

D Areas beyond the waters edge within 1/2m of the

E Areas beyond D

FIG 17 FEEDING POSITION



for explanation see text

b+c After Recher (1966)

drier substrates. Recher considered the drier areas to be poorer feeding grounds (having lower prey densities) and that the plovers were forced to use them due to competitive interaction with other waders. The present study suggests that the dry areas are adequate feeding grounds. However, the mud areas which always had a surface covering of water were definitely more prey rich (see below). Also, the feeding area of the North Shore was only used when it had a surface covering of water.

Invertebrate samples.

A complete record of the invertebrate samples can be found in Appendix 4. Of the three sites sampled, two are the same as those used in the feeding study. Site one was the muddy marsh area. Site two was the feeding area of north-west Old Law. Site three was the beach of east Old Law (see fig. 2). Very little feeding occurs on the east Old Law, though some families do feed there. This is not surprising when the results of the invertebrate samples are considered. The area appears almost barren (see below). The other two areas show very decisive results. The mud site had much more potential food than the feeding area. Both sites had Nereids and tube-building sedentary polychaetes. Their densities were compared by a Mann-Whitney 'U' test. Both were statistically more numerous on the mud site. The mud also contained <u>Hydrobia</u> sp., <u>Macoma balthica</u>, <u>Nereis diversicolor</u> and <u>Corophium volutator</u>, all shown to be food of waders by Goss-Custard (1970). The numbers of these species did not vary greatly between paired samples, but did between different sampling points which is an indication of clumped distributions. The feeding area was characterised by the presence of worm casts from <u>Arenicola</u> sp. The larger of these worms would not be available as food for the plovers, but smaller ones, which were found in the samples, may have been.

These samples only give a first approximation as to the comparative richness of each of these sites. There are several problems. The samples are not showing all of the potential food. Plovers are known to eat Wrack flies (Coelopodae) and Talitrids (Witherby, Jourdain, Ticehurst and Tucker) and these did not occur in the samples. They probably occur in quite large numbers on the east side of Old Law and would account for families feeding in the area. They are both very numerous on Ross Back Sands and are probably the main part of the diet of birds feeding there. Prey availability is another problem. Though potential food items occur in the samples, some of these may not be available to the birds. One way of judging availability is to go out onto the feeding area, and look for what can be seen moving on the surface, as the birds feed by visual cues. On the mud site Corophium, Hydrobia and some Polychaetes could all be seen. Another problem is prey selection by the bird. Just because a certain item is available, it does not necessarily follow that the bird is feeding on it.

Feeding rates.

The initial data for feeding rates consisted of a series of watches on individual birds. The watches consisted of a sequence of individual feeding movements recorded on tape. They were then transcribed and split into sections lasting one minute. Each watch therefore is a series of one minute data. The number of touches, catches and probes in each minute were counted, giving a rate of each per minute. From each watch it is possible to obtain mean rates of touches, catches and probes per minute.

On consideration of the feeding movements, touches are easily explained as the taking of prey items from the surface of the substrate.

Each touch is almost certainly successful. Plovers rely on sight for prey detection and so only peck at something that appears to be a food item. The rate of touches should give an indication of prey availability (though this is complicated by motivation of the bird and selectivity). The number of catches gives some idea of the availability of larger prey items. Probes are rather more difficult to explain. They are presumably an attempt to take prey from below the surface of the substrate probably polychaetes or crustacea with burrows. It is quite possible that probes are less successful than other feeding movements.

Table 12 gives a list of all the feeding watches made, along with their length and their mean rate of total feeding movements, touches, catches and probes. For a list of the individual minute data, see Appendix 4. In order to compare blocks of data, analysis can be carried out in two separate ways:

1) by comparing means of watches. This emphasises the variations between individual birds and is also affected by the area and the state of the tide.
2) by comparing the individual minute data. This brings in factors caused by prey distribution within an area, and short term changes in motivation within an individual bird.

Since all of the feeding data are unlikely to be normally distributed, all the statistical tests used were non-parametric, specifically the Mann-Whitney U test. The statistic z used in the text and tables is equivalent to Student's t with ∞ degrees of freedom.

Differences in feeding rates (total feeding movements per minute) between males and females were investigated. It appeared that females were feeding faster than males (See Table 12). Seven watches were made

Table 12

The information from each feeding watch. The length is given, as are mean rates of feeding movements and the sex of the bird. Some of the watches were originally in more than one part giving a total of 35.
(Taken from Appendix 4).

Table 12

Watch	Sex	Length of watch	Total Feeding Movements	Catches	Probes	Touches
A	M	4min.45sec.	13.05	0.84	3.16	9.05
B	M	13'50"	13.59	0.65	1.45	11.49
C	M	6'10"	19.61	1.94	0.32	17.35
D	M	9'00"	1.40	0	0	1.40
1	F	10'00"	21.70	0.3	0	21.40
2	M	16'00"	12.75	0.31	0	12.44
3	M	9'20"	11.04	0	0.11	10.93
4	M	17'00"	9.00	0.35	0.70	7.95
5	M	5'00"	6.00	0	0	6.00
6	M	40'00"	6.50	1.175	0.475	4.85
7	F	13'00"	17.54	0.15	0.31	17.08
8	M	7'00"	17.14	0	0	17.14
9	F	6'30"	11.08	0.46	1.23	9.39
10	M	6'40"	10.49	0	0.15	10.34
11	M	13'40"	10.17	0.66	0.44	9.07
12	F	6'40"	19.50	0	0	19.50
13	M	5'00"	10.40	0.20	0.20	10.00
14	F	18'00"	26.16	0.06	0.61	25.49
15	F	28'00"	22.25	0.11	0	22.14
16	M	5'35"	18.10	0.36	1.97	15.77
17	M	46'45"	17.45	0.06	0.81	16.58
18	M	14'00"	7.29	0	0	7.29
19	M	4'30"	10.22	0	0	10.22
20	M	10'30"	8.38	1.05	0	7.33

Table 12 (contd)

Watch	Sex	Length of watch	Total Feeding Movements	Catches	Probes	Touches
21	M	4'20"	15.24	0	3.70	11.54
22	M	10'00"	14.10	0.10	1.70	12.30
23	M	33'20"	17.76	0	0.09	17.67
24	-	11'00"	11.27	0	0.82	10.45
25	F	4'30"	12.00	1.33	0	10.67
26	M	2'30"	10.80	0	0	10.80
27	M	12'00"	14.75	0	0	14.75
28	-	14'00"	17.00	0.07	0	16.93
29	F	10'00"	20.70	0	0	20.70
30	M	11'00"	25.73	0.18	0.09	25.46

on females, the mean rate of feeding being 18.60 feeding movements per minute with a standard deviation of 5.57. For males there were 27 watches. The mean rate of feeding was 13.07 feeding movements per minute with a standard deviation of 4.84. The distribution of mean rates of total feeding movements for all of the watches on males were compared with the distribution of means for all of the watches on females. This gave $z = 2.32$ which is not significant. The individual minute data were compared, i.e. all of the one minute feeding rates for males in Appendix 4 were compared with all of the one minute feeding rates for females. The result was $z = 7.32$ ($p < 0.0001$) which is highly significant. This would appear to show that the means of watches were not statistically representative. Inherent variation within watches, when compared, showed the rates of males and females to be significantly different. The reasons for this are not obvious. It could be due to the females having a greater energy requirement for egg production and laying, or it could be that females spend less time feeding than males and therefore have to feed faster. If they do have a greater energy requirement they would have to feed for longer than males, or feed faster for the same length of time or both. To throw more light on this subject it would be necessary to have data on the total time spent feeding by males and females during a day. If the differences in rates were due to egg production it may be expected that female rates of feeding would fall towards the end of the season as laying has ceased. This was not indicated by the present study. However, the number of watches was small ($n = 7$) and more data may have shown it. Also, this breeding season was particularly disastrous for the birds. Not one chick was produced around the feeding area on west Old Law due to egg predation. Consequently, the females may still have been in a physiological state for laying, requiring higher energy input even though the last watches were late in the season. The question of energy requirements towards the end of the season will also be complicated by the moult which follows breeding, again requiring more energy in both males and females.

Feeding rates at the four sites of watches were investigated. The data were compared between pairs of sites to ascertain whether or not there was any difference between :-

1) the total feeding rates between areas.
2) the rate of catching between areas.
3) the rate of probing between areas.

Table 13 shows the mean rate of total feeding movements per minute, mean rate of catching per minute and mean rate of probing per minute for each of the areas calculated from:

1) a pool of the individual minute data.
2) a pool of the means of watches.

Table 14 shows non-parametric comparisons both for the means of watches and minute data, between pairs of sites. As with the male/female feeding rates, the comparisons of distribution of means of watches were all non-significant. Once again the means do not appear to be a good statistical representation of the watches, presumably because the variation within the watches is non-normal. Only the results of the comparisons based on the individual minute data will be dealt with.

By pooling the individual minute data, the differences between individual birds are reduced in importance and differences between areas become more prominent. There is a significant trend in the feeding behaviour at the three different areas on west Old Law. Overall rates of feeding movements are fastest on the sand area (16.57 feeding movements per minute), slowest on the mud area (7.93 feeding movements per minute)

Table 13. The mean rate of total feeding movements per minute, the mean rate of catching per minute and the mean rate of probing per minute calculated from

a) a pool of individual minute data for each area

b) a pool of the means of watches for each area

The number of minutes, and the number of watches pooled are given, as are standard deviations for each mean calculated.

		a			b	
Substrate	No. of mins.	Mean	S.D.	No. of watches	Mean	S.D.
MUD						
Total	57	7.93	5.04	4	9.98	3.06
Catches	57	1.18	1.49	4	1.099	0.21
Probes	57	0.53	1.02	4	1.98	2.37
SAND						
Total	295	16.57	8.04	23	14.61	6.76
Catches	295	0.17	0.55	23	0.22	0.44
Probes	295	0.54	1.33	23	0.69	0.97
MUD/SAND						
Total	30	12.03	7.50	4	12.64	4.58
Catches	30	0.30	0.79	4	0.215	0.31
Probes	30	0.25	0.59	4	0.198	0.18
SEABEACH						
Total	57	12.33	7.32	5	12.10	5.93
Catches	57	0.25	0.61	5	0.19	0.18
Probes	57	0.23	0.60	5	0.16	0.30

Table 14. The results of comparisons between pairs of data from Table 13 by the Mann-Whitney U Test z = Students' t with ∞ degrees of freedom. Where sample sizes are small, no value of z is given as P can be obtained directly.

The object of the test is to show whether or not the rate of total feeding movements (or rate of catching or rate of probing) or means of watches (watches). P. being significant is indicative of a significant difference between the two. NS = not significant.

MUD total against SAND total (mins)	$z = 7.939$	$P < 0.001$	
MUD total against SAND total (watches)	$z = 1.779$	$P < 0.1$	NS
MUD/SAND total against SAND total (mins)	$z = 3.296$	$P < 0.001$	
MUD/SAND total against SAND total (watches)	$z = 1.186$	$P = 0.117$	NS
MUD total against MUD/SAND total (mins)	$z = 2.456$	$P < 0.01$	
MUD total against MUD/SAND total (watches)		$P = 0.343$	NS
SEABEACH total against SAND total (mins)	$z = 4.582$	$P < 0.001$	
SEABEACH total against SAND total (watches)	$z = 1.20$	$P = 0.115$	NS
MUD catches against SAND catches (mins)	$z = 4.035$	$P < 0.001$	
MUD catches against SAND catches (watches)	$z = 2.525$	$P < 0.01$	
MUD/SAND catches against SAND catches (mins)	$z = 0.732$	$P = 0.2327$	NS
MUD/SAND catches against SAND catches (watches)	$z = 0.137$	$P = 0.443$	NS
MUD/SAND catches against MUD catches (mins)	$z = 3.036$	$P < 0.01$	
MUD/SAND catches against MUD catches (watches)		$P < 0.1$	NS
SEABEACH catches against SAND catches (mins)	$z = 0.644$	$P = 0.261$	NS
SEABEACH catches against SAND catches (watches)	$z = 0.03$	$P = 0.48$	NS

/

Table 14 (contd).

MUD probes against SAND probes (mins)	z = 0.21	P = 0.416 NS
MUD probes against SAND probes (watches)	z = 0.546	P = 0.291 NS
MUD/SAND probes against SAND probes (mins)	z = 6.827	P < 0.001
MUD/SAND probes against SAND probes (watches)	z = 0.341	P = 0.367 NS
MUD probes against MUD/SAND probes (mins)	z = 4.514	P < 0.001
MUD probes against MUD/SAND probes (watches)		P = 0.343 NS
SEABEACH probes against SAND probes (mins)	z = 0.857	P = 0.195 NS
SEABEACH probes against SAND probes (watches)	z = 1.47	P = 0.708 NS

with those on the muddy sand intermediate between the two (12.03 feeding movements per minute). The number of catches per minute appears to be greater on the mud area (1.18 catches per minute) than on either the sand (0.17 catches per minute) or the muddy-sand (0.30 catches per minute) areas. The number of probes per minute is similar on the mud (0.53 probes per minute) and sand (0.54 probes per minute) areas but is significantly lower on the muddy-sand area (0.25 probes per minute).

Comparisons were made between the sandy feeding area on west Old Law and the sandy sea-beach at Ross. The overall rate of feeding was much faster on the feeding area (16.57 feeding movements per minute compared to 12.33 feeding movements per minute), the number of catches per minute were similar (0.17 catches per minute for the feeding area and 0.25 catches per minute for Ross), as were the number of probes (0.54 probes per minute for the feeding area and 0.23 probes per minute for Ross).

Though there were definite differences in rates at the different sites, it is not straight forward to attribute these differences to prey distribution. There are several complications such as prey availability, prey nutritional value and the bird's selectivity. Does a higher feeding rate indicate greater prey availability in an area? Observations suggest that the sand area has more potential prey than the muddy-sand area. The results show that feeding rate is faster on the sand than on the muddy-sand so that this could be attributed, at least partly, to prey availability. The feeding rate on the sea-beach is slower than on the sandy feeding area. Once again this may concern prey availability, but it is quite likely that different prey are being taken at the two areas so that care has to be taken in interpretation. The results show that feeding rate on the mud area is the slowest. However, the invertebrate samples appear to show that there is more potential prey on the mud area than on the sandy feeding area. It is possible that the samples are not showing all of the prey present, particularly Talitrids and Wrack flies (Coelopids) and that prey availability also has some influence. A further consideration is the nutritional value of the prey taken. If the average nutritional value of a prey item is greater on the mud site than on the sandy feeding area, a slower feeding rate will result in the same nutritional gain. The number of catches in an area gives an indication of larger and presumably nutritionally greater prey items taken. The results show that the rate of catching per minute is about six times greater on the mud site than on the sandy feeding area. A further complicating factor is cover. The mud area is surrounded by Spartina marsh, while the feeding area is open sand flats. It is possible that birds spend more time watching for predators in the marsh area, which would slow their feeding rate.

The whole of the feeding data were pooled to produce a picture of feeding variation after the tidal cycle (fig. 18). The results do not appear to show a conclusive cycle. A fall off of feeding rates towards high water is apparent, as is an increase after high water. This is definitely the case for the feeding area of north-west Old Law, as it is submerged at high tide. However, high tides did not appear to prevent feeding from occurring on Ross Back Sands or on the south-west point of Old Law, where only the highest tides covered the whole feeding area. If each area was studied separately the results would probably be more easily interpreted.

Differences in feeding rates at different periods of the breeding season are difficult to show. What was noted, though, was that birds spent less time feeding while they were incubating or looking after chicks. This may lead to differences in rate.

Fig. 18 Feeding over the tidal cycle.

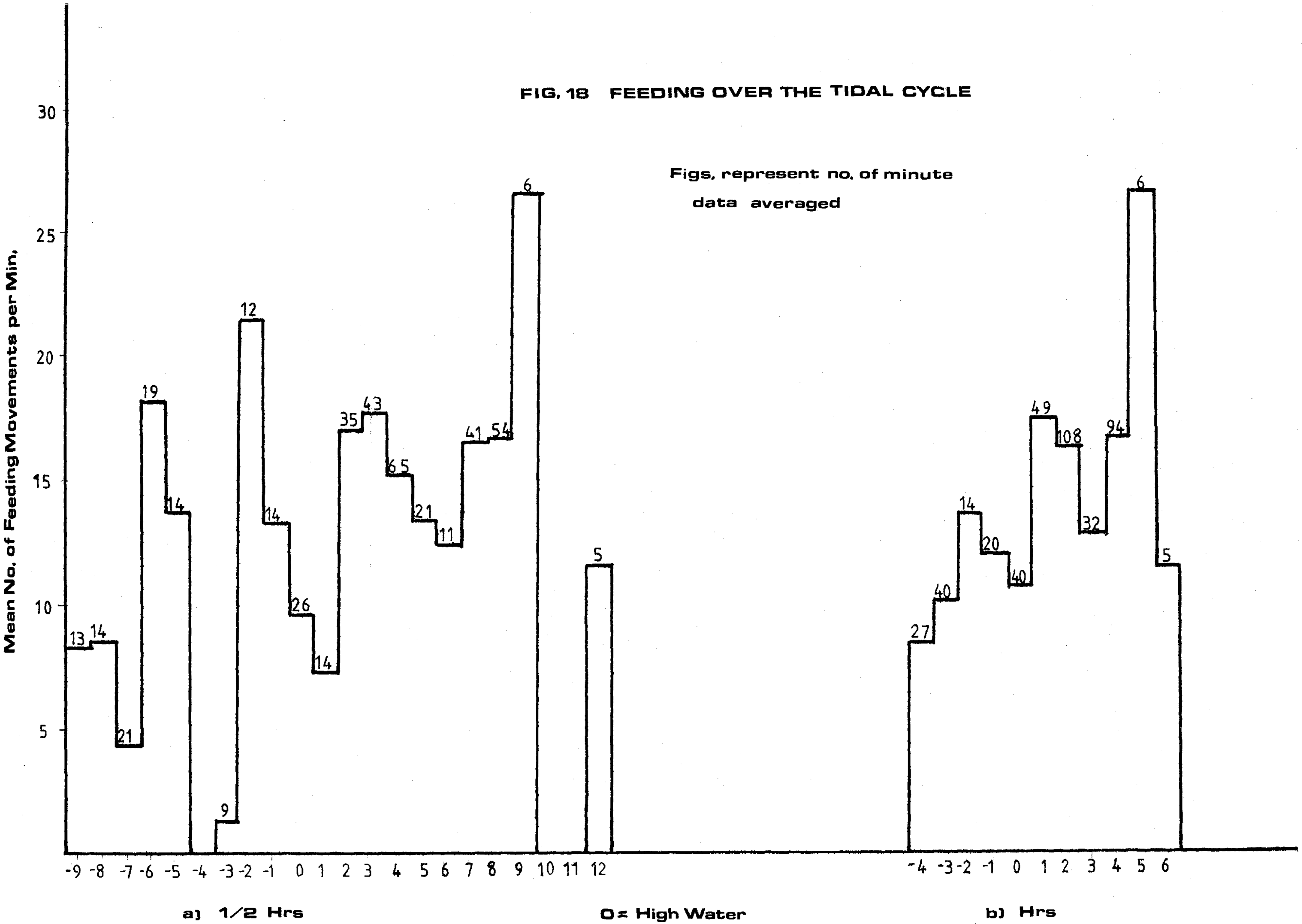
The mean number of feeding movements per minute for

a) $\frac{1}{2}$ hour periods through the tidal cycle and

b) for 1 hour periods through the tidal cycle.

0 represents high water. The figures at the head of each bar gives the number of minutes data averaged to produce the height of the bar.

FIG. 18 FEEDING OVER THE TIDAL CYCLE



DISCUSSION

Breeding Strategy

The breeding strategy of the Ringed Plover is a common one of monogamy based on a pair bond which lasts through the season. Both parents take turns in incubating the eggs. The young are nidifugous and are attended most of the time by both parents. In some other waders there has been a weakening of the pair bond and a double-clutch system has evolved. The female lays two clutches in rapid succession. One is looked after solely by the male and the other by the female, e.g. Temminck's Stint Calidris terminckii (Hilden, 1975). There are several aspects of Ringed Plover parenthood which require both parents. Poor synchrony of hatching is quite common, and often the young are led from the nest by one bird while the other continues to incubate the remaining eggs. The anti-predator strategy of the Ringed Plover involves two birds. During incubation, one bird sits, the other keeps watch for predators and calls the first off the nest at any sign of danger. In arctic areas the terrain is so exposed that the sitting Ringed Plovers were called off nests while the predator was over a distance of half a kilometer away (Pienkowski, pers. com.). Both birds also take part in leading predators away from chicks. Retaining the pair bond through the season makes the laying of a replacement clutch more straight-forward. The birds do not have to spend time searching for a new mate. The replacement clutch capability of the Ringed Plover is obviously an adaptation to low hatching success. However, it only occurs in the moderate conditions of the temperate zone. In Greenland, only one clutch is laid. The breeding season is so short that there is no time to lay a second.

Only one case of double-brooding was noted in 1979. The pair was the first to hatch chicks in early June. It was not known whether the first brood fledged before the second clutch was laid. There was sufficient time for this to occur according to records, but there is also a possibility that the second clutch was laid in response to the first brood being predated.

It appears that some birds either do not have the ability to lay replacements, or do not use it. In 1979 some birds made only one attempt to breed, their clutches being predated in early June, whilst other birds were still laying half way through July. This can probably be attributed to variation in the physiological condition of the birds. The proximate factor responsible for the termination of laying will be the decreasing activity of sex hormones. Waders are relatively long-lived and consequently it is not beneficial to risk too much loss of condition in one year, extra clutches probably being physiologically quite stressful.

Evolutionary constraints on further clutches would be expected to occur with the advent of the end of the season. Young produced must have sufficient time to fledge, and the parents time to moult. Pienkowski found evidence that young had less chance of survival as the season progressed. There is, then, obviously a time when the risk of failure of young would be too great for the parents to invest time and energy in them.

Observations in 1979 gave the impression that some birds do not breed at all. However, this fact is difficult to prove. Most of the Northumberland coast provides reasonable breeding grounds and it is possible that birds failing to breed in one area may move to another area and try again. One pair, during the period of work by Pienkowski were seen at Goswick, the Snook, Tealhole Point and Ross, all in one season.

Some first year birds breed in the area of the reserve, others do not. It is not known whether the latter birds breed during the first year or not. Some birds missing for the first year reappear on the reserve in the second year (Pienkowski, pers. com.).

Breeding Season.

It was thought for a long time after the initial work of Rowan (1926) and Baker (1938) that birds laid their eggs at the correct time for the young to be hatched during a time of plentiful food supply. For this to be so, laying has to take place during a period when food is more scarce. Many observations on different species have shown that the earlier a bird breeds, the better chance of survival of the young. (However, this is only true of single brooded species). There should, therefore, be a great selective advantage for those birds which bred earlier in the season. Yet, by way of example, extremes of laying of different adults in the same area in the same year may be as much as three weeks apart in the Great tit (Parus major) and four weeks apart in the Manx Shearwater (Puffinus puffinus). There must therefore be some kind of balancing disadvantage to early breeding. It was suggested by Perrins (1969) that this disadvantage was related to the food supply present at the time of laying. A female cannot lay until she has food sufficient to do so, without risking her own life.

The classical view of feeding-related constraint to the breeding season does not appear to apply to the Ringed Plover. Pienkowski found that, at no stage, was the Ringed Plover under any stress concerning its feeding. Throughout the year it has adequate food supplies. Egg laying in many birds is correlated with Spring temperatures e.g. Kentish Plover, Charadrius alexandrinus (Rittinghaus, 1956), Redshank Tringa totanus (Grosskopf, 1958) and Dunlin Calidris alpina (Soikkeli, 1967) and this may be the case in the Ringed Plover, though no evidence of this has been obtained. Predation may also play a part. Pienkowski found that the chance of egg predation was higher earlier in the season, decreasing as it progressed. Consequently clutches laid a little later have more change of survival. The results for 1977 were not consistent with this. Fig. 15 shows that the hatching success was highest at the beginning of the season.

Factors controlling the end of the season are probably quite different. During the season the birds have to produce young, tend them until fledging, and then moult. In the arctic, weather conditions allow just enough time to complete everything. In the temporate zone there is far more time. There is no sharp end to the breeding season, but observations make it obvious that breeding is drawing to a close around the beginning of August and that most chicks will be fledged by the beginning of September.

There can be two alternative strategies:-
to try to produce 2 broods/year for x years or
to try to produce 1 brood/year for 2x years.
The Ringed Plover appears to struggle to maintain the second strategy, but occasionally a pair is lucky enough to be able to produce two broods. Some individuals may have longer breeding seasons than others as dictated by the production and maintainance of the sex hormones.

Population Dynamics.

Boyd (1962) estimated, from B.T.O. ringing recoveries, that the mean annual mortality for the Ringed Plover was $42 \pm 5.48\%$. This means that on average each pair must fledge 1.18 chicks each year to keep the population stable. In 1977, which was a reasonably successful year 241 eggs were laid by 54 pairs. The fledging success is difficult to measure accurately as birds tend to leave the area on fledging, but for 1977 it was calculated to be between 11.1 and 24.5% of eggs. This is between 0.49 and 1.09 chicks per pair which is not enough to support the population. In 1979 which was a bad year 154 eggs were laid by 42 pairs. Fledging success was placed somewhere between 5.8 and 12.58% of eggs. This is between 0.21 and 0.48 chicks per pair, far too low to support the population. This assumes that Boyd's calculations are correct. In practice, I suspect adult survival to be greater than Boyd suggested. The Lindisfarne population is stable (except for the drop in the number of pairs in 1979) so there must be immigration of birds into the area. Where they come from is not known. It is possible that they could come from the rest of Northumberland coast or even Scotland.

Breeding success varies from year to year, but as shown in 1979, predation, particularly of the eggs, can be disastrous. One or two predators can clear an area. The major agents of predation vary from year to year. In the past, fox predation was rife on the North Shore, and has also been a problem on Old Law. In 1979 crow predation was the major problem on Old Law, and to some extent on the North Shore. Human disturbance also takes its toll. Directly, birds are driven off the nest by the presence of people. Too much of this may affect normal incubation. Indirectly, people may help predators. Crows, in particular, may watch birds come off and return to the nest and discover the location of the eggs. People, and particularly dogs with them, visiting scrapes may lay scents which foxes could follow.

Territoriality.

It is possible that territoriality is controlling breeding density at Guile Point and the enclosure on the North Shore. Here all of the territories are touching, suggesting that the area is full, and there would appear to be exclusion of birds from these areas. It is unlikely that competition is as fierce in the rest of the areas of the reserve. The position of territories is constant from year to year. In Greenland territory uptake is abrupt, coinciding with snow clearance (Pienkowski, pers. com.). The cleared areas start off fairly small and the birds are packed tightly together, but as the areas extend, the birds even themselves out. Some are excluded and disappear. Exclusion experiments have been carried out in waders. Harris worked on Oystercatchers Haematopus ostrelagus on Skokholm and found that if birds were removed from a territory, it was rapidly filled by another pair, suggesting that territoriality is controlling breeding density, at least in that area.

There is very little information on territory uptake. As mentioned earlier, unlike Greenland, uptake on the reserve is a very gradual process. If there was any advantage in early uptake, the older, more experienced birds would be expected to establish territories first. It may possibly allow retention of a particular territory from year to year. There is evidence that birds tend to return to the same area, if not the same territory year after year. This would tend to suggest that once a bird has chosen a territory for the first time, it is 'fixed' in that position (However, it may move between years if nesting fails). Consequently if a bird manages to obtain a 'good' territory in part of the main area (especially on the North Shore Ross or Old Law) in its first year it is liable to remain there for the rest of its breeding life.

If it only manages to find a territory in a peripheral area, observations by Pienkowski show that it is likely to move around more from year to year, but having become a 'peripheral bird' it tends to remain so. There is some evidence to suggest that the plovers return to the areas where they hatched in an attempt to find a territory. This might suggest that birds hatched in the 'best' areas will become owners of the 'best' territories, while those of the peripheral areas will remain 'peripheral birds'. (There is little or no evidence to suggest that some areas are more suitable for breeding than others, except for the fact that birds appear to 'prefer' some of the sites, and breeding density is higher there, though breeding success is not necessarily higher). A similar situation occurs in the Kittiwake Rissa tridactyla (Coulson, 1968). Here it was shown that there was a definite difference in breeding success between the 'centre birds' with the best territories and the 'edge birds' with peripheral territories. It is unlikely, however, that such a system is as rigidly adhered to in the Ringed Plover as it is in the Kittiwake.

A critical question concerning the above hypothesis is 'when does a young plover become aware of its geographical position?' If this is while in the feeding territory, then it may become imprinted on it. But if it is not aware of where it is until it has fledged, and possibly by then moved several kilometers from the nest site, then it would not be surprising that many young return to the Lindisfarne reserve but not to their particular birthplace. Most fledged young on the reserve have been colour-ringed for the last 5 years. Most of the pairs in 1979 were unringed suggesting hefty immigration of young birds from elsewhere (and perhaps dispersal of some Lindisfarne young to breed elsewhere).

The reasons for territoriality in Ringed Plovers are not obvious. It is very unlikely to be a question of food supply for, as stated previously, the birds have a more than adequate food supply for the whole of the breeding season. It may involve the spacing out of nests; an anti-predator ploy first hypothesised by Tinbergen (1953). The more spaced out nests are, the less likely it is for predators, having found one clutch, to locate adjacent ones. In 1979, this was shown not to work all of the time. The nests at Guile Point were packed so closely that three adjacent clutches were found by crows at the same time. However, the nests spaced further apart, e.g. on Ross Back Sands, did survive better. There must obviously be other factors affecting territory size at Guile Point and in the enclosure on the North Shore, which cause the birds to produce smaller territories and risk location of scrapes by predators.

This leads to the question of territory preference. If there is a greater breeding density at Guile Point and on the North Shore, this would tend to suggest that there is more competition for these areas, and hence they must be preferred areas. They must, therefore, have certain factors which make them appealing to the birds. Both areas have shingle beaches. The eggs of the Ringed Plover are adaptively coloured to be well camouflaged against a shingle substrate. Chicks are also probably better camouflaged against a shingle background. However, the majority of birds on the reserve do not nest on shingle, but on sand (60% of scrapes), so that a shingle substrate does not appear to be too important. Both the North Shore and Guile Point are in the proximity of a preferred feeding area. An important factor may be that birds should be able to see their nest sites while feeding. The North Shore and Guile Point both have long straight stretches of beach which may make it possible for potential predators to be seen at a greater distance. Consideration of other nesting areas show that a clear all round vision from a nest site is quite important. Whatever the factors involved, they are, however, not related to success. Neither the birds at Guile Point nor in the enclosure on the North Shore succeeded in hatching any chicks in 1979. In the past, the North Shore has always shown poor breeding success. The success of the Guile Point birds is usually no better than birds nesting around the rest of Old Law, so that these 'preferred' areas are certainly not the most successful.

Variation in Breeding Success.

Several of the results cited portray the great difference in breeding success between the island and the mainland. The two most important areas are the North Shore on the island and Old Law on the mainland. In the past the number of territories in these two areas was similar (15 on Old Law and 17-18 on the North Shore), but in 1979 the number on Old Law increased (19) and on the North Shore, decreased (11). More eggs are laid on the mainland than on the island, but the most important difference is hatching success. Table 11 shows the considerable difference in hatching success between the areas over the years.

There are a few obvious possible reasons for these differences and the overall answer is probably a combination of all of them and more. The main difference between the two areas is in human disturbance. The 'best' areas of the two places are both shingle beaches. Guile Point on Old Law probably receives as few as 20 or 30 visits per season by holiday-makers, as the only way to reach Old Law is by walking the length of Ross Back Sands. The enclosure on the North Shore, however, is right next to a small tourist car park and is one of the most important holiday areas on the island probably receiving visits from tourists on most days of the peak holiday season. The action of human disturbance has been discussed earlier.

Feeding sites may be important. The Old Law birds have the feeding area on the north-west shore. There was evidence that birds flew across the spit to feed there. More important, however, may be that the Spartina Marsh makes a very good area for hiding and feeding chicks. The North Shore territories have feeding areas within them which are used by the birds, but there is a further area well away from the territories which is also widely used. The difference is distance between these 'auxiliary' feeding areas, quite close on Old Law and quite distant on North Shore may be important, particularly concerning the watching of the territory whilst feeding.

The beaches of Old Law are difficult to approach, without being seen. Many are backed by dune cliffs so that predators can only approach via the open beach. The Snook has a vast dune expanse and most areas of the beach can be approached from behind making it easier for foxes and other predators.

Old Law has a ternery close by, on Black Law which may act as an early warning system for the plovers, particularly concerning aerial predators.

For many years Old Law was part of a large estate which employed a keeper. This may have affected fox predation on Old Law, which in the past has been the main nuisance on the Snook. Both areas are now becoming subject to egg predation by crows, and this, considering the 1979 data, could be disastrous for the plovers if allowed to continue year after year.

The question arises as to how much the biologists are disturbing the area they are trying to study. At Lindisfarne they are unlikely to produce differential effects between the island the mainland. Ordinary observations should not have any adverse effects, but care must be taken when visiting scrapes that no clues are left for crows to follow, or no scent trails are left for foxes to follow. Ringing chicks probably also has little effect, but ringing of adults, particularly those incubating at the time, is not advised as it may lead directly or indirectly to the destruction of the clutch.

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An experiment on spacing out as a defence against predation.

APPENDIX 1

Histories of Colour Ringed Birds.

Y/M G/W ♀ Ringed as adults on Ross Back Sands. 300 yards north of footpath in 1975.

1975 Territory 4th Bay south of Wide Opens - Successful - Mate no rings

1976 Territory 2nd Bay south of Wide Opens - Successful - Mate no rings

1977 Territory South-east Old Law - Successful - Mate no rings

1979 Territory 1st Bay South of Wide Opens - Successful - Mate no rings

Y/M Y/W ♂ Ringed as adult 4th Bay south of Wide Opens 3/7/75

1975 Territory 4th Bay south of Wide Opens

1976 Territory South of NNR sign - Ross Back Sands

1977 Territory 4th Bay south of Wide Opens - Successful - Mate no rings

1977 Seen on March at Budle

1979 Territory Budle Bank - Successful - Mate no rings

Y/M G/R ♀ Ringed as adult on 28/6/75 at Snook Point

1975 Territory Snook Point Successful

1976 Territory Snook Point

1977 Territory Snook Point Unsuccessful - Mate no rings

1979 Territory Snook Point Unsuccessful - Mate no rings

Y/M Y/G ♂ Ringed as adult opposite Tower north shore of Snook 1975

1975 Territory Opposite Tower north shore of Snook

1976 Territory Opposite Tower in March but not seen later

1977 Seen at Wide Opens only twice - no mate

1979 Territory Enclosure, north shore of Snook Unsuccessful - Mate no rings

$^{R}/_{M}$ $^{R}/_{B}$ ♀ Combination used twice. Either 1 of brood of 4 ringed as chick on the Snook 17/6/77 or 1 of brood of 4 ringed as chick Old Law 2/7/77.

1979 Territory South-west Old Law - Successful - Mate no rings

$^{R}/_{M}$ $^{R}/_{Y}$ ♂ 1 of brood of 4 ringed as a chick on the Snook 17/6/77

1979 Territory North shore of Snook - Successful - Mate no rings

$^{R}/_{M}$ G only ♀ Must have lost a ring. Could be $^{R}/_{M}$ $^{B}/_{G}$ 1 of brood of 3 ringed Old Law 25/6/77 or $^{R}/_{M}$ $^{G}/_{R}$ or $^{R}/_{M}$ $^{G}/_{O}$ South side of Snook. Ringed as chicks 7/6/77

1979 Seen at Chare Ends March-June. Seen north shore of Snook June-July.

$^{R}/_{M}$ $^{G}/_{W}$ 1 of brood of 1 ringed as chick 1/7/73 Old Law. Last seen 20/10/73 ($^{M}/_{R}$ $^{G}/_{W}$ was ringed as a chick 1 of a brood of 4 Old Law 30/5/77)

1979 Seen south side of Snook

$^{R}/_{M}$ $^{O}/_{W}$ 1 of a brood of 3 ringed as chick south side of Snook 12/6/77

1979 Seen May Chare Ends - June-July North shore of Snook

$^{R}/_{M}$ $^{R}/_{O}$ 1 of brood of 4 ringed as chick 17/6/77 Snook
All from same brood.

1979 Territory? North-east Old Law No nesting seen Mate no rings.

M $^{Y}/_{R}$ ♂ Has lost a ring 5 most probable 3 young ringed 1977 on Old Law, one young ringed on north shore of Snook 1975 (known to have fledged) or one young ringed 1976, north end of Budle Bay (known to have fledged).

1979 Territory South west Old Law. - Unsuccessful Mate no rings

M only ♂ (x2) Probably chicks from 1974

1979 a) Territory north shore of Snook (also earlier south side of Snook Unsuccessful - Mate no rings

b) Territory north-east Old Law - Successful - Mate no rings

$^{B}/_{M}$ $^{B}/_{G}$ ♂ 1 of brood of 4 ringed as chick east side of Old Law 25/7/75

1976 Seen often at Guile Point north west Old Law

1977 Territory North-west Old Law - Successful - Mate $^{Y}/_{M}$ $^{W}/_{G}$

1979 Territory North-west Old Law Unsuccessful - Mate no rings

$^{B}/_{M}$ $^{G}/_{B}$ ♀ 1 of brood of 4 ringed as chicks on north shore of Snook 12/6/75

1976 Seen on north shore of Snook

1977 Territory North-west Old Law Successful - Mate no rings

1979 Territory North-west Old Law Unsuccessful - Mate no rings

$^{M}/_{O}$ $^{B}/_{R}$ ♂ 1 of brood of 3 ringed as chick 1976 3rd Bay south of Wide Opens

1977 Territory East Pinnacle north Old Law Successful - Mate no rings

1979 Territory East Pinnacle north Old Law Successful - Mate no rings

$^{M}/_{O}$ $^{G}/_{B}$ ♀ 1 of brood of 4 ringed as chick at Wide Opens 7/8/76

1977 Seen on north shore of Snook and Ross Back Sands Mate no rings

1979 Seen on north shore of Snook.

$^{M}/_{O}$ $^{W}/_{B}$ ♂ 1 of brood of 4 ringed as chick at Guile Point 1976

1977 Seen at Heather Cottage, Budle and north Old Law

1979 Territory South-east Old Law Unsuccessful - Mate no rings

$^{W}/_{M}$ $^{W}/_{G}$ 1 of brood of 3 ringed as chick on north shore of Snook 2/6/74.

1975 Seen Eden Estuary, Fife

1979 Seen north west Old Law.

$^{W}/_{M}$ $^{R}/_{W}$ ♀ 1 of brood of 4 ringed as chick north shore of Snook 25/6/74.

1975 Seen

1977 Seen

1979 Territory Primrose Bank - Mate no rings

$^{W}/_{M}$ $^{R}/_{G}$ 1 of brood of 3 ringed as chick on north shore of Snook 30/5/74.

1979 Seen Primrose Bank.

$^{M}/_{B}$ $^{R}/_{O}$ ♂ 1 of brood of 2 ringed as chick Goswick 1/8/75

1976 Seen at Guile Point, Teal Hole Territory Sandham - Unsuccessful - Mate no rings

1977 Territory west Old Law - Unsuccessful - Mate no rings

1979 Seen May north-west Old Law, June north-east Old Law, July north-west

$^{M}/_{W}$ $^{W}/_{R}$ ♀ 1 of brood of 3 ringed as chick east Old Law 25/5/78

1979 Territory Sandham Bay Mate no rings

$^{M}/_{W}$ $^{B}/_{O}$ 1 of brood of 4 ringed as chick Guile Point 8/6/78

1979 Seen north shore Snook.

$^{G}/_{M}$ $^{R}/_{O}$ ♂

1974 Territory Goswick

1975 Seen on Snook

1976 Territory Snook - Successful

1977 Seen

1979 Seen of north shore of Snook

$^{G}/_{M}$ R only ♂ Has lost a ring Could be 1 of 3 $^{R}/_{G}$ 1 of brood of 1 ringed as chick on Long Nanny Beadwell 20/7/77 or $^{O}/_{R}$ 1 of brood of 3 ringed as chick Football Hole 9/8/77 or $^{R}/_{Y}$ nesting Goswick 1974-75-76

1979 Territory North shore of Snook - Unsuccessful - Mate no rings

$^{O}/_{M}$ $^{R}/_{B}$ 1 of brood of 4 ringed as chick Guile Point 19/7/76

1979 Seen at Chare Ends.

$^{O}/_{M}$ $^{W}/_{Y}$ 1 of brood of 3 ringed as chick Guile Point 16/6/76

1977 Territory Chare Ends - Unsuccessful - Mate no rings

1979 Seen at Chare Ends

$^{R}/_{M}$ $^{W}/_{R}$ 1 of brood of 2 ringed as chick Ross Back Sands 24/6/77

1979 Seen on feeding ground north shore of Snook

APPENDIX 2

Data on Individual Pairs

1st Bay before Wide Opens (S. end). Y/$_M$ G/$_W$ ♀ + UR♂

Territory taken up before April 24. Scrape in sand 10^x S of pole with fishbasket at bottom. April 30 birds seen mating. soliciting by crouching in scrape - spreading of wings and calling. May 4 scrape found near pole. No eggs found, but there were crow footprints around the scrape. Could this have been first attempt at breeding?
May 22 4 eggs found. Scrape in plain sand about 20^x N of pole (fb.b.). 20^x - 30^x above HWM. June 10 eggs gone from scrape. 1 chick seen on high water line. This date means that the eggs must have been layed between about 15 - 20 May. Chicks not seen for some time. Due to spending a lot of time in the marram behind the beach 1 chick was found on 28 June. 1 chick found and ringed on 29th.

Chick ringed
BV36115 M/$_R$/$_O$ lt O/$_R$ rt Bill 15.9mm Wt. 49.5gms.
1°/3 1°cou/4 2°/4 Head/4 Back/4 Tail/3 Br/4 Rump/downy
probably about 2½ weeks old.
From around July 1 birds seemed to be in the territory less of the time.
July 12 both parents seen with 2 fledglings. 1 ringed as above 1 unringed. There had been another pair at the N. end of the bay but these left before the chicks were layed and the birds home range stretched out to encompass the rest of the bay. An unringed ♂ only was seen on July 20.

1st Bay S. of Wide Opens N. end. Unringed pair. Territory taken up before April 28, but not before April 24. May 15 Scrape in plain sand 30^x above high water mark 1 egg present. May 22 4 eggs present. June 6, adult ♂ ringed by clap-net on the scrape.

Adult ringed

BV86-96 M/R/O lt R/O rt Wing 140mm Bill 16mm Wt. 70gms.

Unfortunately disturbance of sand was located by crows and eggs taken on June 7. The territory was deserted soon after.

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South-West Point Old Law R/M R/B ♀ + UR ♂

Territory taken up before April 24. No nesting activity was recorded but 3 chicks appeared at the S. end of the Spartina marsh on June 6. At most they were only 2-3 days old.

Chicks ringed

1) BV36098 M/R/O lt R/G rt Wt. 11gms Bill 9mm

2) BV36099 M/R/O lt R/B rt Wt. 7.5gms Bill 7.4mm

3) BV36100 M/R/O lt R/W rt Wt. 11gms Bill 8.5mm

Allowing 26 days for incubation the eggs must have been layed around May 11.

300^x N. of S.W. point. Scrape in sand and straw 4^x above HWM. 4 eggs 27 June Hatched 18 July 2 chicks seen on 20 July. 1 caught wt. 8gms. NB This is a 2nd brood. Hatching date suggest eggs layed between 23 and 26 June. 21 July 2 chicks caught

1) Wt. 9gms 2) Wt. 9.5gms.

100^{x} S. of jutting Dune W. Old Law Unringed pair. Territory taken up before May 12. 15 May, scrape in plain sand. 10' up dune face, hidden by marram roots. 3 eggs present. 22May, eggs taken.

June 1 300^{x} S. of juttung dune Scrape on beach-sand and shell, on HWM. 4 eggs present Adult ♂ ringed on 6 June.

Adult ringed

BV36097 M/R/O lt R/Y rt Wing 143mm Bill 15mm Wt. 81gms.

Eggs taken by crows before 12 June.

Birds still present on July 20 but no further sign of breeding.

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150^{x} N. of jutting Dune W. Old Law Both birds unringed. Territory taken up before April 24. 10 May, scrape in sand with straw 1 egg 13 May, still only 1 egg Egg taken before 15 May. 1 June - new scrape was seen being made.

27 June Scrape in sand in grass 1 egg 200^{x} N. of Jutting dune. 3^{x} above HWM 29 June 2 eggs Eggs gone 1 July

Birds still present 20 July

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Shingle Bay next to the feeding area W. Old Law. Both birds ringed. Territory taken up before April 24 27 June, scrape in sand covered in marram on the HWM 1 egg Egg taken by crows on 29 June.

Birds still present 20 July.

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100^{x} N. of S.W. Point Old Law M only Y/R ♂ UR ♀ Territory taken up before May 12. 27 May Scrape in sand on face of dune under marram roots. 3^{x} above high water mark. 2 eggs present. Eggs taken on or before June 11. Birds seen mating. Pre-mating display ♂ walks up to stands close to her, cranes his neck, keeping his head level, then kicks his legs high in front of him, a kind of 'goose-step' on the spot.

27 June. 70^x N. of S.W. point. Scrape in sand on face of dune under marram roots. 3^x above HWM. 1 egg present 29 June 2 eggs present 1 July 3 eggs present. Slutch of 3 only 27 July 3 eggs buried under dune collapse.

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300^x N. of S.W. Point Old Law Unringed pair. Territory taken up before 24 April. May 2 Scrape in sand 1 egg. 10 May 2 eggs only. The nest must have been deserted around May 4 which coincides with tyre tracks along the shore. The eggs were taken by crows on May 12. Birds still present on 26 and 27 May, also seen on 11 June but no more nesting activity was recorded.

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Point nest to the bend W. Old Law. Both birds unringed. Territory taken up before April 24. 10 May, scrape in sand and pebbles.

June 1 15^x N. of point. Scrape in pebbles with shell 1 egg June 6 3 eggs June 7 4 eggs. June 11 eggs gone.

27 June 20^x N. of point. Scrape in sand 1 egg 3^x above HWM. Egg taken by crows 29 June. Birds still present 20 July.

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50^x N. of the point N.W. Old Law Both birds unringed. Territory taken up before April 24. May 26, Scrape in pebbles and straw. 3 eggs Taken before 7 June. 12 July Scrape in sand and pebbles, + shell. 2 eggs Eggs taken by 18 July Birds still present on 20 July.

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100^x N. of point N.W. Old Law B/M B/G ♂ + UR ♀ Territory taken up before April 24. May 13, 2 scrapes in sand and pebbles. May 22 4 eggs Scrape in sand and shell. Scrape $2-3^x$ above HWM. Eggs taken before June 7. Birds still present on July 20.

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200^x N. of point N.W. Old Law B/M G/B ♀ + UR ♂ Territory taken up before April 24. May 15. Scrape in plain sand 2 eggs. Eggs taken by crows before 16 May. 50^x S of W. pinnacle. June 6. 150^x S. of W. pinnacle. Scrape in pebbles with shell. 3 eggs. Clutch taken June 7. June 27 Scrape in sand in marram. 3^x above HWM. Clutch taken by gulls - 12 July,

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20^x W. of E. pinnacle NE Old Law. W/G M/W ♀ + UR ♂ June 1. Scrape in sand under marram 4 eggs. Clutch taken before June 11, by crows.

In dunes beind E. pinnacles. Scrape in sand under marram 30^x above HWM. 3 eggs 1 July.

Birds seen for the first time on 1 June.

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50^x E. of E. pinnacle N.E. Old Law B/R M/O ♂ + UR ♀ Territory taken up before April 28. No scrape found. 18 July - 2 chicks seen - 3 wks. old.

1 chick ringed (18 July)

M/R/O lt O/Y rt BV86116 Wt. 52gms Wing 105mm Bill 13.6mm

$1^o/4$ 1^ocou/4 $2^o/4$ GT COV/5 M.L.COV/5 BR/4 Tail/4 Back/4 Head/5 Rump/Downy

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<u>100^{x} E. of E. pinnacle N.E. Old Law</u> Both birds unringed. Territory taken up before April 28. June 21. Scrape in sand under marram high up into the dunes at the back of the beach 25^{x} from HWM. <u>3 eggs</u> Eggs gone before 12 July.

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<u>150^{x} S.E. of E. pinnacle N.E. Old Law</u> M left ♂ UR ♀ 1st inlet S. of pinnacles. Territory taken up before April 28. 12 July <u>4 eggs</u> Scrape in sand under marram 20^{x} above HWM. 12 July eggs hatched. 3 chicks seen on sand. 18 July 1 chick ringed.

<u>Chick ringed</u>

BV86117 M/R/O lt O/G rt Wt. 31.5gm Wing 50mm Bill 12.5mm 1^{o}/2

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<u>700^{x} S. of E. pinnacle E. Old Law</u> R/M R/O + UR Territory taken up before April 24. There is a large blowout in the dunes where these birds have been seen. Several scrapes have been found but no eggs. These birds tend to move about a lot. They are usually missing at low tide. R/M R/O has been observed feeding on the feeding area, W. Old Law. The birds have also been observed in the shingle inlet.

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<u>Shingle Inlet E. Old Law</u> Unringed pair. Territory taken up before June 1. Scrape found. ♂ soliciting behaviour was observed. No eggs were found. There was no sign of the birds after June 27.

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Shingle Inlet E. Old Law   Unringed pair. Territory was at the rear of the inlet. Taken up before June 4. June 7, Scrape in sand, shingle and bits of shell. 100^{x} from HWM 4 eggs Eggs taken before June 21. Birds not seen since that date.

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200^{x} S. of Shingle Inlet   Unringed pair. Blowout in the dunes. Territory taken up before April 24. 15 May. Scrape in plain sand 3 eggs Eggs taken by the 16 May. June 7. Scrape in plain sand on HWM. 1 egg Egg gone by 11 June.

21 June, Scrape in sand under marram on dune side 1 egg.
Egg gone by the 27 June. Birds not seen since.

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200^{x} N. of S.E. corner Old Law. $^{M}/_{O}$ $^{W}/_{B}$ ♂ + UR ♀   Territory taken up before April 24. The birds were often missing from the territory and moved about a lot, often seen on N.W. Old Law. After the above pair left, this pair moved further N. and layed. 300^{x} N. of S.E. corner Old Law. Scrape in sand covered by marram 1 July 20^{x} above HWM. 4 eggs Eggs predated by 27 July.

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10^{x} N.E. of Oil Drum, Grass bank, Budle Bay. $^{Y}/_{M}$ $^{Y}/_{W}$ ♂ + UR ♀
Territory taken up before May 27. May 31, scrape in sand, grass and seaweed 4 eggs Eggs hatched before June 27. 1 chick seen July 1 up Ross Back Sands. 3rd Bay S. of Wide Opens.

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400^{x} N.E. of Oil Drum, Grass bank, Budle Bay. $^{M}/_{W}$ $^{R}/_{G}$ ♀ + UR ♂
Territory taken up before May 27. May 31 Scrape in grass with shells 4 eggs. 1 egg taken 7 June. Rest of clutch taken before 11 June.

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<u>Snook Point</u> Y/M G/R + UR Territory taken up before April 26. No sign of nesting activity. Birds not seen on territory after 21 May.

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<u>200^x E. of Snook Point</u> Unringed pair. Territory taken up before May 6. Scrape in sand, with bits of shell. <u>1 egg</u> 2ft. above HWM. Egg taken by 11 May. 25 May - scrape in sand, in marram cover on bank. 3^x above HWM. <u>2 eggs</u>. Eggs taken before May 28. Birds last seen 11 July.

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<u>E. of Crate 500^x E. of Snook Point</u> Unringed Pair. Territory taken up before May 14. No sign of nesting up to end of May. Birds then moved. Unringed birds seen at same point on 26 June.

11 July - unringed pair present 800^x further E. along beach, on W. side of high dune before life boat station. A great deal of agitation from parents - chicks suspected. 16 July - 2 chicks sighted. 18 July - 1 chick caught.

<u>Chick ringed</u>

BV86119 M/R/O lft O/W rt Nill 13mm Wing 77mm Wt. 45gms

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<u>200^x E. of Crate</u> G/M R only ♀ + UR ♂ Territory taken up before April 26. Scrape present 6 May. Sand and shell 10' above HWM No sign of eggs. Nothing more seen. Birds last seen present 16 July.

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100^{x} W. of high dune (200^{x} W. of life boat station). R/Y R/M ♂ + UR ♀ Territory taken up before May 11. Scrape in sand and pebbles and bits of shell 1 egg Egg taken before May 14. Birds moved territory to slacks by life boat station. 11 July - a great deal of agitation from parents - chick suspected. 16 July - 1 chick seen on sands. 18 July 1 chick caught.

Chick Ringed

BV86118 M/R/O lft O/B rt Bill 12.8mm Wing 58mm Wt. 36gms

1^{o}/2 2^{o}/3

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Area of beach from lift boat station to West Tape End. M/W B/O ♂ seen several times but no territoriality seen. 6 May 11 July 16 July

M/W G/O (combination not used) seen twice 14 May 16 July.

R/M O/W ♂ also seen once 11July

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West Tape End M/O G/B ♂ + UR ♀ Territory ? taken up before 11 May. No sign of nesting activity. Birds last seen 16 July

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200^{x} E. of West Tape End Y/G Y/M ♂ + UR ♀ Territory taken up before May 8. 11 May Scrape in sand with shell, under a branch on beach. 4 eggs Eggs taken before 21 May (3 taken, 1 deserted). 13 June Scrape in sand in marram cover. 20^{x} E. of last clutch. 4 eggs. Eggs taken before June 23. Birds last seen July 11.

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<u>East End of Tape</u> 4 pairs of unringed birds. 1st Territories taken up before May 6.

6 May. Scrape in pebbles and bits of shell 100^{x} from E.T.E. <u>1 egg</u>
Egg taken before 11 May.

Scrape in sand and pebbles <u>1 egg</u> 14 May. Gone by 21 May.

Scrape in sand and pebbles <u>2 eggs</u> 21 May. <u>3 eggs</u> 25 May <u>4 eggs</u> 28 May. Eggs taken by June 23.

Scrape in pebbles and shell <u>2 eggs</u> 23 June <u>4 eggs</u> 26 June.
2 eggs taken before 11 July 2 eggs gone 16 July.

Scrape in pebbles and shell <u>4 eggs</u> 18 July.

Reports of clutch on shingle ridge behind beach, early July.

4 pairs still present 11 July All above scrapes within 50' .

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<u>Grass area nest to Snook House road, South Snook.</u> M left only ♂ + UR ♀ Territory taken up before April 29. Territory switched to north shore May 14. Seen ar various places along north shore. 30 June Scrape in sand in marram cover on bank. <u>4 eggs</u> Eggs taken by crows July 21.

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<u>600^{x} S. of Power Cable Sign, Primrose Bank</u> Unringed pair. Territory taken up before 7 May. 16 July - e juveniles seen accompanied by parents.

<u>500^{x} of Power Cable Sign, Primrose Bank</u> $^{W}/_{M}$ $^{R}/_{W}$ ♂ + UR ♀
Territory taken up before May 7. No nesting seen. Reports of possible brood mid-June. Seen on north shore 16 July.

<u>400^{x} S. of Power Cable Sign, Primrose Bank.</u> Unringed pair. Territory taken up before May 7. No sign of nesting activity. Last seen 8 June. only 2 pairs present on Primrose bank of 23 June.

<u>Chare Ends</u>   Reports of nesting attempt in plough fields behind shore. No sign found. Birds seen at Chare Ends.

$^{R}/_{M}\ ^{O}/_{W}$ + $^{O}/_{M}\ ^{R}/_{B}$ + 2 UR   May 11

$^{R}/_{M}$ G only ♀ + UR ♂ + UR   May 25)
) Seen off north shore 11 July
$^{R}/_{M}$ G only ♀ + UR ♂   June 5)

$^{O}/_{M}\ ^{W}/_{Y}$ ♂   June 23

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<u>Sangham Bay, Pebbles E. end</u> $^{W}/_{R}\ ^{M}/_{W}$ ♀ + UR ♂   Territory taken up before April 26. Scrape in pebbles with shell <u>1 egg</u> 21 May <u>3 eggs</u> 25 May 30 May - eggs taken - 2 deserted. Pair left site.

23 June birds return - begin new scrapes 11 July Scrape - sand 2^{x} above HWM <u>4 eggs</u>.

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<u>Sandham Bay, Pebbles E. end</u>   Unringed pair. Took over above territory before 26 May. 30 May <u>4 eggs</u> Scrape in sand under marram roots on bank. Eggs taken before June 23. Birds left site.

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<u>Sandham Bay, Centre Sand</u>   Unringed pair. Territory taken up before April 26. 21 May Scrape - plain sand. <u>4 eggs</u> Eggs taken before June 8

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<u>500^x W. of Sandham Bay - Bove patch</u> Unringed pair. Territory taken up before May 30. Scrape - depression in soil and bits of shell.

<u>1 egg</u> Egg taken before June 2. June 26 Scrape - depression in soil

<u>4 eggs</u> 11 July eggs gone - parents very agitated - suspect chicks. 15 July chicks seen W. end Sandham Bay (4). July 23 3 chicks seen towards E. end of sand. 2 captured.

(1) Wt. 26gms (2) Wt. 32gms

$1^o/1$ 1^o/cov 1 $2^o/1$ 2^ocov/1 $1^o/2$ 1^ocov/2 $2^o/2$ 2^ocov/2

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APPENDIX 3

The results of the invertebrate sampling around Old Law.

S = Spartina Marsh

E = East Seabeach

F = Feeding Area on West Old Law

The figures give the number per sample (approximately 80 cm^2) and the figures in parentheses are the number per m^2.

Any samples not given contained no invertebrates.

(Paired
(
(Samples

Appendix 3

Site	Hydrobia	Macoma	Nereis	Nereids	Nephtis	Scoloplos	Tube Building Polychaetes	Corophium	Arenicola	Talitrids	Euridice	Cardium
(S1	31 (3947)	- -	8 (1019)	7 (891)	3 (382)	-	150 (19,099)	2 (255)	-	-	-	-
(S2	27 (3438)	-	10 (1273)	13 (1655)	3 (382)	-	85 (10,823)	9 (1146)	-	-	-	-
(S3	20 (2546)	2 (255)	3 (382)	2 (255)	5 (637)	2 (255)	30 (6366)	4 (509)	-	-	-	-
(S4	18 (2292)	3 (382)	1 (127)	12 (1528)	1 (127)	1 (127)	25 (3183)	16 (2037)	-	-	-	-
(S5	14 (1782)	7 (891)	1 (127)	7 (891)	1 (127)	1 (127)	180 (22,918)	1 (127)	-	-	-	-
(S6	30 (3820)	8 (1019)	1 (127)	4 (509)	1 (127)	2 (255)	45 (5730)	5 (637)	-	-	-	-
(S7	15 (1910)	8 (1019)	2 (255)	6 (764)	2 (255)	1 (127)	165 (21,008)	8 (1019)	-	-	-	-
(S8	6 (764)	8 (1019)	1 (127)	7 (891)	2 (255)	4 (509)	360 (45,837)	19 (2419)	-	-	-	-
(S9	14 (891)	2 (255)	2 (255)	11 (1401)	-	4 (509)	300 (38,197)	4 (509)	-	-	-	-
(10)	14 (1783)	2 (255)	2 (255)	14 (1783)	-	10 (1273)	450 (57,296)	7 (891)	-	-	-	-

Site	Hydrobia	Macoma	Nereis	Nereids	Nephtis	Scoloplos	Tube Building Polychaetes	Corophium	Arenicola	Talitrids	Euridice	Cardium
(S11	2 (255)	-	1 (127)	6 (764)	-	6 (764)	240 (30,558)	-	-	-	-	-
(												
(12	8 (1019)	1 (127)	-	16 (2037)	-	5 (637)	320 (40,744)	-	-	-	-	-
(S13	9 (1146)	2 (255)	-	12 (1528)	-	1 (127)	210 (26,738)	-	-	-	-	-
(												
(14	3 (382)	-	-	13 (1655)	-	2 (255)	340 (43,290)	-	-	-	-	-
(S15	-	-	-	11 (1401)	-	2 (255)	300 (38,197)	1 (127)	-	-	-	-
(												
(S16	-	-	-	4 (509)	-	1 (127)	170 (21,645)	-	-	-	-	-
(S17	-	-	-	3 (382)	-	1 (127)	80 (10,186)	-	-	-	-	-
(												
(S18	-	-	-	7 (891)	-	4 (509)	160 (20,372)	-	-	-	-	-
(E17	-	-	-	-	-	-	-	-	-	-	1 (127)	1 (127)
(												
(E18	-	-	-	-	-	-	-	-	-	-	-	1 (127)

Site	Hydrobia	Macoma	Nereis	Nereids	Nephtis	Scoloplos	Tube Building Polychaetes	Corophium	Arenicola	Talitrids	Euridice	Cardium
(F1	-	-	-	2 (255)	1 (127)	-	40 (5093)	-	-	-	-	-
(F2	-	-	-	2 (255)	-	-	40 (5093)	-	2 (255)	-	-	-
(F3	-	-	-	5 (637)	-	3 (382)	20 (2546)	-	-	-	-	-
(F4	-	-	-	5 (637)	-	-	35 (4456)	-	2 (255)	-	-	-
(F5	-	-	-	2 (255)	-	-	10 (1273)	-	2 (255)	-	-	-
(F6	-	-	-	3 (382)	-	-	8 (1019)	-	4 (509)	-	-	-
(F7	-	-	-	5 (637)	-	-	15 (1910)	-	11 (1401)	-	-	-
(F8	-	-	-	5 (637)	-	-	20 (2546)	-	5 (637)	-	-	-
(F9	-	-	-	2 (255)	-	-	6 (746)	-	4 (509)	1 (127)	-	-
(F10	-	-	-	9 (1146)	-	-	13 (1655)	-	6 (764)	-	-	-

Site	Hydrobia	Macoma	Nereis	Nereids	Nephtis	Scoloplos	Tube Building Polychaetes	Corophium	Arenicola	Talitrids	Euridice	Cardium
(F11	-	-	-	3 (382)	-	-	30 (3820)	-	5 (637)	-	-	-
(F12	-	-	-	3 (382)	-	-	8 (1019)	-	2 (255)	-	-	-
(F13	-	-	-	3 (382)	-	-	-	-	-	-	-	-
(14	-	-	-	2 (255)	-	-	6 (764)	-	1 (127)	-	-	1 (127)
(F15	-	-	-	2 (255)	-	-	15 (1910)	-	1 (127)	-	1 (127)	-
(F16	-	-	-	2 (255)	-	-	20 (2564)	-	3 (382)	-	-	-
(F17	-	-	-	3 (382)	-	-	2 (255)	-	1 (127)	1 (127)	-	-
(F18	-	-	-	6 (764)	-	-	20 (2546)	-	-	-	-	-

Nos. represent nos. per sample Nos. in parentheses are nos. per m^2

S = Spartina marsh E = East Old Law F = Feeding Area West Old Law

(Paired
(Samples

APPENDIX 4

Feeding data

Total = Total feeding movements over the whole watch

Total C = Total number of catches

Total P = Total number of probes

1 min = Feeding rates per minute

5 min = Feeding rates per 5 minutes.

Watch A   MUDFLATS - S.W. OLD LAW.   12 May.

M only Y/R ♂   Start 78 mins after high water   Length 4 min 45 sec

Total

Total = 62   Total C = 4   Total P = 15   %C = 6.45   % P = 24.19

Mean = 13.05   Mean C = 0.84   Mean P = 3.16

1 min

Total	14	C	1	P	0
	13		1		4
	15		2		4
	15		0		3

Watch B   SAND - N.W. OLD LAW   12 May

B/M B/G ♂   Start 123 min after high water   Length 13 min 50 sec

Total

Total = 188   Total C = 9   Total P = 20   %C = 4.79   % P = 10.6

Mean = 13.59   Mean C = 0.65   Mean P = 1.45

1 min

Total:	9	19	11	Total C :	0	1	0	Total P :	1	1	2
	3	11	5		1	2	0		0	2	1
	17	14	14		1	2	1		2	4	0
	26	14			0	1			0	3	
	13	8			0	0			2	0	

5 min.

A)	Total	73	Mean = 14.6	A) C	2	Mean = 0.4	A) P	5	Mean = 1
B)		139	Mean = 27.8	B)	6	Mean = 1.2	B)	10	Mean = 2

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Contd. 146 mins after high water Length 6 min 05 sec.

Total

Total = 31 Total C = 1 Total P = 3 %C = 3.2 %P = 0.97

Mean = 5.1 Mean C = 0.16 Mean P = 0.49

1 min

Total	6	2	C 1	0	P 1	0
	10		0		1	
	4		0		0	
	3		0		0	
	3		0		1	

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Contd. 160 mins after high water Length 13 min

Total

Total = 157 Total C = 11 Total P = 30 %C = 7 %P = 19.1

Mean = 12.08 Mean C = 0.85 Mean P = 2.31

1 min

Total	19	11	9	C	2	0	1	P	12	0	3
	17	15	12		1	0	1		1	0	0
	15	7	5		2	0	0		3	2	1
	11	9			2	0			2	1	
	15	12			1	1			4	1	

5 min

A)	Total	77	Mean = 15.4	A) C	8	Mean = 1.6	A) P	22	Mean = 4.4
B)		54	Mean = 10.8	B)	1	Mean = 0.2	B)	4	Mean = 0.8

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Watch C SAND S.W. POINY OLD LAW 16 May

M only Y/R ♂ Start 179 mins before high water Length 6 min 10 sec

Total

Total = 121 Total C = 12 Total P = 2 %C 2 9.92 %P = 1.65

Mean = 19.61 Mean C = 1.94 Mean P = 0.32

1 min

Total	35	24	C	3	1	P	0	1
	16			2			0	
	10			0			0	
	7			1			0	
	23			5			1	

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Watch D SAND N.W. Old Law 16 May

B/M B/G ♂ Start 90 mins before high water Length 9 min

Total

Total = 13 Total C = 0 Total P = 0

Mean = 1.4

1 min

Total	2	0
	2	0
	3	0
	2	1
	3	

5 min

A) Total = 12 Mean = 2.4

Watch 1 SAND 1st BAY BEFORE WIDE OPENS 24 MAY

Y/M G/M ♀ Start 58 mins before high water Length 10 min

Total

Total = 217 Total C = 3 Total P = 0 %C = 1.38

Mean = 21.7 Mean C = 0.3

1 min

Total	30	35	C	0	0
	23	23		0	0
	25	18		2	0
	18	3		1	0
	28	13		0	0

5 min

A)	Total	124	Mean = 24.8	A)	C	3	Mean = 0.6
B)		92	18.4	B)		0	0

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Watch 2 SAND 1st MAY BEFORE WIDE OPENS 26 May

UR ♂ Start 19 mins before high water Length 16 min

Total

Total = 204 Total C = 5 Total P = 0 %C = 2.45

Mean = 12.75 Mean C = 0.31

1 min

Total	14	12	14	11	Total C	3	0	0	0
	14	6	15			1	1	0	
	21	9	11			0	0	0	
	16	9	9			0	0	0	
	6	12	24			0	0	0	

5 min

A)	Total	71	Mean = 14.2	A)	C	4	Mean = 0.8
B)		48	9.6	B)		1	0.2
C)		73	14.6	C)		0	0

Watch 3 SAND 1st BAY BEFORE WIDE OPENS 26 May

UR ♂ Start 1 min after high water Length 9 min 20 sec

Total

Total = 103 Total C = 0 Total P = 1 %P = 067

Mean = 11.04 Mean P = 0.11

1 min

Total	13	16	P	0	0
	13	11		0	1
	9	7		0	0
	10	11		0	0
	12			0	

5 min

A) Total 57 Mean = 11.4

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Watch 4 1st BAY BEFORE WIDE OPENS 26 May Overcast

Waters edge UR♂(South Bay) 11 mins after high water Length 17 min

Total

Total 153 Total C 6 Total P 12

Mean = 9 Mean = 0.35 Mean 2 0.70

1 min

Total	14	8	10	1	C	0	0	0	0	P	1	2	3	0
	24	10	10	2		0	0	1	1		0	1	1	0
	12	16	2			0	0	2			2	0	0	
	7	10	4			0	1	0			0	0	1	
	9	5	8			0	1	0			0	1	0	

5 min

Total	A)	66	Mean	13.2	C	A)	0	Mean	0	P	A)	3	Mean	0.6
	B)	49		9.8		B)	2		0.4		B)	3		0.6
	C)	34		6.8		C)	3		0.6		C)	4		0.8

Watch 5 1st BAY S. FO WIDE OPENS 27 May Rain

SAND UR♂ (North Bay) 212 mins before high tide Length 5 min.

Total

Total 30 Mean = 6

1 min

12	7	4
4	3	

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Watch 6 500[x] N. OF S.W. POINT OLD LAW 27 MAY RAIN

SPARTINA MARSH UR ♂ 227 mins before high water Length 40 min

Total

Total 260 Total C 57 Total P 19 %C = 18.08 %P = 7.3

Mean = 6.5 Mean C = 1.175 Mean P = 4.75

1 min

Total	12	11	9	9	0	0	4	C	5	3	2	1	0	0	3	0
	0	10	5	9	0	9	7		0	2	0	0	0	0	1	0
	0	11	11	1	5	12	2		0	2	1	0	0	1	0	1
	14	11	8	0	15	11	1		7	1	2	0	1	1	0	0
	10	10	12	0	9	11	1		1	3	3	0	1	5	0	0

P	0	0	0	3	0	0	0	0
	0	0	0	3	0	2	1	0
	0	0	1	1	0	1	0	0
	0	1	1	0	0	0	1	0
	0	1	1	0	1	0	1	0

5 min

Total	A)	36	Mean	7.2	C	A)	13	Mean 2.6	P	A)	0	Mean 0
	B)	53		10.6		B)	11	2.2		B)	2	0.4
	C)	45		9.0		C)	8	1.6		C)	3	0.6
	D)	19		3.8		D)	1	0.2		D)	7	1.4

Total	E)	29	Mean	5.8	C	E)	2	Mean 0.4	P	E)	1	Mean 0.2
	F)	43		8.6		F)	7	1.4		F)	3	0.6
	G)	20		4.0		G)	4	0.8		G)	3	0.6
	H)	15		3.0		H)	1	0.2		H)	0	0

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Watch 7   500^x N.OF S.W. POINT OLD LAW   27 MAY   RAIN

SAND UR ♀   164 mins before high water   Length 13 min

Total

Total 228   Total C 2   Total P 4   %C = 0.88   %P = 1.75

Mean = 17.54   Mean C = 0.15   Mean P = 0.31

1 min

Total	7	21	26	C	0	1	0	P	0	2	0
	4	21	22		0	0	0		0	2	0
	0	30	28		0	0	0		0	0	0
	4	28			0	0			0	0	
	9	28			1	0			0	0	

5 min

Total	A)	24	Mean	4.8	C	A)	1	Mean 0.2	P	A)	0	Mean 0
	B)	128		25.6		B)	1	0.2		B)	4	0.8

Probably this ♀ was picking up grit!

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Watch 8   JUTTING DUNE W. OLD LAW   27 MAY   RAIN

SAND UR ♂   129 mins before high water   Length 7 min

Total

Total 120   Mean = 17.14

1 min

Total	20	4
	20	10
	27	
	29	
	10	

5 Min

Total A) 106   Mean 21.2

Watch 9   100^x S. OF W. PINNACLE N.W. OLD LAW   1 JUNE   SUNNY

SAND   B/M G/B ♀   149 mins before high water   Length 6 min 30 sec

Total

Total 72   Total C 3   Total P 8   %C = 4.17   %P = 11.11

Mean = 11.08   Mean C = 0.46   Mean P = 1.23

1 min

Total	15	14	C	0	2	P	3	2
	15	4		0	0		0	0
	9			0			3	
	8			0			0	
	7			1			0	

5 min

Total A) 54   Mean 10.8   C A)1 Mean 0.2   P A) 6 Mean 1.2

Watch 10   100^x N. OF S.W. POINT OLD LAW   3 JUNE   FAIR

SAND/MUD   M only Y/R ♂   371 mins after high water   Length 6 min 40 sec

Total

Total 70   Total P 1   %P 1.42

Mean = 10.49   Mean P = 0.15

1 min

Total	15	9	P	0	0
	13			1	
	15			0	
	6			0	
	(3)			0	
	9				

5 min

Total A) 58   Mean = 11.6   P A) 1   Mean = 0.2

Watch 11 S.W. POINT OLD LAW 10 JUNE SUNNY

SAND/MUD M only Y/R ♂ 121 mins after high water Length 13 min 40 sec (see sheet for timing)

Total

Total 139 Total C 9 Total P 6 %C = 6.4 %P = 4.31

Mean = 10.17 Mean C = 0.66 Mean P = 0.44

1 min

Total	13	0	16	C	0	1	0	P	2	2	0
	16	18	18		0	3	0		0	0	1
	18	5	10		0	0	1		0	0	1
	12	2			3	0			0	0	
	1	1			0	1			0	0	
		6									

5 min

Total	A) 60	Mean = 12	C,	A) 3	Mean = 0.6	P	A) 2	Mean = 0.4
	B) 32	2 6.4		B) 5	= 1.0		B) 2	= 0.4

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Watch 12 S.W. POINT OLD LAW 10 JUNE SUNNY

SAND/MUD 168 mins after high water UR ♀ Length 6 min

Total

Total 117 Mean = 19.5

1 min

Total	24	1
	27	
	27	
	14	
	23	

5 min Total A) 115 Mean = 23

Watch 12 (A)   S.W. POINT   OLD LAW   10 JUNE   SUNNY

SAND/MUD   M only   Y/R ♂   180 mins after high water   Length 5 min

Total

Total 52   Total C 1   Total P 1   %C = 1.92   %P = 1.92

Mean = 10.4   Mean C = 0.2   Mean P = 0.2

1 min

Total	10
	8
	6
	15
	13

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Watch 13   S.W. POINT   OLD LAW   11 JUNE   SUNNY

SAND   UR ♀   64 mins after high water (split times)   Length 18 min

Total

Total 471   Total C 1   Total P 11   %C = 0.21   %P = 2.33

Mean = 26.16   Mean C = 0.06   Mean P = 0.61

1 min

Total	30	29	27	26	P	2	1	0	1
	22	30	31	21		4	0	0	0
	22	24	29	16		0	0	0	0
	26	28	29			0	1	1	
	31	25	25			1	0	0	

5 min

Total	A)	131	Mean 26.2	P	A)	5	Mean 1.0
	B)	137	27.4		B)	2	0.4
	C)	141	28.2		C)	1	0.2

Watch 14 200^{x} N. OF S.W. POINT OLD LAW 11 JUNE SUNNY

SAND UR ♀ 116 mins after high water Length 28 min

Total

Total 623 Total C 3 %C = 0.48

Mean = 22.25 Mean C = 0.11

1 min

Total	15	27	23	22	20	10	C	3	0	0	0	0	0
	16	23	25	27	17	7		0	0	0	0	0	0
	16	25	27	26	28	7		0	0	0	0	0	0
	18	28	43	28	23			0	0	0	0	0	
	30	23	18	27	21			0	0	0	0	0	

5 min

Total	A)	95	Mean = 19	C	A) 3	Mean = 0.6
	B)	126	Mean = 25.2		B) 0	Mean = 0
	C)	136	Mean = 27.2			
	D)	130	Mean = 26.0			
	E)	109	Mean = 21.8			

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Watch 15 POINT N.W. OLD LAW 27 JUNE SUNNY

SAND UR ♂ 71 mins after high water Length 5 min 35 sec
(redecing tide edge)

Total

Total 101 Total C 2 Total P 11 %C = 1.98 %P = 10.89

Mean = 18.10 Mean = 0.36 Mean P = 1.97

1 min

Total	19	(12)	C	1	P	0
	21			1		2
	25			0		5
	11			0		2
	13			0		2

5 min

Total A) 89

Mean = 17.8

C A) 2

Mean = 0.4

Watch 16. FEEDING AREA (N.W. OLD LAW) 27 JUNE SUNNY

SAND AT TIDE EDGE UR ♂ 78 mins after high water Length 45 min 45 sec

Total

Total 816 Total C 3 Total P 38 %C = 0.37 %P = 4.66

Mean = 17.45 Mean C = 0.06 Mean P = 0.81

1 min

Total	20	15	12	12	10	16	26	28	10	
	22	11	21	9	20	19	24	28	10	17
	19	10	19	13	23	18	17	18	18	(12)
	18	18	12	11	19	33	15	18	16	
	22	18	21	14	22	27	29	20	15	
Total C	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	1	0	(0)
	0	0	0	0	0	0	0	1	0	
	0	0	0	0	0	0	0	0	0	
	0	0	0	0	0	1	0	0	0	
Total P	2	0	1	0	0	1	0	0	0	0
	2	0	1	1	1	0	2	5	1	(0)
	1	0	0	0	0	0	0	8	3	
	1	0	0	0	1	1	0	0	0	
	1	1	0	0	1	0	0	2	1	

5 min

Total	A)	101	Mean = 20.2	C	A)	0	Mean = 0	P	A)	7	Mean = 1.4
	B)	72	12.4		B)	0	0		B)	1	0.2
	C)	85	17.0		C)	0	0		C)	2	0.4
	D)	59	11.8		D)	0	0		D)	1	0.2
	E)	94	18.8		E)	0	0		E)	3	0.6
	F)	113	22.6		F)	1	0.2		F)	2	0.4
	G)	111	22.2		G)	0	0		G)	2	0.4
	H)	112	13.8		H)	2	0.4		H)	15	3.0
	I)	69	13.8		I)	0	0		I)	5	1.0

Watch 17 S.W. POINT OLD LAW 28 June FAIR

SAND M only Y/R ♂ 38 mins after high water Length 14 min

Total

Total 102 Mean = 7.29

1 min

Total	6	0	14
	0	0	9
	11	17	20
	7	9	6
	0	2	

5 min

Total	A)	24	Mean = 4.8
	B)	28	5.6

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Watch 18 S.W. POINT OLD LAW 15 JULY OVERCAST

SAND M only Y/R ♂ 233 mins before high water Length 4 min 30 sex (split time)

Total

Total 46 Mean = 10.22

1 min

Total 13
13
6
11
(3)

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Watch 19 SPARTINA MARSH, W. OLD LAW 20 JULY OVERCAST

MUD UR ♂ 128 mins after high water Length 10 min 30 sec (split time)

Total

Total 88 Total C 11 %C = 12.5

Mean = 8.38 Mean C = 1.05

1 min						5 min	
Total	9	17	C	1	1	Total	A) 41
	(1)	11		(0)	1	Mean = 8.2	
	(4)	7		(0)	2		
	9	7		4	1	C	A) 6
	12			0		Mean = 1.2	
	6			1			
	5			0			

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Watch 20 FEEDING AREA N.W. OLD LAW 20 July OVERCAST

SAND UR ♂ 258 mins after high water Length 4 min 20 sec

Total

Total 66 Total P 16 %P = 24.24

Mean = 15.24 Mean P = 3.70

1 min

Total	14	P	7
	12		1
	21		4
	16		4
	(3)		(0)

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Watch 21 FEEDING AREA N.W. OLD LAW 20 JULY OVERCAST

SAND UR ♂ 204 mins after high water Length 10 mins

Total

Total 141 Total C 1 Total P 17 %C 0.71 %P 12.06

Mean 14.1 Mean C 0.1 Mean P 1.7

1 min

Total	20	9	C	0	0	P	6	0
	18	16		0	0		1	0
	10	9		0	0		1	0
	15	14		1	0		3	0
	13	17		0	0		1	5

5 min

Total	A)	76	Mean	15.2	C	A)	1	Mean	0.2	P	A)	12	Mean	2.4
	B)	65		13.0		B)	0		0.0		B)	5		1.0

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Watch 22 FEEDING AREA, N.W. OLD LAW 20 JULY OVERCAST

SAND R/M R/O ♂ 218 mins after high water Length 33 min 20 sec (split time)

Total

Total 592 Total P 3 %P 0.51

Mean 17.76 Mean P 0.09

1 min

Total	16	19	(6)	21	19	10	P	0	0	(0)	0	0	0	0
	16	16	18	19	17	6		1	0	0	0	0	0	0
	17	15	18	19	18	14		0	0	0	0	1	0	0
	17	19	15	16	24			0	0	0	0	0	0	
	14	20	18	24	17			0	0	0	1	0	0	
			21							0				

5 min

Total	A)	80	Mean	16.0	P	A)	1	Mean	0.2
	B)	89		17.8		B)	0		0.0
	C)	93		18.6		C)	0		0.0
	D)	112		22.4		D)	1		0.2
	E)	87		17.6		E)	1		0.2
	F)	95		19.0		F)	0		0.0

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Watch 23 FEEDING AREA, N.W. OLD LAW 20 July OVERCAST

SAND UR Juvenile 258 mins after high water Length 11 min (split time)

Total

Total 124 Total P 9 %P = 7.26

Mean = 11.27 Mean P = 0.82

1 min

Total	16	14	2	P	0	0	0
	13	16			0	0	
	14	12			1	1	
	16	11			0	2	
	7	3			4	1	

5 min

Total	A) 66	Mean =	13.2	P	A) 5	Mean =	1.0
	B) 56		11.2		B) 4		0.8

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Watch 24 S.W. POINT OLD LAW 21 July SHOWERS

MUD UR ♀ 107 mins after high water Length 4 min 30 sec (split time)

Total

Total 54 Total C 5 %C 0.11

Mean 12.0 Mean C 1.33

1 min

Total	7	C 1
	19	3
	11	1
	(2)	(1)
	15	0

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Watch 25 FEEDING AREA N.W. OLD LAW 21 July SHOWERS

SAND UR ♂ 215 mins after high water Length 2 min 30 sec

Total

Total 27 Mean = 10.8

1 min

Total	13
	13
	(1)

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Watch 26 FEEDING AREA N.W. OLD LAW 21 July SHOWERS

SAND UR♂ 218 mins after high water Length 12 min

Total 177 Mean 14.75

1 min

Total	18	11	14
	21	15	9
	15	22	
	13	13	
	9	17	

5 min

Total	A)	76	Mean	15.2
	B)	78		15.6

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Watch 27 N.W. OLD LAW 21 July SHOWERS

SAND UR Juvenile 235 mins after high water Length 14 min

Total

Total 238 Total C 1 %C 0.42

Mean 17.0 Mean C 0.07

1 min

Total	23	24	12	C	0	0	1
	22	20	20		0	0	0
	22	8	8		0	0	0
	21	16			0	0	
	24	18			0	0	

5 min

A) 112 Mean = 26.4

B) 86 Mean = 17.2

Watch 28 N.W. OLD LAW 21 July SHOWERS

SAND B/G B/M ♂ 252 mins after high water Length 10min

Total

Total 207 Mean = 20.7

1 min

Total	21	21
	14	22
	19	24
	18	13
	28	27

5 min

Total	A)	100	Mean	= 20.0
	B)	107		21.4

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Watch 29 N.W. OLD LAW 21 July SHOWERS

SAND R/M G only ♂ 265 mins after high water Length 11 min

Total

Total 28.3 Total P 1 Total C 2 %P 0.35 %C 0.71

Mean = 25.73 Mean P = 0.09 Mean C = 0.18

1 min

Total	17	27	2	C	0	0	0	P	0	1	0
	24	32			0	0			0	0	
	25	30			0	0			0	0	
	30	35			1	0			0	0	
	27	34			0	1			0	0	

5 min

Total	A)	123	Mean	= 24.6	C	A)	1	Mean = 0.2	P	A)	0	Mean	0.0
	B)	160		32.0		B)	1	0.2		B)	1		0.2

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ACKNOWLEDGEMENTS

My grateful thanks to my supervisor Dr. P.R. Evans for help and encouragement, to Mr. M. Pienkowski and Mr. P.A. Snell for allowing my use of their data, and to Mr. M. Pienkowski and Dr. J.C. Coulson for helpful discussion and criticism.