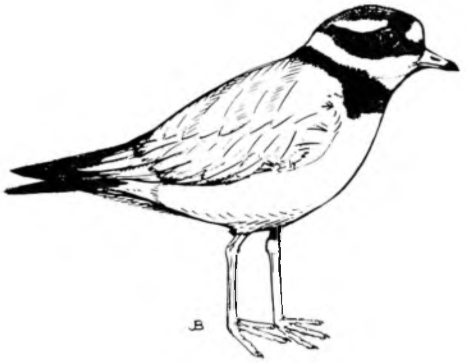
Limitation by nesting habitat of the density of breeding Ringed Plovers *Charadrius hiaticula*: a natural experiment.



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Some previously stony nesting areas of Ringed Plovers at Lindisfarne, Northumberland, became covered by sand over about ten years whilst feeding areas remained at least as suitable. Breeding numbers declined in changed areas but remained more constant in others. Densities in new sandy areas became similar to those sandy throughout the period. This is discussed in relation to adaptations to breeding habitat, and with respect to conservation implications.

Although bird populations have become adapted to particular habitats (e.g. Fuller 1982), we are not always certain as to the nature of the adaptation, i.e. which, if any, features of the environment are critical to these populations.

Markedly different habitat preferences can occur between wader species in the same general area, e.g. northeast Greenland (Ferns 1978), and the Outer Hebrides (Fuller *et al.* 1986). Two broad hypotheses have been advanced to account for habitat selection in breeding waders. Ferns (1978, 1983) attributed such habitat differences to specializations to particular prey or feeding methods, thereby minimising competition, whilst Pienkowski (1984a) argued that habitat specializations enabled wader eggs and/ or plumages to evolve markings closely matching the habitat, and thus reduce egg predation. Similarly Holmes (1970) related geographical variation in the density of territories of breeding Dunlins *Calidris alpina* in Alaska to variations in food density, whilst Pienkowski (1984a) considered that such variations in Ringed Plovers *Charadrius hiaticula* in Britain and Greenland could be related to the degree of match of appearance between eggs and habitat: the worse the match the more the birds spaced out their territories and nests.

Both food-supply and nest-site hypoheses may hold true for different populations or in different environments. Indeed, this is clearly the case for example in various raptors in which densities may be related either to food-supply or nest-site availability (Newton 1979). A problem in distinguishing between such hypotheses for waterfowl is that conditions often co-vary amongst sites in such ways that the expectations of both models run parallel. However, a "natural experiment" occurring over decades at Lindisfarne National Nature Reserve, northeast England, was documented from 1973. The major change was a progressive covering of much of the previously stony areas of shore by deep sand, so that nesting habitat of Ringed Plovers was modified far more than was feeding habitat. This paper describes the changes both in habitats and the densities of breeding birds which took place.

We argue that this case provides an example in which local breeding population size and distribution varies with the extent of nesting (as opposed to feeding) habitat. In some previous studies, comparable examples have related to a shortage of nest-sites, such as trees or holes. In the present case of a ground-nesting species, the limitation appears to relate to the extent and degree of suitability of habitat in which to hide a camouflaged nest.

Methods

Detailed studies of Ringed Plovers were made at Lindisfarne from 1974 to 1976. Methods are described by Pienkowski (1983, 1984a,b). After the detailed study, observations in later years were more sporadic until the extent and nature of the changes were realised.

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The study area and the habitat changes

Lindisfarne NNR is an area of tidal sand and mud-flats with associated dunes lying between Holy Island and the mainland of Northumberland. Ringed Plovers defend breeding territories, which include the nest-sites along the shores and adjacent areas. Some pairs feed mainly within their territories but non-territorial feeding areas are also used to different extents (Pienkowski 1984a).

Nesting areas

The principle nesting habitats for Ringed Plovers at Lindisfarne are areas of gravel (where territories and nests may be closely packed) and of sand (where pairs tend to be more widely spaced). Other nesting habitats used include saltmarsh, fields and sand-dunes (Pienkowski 1984a).

In this section, the main nesting areas and the changes in them since 1973 are outlined; these are placed in the context of changes over a longer period. The changing physiography of the area and the locations mentioned below are shown in Figure 1.

Rig. This ridge of sand appears not to have changed systematically since 1974, but its level varies so that it is more liable to tidal or storm flooding in some years than in others. Rather more remains above normal spring high-water levels than indicated in Figure 1 (f).

Snook. Much of this area of sand dunes overlies shingle and solid rock. In 1974–76 the north shore supported a very high density of Ringed Plovers which nested mainly on an area of gravel about 3 m wide and above the level of normal high tides. This gravel area has been progressively covered by wind-blown sand, so that by 1984 almost the whole of the area was covered, in some places to a depth of over 2 m (Fig. 2). The previously eroding seaward side of the dune is now an area of sand deposition. The deposition of sand has pushed the normal high-water-mark up to about 25 m further seaward from the dunes on some northern and western parts of the Snook than ten years earlier. Just south of the western extremity of the Snook, cord-grass *Spartina* is establishing, also causing increased sand accumulation on the flats. Some gravel areas occur also in slacks within the dune area of the Snook, particularly near the north shore, and are used as nest-sites, but parts of these have also been covered by wind-blown sand.

Holy Island Links and shores. Rocky headlands, and two bays, with varied shore types, occur on the north side of Holy Island proper. To the south of these are areas of dunes and stony slacks raised on a rocky plateau. This area changed little during the period. Ringed Plovers nest in the slacks and on the shore at several places around the island proper.

Elwick shore. In 1974–75, Ringed Plovers nested on gravel patches on the shore between the sand-dunes and the *Spartina* marsh. By 1976 the gravel was covered by sand, with vegetation growth.

Old Law. This area has similarities in structure to the Snook, with Ringed Plovers nesting primarily on gravel, both on the shore and in dune slacks, but also on the more sandy beach, the latter particularly towards the south. Although considerable sand movement has occurred, much more gravel remains exposed than on the Snook.

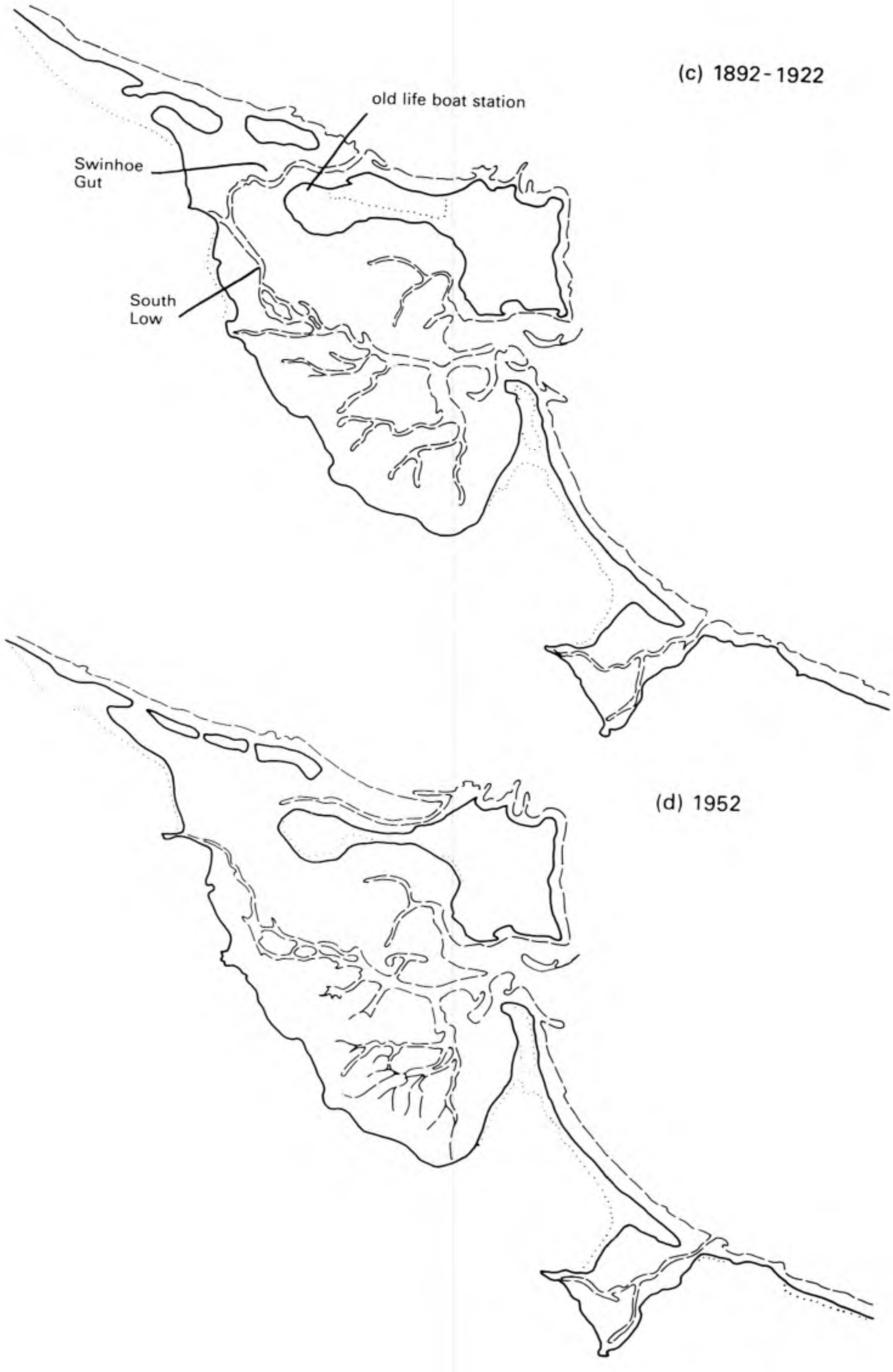
Ross Back Sands. Throughout the study period, this area consisted of sand-beach backed by dunes. However, the width of the bare sand area between the marram-covered dunes and the normal spring high-water-mark decreased from about 50 m in 1975 to about 10 m in many parts in 1984.

Budle Bay. The nesting area in Budle Bay includes a spit extending Ross Back Sands, and an area of saltmarsh on the northwestern side of the Bay. These areas appear to have changed rather little during the study period. The height of the spit varies but in some years rather more remains above normal spring high-water levels than is indicated in Figure 1 (f).

Longer term changes

It is clear that the changes outlined above form part of a longer-term pattern (Fig. 1). The most obvious changes are in the course of the Swinhoe Gut. About 100 years ago, this branch of the South Low channel

Figure 1. Holy Island and its surroundings as mapped by (a) Captain Grenville Collins (1695); and the Ordnance Survey in (b) 1859–61, (c) 1892–1922, (d) 1952, (e) 1963–64 and (f) 1981–82.
--- low-water-mark; ___ high-water-mark; .... upper limit of open sand (where information available). Crown Copyright reserved on (c) to (f).


(c) 1892-1922
old life boat station
Swinhoe
Gut
South
Low
(d) 1952

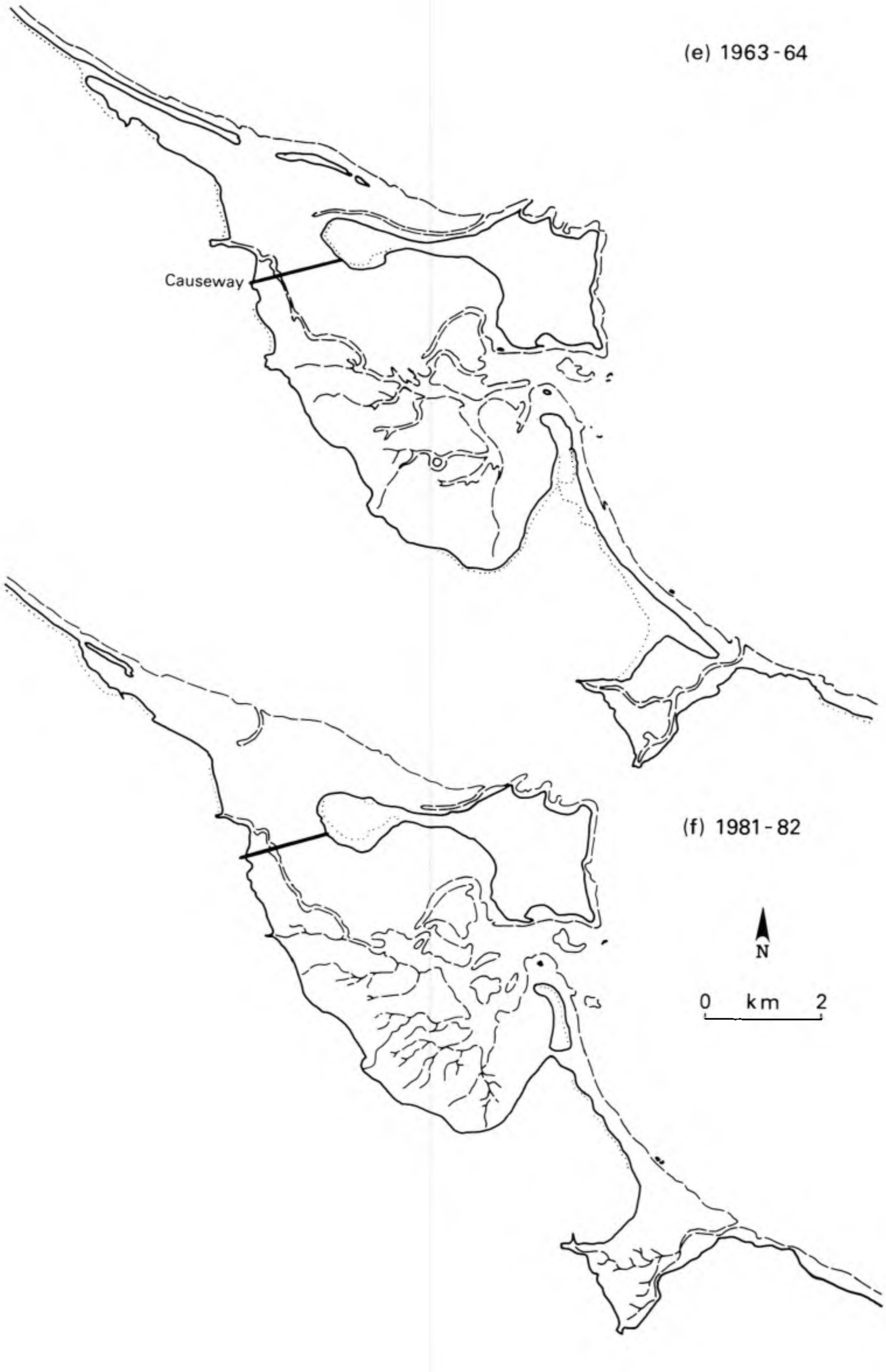

(e) 1963-64
Causeway
(f) 1981-82
N
0 km 2

Figure 2. View eastwards along the north shore of Holy Island Snook in (a) 1976, and (b) from the same position in 1983. The shingle nesting area of 1976 had been covered by up to 2 m of sand by 1983.

flowed northwards to the sea from its separation from the main South Low, near Beal Point. In later years, the Swinhoe Gut was deflected eastwards towards the north shore of the Snook. This appears to have had the effect of reducing the area of high sand beach north of the Snook but exposing shingle near the north shore of the Snook. In 1839 and 1869 lifeboat stations (the foundations of one of which are still present) were built on the Snook to allow direct access by the lifeboat to the dangerous shore of the Rig (Perry 1946). Later changes involved the progressive filling of the Swinhoe Gut from the west (the lifeboat station closing in the early 20th century). The Gut still required deep wading at low-water in the 1940s (Perry 1946) but this infilling has continued, to a noticeable extent during the ten years reported here. Meanwhile the northern inlet from the sea to the flats is again cutting back into the Rig (Fig. 1f).

It is not known what factors underlie the changes described above, nor whether the events form part of a long-term cycle. Maps made before 1860 are rather difficult to obtain, but Collins (1695) showed a northerly channel through the flats (Fig. 1a). Possibly the high frequency of westerly winds in the first half of the 20th century (e.g. pp. 50, 259 in Lamb 1982) may have been involved in the eastward movement of sand of the Rig and deflection of the Swinhoe Gut, with the subsequent increase in northerlies aiding its infilling along the North Shore of the Snook. Alternatively or additionally, hydraulic or other factors may be involved, or even factors relating to the building of the road causeway in the 1950s.

Numbers of breeding Ringed Plovers

The number of pairs of Ringed Plovers holding territory at Lindisfarne declined progressively from over 60 in 1974 to about 30 in 1984 (Table 1). The decline was not equal in all areas (Table 1). Numbers on the main area at the Snook and other sites such as Elwick and Ross declined whereas little or no decline was evident at Old Law, Budle and Holy Island proper.

No detailed counts of breeding pairs are available for earlier years, but high densities of nests on shingle were noted by Bolam (1912): at "Ross Links [which, in his usage, could include Old Law], as well as upon Holy Island [including the Snook], the birds breed in little scattered colonies, both on the shore, just above high-water-mark, and in stony depressions amongst the sandhills; and in such situations I have sometimes seen three or four nests, all containing eggs, within ten or twenty yards [approx. 10–20 m] of one another".

Feeding areas

As it was not known in advance that these changes in areas of habitat and numbers of birds would take place, no systematic programme was undertaken to investigate temporal changes in the densities of the invertebrates on which Ringed Plovers feed. However, sampling was undertaken for other studies on the main feeding area used by breeding Ringed Plovers at the Snook: the intertidal area on the North Shore. In all cases a common method was used, the substratum being sampled using

Table 1. Numbers of territorial pairs of Ringed Plovers at Lindisfarne National Nature Reserve and adjacent areas.

Site	Year							
	1974	75	76	77	79	81–82[1]	83	84
Rig	2	2	3	+	2	4	1	0
Snook	19	18	17	16	14	5+	9	5
Holy Island	5	5	5	4	5	–[2]	–	6
Teal Hole	1	1	1	1	0	–	–	0
Elwick	4	3	0	1	0	0	0	0
Old Law	13+	15	15	15	18	13	10+	12
Ross Back Sands	6	6	6	6	2	2	2	3
Budle Bay	3	3	3	2	2	–	–	4
SUBTOTAL[3]	53+	53	50	45+	43	–	–	30
Other areas	7	6	7	–	–	–	–	–
TOTAL	60+	59	57	–	–	–	–	–

[1] Data for northern sites gathered in 1981 and southern ones in 1982.
[2] – = no data
[3] Subtotals given for those years of complete count for the sites listed above the sub-total line.

10 x 10 cm corers, the sample then being washed through a sieve of square holes with sides of 0.9 mm. The animals retained were identified and counted.

The data from these samples must be viewed with caution because of the high variance often found in densities of intertidal invertebrates. Also, some species, e.g. the amphipod *Bathyporeia pelagica*, move on each tide so that densities vary greatly over short periods. However, several features are apparent (Fig. 3). First, all the common invertebrates present in 1973 remained present throughout the period. Second, no species appear to be consistently less abundant in the 1980s than in 1973. Third, the thin red polychaete worms *Scoloplos* and *Notomastus*, the principal prey items of Ringed Plovers at Lindisfarne (Pienkowski 1983), appear to have become more abundant over the period.

Ringed Plovers at the Snook feed also on flies (Diptera) associated with tide-wrack, and sandhoppers *Talitrus* above the high-water-mark. Because the changes in ground described above will have affected the sampling efficiency of the pitfall trapping method used above the high-water-mark, quantitative comparison is not possible between data collected in 1976 and 1984. However, observations and pitfall trapping in 1984 revealed these animals to be still extremely abundant, and wrack was washed up in the 1980s as often as it was in the 1970s.

Discussion

The timing of the decline in numbers of Ringed Plovers in the various parts of Lindisfarne NNR coincides closely with the changes in nesting habitat. The early cessation of use of the Elwick shore coincided with the covering of that area by sand and vegetation. The progressive decline at the Snook between 1974 and the early 1980s matches the increasing coverage of that area by wind-blown sand. The exact timing of the narrowing of the shore at Ross is not known (except that it was later than 1977), so the temporal relationship with the decline in Ringed Plovers here cannot be determined. Old Law, Budle Bay and sites on Holy Island proper have not been subject to such marked changes in nesting habitat, and Ringed Plover numbers have been maintained or declined only slightly.

The change in the shore of the Snook from predominantly shingle to entirely sand did not lead to a total loss of Ringed Plovers but a marked decrease in breeding density. This latter density was fairly similar to the more constant density on those areas sandy throughout the period, i.e. Ross Back Sands and Budle Bay, and much lower than the main remaining shingle area, i.e. part of Old Law. In summary, a decrease in nesting density (and numbers) occurred where a shingle surface was replaced by sand (Snook), and a decrease in numbers (but not in density) where the area of sand habitat was reduced (Ross). Numbers of pairs remained fairly constant where the nesting habitat was little changed, whether this was primarily gravel (Old Law), sand (Budle) or mixed (Holy Island proper).

These observations tend to support Pienkowski's (1984a) suggestion that Ringed Plovers in this situation adjust their nesting density to the match between egg camouflage and the ground: the match is very close on shingle, but on sand the birds nest much further apart. Increased inter-nest distance would make nest finding by predators more difficult. For example, Tinbergen *et al.* (1967) and Goransson *et al.* (1975) gave experimental evidence of higher incidences of nest-predation at higher nest site densities; and Pienkowski (1984a) presented evidence that predators tended to find on the same day Ringed Plovers nests which were close together. Note that this pattern relates to nesting birds which tend not to use communal defence against predators; for those that do so, other factors come into play in density relations.

An alternative explanation is that sand is an unsuitable nesting habitat for reasons other than as a background for the camouflage of eggs. Sand is mobile and nests on it could be vulnerable to burying. If this were the case, once an area became covered with sand, the number of nesting sites would immediately be reduced to those in sheltered locations. The reduction in numbers of breeding Ringed Plovers on Ross Back Sands following the narrowing of the shore there does not support this alternative idea, as the availability of sheltered localities, being related mainly to length of shore, would not have decreased with narrowing of the shore. The relative

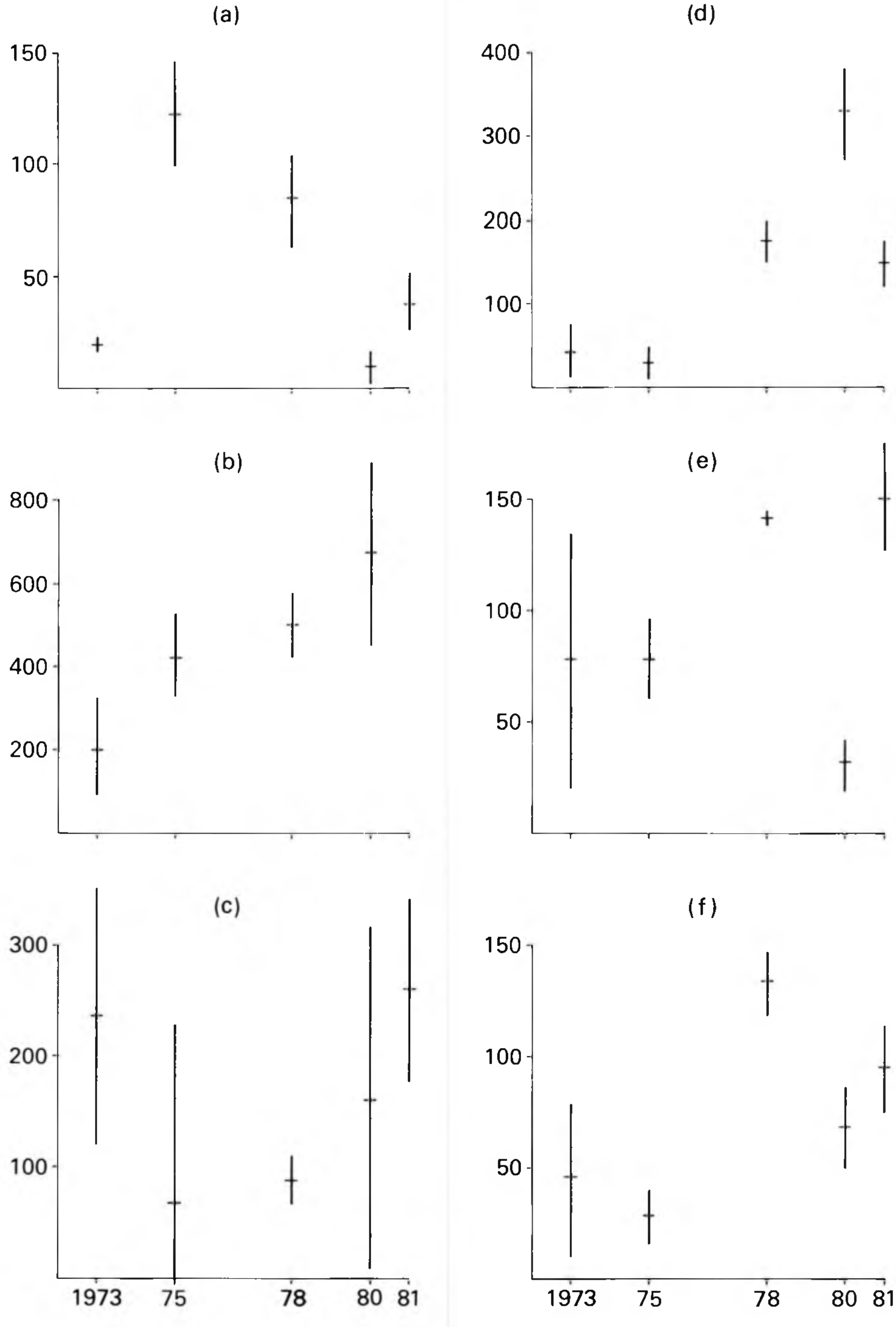


Figure 3. Densities (m^{-2}) of various invertebrates in the intertidal sand of the north shore of Holy Island Snook. Given as mean ± 1 standard error. (a) amphipod crustacean *Bathyporeia pelagica*, (b) polychaete worms *Scoloplos armiger* and *Notomastus latericeus*, (c) small worms Spionidae, (d) bivalve mollusc *Tellina tenuis*, (e) bivalve mollusc *Macoma balthica*, (f) bivalve mollusc *Cardium edule*.

infrequency of losses of nests to blown sand (only one recorded in the detailed study – Pienkowski 1984a) also runs counter to this explanation, as does the lack of consistent differences in nest survival rates in relation to ground-type (Pienkowski 1984a). The anti-predation model involves the birds adjusting nesting density to give approximately equal average nest survival rates in different habitats. Whichever model is correct, the argument that it is the availability of suitable nesting habitat which limits nesting density in this population is not weakened.

Further testing of the increased risk of predation of nests on sand could be undertaken by placing suitably painted eggs in artificial scrapes at the same density on different ground-types, provided that suitably matched areas could be located. This would be a conservative test, as additional features which may make sand less suitable are the trails of footprints of the breeding birds to and from nests in sand.

It seems unlikely that any changes in feeding conditions underlay the changes in breeding density recorded. The main food organisms appear to have remained at least as abundant as previously. Furthermore, at no stage in the breeding cycle was food supply critically low for Ringed Plovers at Lindisfarne in studies in 1974–76 (Pienkowski 1983, 1984b). In addition, alternative rich feeding areas on Holy Island Sands, used by Ringed Plovers throughout the year (Pienkowski 1982), are closer to the Snook nesting sites than the distance between feeding and nesting areas of some birds nesting on Ross Back Sands and Old Law (Pienkowski 1984a).

Thus, in the present case, availability of suitable nesting habitat appears to limit the breeding population of Ringed Plovers at Lindisfarne. This does not, of course, exclude the possibility that, in other circumstances, feeding conditions may limit breeding density.

Although a number of Ringed Plovers were individually colour-marked in the early years of the study period, shortage of resources prevented both detailed behavioural observations and maintenance of a high level of marking effort in later years. Thus it is not known whether the change in breeding distribution at Lindisfarne resulted from relocations of established breeders, lack of recruitment to certain areas when breeding birds had died, or a combination of these. Although both site-fidelity and change of site have been observed in marked Ringed Plovers breeding at Lindisfarne in 1974–76, most were site-faithful.

Pienkowski (1984a) noted that, in certain areas at Lindisfarne, including the Snook, Ringed Plovers did not produce enough young to maintain numbers without immigration. However, other areas produced a surplus. It seems unlikely that shortage of recruits caused the changes in breeding numbers reported here, because Lindisfarne chicks ringed even as late as 1978 (after which few chicks were marked) continued to recruit to areas away from Lindisfarne as well as near their natal areas (Table 2).

The breeding numbers of several species such as Ringed Plover, Oystercatcher *Haematopus ostralegus* and several terns *Sterna* spp. have decreased markedly on beaches in recent years, especially in southern Britain, and increased human usage of

Table 2. Dispersal of Ringed Plover chicks from Lindisfarne.

Year of hatching	No. chicks ringed	No. (%) breeding in a later year at: Lindisfarne	Elsewhere	Ratio: Lindisfarne/ Elsewhere
1973	7	3 (43%)	0	–
1974	15	4 (27%)	1 (7%)	4.0
1975	46	15 (33%)	2 (4%)	7.5
1976	58	12 (21%)	4 (7%)	3.0
1977	71	12 (17%)	2 (3%)	6.0
1978	18	4 (22%)	1 (6%)	4.0
1979	8	2 (25%)	0	–

Note. 'Elsewhere' includes the coasts of NE England and SE Scotland. Coverage varied from year to year.

beaches, mainly for recreation, has been suggested as the main cause (see Parslow 1973, Prater 1976, Sharrock 1976). De Roos (1981) demonstrated lowered nesting densities of several wader species as intensity of tourism increased, and evidence for low nesting success of Ringed Plovers at Lindisfarne in areas of highest frequency of human visits was discussed by Pienkowski (1984a). However, the temporal changes in nesting distribution described in this paper cannot readily be related to changes in human usage. For example, declines in Ringed Plovers occurred at Elwick with no increase in human usage but not at Holy Island Links where visitors increased.

The results reported here have implications for the conservation of this, and other, species which nest on open ground. If successful open-ground nesting depends on a good match between egg camouflage and the ground, the species concerned may be very habitat-specific. Open ground at temperate latitudes is often unstable, as stable ground is generally colonised by vegetation. Therefore, these habitats tend to be both small in area and variable in location. As land tenure practices cause nature reserves to occupy fixed locations, effective conservation of species nesting on open ground may require a relatively large number of reserves (not all of which are suitable for use by the species concerned at any one time), as well as habitat management in existing reserves, which may be difficult, although exclusion of predators may be feasible in some circumstances (e.g. Forster 1975) to allow use of suboptimal sites. Conservation measures outside nature reserves are an obvious additional measure but may be difficult because of the conflict between recreational uses and the lack of disturbance required by breeding birds.

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