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SCIENCE DIRECT
Biological Conservation 117 (2004) 151–166
BIOLOGICAL CONSERVATION
www.elsevier.com/locate/biocon

Long-term population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (*Erinaceus europaeus*)

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Received 27 September 2002; received in revised form 11 June 2003; accepted 19 June 2003

Abstract

In 1974, hedgehogs (*Erinaceus europaeus*) were introduced to the island of South Uist, which forms part of an area holding one of the largest concentrations of breeding shorebirds in Western Europe. By the 1990s these mammals had spread widely and become major predators of shorebird eggs. Breeding shorebirds were surveyed in 1983, when hedgehogs were confined to a small part of South Uist. They were surveyed again in 2000 by when hedgehogs had occupied all of the southern part (South Uist and Benbecula) of the 250 km^2 of lowland shorebird nesting habitat for at least 10 years but had not yet colonised large parts of North Uist and adjacent small islands. Between surveys the overall numbers of shorebirds in the hedgehog-free northern zone increased by 9% but in the southern zone, where hedgehogs were present, numbers decreased by 39%. Population changes differed among species, but for all species the population in the hedgehog-free northern zone outperformed that in the southern zone. The most marked differences occurred in northern lapwing (*Vanellus vanellus*) and common redshank (*Tringa totanus*), which both showed large declines in the southern zone and moderate to large increases in the northern zone. The north–south differences in population change could not be explained in terms of habitat change and were probably largely driven by hedgehog predation.

Keywords: Breeding shorebird; Introduced predator; Population change; Hedgehog; Machair

1. Introduction

Predators have been introduced to many parts of the world, frequently with catastrophic consequences for native animal species, especially on islands. Identifying, predicting and mitigating the effects of introduced predators has become a major focus of conservation science (Atkinson, 1996; Dickman, 1996; Sinclair et al., 1998; Martin et al., 2000, Dowding and Murphy 2001). Although most of the striking examples come from oceanic islands, Australia and New Zealand, impacts are being increasingly recognised in the Old World (Ferreras and Macdonald, 1999; Manchester and Bullock, 2000, Nordström et al., 2002, 2003). In this paper, we report reductions in internationally significant populations of shorebirds (Charadrii) in the southern islands of the Outer Hebrides archipelago, Scotland, that are almost certainly caused by the recent introduction of hedgehogs (*Erinaceus europaeus*).

These islands rank among the foremost breeding grounds for shorebirds in Europe and support the largest concentrations of breeding shorebirds in Britain (Fuller et al., 1986). The birds are concentrated into ca. 250 km^2 of relatively fertile, flat lowland ground fringing the Atlantic shores of the islands of South Uist, Benbecula and North Uist together with smaller islands in the Sound of Harris (we refer to this collection of islands as 'the Uists'). Six species breed at high density: Eurasian oystercatcher (*Haematopus ostralegus*), ringed plover (*Charadrius hiaticula*), northern lapwing (*Vanellus vanellus*), dunlin (*Calidris alpina*), common snipe (*Gallinago gallinago*) and common redshank (*Tringa totanus*). Six other

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0006-3207/$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/S0006-3207(03)00289-1

shorebird species also regularly breed on these islands but these are not considered here because they are either rare or largely confined to the peaty moorland areas occupying the eastern half of the islands.

Hedgehogs were introduced at the southern end of South Uist in 1974 when four individuals are thought to have been released (Morton, 1982). By the mid 1990s hedgehogs were abundant throughout the more fertile areas of South Uist, Benbecula and the extreme south of North Uist, but were absent from the northern and western parts of North Uist (Watt, 1995; Jackson and Green, 2000). Partial surveys in the 1990s indicated that populations of some shorebird species were declining (Whyte and O'Brien, 1995; Fuller and Jackson, 1999) and research revealed high levels of egg predation by hedgehogs (Jackson and Green, 2000). Experiments have demonstrated that, in the presence of hedgehogs, the chances of nest success are reduced by a factor of ca. 2.4 (Jackson, 2001).

The first comprehensive survey of these shorebird populations was in 1983 (Fuller et al., 1986), at which time hedgehogs only occurred in the southern quarter of South Uist and their population density was apparently low (Morton, 1982). In 1999 and 2000, a further comprehensive survey was made. These data are particularly valuable because they cover a period during which predation pressure from hedgehogs has been high for several years on some islands but not on others. These data present the opportunity to distinguish, at a population level, between natural fluctuations and the impacts of an introduced predator. Furthermore, for three of these species, accurate measures of site fidelity have been made on the islands and these help determine the likely extent of redistribution of individuals between islands (Jackson, 1994).

We describe the geographical pattern of shorebird population changes between 1983 and 2000 in relation to the status of hedgehogs. This provides a test of the hypothesis that those shorebird species most susceptible to predation by hedgehogs will have undergone larger declines in areas colonised by hedgehogs than in areas without hedgehogs. Jackson and Green (2000) reported the following daily nest failure rates due to hedgehogs: common redshank (7.5%), dunlin (5.0%), common snipe (4.9%), northern lapwing (1.4%), ringed plover (0.5%), Eurasian oystercatcher (0.0%). Using additional survey data from two sites on South Uist, we also consider the timing of the onset of declines relative to when hedgehogs first became established in an area and whether, over the longer term, shorebird numbers can be expected to stabilise or decline further.

2. Study area and history of hedgehog population expansion

The areas that are occupied by high densities of shorebirds comprise a mosaic of semi-natural grasslands, sand dunes, marshes and arable land. Two distinct landforms can be identified throughout much of the study area. First, the land closest to the west coast, typically within 2 km, forms a level plain dominated by 'machair' soils composed of calcareous shell-sand (Ritchie, 1979). These machair habitats cover ca. 110 km^2 and include dunes, arable land, dry and damp grassland, and marsh. Immediately inland lies a zone of less even, more peaty land, often with rocky outcrops, extensive damp grassland and marsh. This is known as 'blackland' and covers ca. 140 km^2. The composition of shorebird assemblages can vary substantially over quite short distances depending on the exact make-up of habitats (Fuller, 1981; Fuller et al., 1986). This mosaic of habitats is probably unique in northwest Europe and is managed by low-input crofting agriculture based on cattle and sheep rearing. In recognition of their importance, large parts are protected by national and international conservation designations, and most crofters (farmers) receive agri-environment payments for using farming methods that are sympathetic to breeding birds. These habitats have particular importance for ringed plover and dunlin; in 1983 they were estimated to hold approximately a quarter and a third respectively of the UK breeding populations (Fuller et al., 1986).

Since the 1983 shorebird survey, hedgehogs have massively extended their range on the islands. A survey in 1981, seven years after their introduction, found that hedgehogs were restricted to the southern end of South Uist, and all records were within 5 km of the original release site (Morton, 1982). There is strong evidence that they were absent from the northern half of South Uist until at least 1987. None was seen there (despite spot lamp searches on machair conducted to catch shorebirds for ringing), nor suspected as a predator of eggs, during intensive studies on shorebird breeding success at several machair sites between 1983 and 1987 (Jackson, 1988; Jackson and Green, 2000). Furthermore, there are no records of hedgehogs killed on the roads in this half of the island in this period. After this, they must have spread rapidly because by the early/mid-1990s (Angus, 1993; Watt, 1995) the distribution was similar to that in 2000 (Fig. 1), except that it was probably a little more restricted in North Uist, and the small island of Grimsay may not then have been colonised. The approximate rate of spread north from the initial release site in 1974 (Daliburgh in southern South Uist) can be calculated from records (Morton, 1982; Angus, 1993; Watt, 1995). These show that hedgehogs probably did not reach the north coast of South Uist—a distance of 25 km from the original release site—until about 1990, an average progression north of approximately 1 km per year over the first 6 years, and 2 km per year thereafter.

It is not known whether people aided the spread across South Uist, but natural spread appears likely

Fig. 1. The distribution of hedgehogs on the Uists and adjacent islands in 2000. The star indicates the approximate location where hedgehogs were introduced on South Uist in 1974.

given that the range appears to have expanded progressively and relatively slowly, and there are no serious dispersal barriers. The establishment of hedgehogs as early as 1991 in northern Benbecula and in southern North Uist, suggests that colonisation of these islands was directly aided by people. Anecdotal accounts of animals being deliberately released on these islands at around this time support this (Angus, 1993). Therefore, although the three main islands are linked by causeways and inter-tidal strands, the populations on North Uist and Benbecula may be derived from separate introductions (probably of animals from South Uist). It is almost certain there have been later unaided movements between the islands, at least between South Uist and Benbecula.

Mark recapture studies on hedgehogs (Jackson and Green, 2000; Jackson, 2001) and records of road kills show that hedgehog densities vary according to habitat. In general, machair habitats support high densities (30–50 adults/km^2), blackland and grassy moorland hold moderate densities (15–25 adults/km^2) and the eastern hills and peatlands have unquantified, but probably low, densities.

3. Methods

3.1. Bird surveys

Most of the survey work in 1983 and 2000 involved extensive transect surveys of a series of large sites considered to hold the highest densities of shorebirds. These sites were dominated by machair habitats, but included substantial areas of blackland (Fig. 2). The total area covered by the 2000 transect surveys was 113 km^2 (Table 1), about 45% of the total suitable lowland shorebird habitat in the Uists, and includes virtually all of the machair habitats. The 2000 results incorporated data for three sites that were surveyed in 1999 but not in

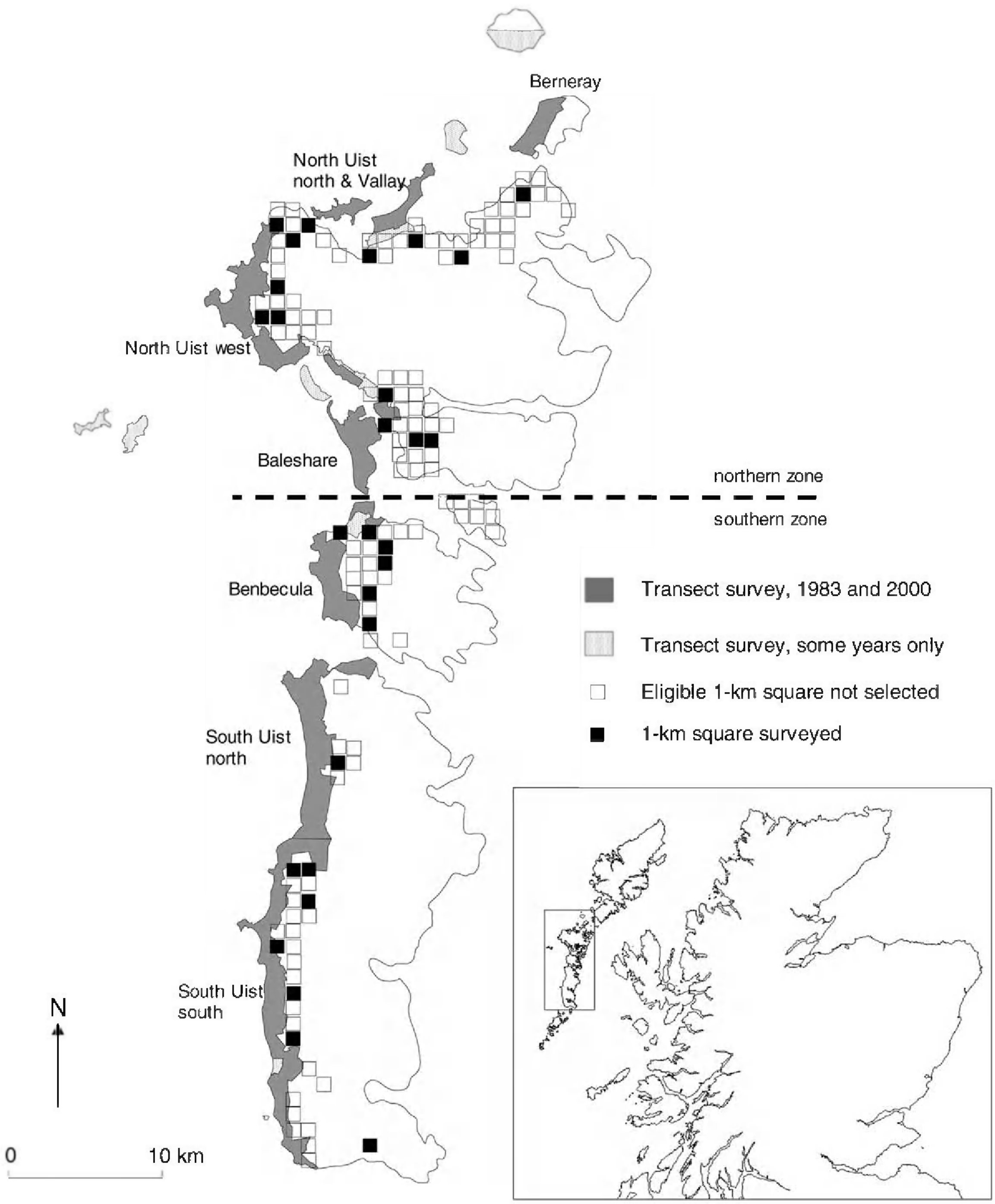

Fig. 2. Map of the Uists and adjacent islands showing where breeding shorebird surveys were undertaken using either transect or random 1-km square survey methods. Also shown are the names and boundaries of the seven large machair sites (shaded dark grey) that were surveyed in both the 1983 and the 2000 surveys and used to assess population change. See text (Section 3.1) for description of selection of 1-km squares. The 'North Uist west' site includes the two small areas marked on North Uist lying to the north and to the east of Baleshare. See Fig. 1 for the names of the smaller islands.

Table 1
The estimated numbers of pairs of waders recorded on surveys of the Uists in 2000[a]

Area and survey method	Zone (southern or northern)	Eurasian oystercatcher	Ringed plover	Northern lapwing	Dunlin	Common snipe	Common redshank	All species	Area (km^2)	Density (pairs km^{-2})
Transect surveys										
South Uist south	S	415	202	657	144	82	376	1876	27.8	67.5
South Uist north	S	439	284	374	558	126	197	1978	22.0	89.9
Benbecula	S	291	99	278	201	75	196	1140	13.5	84.4
Baleshare	N	330	55	334	141	49	165	1074	8.6	124.9
North Uist west	N	677	130	615	219	89	424	2154	21.5	100.2
North Uist north (1999)	N	158	141	173	99	6	50	627	4.4	142.5
Vallay	N	117	1	60	9	5	38	230	2.5	92.0
Berneray (1999)	N	161	58	225	135	9	92	680	5.2	130.8
Pabbay (1999)	other	57	8	36	12	11	34	158	3.8	41.6
Monach Isles (2001)	other	95	27	20	15	11	24	192	3.6	53.3
Random squares surveys (areas not covered by transects)										
South Uist, Benbecula and Grimsay	S	515	13	728	59	323	419	2057	60.0	34.3
North Uist	N	888	16	837	285	287	1201	3514	76.0	46.2
Grand total		4143	1034	4337	1877	1073	3216	15,680	248.9	63.0

[a] All counts are based on survey work in 2000 except where indicated, in which case the most recent count available is used. The area covered by transect surveys in 1999 and 2000 includes an additional 12.6 km^2 that were not covered in 1983. (This accounts for apparent discrepancies with Table 3). Figures for dunlin and common snipe are corrected for under-recording by ×1.5 and ×1.74, respectively (see Section 3.3). The estimates for the random squares survey areas were derived by bootstrapping (see Table 2).

2000 (the island of Pabbay, the island of Berneray, and the Sollas peninsula of North Uist) and for one site surveyed in 2001 but not in 2000 (the Monach Isles). All the areas covered by transect surveys in 1983 were recounted by the 2000 transect surveys except the islands of Barra, Eriskay (both south of South Uist), Kirkibost (west of North Uist) and Boreray (Sound of Harris) which were not re-counted. Shorebird numbers on these islands are low and form only a very small proportion of the shorebirds breeding on the islands (Webb et al., 1983). The 2000 transect surveys covered 12.6 km^2 on the main islands that was not covered in 1983 (because access was denied, or the suitability of the habitat for waders was not appreciated at the time). Birds counted on this additional ground were excluded from the calculations of population changes between the two surveys.

The method used for the transect surveys was developed in 1983 specifically for use in the Uists (Reed and Fuller, 1983; Fuller et al., 1986; Fuller and Jackson, 1999). Briefly, the method involved a pair of observers making a single visit to each site, walking adjacent parallel transect lines. These were spaced either 100 or 150 m apart depending on habitat, physical conditions and shorebird densities and were typically 0.5–1.5 km long. The same transect lines were walked in different years. The total length of transect lines walked was ca. 680 km (average of 6 km/km^2). Positions of all shorebirds seen were marked on 1:10,000 field maps using standard codes. Later, all registrations were transferred to a single 'composite visit map', and the number of 'breeding pairs' was estimated according to species-specific criteria. For all species except common snipe the counting unit was 'pairs', for common snipe it was 'displaying males'. Birds in flocks not exhibiting any behaviour indicative of breeding (e.g. alarm calling) were excluded from the estimates. Sites were visited once between 28 May and 17 June, the period when most species were easiest to detect because they had young and alarm vigorously. The strengths and limitations of this method are discussed by Fuller and Jackson (1999).

In 2000, in addition to the transect surveys, counts of shorebirds were undertaken in a random sample of 28 squares, each 1 km^2 and demarcated on UK Ordnance Survey maps (Fig. 2). The aim was to estimate the numbers of shorebirds breeding in broadly suitable lowland shorebird habitat outside the sites covered by the transect surveys. In the Uists, potential shorebird habitat is generally associated with the more fertile land. The procedure for defining this potential habitat outside the areas covered by the transect survey followed that used in a Scotland-wide lowland survey of breeding shorebirds (Dodds et al., 1995; O'Brien, 1996). The Macaulay Land Classification of Scotland system (Grant, 1981) was used to identify 1-km squares with at least 75% cover of 'land capability class 5.3', or below. This criterion eliminated infertile land (mainly moorland, blanket bog and mountain habitats) with very low densities of shorebirds. In practice, this resulted in the eligible squares ($n = 136$) comprising mainly blackland

and grassy moorland pasture; squares with machair soils were all covered by the transect survey. The survey method for the 28 randomly selected squares was similar to that used for transect surveys except that each square was covered by a single observer who, instead of walking transects, was instructed to walk within 100 m of all parts of the square.

In addition to the two full surveys (1983 and 2000), a number of smaller scale shorebird surveys have been made at several sites (Fuller and Percival, 1988; Dodds et al., 1995; Whyte and O'Brien, 1995). These are not reported here in detail because (a) the methods were in some cases different to those used in 1983 and 2000, in particular, the timing of visits to some sites was often considerably later, and (b) hedgehog status has continued to change during the 1990s. However, we do present data for two sites in South Uist surveyed in 1984–1987 (Fuller and Percival, 1988) and in 1995 (Whyte and O'Brien, 1995) because they provide the best available evidence on the timing and rate of shorebird decline in relation to hedgehog establishment. The southerly site is ca. 3 km^2 and is located at Kilpheder, close to the original release site of hedgehogs (central grid reference NF 735195). The other site lies 13 km to the north and covers ca. 7 km^2 extending from Peninerine to Drimsdale (central grid reference NF755365). This northerly area was treated as two sites when surveyed but, because they are contiguous and for brevity, they are treated here as a single site. Common snipe were excluded from these last analyses because of differences between the surveys in the way this species was recorded.

3.2. Hedgehog distribution

Data on the distribution of hedgehogs were available from published and unpublished sources (Angus, 1993; Watt, 1995; Slack, 2000), together with information from local people and biologists working on hedgehogs on the islands. Surveys were made of scats (described in Slack, 2000), live individuals using spot-lamps (described in Jackson, 2001), and road-kills in the southern part of North Uist in July 2000 and 2001 to determine the status of hedgehogs in the 'front-line' area.

3.3. Analyses and interpretation

The boundaries of the transect survey sites were chosen in 1983 mainly according to habitat (most of the blackland was excluded) and were believed to cover those areas likely to hold the highest shorebird densities. Therefore, they do not constitute representative samples of the whole breeding grounds, and the results cannot be used to infer bird numbers in any areas of the Uists not surveyed. Although the estimates are essentially absolute counts, they are subject to various sources of methodological error mostly resulting from under- or over-recording caused by variations in species detectability (reviewed by Fuller and Jackson, 1999) and inter-observer recording differences (Fuller, 1984). Fuller and Jackson (1999) suggested that estimates of easily detected species (Eurasian oystercatcher, ringed plover and northern lapwing) are likely to be within 10% of the true figure and those for the less detectable species (dunlin, common snipe and common redshank) are likely to be within 20%.

Dunlin and common snipe are systematically underestimated by these survey methods because they are highly cryptic. The following correction factors were applied to the estimates of these two species as they were used in earlier estimates of the shorebird populations (Fuller et al., 1986; Green, 1985). Based on nest-finding and colour-ringing studies on South Uist, Jackson and Percival (1983) calculated that dunlin estimates derived from the transect counts need to be corrected by a factor of ×1.5. Green (1985) used nest finding to calculate that dawn / dusk surveys of displaying common snipe in east England should be corrected by ×1.74. In the absence of other information, the same correction factor has been used for these Uist surveys. However, the appropriate correction factor for common snipe is likely to be bigger because the Uist survey work was mostly conducted between 2 h after dawn and 2 h before dusk, a period when common snipe display activity is often low unless there is light rain. No correction factors have been applied to the other species.

Although the 28 May–17 June survey period is optimal for most species it is slightly too late for northern lapwing and probably leads to a small systematic underestimation (Fuller and Jackson, 1999). From late May, northern lapwing can start to form mobile flocks (which do not contribute to the survey total) composed of successful adults and newly fledged juveniles. The 2000 breeding season appeared to be unusually early and successful for northern lapwing with the result that 19% of all birds seen on visits before 8 June, and 42% seen later, were in flocks. Exactly how many extra breeding pairs these birds represent is unknown but, if half of them were adults and the remainder juveniles (which is reasonable), then the estimates of breeding pairs are likely to be too low by about 5–10%. Data on the proportion of northern lapwing seen in flocks during previous surveys were not available, but were probably lower. No correction was made for the birds in seen in flocks.

The random square survey was designed to provide a population estimate with confidence limits for the whole area from which squares were selected (see Fig. 2). Confidence limits were calculated by a bootstrapping method based on 999 iterations (Greenwood, 1991). Population estimates from the random square data were derived separately for North Uist and South Uist/Benbecula/Grimsay to match the current distribution of hedgehogs. The estimates of the total numbers of shorebirds breeding on the islands in 2000 were derived from combining the site estimates from the transect surveys with the estimates derived from analysis of the random squares data for the remaining area of potential shorebird habitat.

The distribution of hedgehogs in 2000 (Fig. 1) divides the shorebird breeding grounds into two zones: a 'northern zone' (North Uist and adjacent small islands) where hedgehogs are absent or uncommon, and a 'southern zone' (South Uist, Benbecula and Grimsay) where they are common. Analyses of population change in shorebirds are restricted to those sites that were counted by transect surveys in both 1983 and 2000. These sites were amalgamated into the seven areas shown in Fig. 2. Estimates of population change are presented separately for these seven areas (note that the islands of Pabbay, Boreray, the Monachs, Kirkibost, Eriskay and Barra are excluded). Four of the areas were within the northern zone: (i) the island of Berneray, (ii) northern North Uist which comprises the Sollas peninsula and the nearby island of Vallay, (iii) western North Uist and (iv) the island of Baleshare. Three of the areas were within the southern zone: (v) the island of Benbecula, (vi) northern South Uist, (vii) southern South Uist.

The sites that were counted by transect surveys in both 1983 and 2000 cover virtually all of the machair on the main islands. These counts can, therefore, be treated as a full census of the machair habitats. Furthermore, these assemblages of shorebirds are unique in terms of the mixture of species and the types of habitats they occupy—they do not form part of a wider universe of similar shorebird assemblages on similar habitats. For these reasons it is not considered appropriate to test the statistical significance of the observed changes between 1983 and 2000. The confidence limits determined for the random sample of squares should not be applied to data collected on the transect surveys because the habitats, and therefore the densities of shorebirds, were different.

4. Results

4.1. Hedgehog distribution in 2000/2001

The searches in 2000 and 2001 for evidence of hedgehogs in North Uist confirmed that hedgehogs were restricted to the extreme south of this island (away from the main machair shorebird breeding grounds), and that densities here were low (Fig. 1). The only exception to this was a small area (about 3 km^2) around Carinish village in the extreme south of North Uist where hedgehog densities were moderate.

4.2. Total numbers of shorebirds in 2000

The total numbers of shorebirds breeding on suitable lowland habitat in the Uists in 2000 was estimated at 15,680 pairs (Tables 1 and 2). This total excludes the islands Barra, Eriskay, Kirkibost and Boreray, which were not surveyed. In 1983 these four islands held ca. 250 pairs of waders (Webb et al., 1983), thus the total figure for the Uists in 2000 was likely to be close to 16,000 pairs. Northern lapwing and Eurasian oystercatcher, each with over 4000 pairs, were the two most common species each making up about 27% of the total. The suspected slight systematic underestimation of northern lapwing (explained above) means that the actual number of northern lapwing probably exceeded 4500 pairs. Common redshank with slightly over 3200 pairs (21% of total) was the third most abundant species, followed by dunlin with 1877 pairs (12%). Common snipe (1073 pairs) and ringed plover (1034 pairs) were the least common (each slightly below 7%). The difficulties of counting common snipe mean that the estimates for this species were the least reliable and, for the reasons given earlier, numbers may have been substantially greater than this corrected estimate. For completeness it is worth noting here that small numbers of Eurasian oystercatchers, northern lapwing, common snipe and common redshank bred at low density on the ca. 350 km^2 of unsurveyed less favoured rocky coast and peatland habitats on the eastern half the islands. It is thought (based on occasional visits to these areas by the authors) that together these birds probably amounted to a few hundred additional pairs at most.

4.3. Changes in total numbers and density of shorebirds, 1983–2000

Information on how shorebird numbers have changed is only available for the areas covered by transect surveys. The 2000 transect survey recorded a total 9499 pairs of shorebirds in exactly the same areas (totalling 93 km^2) that were counted in 1983 (Table 3). This is 23% less than the number recorded in 1983. The pattern of overall population change differed across the islands and between species. In general, shorebirds on North Uist and adjacent small islands (the 'northern zone') fared much better than those on South Uist and Benbecula (the 'southern zone') (Table 3). Overall numbers on the transect survey sites in the northern zone increased by nearly 9% between 1983 and 2000, whereas in the southern zone they declined by 39%. South Uist, the island holding the highest number of shorebirds in 1983, experienced the most severe decline, 43%, a loss of ca. 3000 pairs of shorebirds.

A north–south divide was also apparent in the shorebird breeding densities recorded in 2000 (Table 1). Total shorebird densities on the four areas in the northern zone ranged from 100 to 131 pairs km^{-2} (average 120 pairs km^{-2}). In contrast, the three areas in the southern zone ranged from 68 to 90 pairs km^{-2} (average 81 pairs km^{-2}). In 1983, shorebird densities on the same areas in

Table 2
The estimated numbers of pairs of waders breeding in areas of the Uists covered by random 1 km^2 square surveys in 2000[a]

Area	No. of eligible 1-km squares	No. of 1-km squares surveyed	Species	Lower 95% CL (pairs)	Estimate (pairs)	Upper 95% CL (pairs)
South Uist, Benbecula and Grimsay	60	14	Eurasian oystercatcher	396	515	656
			Ringed plover	3	13	29
			Northern lapwing	465	728	1053
			Dunlin	14	59	137
			Common snipe	219	323	460
			Common redshank	295	419	565
			All species	1392	2057	2900
North Uist	76	14	Eurasian oystercatcher	610	888	1182
			Ringed plover	3	16	34
			Northern lapwing	607	837	1134
			Dunlin	126	285	477
			Common snipe	130	287	502
			Common redshank	769	1201	1628
			All species	2245	3514	4957
Grand total	136	28	All species	3637	5571	7857

[a] The survey areas were all parts of the islands that were not covered by transect surveys and that are classified as predominantly Macaulay 'land-capability class 5.3' or lower. The 95% confidence limits were calculated by the bootstrapping method. Figures for dunlin and snipe are corrected for under-recording by ×1.5 and ×1.74, respectively (see Section 3.3).

the southern zone averaged 127 pairs km^{-2}, a figure that was nearly 20% higher than recorded for the northern zone sites in 1983 (106 pairs km^{-2}), and 57% greater than the density recorded in 2000.

Similar north–south differences in density were evident in the 2000 survey results for the blackland/moorland habitats covered by the random square method. In North Uist, the mean density of shorebirds on these habitats was 46 pairs km^{-2}, whereas in South Uist and Benbecula it was 26% lower at 34 pairs km^{-2}.

These patterns of change in total shorebird numbers and density since 1983 masked large between-species differences (Table 3, Fig. 3).

4.4. Changes in numbers of individual species, 1983–2000

Northern lapwing and common redshank showed similar changes between 1983 and 2000 (Table 3, Fig. 3). Both showed moderate increases in the northern zone (+24 and +51%, respectively) and similar sized decreases in the southern zone (−31 and −41%, respectively). Between 1983 and 2000 within the transect areas there was an overall decrease 322 pairs of northern lapwings and 281 pairs of common redshank.

An estimate of the overall net change in numbers within suitable lowland shorebird habitat in the Uists (excluding Pabbay, Boreray, the Monachs, Kirkibost, Eriskay and Barra) was made as follows. It was assumed that the % changes for the southern and northern zone given in Table 3 were representative of all areas within these zones. These % changes were then used to estimate the numbers in the southern and northern zones that were present in 1983, based on the combined transect and random square surveys totals for 2000 (Table 1). As an example, the northern lapwing total in the southern zone in 2000 was estimated as 2037 pairs which, assuming a 31.1% decrease, equates to a population of 2956 in 1983. The northern zone population in 2000 was 2244 which equates to 1815 pairs in 1983, given a 23.6% increase. The net change of northern lapwings was therefore a decrease of 490 pairs. Using this method, the estimated net change for redshank was a decrease of 162 pairs.

Dunlin underwent an overall decline of 49% on the transect survey sites amounting to 1379 pairs (Table 3, Fig. 3). This equates to a net loss of 1626 pairs across the islands. The decline in the southern zone (−56%) was almost twice as severe as in the northern zone (−31%). In the southern zone, all areas showed large declines, though the decline in southern South Uist was particularly severe (−79%). Despite a decline of 47%, the northern half of South Uist remained by far the most important area for dunlin in the islands, supporting 39% of the island-wide population. In the northern zone, changes are markedly different between areas. For example, on Baleshare they remained stable but on Berneray they declined severely.

Although the estimates for common snipe may be inaccurate (see Section 3.3), the same method was used in both surveys and so the observed changes should reflect the actual changes. There was a marked north – south split, with approximately stable numbers (−2%) in the northern zone and a large decline (−57%) in the

Table 3
The estimated numbers of waders breeding in the same areas (total 93 km^2) of the Uists and adjacent islands in 1983 and 2000 based on transect surveys[a]

Area	1983 total (pairs)	2000 total (pairs)	% change 1983 to 2000
All species combined			
South Uist south	3450	1830	−47.0
South Uist north	3269	1975	−39.6
Benbecula	1324	1097	−17.1
Baleshare	816	1074	31.6
North Uist west	2185	2035	−6.9
North Uist north and Vallay	586	857	46.2
Berneray	645	631	−2.2
Southern zone	8043	4902	−39.1
Northern zone	4232	4597	8.6
Total	12,275	9499	−22.6
Eurasian oystercatcher			
South Uist south	349	406	16.3
South Uist north	363	438	20.7
Benbecula	216	278	28.7
Baleshare	178	330	85.4
North Uist west	506	637	25.9
North Uist north and Vallay	166	275	65.7
Berneray	57	161	182.5
Southern zone	928	1122	20.9
Northern zone	907	1403	54.7
Total	1835	2525	37.6
Ringed plover			
South Uist south	559	192	−65.7
South Uist north	558	284	−49.1
Benbecula	170	93	−45.3
Baleshare	110	55	−50.0
North Uist west	293	130	−55.6
North Uist north and Vallay	157	142	−9.6
Berneray	200	58	−71.0
Southern zone	1287	569	−55.8
Northern zone	760	385	−49.3
Total	2047	954	−53.4
Northern lapwing			
South Uist south	841	645	−23.3
South Uist north	739	372	−49.7
Benbecula	289	270	−6.6
Baleshare	228	334	46.5
North Uist west	645	572	−11.3
North Uist north and Vallay	126	233	84.9
Berneray	105	225	114.3
Southern zone	1869	1287	−31.1
Northern zone	1104	1364	23.6
Total	2973	2651	−10.8
[1983 lapwing estimates are from the 1983 visit that mostly closely matches the date of the 2000 visit. This was not always the peak count made in 1983 (see text)].			
Dunlin			
South Uist south	638	134	−79.0
South Uist north	1049	558	−46.8
Benbecula	330	192	−41.8
Baleshare	144	141	−2.1
North Uist west	332	219	−34.0
North Uist north and Vallay	86	108	25.6
Berneray	242	90	−62.8

(continued on next page)

Table 3 (*continued*)

Area	1983 total (pairs)	2000 total (pairs)	% change 1983 to 2000
Southern zone	2017	884	−56.2
Northern zone	804	558	−30.6
Total	2821	1442	−48.9
[Dunlin figures are corrected for under-recording by a factor of ×1.5 (see text)].			
Common snipe			
South Uist south	392	82	−79.1
South Uist north	165	126	−23.6
Benbecula	98	72	−26.5
Baleshare	43	49	14.0
North Uist west	96	89	−7.3
North Uist north and Vallay	14	11	−21.4
Berneray	4	5	25.0
Southern zone	655	280	−57.3
Northern zone	157	154	−1.9
Total	812	434	−46.6
[Snipe figures are corrected for under-recording by a factor of ×1.74; this correction is likely to be too small (see text)].			
Common redshank			
South Uist south	671	371	−44.7
South Uist north	396	197	−50.3
Benbecula	221	192	−13.1
Baleshare	98	165	68.4
North Uist west	313	388	24.0
North Uist north and Vallay	37	88	137.8
Berneray	38	92	142.1
Southern zone	1288	760	−41.0
Northern zone	486	733	50.8
Total	1774	1493	−15.8

[a] The Southern Zone comprises South Uist and Benbecula and since 1983 has become colonised by introduced hedgehogs. The Northern Zone comprises North Uist, Baleshare, Berneray and Vallay and remains essentially hedgehog-free. See text for full details

southern zone (Table 3, Fig. 3). The small declines for some areas in the northern zone may result from stochastic errors rather than genuine declines.

Ringed plover declined on the transect sites by 53%, amounting to a loss of 1093 pairs (Table 3, Fig. 3). The net loss across the islands was estimated to be 1145 pairs. Compared with other species, the decline of ringed plover has been remarkably even across the islands, though it is 7% greater in the southern zone.

Eurasian oystercatcher was the only species to show a population increase across all sites amounting to a 38% increase (Table 3, Fig. 3). The estimated net increase across the islands was 1111 pairs. The increase in the northern zone (55%) was over twice that in the southern zone (21%). Numbers on Berneray increased particularly dramatically, by 183%.

The differences between north and south are also reflected in density, with overall densities on the transect sites being more than 40% higher in the northern zone. Therefore, it is likely that the north–south difference was a result of the northern sites outperforming, rather than 'catching up' with, the southern sites.

4.5. Onset of shorebird declines and population trends with time

The additional survey results obtained by Fuller and Percival (1988), and Whyte and O'Brien (1995) are presented for two sites on South Uist as they provide evidence of the timing of the onset of declines relative to hedgehog establishment and the subsequent population trends (Fig. 4). The trend lines shown in the figs. are provided for clarity only and should not be taken as a reliable guide as to what happened in the years with no estimates. For a variety of reasons, count estimates from relatively small sites such as these are more susceptible to errors than counts from large areas. The importance of these counts lies in the between-site differences in the cumulative trend over time rather than the magnitude of annual fluctuations.

The Kilpheder site was only about 3 km from the original hedgehog release point. By 1987 hedgehogs had probably been established at this site for at least 6 years as the 1981 hedgehog survey received several records from this area (Morton, 1982). However, it is unlikely that they could have been common here until the early

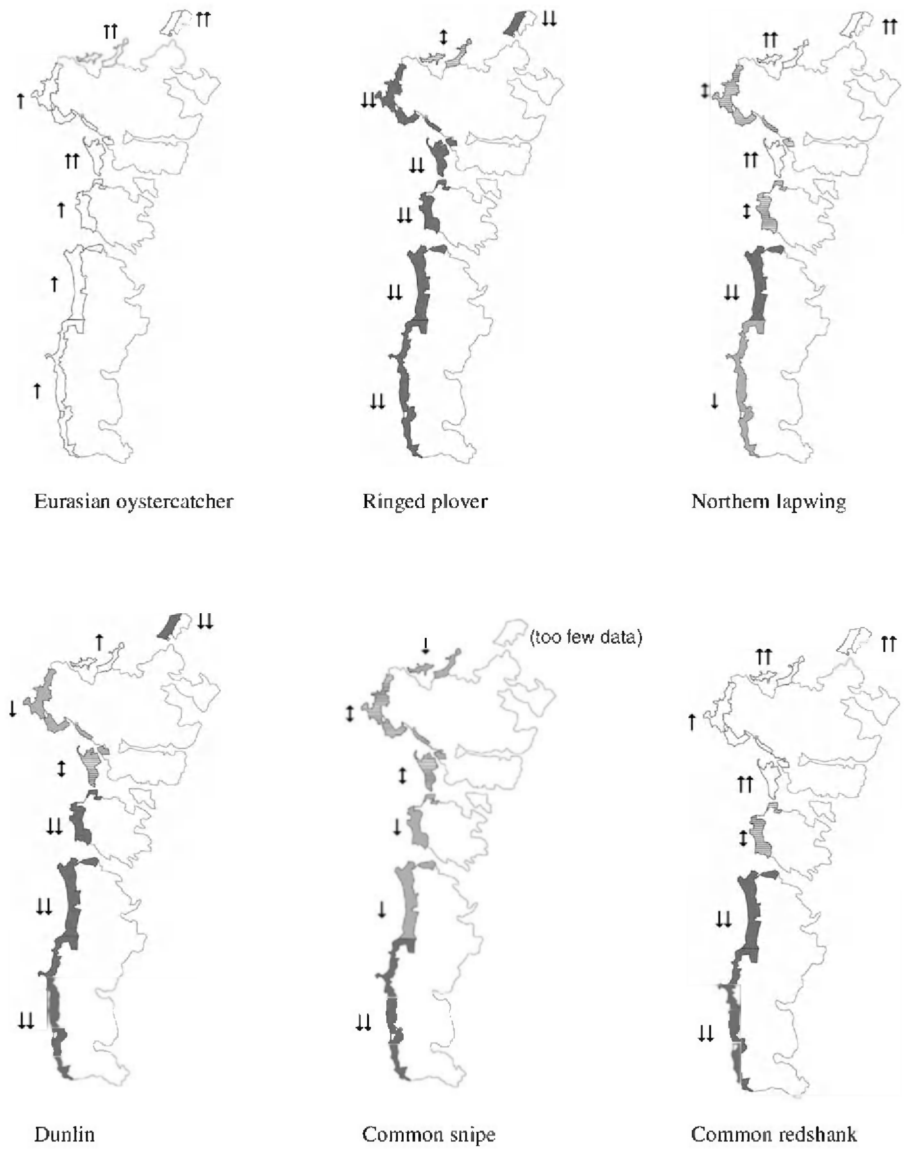

Fig. 3. The geographical pattern of shorebird population change between 1983 and 2000 for seven areas on the Uists. The shading and arrows indicate the magnitude of the change in estimated population size as follows: dark grey shading and $\downarrow\downarrow$, large declines (at least −41%); mid-grey shading and $\downarrow$ moderate declines (−16 to −40%), horizontal hatching and $\updownarrow$, stable (−15 to +15%); solid white and $\uparrow$, moderate increase (+16 to +40%); and solid white and $\uparrow\uparrow$, large increase (at least +41%). Changes in common snipe numbers on Berneray are not shown because very few occurred there. The actual values for population changes are shown in Table 3.

1980s because of insufficient time for population growth and spread; the founder population is believed to have consisted of only four animals released in 1974/1975 (Morton, 1982). The larger and more northerly site was situated about two-thirds the way up South Uist and was first colonised by hedgehogs some time after 1987 and before 1991.

At both sites, the time series pattern of estimated population changes from 1983 to 2000 was broadly similar for dunlin and common redshank. At the Kilpheder site, numbers of these species underwent moderate to large declines (−46% to −60%) by 1987, and thereafter declined at a much slower rate or stabilised (Fig. 4). In contrast, at the more northerly site, these species underwent small declines up to 1987, probably within 'normal' year-to-year fluctuations for these species counted by this method (Fuller and Jackson, 1999). Then, between 1987 and 1995 numbers underwent moderate to large declines similar in magnitude to those at the more southerly site. Northern lapwing numbers at the two sites followed the same temporal pattern but, at around −35%, the overall size of the declines has been smaller (Fig. 4). These results indicate that, for these three species, the timing of the large decline occurred ca. 5–10 years later at the more northerly site, a lag consistent with the difference in the arrival time of hedgehogs between the two sites. For ringed plover and Eurasian oystercatcher, the population trends and their timing are very similar at both sites.

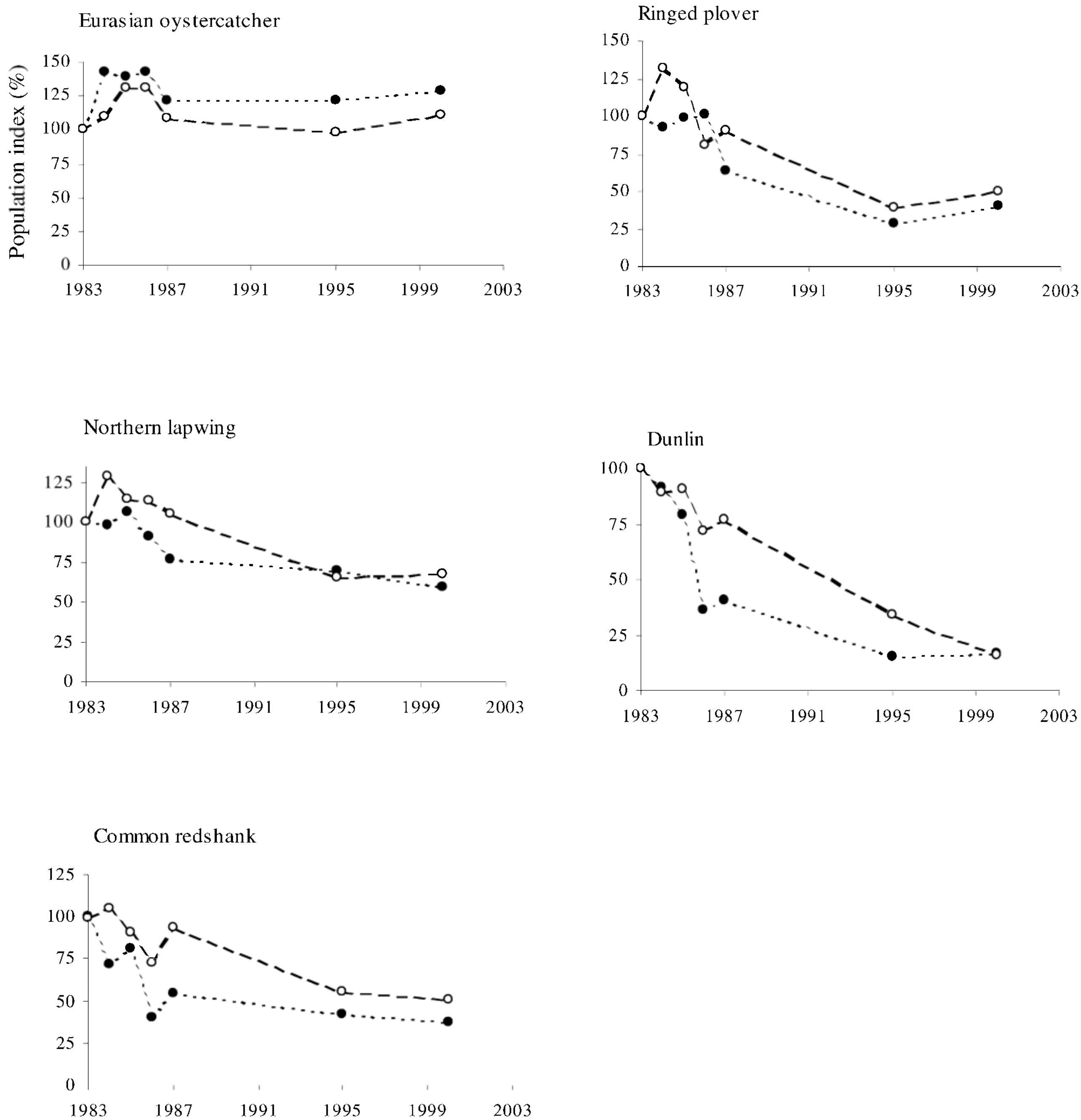

Fig. 4. The changes over the period 1983–2000 in the estimated shorebird numbers breeding on two sites in South Uist. The filled circles and dotted lines show estimates for the southerly site (Kilpheder) that was colonised by hedgehogs in the early 1980s. The open circles and dashed lines show estimates for the northerly site (Peninerine to Drimsdale), that was colonised by hedgehogs in the late 1980s. The initial estimated number of pairs shown as 100% were as follows (southerly site given first): Eurasian oystercatcher 28, 146; ringed plover 35, 111; northern lapwing 90, 237; dunlin 47, 99; common redshank 118, 168. The data are taken from Fuller and Percival (1988) and Whyte and O'Brien (1995). Details are given in Section 3.1.

5. Discussion

5.1. Impacts of hedgehogs on shorebird numbers

Between 1983 and 2000, there were large changes in the numbers of shorebirds breeding on the Uists. The size and direction of these population changes varied between species and islands. In general, however, shorebird numbers fared well in the areas without hedgehogs (the northern zone) and fared relatively poorly in areas where they were well established (the southern zone). Exceptions to this pattern are discussed in Section 5.3. This geographical pattern of changes provides further evidence that the introduction and spread of hedgehogs has been the principal factor driving declines in shorebird numbers. Especially when coupled with the results from earlier work on shorebird breeding success and hedgehog removal experiments (Jackson and Green, 2000; Jackson, 2001), these analyses of changes in shorebird numbers amount to strong evidence that hedgehogs have exerted major impacts at a regional population level. It can be concluded that hedgehogs limit the breeding success and breeding density of some shorebird species on these islands.

Northern lapwing, dunlin, common snipe and common redshank, have been shown to be particularly vulnerable to hedgehogs, which accounted for between 36% and 64% of nest failures of these species in South Uist in 1996–1997 (Jackson and Green, 2000). The hypothesis that these species would show the strongest evidence of relatively poor population performance in areas with hedgehogs was supported (Fig. 3). The differences in population changes from 1983 to 2000 between the areas with and without hedgehogs is probably almost entirely attributable to egg predation by hedgehogs. Although good quantitative data are lacking, the extent of habitats and the status of other predators (notably corvids and gulls) between the northern and southern areas do not appear to have changed over this period.

Ringed plover are less vulnerable to hedgehog predation than the other small wader species, probably because most nest in dry habitats that appear to be relatively unattractive to foraging hedgehogs (Jackson and Green, 2000). This species underwent large declines in several areas not occupied by hedgehogs and possible reasons are discussed in Section 5.3. Although Jackson and Green (2000) recorded no confirmed cases of hedgehogs taking the eggs of oystercatcher, further studies on South Uist have shown that hedgehogs are responsible for about 11% of oystercatcher nest failures ($n = 28$) (D. Jackson, unpublished data). Given this relatively low rate of predation of oystercatcher eggs by hedgehogs, it is not surprising that oystercatcher numbers have not decreased where hedgehogs are present. Nevertheless, the difference in the population increase between the southern zone (21%) and the northern zone (55%) over the past 17 years may result from a moderate reduction of breeding success caused by hedgehogs. Adult oystercatchers are larger and probably better able to protect their eggs from mammalian predators than the other shorebird species. It is also possible that hedgehogs have difficulty biting into eggs as large as those of oystercatcher.

Dunlin, common redshank and northern lapwing at sites in South Uist started to decline rapidly within about 5 years of hedgehogs becoming established. Rapid decline (ca. 5–10% per annum) occurred for several years, after which the decline slowed and in some cases, at least, numbers became approximately stable. The situation in the islands as a whole is unknown and there are likely to be significant year-to-year and site-to-site variations in performance of both shorebirds and hedgehogs, mainly caused by weather and habitat conditions (Jackson, 1988; 2001).

5.2. Shorebird redistribution

Significant redistribution of individual shorebirds between sites could potentially mask localised differences in breeding performance and survival (for example, those caused by hedgehogs). Such processes could reduce the spatial and temporal coincidence between hedgehog occurrence and changes in shorebird numbers. Knowledge of shorebird dispersal allows this issue to be addressed.

There are large differences in philopatry and adult site fidelity between the species of shorebirds nesting on the Uists (Jackson, 1994). Thus, the extent to which shorebirds on the different islands behave as independent populations will vary. Dunlin exhibit strong philopatry and adult site-fidelity and are unlikely to disperse between islands. Therefore, the declines of dunlin recorded in western North Uist and Berneray are very unlikely to be an effect of low breeding success further south, and are more likely to be caused by locally depressed breeding success or increased mortality.

In the Uists, common redshank typically exhibit dispersal movements of a few kilometres (Jackson, 1994). Dispersal into Benbecula, from adjacent sites to the north (unaffected by hedgehogs) may have augmented numbers in Benbecula but not South Uist. This may account for the larger decline on South Uist than Benbecula.

Ringed plover disperse widely within the islands, and settle to breed in new places in response to habitat quality (Jackson, 1994). Population changes at a site can therefore be influenced by breeding performance over a far wider area. This could explain why the decline of ringed plover is so consistent across the islands. It is theoretically possible that sustained low breeding success in the southern zone could generate a population decline throughout the islands, but this is unlikely to have occurred as this species experiences relatively low rates of predation by hedgehogs (Jackson and Green, 2000).

5.3. Other causes of shorebird population change

Some species have undergone substantial declines at some sites without hedgehogs over the past 17 years, showing that other factors must be involved. Of all the sites in the northern zone, the changes in shorebird numbers on the island of Berneray are the most anomalous, especially for dunlin and ringed plover, which have undergone marked declines in striking contrast to most areas on North Uist. The causes are unclear but several hypotheses are discussed by Fuller and Jackson (1999).

The general increases in the northern zone in Eurasian oystercatcher, northern lapwing and common redshank, and decreases in dunlin and ringed plover, may reflect cumulative changes in winter survival in recent years. However, birds from different breeding sites are mixed on the wintering areas so any such changes in survival would be expected to affect breeding numbers at all sites within a region. Therefore, winter survival is unlikely to explain site-to-site and island-to-island differences. Site-to-site differences within the northern zone are most likely to be caused by local processes on the breeding grounds.

Changes in farming practice could potentially have affected the suitability of sites for shorebirds. Farming on the islands is based on extensive livestock rearing, including the growing of grass and cereal fodder crops, and this broad pattern has changed little over the past two decades. However, there have been local changes, for example in the balance between, and intensity of, cattle and sheep grazing. A possible explanation for the declines of dunlin on Berneray is a subtle change in grazing management favouring Eurasian oystercatcher and northern lapwing (these prefer a short sward) but disadvantaging dunlin (which prefer somewhat longer vegetation), though we have no evidence for this. A further possible explanation for the decline in dunlin on Berneray is interference from the larger species whose numbers have greatly increased. Eurasian oystercatchers in particular can be aggressive to other birds and have been recorded taking the eggs of other species, though not in the Uists (Cramp and Simmons, 1983).

Finally, predation by gulls or corvids may have increased at some sites more than others; this was discussed in detail by Fuller and Jackson (1999), especially in relation to the declines of dunlin and ringed plover on Berneray. Predation of ringed plover eggs by common gulls (*Larus canus*) has increased (Jackson and Green, 2000). This is probably at least as important a cause of decline in ringed plover as predation by hedgehogs. The increase in gull predation has occurred in the absence of a major increase in gull populations, which suggests that a change in foraging behaviour of gulls has taken place. It is possible that increased predation by gulls has contributed to declines in other species of shorebirds. Between the 1980s and 1990s, dunlin underwent a significant increase in rate of nest failures due to predators other than hedgehogs (Jackson and Green, 2000).

There was one exception to the large declines in ringed plover numbers across the islands, and this was at the small area (4.4 km^2) of machair at Sollas in the north of North Uist. Ringed plover numbers here declined by only 7%, and in 2000 this site held ca. 13% of the Uist population. This anomaly is probably linked to a large arctic tern (*Sterna paradisaea*) colony at this site which is likely to afford incidental protection from gulls.

5.4. Future outlook for Uist shorebirds and hedgehogs

The results from the two South Uist sites (Fig. 4) give the best insight available as to how shorebird populations may fare in the longer term alongside a hedgehog population not controlled by human intervention. Following a period of decline after hedgehogs first establish in an area, the mostly likely course of events is that populations of the most vulnerable species eventually become approximately stable. The new equilibrium level is likely to depend both on a species' vulnerability to hedgehogs and on local habitat composition. If the two South Uist sites are representative, populations appear to approach stability when numbers have fallen by about 80% in the case of dunlin, 50% in the case of redshank and 40% in the case of northern lapwing. However, the fact that birds are free to redistribute between sites needs to be considered (see Section 5.2). Patterns observed at the site-scale may not hold throughout the islands, especially if some places act as sinks and others as sources (Pulliam, 1988).

The worst-case scenario is that some species eventually become extinct on the islands with hedgehogs. The fact that dunlin and snipe declines have been greatest where hedgehogs have been established longest (southern South Uist) supports this possibility. The passive method by which hedgehogs are believed to locate shorebird eggs, and the low importance of eggs in the hedgehogs' diet (Jackson and Green, 2000), mean that the risk of egg predation by hedgehogs is expected to be independent of egg density. Therefore, theoretically, it is possible for hedgehogs to cause extinction. Reduction in predation risk is more likely to arise through birds tending to nest more frequently in sites or habitats where eggs are less at risk than through a change in hedgehog behaviour. Trends in Uist shorebird populations will also depend on how hedgehog populations change. Some mammal species introduced to islands elsewhere in the world have decreased from initially higher densities (e.g. Scheffer, 1951), but there is no sign of this occurring on the Uists. Surveys of hedgehog densities repeated annually from 1997 to 2001 at two sites on South Uist where they had already been well established for at least five years showed no evidence of a trend to increase or decrease (D. Jackson, unpublished data).

6. Implications for conservation

The 2000 survey showed that the Uists and adjacent small islands still support exceptionally large numbers of breeding shorebirds, totalling ca. 16,000 pairs. This reconfirms the Uists as the single most important shorebird breeding area in the UK both because of the high densities within a relatively small area, and because they contain high proportions of the UK's breeding populations of several species. Fuller et al. (1986) highlighted the importance of the Uist populations of dunlin and ringed plover but the significance of the common redshank and northern lapwing populations should also be recognised because these species have been decreasing strongly elsewhere in their British range (Gibbons et al., 1993; Wilson et al., 2001).

The random square survey element of the 2000 survey enabled the proportion of shorebirds breeding outside the transect survey sites to be estimated for the first time. This indicated that these areas (consisting mostly of blackland and grassy moorland) contain ca. 35% of the islands' shorebirds, including 36% of the northern lapwing, 18% of the dunlin, 57% of the common snipe and 50% of the common redshank. The mean shorebird densities in the random squares were around 40 pairs km^{-2}. Although this is less than half that typically recorded on the mainly machair areas covered by the transect method, it is very high by mainland standards (O'Brien et al., 2002). The importance of the blackland/grassy moorland habitat for breeding shorebirds on the Uists has before now not been fully appreciated [though see Fuller (1981) and Pienkowski et al. (1986)]. In recognition of this, some of these areas probably merit protection, for example through statutory nature conservation designations. The size of the shorebird declines on the Uists means that, with the exception of Eurasian Oystercatcher, populations of these species should currently be regarded as not having a 'favourable conservation status' as defined in the EU Birds Directive. In 2000, a new introduced predator, the American mink (*Mustela vison*), arrived in the Uists from islands to the north, posing another possible threat to ground-nesting birds. In addition, introduced populations of brown rat (*Rattus norvegicus*) and polecat-ferret (*Mustela furo*) have existed on the islands for many years though neither are important predators of wader eggs on the Uists (Jackson, 1998; Jackson and Green, 2000).

Hedgehogs in North Uist have been slowly spreading north and, unless checked, it is inevitable that the whole of the island will be colonised. If they spread at 1–2 km per year, as on South Uist, they will become established in the main shorebird nesting areas in the west of North Uist by about 2005 and, perhaps, eventually spread to the causeway-linked islands of Baleshare and Berneray. The shorebird populations in these areas would then decline like those further south. Conservation organisations have attempted to prevent further hedgehog spread in North Uist by using barrier fences and trapping, but fences are not expected to be fully effective because hedgehogs can avoid them by using roads, inter-tidal ground and rabbit (*Oryctolagus cuniculus*) burrows (Jackson, 2001). In 2003, Scottish Natural Heritage and the Scottish Executive, supported by RSPB Scotland, started the Uist Wader Project. This involves removal of hedgehogs from blackland in the south of North Uist as a short-term emergency measure to reduce the chances of hedgehogs colonising the machair of North Uist. The Uist Wader Project is also developing a wide-scale and long-term hedgehog management plan aimed at preventing further declines in breeding wader numbers and facilitating the recovery of wader populations that have been reduced by hedgehog nest predation. To achieve these aims, the Uist hedgehog population will have to be significantly reduced and, ideally, eradicated.

Humans have introduced hedgehogs to many other islands around the world including most of the inhabited islands around Scotland, islands off Germany (Grosskopf, 1989) and New Zealand (Brockie, 1975), and at many of these they have impacted on ground-nesting birds. Coupled with the experience of the Uists, this indicates that hedgehogs establish easily from small founder populations, especially where their major predators [Eurasian badger (*Meles meles*) and red fox (*Vulpes vulpes*)] are absent. The avoidance of similar problems on islands elsewhere will require education at all levels, sound policies, great vigilance and strong, well enforced legislation.

Acknowledgements

We would like to thank those who had the foresight to establish base-line population estimates in the 1980s in particular Harry Green, Mike Pienkowski and Tim Reed. The 2000 surveys were a team effort and thanks are due to everyone involved. The surveys were undertaken by Dawn Balmer, Fiona Harmer, Andy Wilson, Pete Wilson and the authors. Andrew Stevenson provided shorebird counts for The Monach Islands in 2001. We are grateful to the islanders and to landowners for allowing us access to survey sites. Katy Proctor is thanked for recounting the map registrations. Jerry Wilson and David Gibbons are thanked for constructive comments on the draft. Jeremy Greenwood provided analytical advice. The surveys in 2000 were financed by RSPB.

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