

# The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland

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Received 6 June 1999; received in revised form 3 August 1999; accepted 5 August 1999

## Abstract

Populations of waders (Charadrii) on machair habitats on the island of South Uist were counted and wader nests were monitored to determine nest success and causes of failure. There were large declines in wader numbers and nest success following the spread of the introduced hedgehog throughout the island. Predation of wader eggs by hedgehogs was frequent, but susceptibility varied among wader species, being between 0 and 60% of the nests started. Wader species that were susceptible to hedgehog predation tended to suffer larger population declines than those that were less susceptible, with the exception that the ringed plover (*Charadrius hiaticula*) population declined markedly even though their nests were depredated by hedgehogs infrequently. A combined analysis of mark-resighting and radio-tracking data produced an average hedgehog population density estimate of 57 adults km<sup>-2</sup>. It was estimated that wader eggs only provided 0.7–5.5% of the energy requirements of hedgehogs, even during the season when most eggs were taken. From this it is argued that the abundance of hedgehogs and the intensity of their predation on wader eggs are unlikely to diminish in response to wader population declines. Unless some presently unidentified density-dependent mechanism compensates for low nest success, local extinctions of susceptible wader species are likely if no action is taken to reduce hedgehog predation. This appears to be the first documented case of hedgehogs threatening an internationally important bird population with regional extinction. © 2000 Elsevier Science Ltd. All rights reserved.

**Keywords:** Egg-predation; Introduced predator; Island

## 1. Introduction

The islands of North Uist, Benbecula and South Uist, in the Outer Hebrides archipelago in Scotland, support large numbers of six species of ground-nesting wading birds (Charadrii); ringed plover (*Charadrius hiaticula*), lapwing (*Vanellus vanellus*) oystercatcher (*Haematopus ostralegus*), dunlin (*Calidris alpina schinzii*), redshank (*Tringa totanus*) and snipe (*Gallinago gallinago*) (Webb et al., 1983; Fuller et al., 1986). About one third of the UK's breeding population of dunlin is found on the machair, the shell-sand enriched arable and grassland area at the western edge of the islands (Fuller et al., 1986).

The hedgehog (*Erinaceus europaeus*) was introduced to South Uist in 1974 (Angus, 1993). Before this, the species had been absent from the archipelago, at least in historical times (Corbet and Harris, 1991). By the 1990s hedgehogs had spread throughout the island and onto nearby islands linked to South Uist by causeways (Arnold, 1993). Counts of breeding waders in 1983 (Webb et al., 1983; Fuller et al., 1986), and 1995 (Whyte and O'Brien, 1995) show that numbers of dunlin, ringed plover, redshank and snipe have declined greatly in recent years. This study compares wader population density and nest success before and after the arrival of hedgehogs and estimates the population density of hedgehogs on machair and the rate of their predation of wader eggs. The probable importance of wader eggs to hedgehogs, in terms of the contribution to their food in spring and summer, is also assessed.

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## 2. Study areas

The study was carried out on the machair habitat of South Uist (57° N, 7° W), which is about 90 km west of mainland Scotland. Machair is a flat dune grassland formed from wind-blown shell sand, occurring as a 1–2 km wide strip along the Atlantic fringe of the island (Ritchie, 1979). Vegetation communities range from dry dunes, through damp grassland to marsh. Human use of the machair is traditional low intensity farming (crofting), which involves seasonal grazing by cattle and sheep, rotational cultivation of fodder rye and oats and hay or silage cropping. In the spring and early summer the machair vegetation is typically closely grazed and is too sparse to provide hedgehogs with suitable cover above ground for day-time refuges. Rabbits (*Oryctolagus cuniculus*), introduced many years ago, have an important influence upon the machair. They are abundant in areas with well-drained sandy soil, and their grazing and burrowing has a large impact on the habitat. Rabbit burrows provide an abundance of suitable refuges for hedgehogs.

Hedgehog surveys were conducted on three rectangular survey plots located at three sites in South Uist, Ormiclate (30 ha), Drimore (71 ha) and Loch Bee (42 ha) (Fig. 1). The sites were selected to be representative of the range of machair habitats and wader communities on the islands. Machair was the habitat selected for study because it has the highest overall population density of waders and is particularly important for dunlin and ringed plover. A 100 m grid of numbered white pegs was set up on each plot to guide surveyors and provide reference points for recording of hedgehogs.

Data on changes in wader numbers since the arrival of hedgehogs were available for all sites from surveys of areas that overlapped or included the hedgehog survey plots. The size of the wader survey plots was; Ormiclate, 65 ha, Drimore, 197 ha and Loch Bee, 55 ha. There were data on wader breeding success from the 1980s before hedgehogs arrived in these areas and comparable data from 1996–1997 after the arrival of hedgehogs. All sites had an approximately equal mixture of dry (with rabbit burrows) and damp machair habitats. In general, wader nests occurred at higher density in the damp areas. The plots were bounded on three sides by similar machair habitat and on the fourth by either the coast or a brackish-water lake shore.

## 3. Methods

### 3.1. Estimation of wader density and population change

Results from two surveys of waders in the Uists (Webb et al., 1983, Whyte and O'Brien, 1995) were used to estimate the wader numbers and densities on the

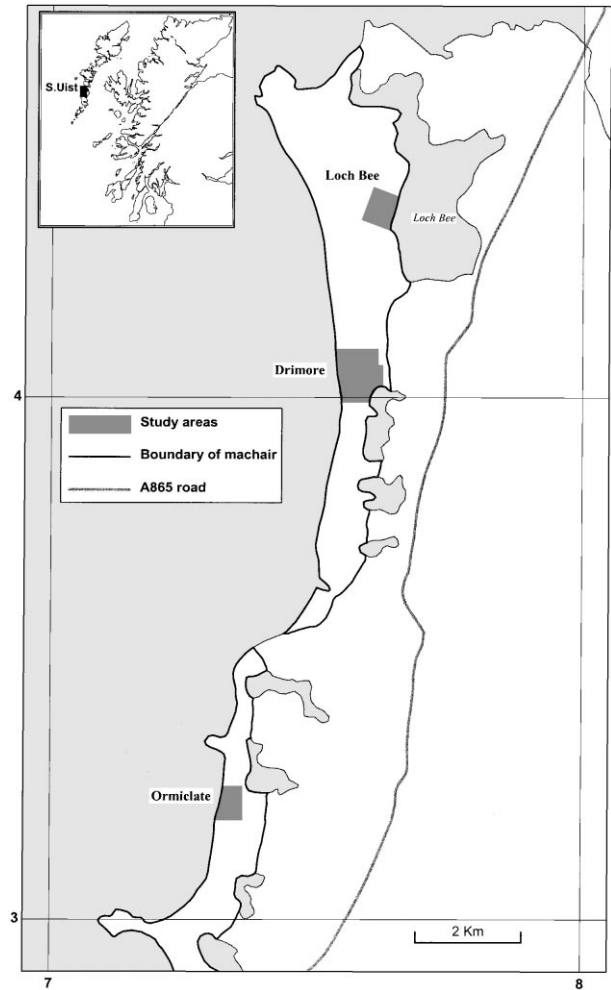


Fig. 1. Map showing the location of South Uist within the Outer Hebrides archipelago of Scotland (inset) and the study areas in the northern part of the island. Areas of sea and lakes are shown in light stipple.

hedgehog survey plots and adjacent areas of similar machair habitat. These were the same areas within which nest success was monitored (see below). The first survey was undertaken in 1983, before hedgehogs colonised the sites (Webb et al., 1983; Fuller et al., 1986). A repeat survey was carried out in 1995 (Whyte and O'Brien, 1995), several years after hedgehogs are thought to have arrived. The survey method is described in Reed and Fuller (1983). In the case of dunlin, the number of pairs counted is known to underestimate the true number present by a approximately one third, so a correction factor of  $\times 1.5$  was applied (Jackson and Percival, 1983). The counts of snipe were also likely to be lower than the number of pairs present. Although Green (1985) found that peak densities of nests averaged 1.74 times the mean density of displaying snipe, this correction factor is not directly applicable to our surveys, which were made throughout the day, because he used counts of displaying males in the early morning and late evening when snipe are easier to detect (Tuck, 1972). Therefore,

we have assumed that densities of snipe were twice the density of birds counted. Failure of this assumption would make little difference to our conclusions because few snipe nest on the study sites.

These estimates of the number of pairs of waders breeding on the sites are considered to give adequate measures of the number of pairs breeding on the sites during this study, and of the size of wader population changes that have occurred since hedgehogs colonised. The 1995 wader survey was carried out two years before the hedgehog surveys and the impression gained by field-workers in 1996–1997 was one of moderate further declines of some species.

### 3.2. Estimation of wader nest success

Nests of waders were monitored at two sites, Drimore and Loch Bee, in 1996 and 1997, but not at Ormiclate. To achieve adequate sample sizes, nests were located within the hedgehog survey plots and in adjacent areas up to 500 m away with similar machair habitat. Data on nest success for some species was also available for Drimore from 1985–1987, shortly before hedgehogs colonised the area (Jackson, 1988).

Nests were found by watching the adults and by intensive ground searches. Nest positions were mapped carefully and markers were not used for relocation to avoid the possibility that predators could also use them. Nests were checked at intervals of about 7 days. The presence on the nest of incubating lapwing, oystercatcher and ringed plover could often be checked through a telescope without disturbance. A visit was required for nests that were hidden by vegetation. Care was taken to avoid trampling vegetation around nests. Nest visits were not made if gulls (*Laridae*) were in the vicinity or during rain.

A nesting attempt was considered successful if at least one egg hatched. Three types of evidence were used to indicate that hatching had occurred: seeing chicks, seeing adults in the vicinity of the nest behaving in a manner indicating the presence of chicks and the occurrence in the nest lining of small chippings of eggshell and ‘chick-down dust’.

Daily failure rates and survival probabilities of clutches during egg-laying and incubation were calculated by the method of Mayfield (1975). Failures were assumed to occur mid-way between nest checks. In addition to the failure rate to all causes, daily failure rates attributable to specific causes (see Results) were also calculated by the Mayfield method. The proportion of nests that survived from the laying of the first egg until hatching was calculated by raising the daily survival rate to a power equal to the combined duration of egg-laying and incubation typical for the species. These periods were; for oystercatcher, redshank and ringed plover, 29 days; for lapwing, 30 days, for dunlin 27.5

days and for snipe, 22 days (Tuck, 1972) for snipe, Cramp and Simmons (1983) for other species]. The standard error of nest survival from the laying of the first egg to hatching was calculated by Hensler’s (1985) method.

The Julian date of the laying of the first egg was calculated for clutches found during laying, by assuming that an egg was laid every 1.5 days and, for clutches where hatching was observed, by subtracting the typical egg-laying to hatching period (see above) from the hatching date. First clutches were assumed to be those with first-egg dates before the following Julian dates; lapwing, day 120; redshank, snipe, ringed plover and oystercatcher, day 135; dunlin, day 151. These dates were based on inspection of histograms of first-egg laying dates and may misclassify some clutches. However, such misclassifications are unlikely to affect the conclusions.

The influence of period (1985–1987 or 1996–1997), wader species and clutch (first or later) on overall and cause-specific daily failure rates were tested using logistic models. The outcome of each day that a clutch was exposed to the risk of failure was regarded as a binary dependent variable. Period, species and clutch (first or later) were treated as independent factors. Models were fitted using GLIM (Crawley, 1993). The fit of models was compared using likelihood-ratio tests.

### 3.3. Identification of nest predators

The area within a 5 m radius of a failed nest was carefully examined for signs that could help determine the cause of failure. The signs recorded were the size and number of egg shell fragments, the state of the nest lining, and the presence or absence of traces of yolk, fresh predator scats, vehicle tracks, hoof-prints of sheep or cattle and flood water. Nest destruction through agricultural machinery, livestock trampling or flooding was usually self-evident. Clutches that disappeared from the nest were assumed to have been taken by predators. Eggshell fragments were examined for puncture marks and crushed edges as described by Green et al. (1987).

For most depredated wader nests the most likely predator was identified from signs. It was first necessary to discover characteristic signs left by particular predators. There was a relatively small number of potential mammal and bird egg predators. The following mammals that might take eggs were present on the island; hedgehog, brown rat (*Rattus norvegicus*), wood mouse (*Apodemus sylvaticus*), feral cat (*Felis catus*), otter (*Lutra lutra*) and feral ferret (*Mustela furo*). All of these species were seen during the night-time searches, though hedgehogs were seen by far the most frequently (Table 1). Several wood mice were seen on a typical search, but they were not counted. There was no indication that humans were removing eggs from wader nests on South Uist. The following birds were seen taking wader eggs at

some time during several years of fieldwork throughout the Uists; common (*Larus canus*), black-headed (*L. ridibundus*), herring (*L. argentatus*), and greater black-backed gulls (*L. marinus*), arctic skua (*Stercorarius parasiticus*), hooded crow (*Corvus corone cornix*), raven (*C. corax*) and hen harrier (*Circus cyaneus*). All of the mammal species were active above ground on the machair mainly at night, whereas foraging by all of the birds only occurred by day.

The only birds seen to depredate wader nests in the study areas during the present study were common gulls, which caused the complete failure of 19 wader clutches (5 dunlin, 4 lapwing, 1 redshank, 7 ringed plover and 2 snipe) in daylight (11.00–20.00 GMT). Subsequent examination showed none of the characteristics of depredation by mammals (Green et al., 1987). No nests showed disturbance to the nest lining or shell fragments with crushed edges and none had fresh hedgehog faeces near the nest. Shell fragments were only present in 16% of the nests and were all < 6 mm in diameter. No nest had more than two fragments > 2 mm in diameter. In three cases some eggs were left abandoned in the nest. A further 12 clutches were seen to be partially depredated by common gulls, but incubation continued. It is concluded the common gull was the main avian predator of wader nests in the study areas.

Two clutches were seen to be depredated by mammals; these were night-time observations (22.00–23.00 GMT) of hedgehogs eating the eggs from a dunlin nest and a lapwing nest in different years and areas. The signs left at these nests were very different from those at nests depredated by common gulls. The nest lining was disturbed in both cases and there were 17 and 19 eggshell

fragments > 2 mm in diameter. Shell fragments had crushed edges and, in one clutch, tooth-holes similar to those recorded for hedgehogs by Green et al. (1987). However, hedgehog scats were not found near these nests. The remains were similar to those of eggs fed to captive hedgehogs.

Further information on the identity of egg predators came from the monitoring of nest temperature with time and temperature data loggers [TinyTalk, Gemini Data Loggers (UK) Ltd], which were used to determine the time of predation and thereby distinguish between diurnal and nocturnal predators. The logger was placed close to the nest and connected to a thermistor by 0.5 m of fine wire. The thermistor tip was passed vertically upwards through the bottom of the nest so that it was a few millimetres above the nest lining and at the centre of the clutch. The logger and wire were buried and care was taken to avoid disruption of the vegetation and ground around the nest. Loggers were set to record nest temperature every four minutes. The logger was retrieved after the nest had failed and its data were downloaded. A graph of temperature against time was used to determine the time of the abrupt and permanent change from incubation to ambient temperature that was assumed to coincide with nest predation.

The time of failure caused by egg predation was determined at 26 nests (11 dunlin, 8 redshank, 5 lapwing, 1 ringed plover, 1 snipe). Of these, eight failed during daylight and 18 during darkness; all of the latter outside the period of civil twilight (Fig. 2). There was no disturbance of the nest lining in any of the nests that failed during daylight. There were eggshell fragments in

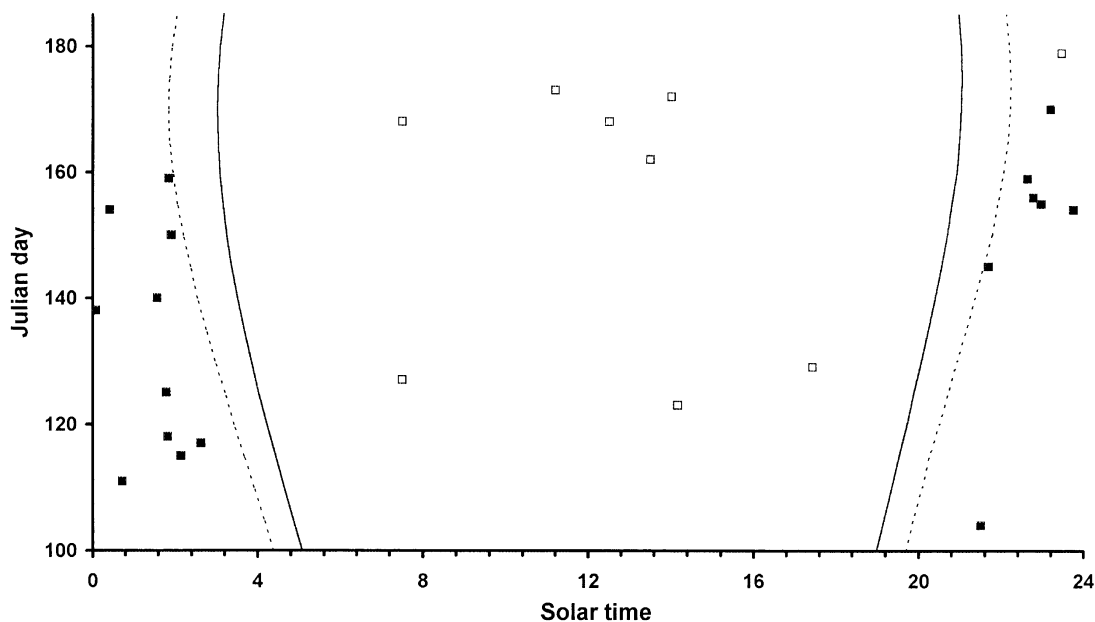


Fig. 2. Solar time and date of failures of depredated nests monitored by temperature-time data loggers. Filled squares denote nests at which signs indicated predation by hedgehogs and open squares denote predation by another species. The curves show the times of sunrise and sunset (solid lines) and of civil twilight (sun zenith angle =  $96^\circ$ ; dotted lines).

or near 38% of the nests that failed during daylight, but none of them had crushed edges and there were no fragments > 2 mm in diameter. These signs are entirely consistent with those at nests seen to have been depredated by common gulls, which are diurnal egg predators.

By contrast, the nest lining had been disturbed at 83% of the nests that failed at night, 94% had eggshell fragments and 89% had at least three fragments more than 2 mm in diameter. There were fresh hedgehog scats near 17% of these nests and eggshell fragments with tooth-holes at 28%. Yolk staining was seen at nests depredated during the day and the night. Hence, most of the nests that failed at night had signs similar to those at the two nests seen to have been depredated by hedgehogs and to the egg remains left by captive hedgehogs.

The tooth-holes seen in eggshell fragments at nests depredated at night resembled those attributed to hedgehogs by Green et al. (1987) and none of the tooth-holes were in the widely spaced pairs characteristic of mustelids. Another difference between the appearance of these nests and those whose failure was attributed to mustelid predation by Green et al. (1987) was the disturbance of the nest lining. This was hardly ever observed in nests depredated by mustelids (R.E. Green, unpublished data). Among the larger sample of failed nests found in the study areas, there was one failed dunlin nest in which two eggs were damaged and there were small rodent droppings. This failure was attributed to a wood mouse. One clutch was found with widely spaced, paired tooth-holes of the kind attributed to mustelids by Green et al. (1987). Rat droppings were found in several ringed plover and arctic tern (*Sterna paradisea*) nests on beaches outside the study areas. The egg remains in these nests were distinctive; a large hole had been made in the side of the egg and the inside was left yolky. No nest failures with these signs were seen in the machair study areas. There was no indication that feral cats were taking significant numbers of wader eggs and only one cat was seen on the machair during night-time searches (Table 1).

On the basis of these findings we identified the predator most likely to have caused nest failure as hedgehog if any of the following signs was present: disturbed nest lining, at least three shell fragments > 2 mm in or near to nest, single tooth puncture holes similar to those

known to have been produced by hedgehogs or the presence of fresh hedgehog scats by the nest. Depredated nests without any of these signs were attributed to other predators. Most of these nests had almost certainly been depredated by common gulls, but the possibility that mustelids removed eggs from some of the nests in this category cannot be excluded. This seems a plausible explanation for the dunlin nest, shown by the data logger to have failed at night, at which there were no eggshell fragments and no disturbance of the nest lining (Fig. 2).

### 3.4. Hedgehog surveys and mark-recapture

Hedgehog density was estimated by mark-recapture surveys on each of the three plots. Systematic searches for hedgehogs were undertaken between sunset and solar midnight on several occasions between April and August 1997 (11 searches at Ormiclate, 6 at Drimore and 10 at Loch Bee). On most occasions (67% of visits) two to four surveyors walked along adjacent parallel transect lines, until the whole plot was covered. Depending on the number of surveyors and the size of the plot, complete surveys took between one and two hours to complete. On the other occasions two surveyors made incomplete searches of a plot which lasted for approximately half the time required for a complete survey. For each visit, a record was kept of the number of surveyors and the total time each spent searching for hedgehogs.

Transects across the plots were spaced 50 m apart, except on extensive areas of flat short sward where they were spaced 75 m apart because hedgehogs were more easily seen. Surveyors scanned the ground either side of their transect, using hand-held 200,000 candle power spot lamps. None of the hedgehogs seen was able to escape and all were caught by hand. Unmarked animals were put in numbered sacks and marked at the end of the survey using individually distinct combinations of coloured heat-shrink plastic tubing attached as sleeves to five anterior dorsal spines. The colour-marks were not conspicuous, being only visible from ca. 5 m, so marked and unmarked animals were equally likely to be detected by surveyors. The identity and position of previously marked animals were noted. Animals were sexed using the criteria in Reeve (1994). Totals of 23, 23 and 19 adult hedgehogs were captured in the plots at Ormiclate, Drimore and Loch Bee respectively, and there were 27, 8 and 11 recaptures of animals marked on previous visits. Two juveniles were caught in August, but were excluded from the analysis. All other mammals, except mice, that were potential egg predators were also recorded.

Eighteen individuals, six from each plot, were also fitted with radio transmitters on the initial visits to allow the estimation of search efficiency and the probability of animals being inside the boundaries of the plot. Radio packages (15 g) covered with Velcro 'hooks'

Table 1  
Numbers of mammals, considered to be potential egg predators, seen during night-time searches of hedgehog survey plots on South Uist

Site	Hedgehog	Rat	Feral cat	Otter	Feral ferret
Ormiclate	49	2	1	0	1
Drimore	29	0	0	0	0
Loch Bee	29	0	0	3 <sup>a</sup>	2
Total	107	2	1	3 <sup>a</sup>	3

<sup>a</sup> Female with 2 cubs swimming in lake at edge of site.

were attached to a 20×35 mm area of clipped spines in the middle of the back to which a Velcro strip was glued, so that they could be quickly attached or removed. Radio-tagging did not appear to cause harm to the animals, except that one hedgehog tagged during the first search at Ormiclate was found dead soon after release. This animal was noted to be in poor condition at capture and was probably diseased. Because tagging may well have been a contributory cause of death it was excluded from the analyses.

On occasions where a full search of a plot was made, a surveyor with a radio-receiver and Yagi antenna walked around the edge of the plot, beginning about twenty minutes before the search was completed. The identity of radio-tagged hedgehogs inside the plot was determined. Typically, signal strength was sufficient to detect radio-tags from at least 1 km away.

Details of the methods used to estimate population density from the mark-recapture and radio-tracking data are given in Appendix A.

### 3.5. *Estimation of the number of wader clutches eaten by hedgehogs*

Our purpose in calculating the number of wader clutches eaten by hedgehogs per unit area, was to assess the probable contribution of wader eggs to the hedgehogs' total energy requirements. The approach adopted was first to estimate, for each wader species, the number of failed clutches produced per pair. Waders frequently make more than one breeding attempt per year because they lay replacement clutches after failure at the egg stage. Typically, breeding waders that lose a clutch, lay a replacement clutch within about two weeks (Cramp and Simmons, 1983; Green, 1988; Jackson, 1988; Berg, Lindberg and Källebrink, 1992). In calculating the mean number of breeding attempts per pair of waders, we assumed for simplicity that all pairs whose first clutches failed produced replacement clutches. In the case of lapwing, ringed plover and snipe, which have longer breeding seasons than the other species (see below and Green, 1988), we assumed that failed second clutches were also replaced. Hence, the mean number of failed clutches produced per pair per year  $M$  is given by;

$$M = (1 - S_1) + (1 - S_1) * (1 - S_2),$$

for oystercatcher, redshank and dunlin and;

$$M = (1 - S_1) + (1 - S_1) * (1 - S_2) + (1 - S_1) * (1 - S_2)^2,$$

for the other species, where  $S_1$  and  $S_2$  are the nest survival rates from the laying of the first egg to hatching for first and later clutches respectively in 1996–1997. The number of clutches that were taken by hedgehogs per pair of waders was estimated for each species as the

product of  $M$  and the proportion of clutch failures attributed to hedgehogs (see above). This quantity was then multiplied by the mean number of eggs per clutch, as observed at the last nest check at which eggs were present, to give the mean number of eggs taken by hedgehogs per pair of waders. There were too few data for the calculation of reliable site-specific estimates of  $M$ , so combined data from all sites was used. The numbers of clutches and eggs taken by hedgehogs per square kilometre at each site were then obtained by multiplying by site-specific estimates of wader density.

### 3.6. *Estimation of the energy value of wader eggs*

The mean energy ingested by a hedgehog eating the entire contents of an egg of each wader species was calculated as;

$$E \times C \times W,$$

where  $E$  is the energy value of egg contents in MJ kg<sup>-1</sup>,  $C$  is the weight of egg contents as a proportion of the total weight and  $W$  is the mean weight of the egg in kilograms. Wader species-specific values of  $W$  were taken from Cramp and Simmons (1983).  $C$  was assumed to be 0.917; the mean for eight species of Haematopodidae, Charadriidae and Scolopacidae listed by Carey et al. (1980).  $E$  was taken to be 8.02 MJ kg<sup>-1</sup> wet weight; the mean for three species of Scolopacidae listed by Carey et al. (1980).

## 4. Results

### 4.1. *Changes in wader populations*

Comparison of wader surveys at the three study sites in 1983 and 1995 shows that the estimated number of pairs of all species except oystercatcher declined (Table 2). The magnitude of population declines of the four species present at all three sites (dunlin, ringed plover, lapwing and oystercatcher) ranked in similar order in the three sites (Kendall coefficient of concordance,  $W=0.911$ ). The magnitude of the declines on the study sites and the pattern of species differences resemble those for the whole of South Uist and Benbecula (Whyte and O'Brien, 1995). The largest declines occurred in dunlin, redshank and ringed plover. The decline of lapwing was about half as severe as for the previously mentioned species and oystercatchers increased.

### 4.2. *Wader nesting success*

The results of nest monitoring in 1985–1987 and 1996–1997 reveal species differences in overall daily nest failure rate and the proportion of clutches from which

Table 2

Comparison of the estimated number of pairs of waders breeding on three machair study sites on South Uist between 1983, before hedgehogs colonised, and 1995, several years after hedgehogs colonised

Site	Wader species	No. of pairs in 1983 <sup>a</sup>	No. of pairs in 1995 <sup>b</sup>	% change
Ormiclate	Dunlin	42	7.5	–82%
	Redshank	0	0	–
	Ringed plover	54	19	–65%
	Snipe	0	0	–
	Lapwing	31	13	–58%
	Oystercatcher	11	11	0%
Drimore	Dunlin	114	33	–71%
	Redshank	19	3	–84%
	Ringed plover	73	24	–67%
	Snipe	0	0	–
	Lapwing	79	58	–27%
	Oystercatcher	50	59	+18%
Loch Bee	Dunlin	138	58.5	–58%
	Redshank	12	3	–75%
	Ringed plover	11	0	–100%
	Snipe	14	8	–43%
	Lapwing	18	11	–39%
	Oystercatcher	6	11	+83%
All sites	Dunlin	294	99	–66%
	Redshank	31	6	–81%
	Ringed plover	138	43	–69%
	Snipe	14	8	–43%
	Lapwing	128	82	–36%
	Oystercatcher	67	81	+21%

<sup>a</sup> Figures taken from the 1983 joint survey by Nature Conservancy Council and water Study Group (Fuller et al. 1986).

<sup>b</sup> Figures taken from the 1995 RSPB survey (Whyte and O'Brien, 1995).

at least one chick hatched and a marked increase in nest failure since the 1980s for some species (Table 3).

The failure rate of dunlin nests was much higher in 1996–1997 than in 1985–1987. Two-way logistic models of dunlin nest failure rate, including effects of period (1980s vs 1990s) and clutch (first clutch vs later clutches), showed a large and significant effect of period ( $\chi^2_{(1)} = 46.91$ ,  $p < 0.001$ ), but no significant effect of clutch ( $\chi^2_{(1)} = 0.37$ ,  $p > 0.50$ ). When clutch was excluded from the model, the effect of period remained highly significant ( $\chi^2_{(1)} = 51.99$ ,  $p < 0.001$ ). There was no significant interaction between period and clutch ( $\chi^2_{(1)} = 0.93$ ,  $p > 0.30$ ) and the difference in failure rate between periods was significant for first and later clutches considered separately ( $\chi^2_{(1)} = 39.11$ ,  $p < 0.001$  for first clutches and  $\chi^2_{(1)} = 8.72$ ,  $p < 0.005$  for later clutches).

In 1985–1987 the failure rate of first clutches of redshank was significantly lower than for later clutches ( $\chi^2_{(1)} = 5.18$ ,  $p < 0.025$ ), but there were too few nests to allow the separation of first and later clutches in 1996–1997. Comparing nest failure rates between the 1980s and 1990s for both clutch categories combined, there was a significantly higher failure rate in the 1990s than in the 1980s ( $\chi^2_{(1)} = 15.51$ ,  $p < 0.001$ ).

Two-way logistic models of ringed plover nest failure rate, including effects of period and clutch, showed a significant effect of clutch ( $\chi^2_{(1)} = 5.59$ ,  $p < 0.025$ ), but no significant effect of period ( $\chi^2_{(1)} = 0.68$ ,  $p > 0.30$ ). When period was excluded from the model, the effect of clutch remained significant ( $\chi^2_{(1)} = 6.31$ ,  $p < 0.01$ ). Although there was no significant interaction between period and clutch ( $\chi^2_{(1)} = 1.22$ ,  $p > 0.20$ ), the difference in failure rate between clutch categories was significant for

Table 3

Comparison of Mayfield daily failure rate and the proportion of wader nests that hatched at least one egg at Drimore in 1985–1987 and at Drimore and Loch Bee in 1996–97. There were too few data for snipe and redshank in 1996–1997 for division into first and later clutches

Wader species	Clutch	Nests	Exposure days	Failures	Daily failure rate%	Percentage of nests hatching	Standard error
<i>1985–1987</i>							
Dunlin	First	96	1233	23	1.87	59.6	6.4
Dunlin	Later	26	265	8	3.02	43.0	12.8
Redshank	First	45	683	12	1.76	59.8	8.9
Redshank	Later	12	127	7	5.51	19.3	12.0
Ringed plover	First	72	1001	41	4.10	29.7	5.6
Ringed plover	Later	42	449	33	7.35	10.9	4.2
<i>1996–1997</i>							
Dunlin	First	59	532	45	8.46	8.8	3.2
Dunlin	Later	41	349	30	8.60	8.4	3.8
Redshank	All	12	93	11	11.83	2.6	2.9
Snipe	All	5	41	3	7.32	18.8	18.1
Ringed plover	First	36	414	24	5.80	17.7	6.3
Ringed plover	Later	33	345	24	6.96	12.4	5.3
Lapwing	First	110	1005	39	3.88	30.5	5.8
Lapwing	Later	59	810	31	3.83	31.0	6.5
Oystercatcher	First	56	982	9	0.92	76.6	6.8
Oystercatcher	Later	27	440	10	2.27	51.3	10.8

1985–1987 ( $\chi^2_{(1)} = 6.39$ ,  $p < 0.01$ ), but small and non-significant for 1996–1997 ( $\chi^2_{(1)} = 0.43$ ,  $p > 0.50$ ). Hence, the failure rate of ringed plover nests was higher for later clutches than first clutches in 1985–1987, but there was no clear difference in 1996–1997. There was no significant difference in failure rates of ringed plover nests between the 1980s and 1990s.

For lapwing and oystercatcher there were no data available for 1985–1987. In the period 1996–1997 there was no significant difference in nest failure rate between first and later clutches for lapwing ( $\chi^2_{(1)} = 0.00$ ,  $p > 0.90$ ), but first clutches of oystercatcher had significantly lower failure rates than later clutches ( $\chi^2_{(1)} = 3.89$ ,  $p < 0.05$ ).

#### 4.3. Causes of wader nest failure

The causes of nest failure are compared between wader species and periods (1980s vs 1990s) in Table 4. Signs characteristic of predation by hedgehogs were not observed in 1985–1987, but hedgehog predation was a frequent cause of failure in 1996–1997. This increase in the daily rate of nest failures caused by hedgehogs was highly significant in all species (dunlin,  $\chi^2_{(1)} = 88.83$ ,  $p < 0.001$ ; redshank,  $\chi^2_{(1)} = 32.31$ ,  $p < 0.001$ ; ringed plover,  $\chi^2_{(1)} = 8.56$ ,  $p < 0.005$ ).

There was a significant increase in the rate of nest failures caused by predators other than hedgehogs between the 1980s and 1990s only for dunlin ( $\chi^2_{(1)} = 5.87$ ,  $p < 0.025$ ), though the rates for redshank and ringed plover were also higher. There were no significant differences in the rate of nest failures caused by factors other than predation between the 1980s and 1990s for any of the three species.

There was significant variation among wader species in daily rates of nest failure caused by hedgehogs in 1996–1997 ( $\chi^2_{(5)} = 108.80$ ,  $p < 0.001$ ) with the species ranking redshank > dunlin > snipe > lapwing > ringed plover > oystercatcher. During both periods 1985–1987 and 1996–1997 there was significant variation among wader species in daily rates of nest failure caused

by predators other than hedgehog (1985–1987,  $\chi^2_{(2)} = 23.88$ ,  $p < 0.001$ ; 1996–1997,  $\chi^2_{(5)} = 37.40$ ,  $p < 0.001$ ) with the species ranking ringed plover > redshank > dunlin in 1985–1987 and ringed plover > redshank > dunlin > snipe > lapwing > oystercatcher in 1996–1997. Hence, failure rates to predators other than hedgehog ranked the three wader species that could be compared in the same order in both periods. This result would be expected if the species of predators other than hedgehogs, predator behaviour and the effects of wader species-specific anti-predator behaviour on predation rates were similar in the two periods. The ranking of wader species in 1996–1997 was different for failures caused by hedgehogs and other predators. Ringed plover was the wader species most susceptible to predation by predators other than hedgehog, but only oystercatcher suffered a lower rate of predation by hedgehogs. In neither period was there significant variation among wader species in daily rates of nest failure caused by factors other than predation.

#### 4.4. Contribution of wader eggs to the daily energy budget of hedgehogs

The mean population density of adult hedgehogs, weighted for plot area, was 57.0 animals km<sup>-2</sup> (Table 5). The estimated densities varied more than two-fold among the study areas, but the upper 95% confidence limit of a plot-specific density was about six times the lower, so this is likely to represent sampling error rather than true differences among plots.

Wader species-specific estimates of the weight and energy content of wader eggs and clutches taken by hedgehogs are shown in Table 6. These estimates were multiplied by the 1995 population densities of breeding waders from Table 2 to give estimates of the number and energy content of clutches of wader eggs taken per km<sup>2</sup> by hedgehogs at each study site (Table 7). The number of wader clutches present varied substantially with date (Fig. 3). Wader clutches were most abundant

Table 4

Number of nest failures and Mayfield daily failure rates attributable to hedgehogs, other predators and other causes, such as trampling, crushing by agricultural machinery and flooding. No data are available for lapwing and oystercatcher for 1985–1987

Wader species	Period	Number of failures caused by;			Daily failure rate (%) to;		
		Hedgehog	Other predator	Other cause	Hedgehog	Other predator	Other cause
Dunlin	1985–87	0	27	4	0.00	1.80	0.27
Dunlin	1996–97	44	30	1	4.99	3.41	0.11
Redshank	1985–87	0	19	0	0.00	2.35	0.00
Redshank	1996–97	7	4	0	7.53	4.30	0.00
Snipe	1996–97	2	1	0	4.87	2.44	0.00
Ringed plover	1985–87	0	70	4	0.00	4.83	0.28
Ringed plover	1996–97	4	39	5	0.53	5.14	0.66
Lapwing	1996–97	25	35	10	1.38	1.93	0.55
Oystercatcher	1996–97	0	16	3	0.00	1.11	0.21



Table 5

The average number and density ( $\text{km}^{-2}$ ) of adult hedgehogs present at any one time in three machair plots on South Uist. Numbers are estimated using a mark-recapture model (see Appendix A). Bootstrap 95% confidence limits are shown for population densities, but these could not be estimated for females at Drimore

Survey plot	Males			Females			All adults		
	No.	Density	95% C.L.	No.	Density	95% C.L.	No.	Density	95% C.L.
Ormiclate	8.5	28.3	14.2–77.1	6.3	20.9	4.9–36.8	14.8	49.3	13.1–85.3
Drimore	23.8	33.5	13.1–110.3	30.7	43.2	–	54.5	76.7	–
Loch Bee	6.5	15.5	4.8–49.0	5.8	13.7	5.0–46.0	12.3	29.2	15.0–71.7
All	38.7	27.1	8.1–47.3	42.7	27.0	–	81.5	57.0	–

Table 6

Estimates of the weight and energy content of wader eggs, the mean number of eggs taken by predators per clutch and the mean number of clutches taken per pair of waders (see Methods)

	Egg weight (g per egg)	Energy content per egg (MJ)	Final clutch size (eggs)	Energy content per clutch (MJ)	Clutches taken by hedgehogs per pair	Energy content of clutches taken by hedgehogs per pair (MJ)
Dunlin	10	0.080	3.47	0.278	1.03	0.286
Redshank	22	0.176	3.30	0.588	1.22	0.709
Ringed plover	12	0.096	2.86	0.275	0.18	0.050
Snipe	17	0.136	3.80	0.517	1.34	0.693
Lapwing	26	0.209	3.53	0.738	0.54	0.397
Oystercatcher	47	0.377	2.60	0.980	0.00	0.000

Table 7

Number and energy content of wader clutches estimated to be taken per year by hedgehogs at the three study sites and the approximate percentage of hedgehog energy requirements obtained from wader eggs during spring and early summer

	Number of clutches per $\text{km}^2$			Energy (MJ) per $\text{km}^2$		
	Ormiclate	Drimore	Loch Bee	Ormiclate	Drimore	Loch Bee
Dunlin	11.8	17.2	109.0	3.3	4.8	30.5
Redshank	0.0	1.9	6.7	0.0	1.1	3.9
Ringed plover	5.3	2.2	0.0	1.5	0.6	0.0
Snipe	0.0	0.0	19.5	0.0	0.0	10.1
Lapwing	10.8	15.8	10.8	7.9	11.7	7.9
Oystercatcher	0.0	0.0	0.0	0.0	0.0	0.0
Total	27.9	37.1	146.0	12.7	18.2	52.4
Clutches or MJ per hedgehog	0.57	0.48	5.0	0.26	0.24	1.79
Percentage of hedgehog energy	–	–	–	0.8	0.7	5.5

between mid-April and mid-June, when all species were breeding. We calculated the proportion of the hedgehogs' energy requirements met by wader eggs during a period when their importance in the diet is likely to have been greatest. We assumed that all eggs were eaten during a period of 65 days between Julian dates 105–170 and that each adult hedgehog needed to ingest food with an energy content of 0.5 MJ each day (Wroot, 1984). Hence, the total requirement per square kilometre during the period mid-April to mid-June was

taken to be  $65 \times 0.5 = 32.5$  MJ multiplied by the estimated population density of adult hedgehogs. Obviously this calculation is an approximation and tends to overestimate the contribution made by wader eggs to hedgehog energy requirements because not all of the eggs consumed were taken in the 65 day period and the energy costs of hedgehog reproduction were ignored. Even so, the estimated proportion of the energy requirements of hedgehogs was found to be low (mean 2.2%, range 0.7–5.5%; Table 7).

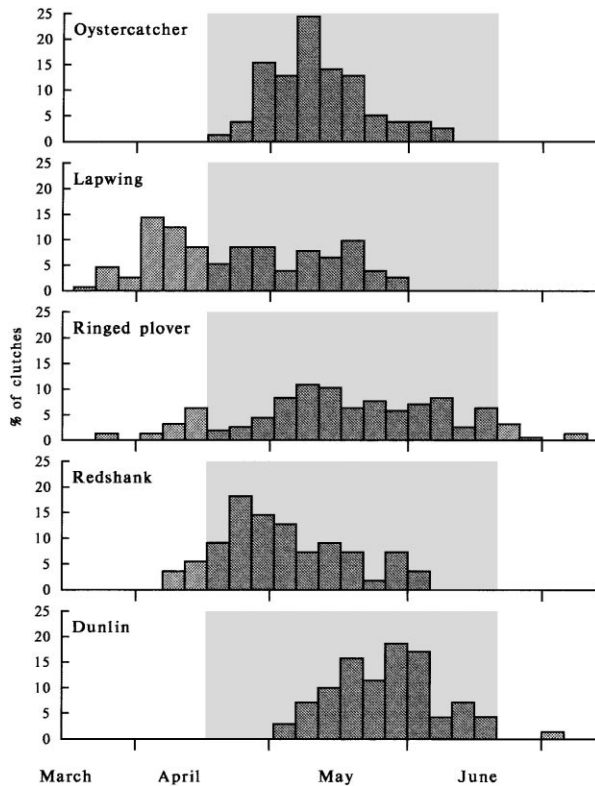


Fig. 3. Distribution of first egg laying dates of five wader species by 5-day periods of Julian date. Numbers of clutches for the species (from top to bottom) are 78, 153, 80, 55 and 70. The shaded area shows the period Julian date 105–170 used in the calculation of the contribution of wader eggs to the energy requirements of hedgehogs (see text).

#### 4.5. Wader population trend in relation to hedgehog predation

An obvious hypothesis about the causation of the decline in wader populations in South Uist is that the increased predation caused by hedgehogs has reduced the number of young fledged per pair of waders and that this has not been compensated for by density-dependent increases in the survival of immatures or adults or immigration from other areas. If this hypothesis is correct, it would be expected that the wader species showing the largest population declines would be those that suffer the highest rates of nest failure due to egg predation by hedgehogs. A test of this hypothesis is shown in Fig. 4, in which the ratio of the population of each species of wader on all of the study areas combined in 1995 is plotted against the estimated proportion of the clutches started that were taken by hedgehogs in 1996–1997. The results for oystercatcher, lapwing, snipe, dunlin and redshank are in accord with the hypothesis that hedgehog predation has caused the wader declines, but the datum for ringed plover is a clear exception. The population of this species has declined markedly even though only a small proportion of ringed plover clutches was taken by hedgehogs. This species also stands out in having the highest nest failure

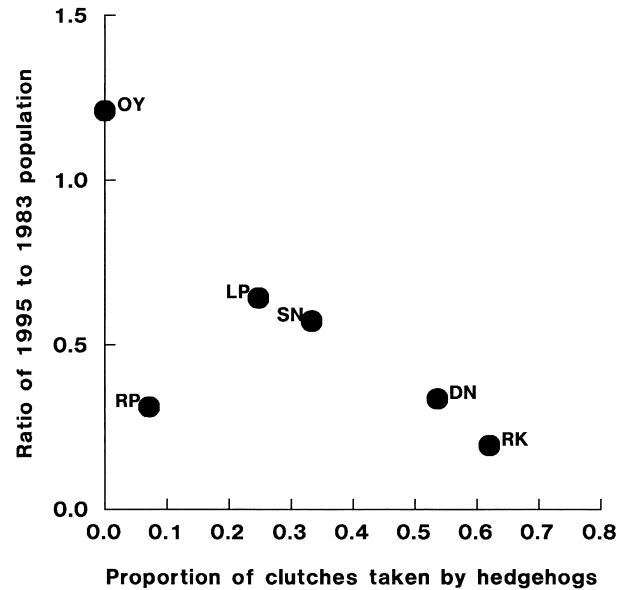


Fig. 4. Ratio of the population of waders in the three study areas combined in 1995 to that in 1983 in relation to the proportion of clutches started that were taken by hedgehogs in 1996–1997. Two-letter codes denote wader species (OY = oystercatcher, RP = ringed plover, LP = lapwing, DN = dunlin, RK = redshank, SN = snipe).

rate in 1985–1987. Hence, the correlation across wader species between population change and the proportion of clutches taken by hedgehogs was not quite statistically significant ( $r = -0.689$ , one-tailed  $p = 0.065$ ).

## 5. Discussion

### 5.1. Reliability of the identification of hedgehog predation of wader eggs

Reliable identification of the causes nest failure is fundamental to this study and its conclusions. Fortunately, the signs remaining after a clutch was eaten by a hedgehog were found to be distinctive. There are three other pieces of evidence supporting the diagnosis of egg predation by hedgehogs. The first is that depredated nests with the characteristic signs were not recorded during 1985–1987, before hedgehogs colonised the study areas. Second, such signs were not recorded in 243 wader nests monitored in 1997 on hedgehog-free machair sites in North Uist (RSPB, unpublished data). Third, in hedgehog enclosure trials in South Uist in 1998, signs of hedgehog predation were absent (infrequent) in areas in which hedgehogs were removed (reduced) (Jackson, 1999).

### 5.2. Differences among wader species in susceptibility to hedgehog predation

The observed differences between species in the rates of loss of eggs to hedgehogs probably result from a

combination of nest defence behaviour and avoidance. The oystercatcher, the largest species with the most vigorous nest defence, is probably sufficiently aggressive to defend its nest from hedgehogs. The next largest and most aggressive species, the lapwing, may also be able to do this in some circumstances. The smaller redshank, snipe and dunlin do not attack predators vigorously and rely upon concealing the nest in vegetation as their main defence against egg predation (Dyrce et al., 1981; Cramp and Simmons, 1983). Ringed plovers suffer low egg losses to hedgehogs even though they are small and relatively timid. It may be that ringed plover benefit from nesting on large expanses of bare or partly vegetated dry ground, in particular on ploughed land, stubbles and fallow. Hedgehogs were seldom seen in these habitats, perhaps because invertebrate prey are scarcer there than on undisturbed, vegetated ground.

### 5.3. Hedgehog density

The estimation of the population density of hedgehogs is made difficult by their relatively large home-ranges, nocturnal habits and the possibility of concealment in vegetation and rabbit burrows. Accurate estimation of numbers requires that allowance is made for animals that are not detected during a survey. Standard Cormack-Jolly-Seber (CJS) methods can be used for this. However, unless the study area was very large or covered all the habitat of a closed population, density would be overestimated because some of the animals estimated to be alive would actually be temporarily absent from the survey plot whilst elsewhere in their home range. This study appears to be the first in which radio-tagged hedgehogs have been used to in combination with CJS to estimate separately both search efficiency and the proportion of animals that are within the study plot.

The mean density of 57 adult hedgehogs  $\text{km}^{-2}$  for machair habitat estimated by this study is broadly similar to densities reported elsewhere in Britain. However, we suspect that hedgehog densities on the South Uist machair may actually be higher than is typical for the British mainland. Reeve (1981) estimated ca. 83 hedgehogs  $\text{km}^{-2}$  on a 0.4  $\text{km}^2$  suburban golf course in London, Morris (1988) estimated ca. 30  $\text{km}^{-2}$  on a 0.55  $\text{km}^2$  rural grassland site on the Isle of Wight, Hampshire, and Doncaster (1992) estimated ca. 24  $\text{km}^{-2}$  in rural Oxfordshire. However, at least some of these study areas may have been selected because they held unusually high densities of hedgehogs and none of the studies attempted to overcome the biases arising from failing to detect individuals and animals not being present within the study site at all times. In at least one study (Morris, 1988), juvenile hedgehogs (born that year) were included. The only other estimate from an island, North Ronaldsay in Orkney, found a density similar (ca. 52 animals  $\text{km}^{-2}$ ) to the average for South Uist (Warwick, cited in Reeve, 1994).

Hedgehog population density is thought to be influenced by predation, road deaths, food supply, parasites, weather and the availability of resting sites and hibernacula. Doncaster (1992) and Micol et al. (1994) showed that hedgehog densities in southern England were correlated with the predation risk from badgers (*Meles meles*). The red fox (*Vulpes vulpes*) is the only other significant wild predator of hedgehogs, though in suburban areas pet dogs also kill many. Motor vehicles are a frequent cause of death (Arnold, 1993). Road deaths and predation may limit hedgehog densities in many parts of England (Doncaster, 1992).

Badgers and foxes do not occur in the Uists (Corbet and Harris, 1991), and the machair has few roads with light traffic. Hence, it is likely that predation and road death rates in Uist are significantly lower than on mainland areas and this may contribute to the high hedgehog densities on the machair. The fact that no radio-tagged individuals died from these causes during the study supports this, and contrasts with radio-tagging studies in southern England which report substantial mortality (e.g. Doncaster, 1992, Morris et al., 1993). The fertile invertebrate-rich habitats, the abundance of rabbit burrows for day refuges and hibernacula, and the mild winter climates in the Uist are all likely to benefit hedgehogs.

### 5.4. Total hedgehog population of South Uist

If the mean density of 57 adults  $\text{km}^{-2}$  found in this study is typical, then a crude estimate can be made of the hedgehog population size on South Uist. Machair covers ca. 35  $\text{km}^2$  of the island, which is now completely colonised by hedgehogs (Angus, 1993; Watt, 1995). This suggests a population size of ca. 2000 adults on the machair of South Uist. In addition there are ca. 90  $\text{km}^2$  of blackland and 130  $\text{km}^2$  of hill and moorland on South Uist. Hedgehog densities on these habitats have not been measured, but the impression gained by fieldworkers is that densities on blackland are about half those found on machair. Densities on moorland are likely to be much lower but road casualties confirm that hedgehogs use this habitat. On this basis, there are likely to be approximately an additional 2500 adults on blackland zone and, perhaps, a few hundred more on the moorland zone of South Uist. This would give an approximate total population for South Uist approaching 5000 adults. On a similar basis there may be ca. 1600 adults on Benbecula, and a few hundred in the southern part of North Uist.

### 5.5. Importance of wader eggs to hedgehogs

This study demonstrates that wader eggs only contribute a small proportion of the energetic requirements of hedgehogs living on the machair of South Uist. It also seems unlikely that hedgehogs require eggs as a

source of calcium, because the machair shell sand supports many calcium-rich prey, such as snails, and because hedgehogs did not usually eat much of the eggshell. Analysis of hedgehog scats also indicates that eggs are not a large component of the hedgehog's diet. Proctor (1998) found eggshell in 13% of 64 scats collected during the wader breeding season from the hedgehog survey plots. A similar rate of occurrence of eggshell in scats (11%) was found by Watt (1995) in a sample of 242 scats collected on South Uist machair. In both these studies, eggshell only formed a small proportion of the contents of scats in which it was present. Arthropods, molluscs and earthworms were the main prey.

#### 5.6. Hedgehog predation on wader chicks

There was no evidence that hedgehogs take significant numbers of wader chicks. Wader chicks are precocial and leave the nest a few hours after hatching. Hence, it seems likely that they would usually be capable of escape if found by a hedgehog. However, young chicks may be vulnerable to hedgehogs, particularly before they leave the nest. A hedgehog that was being radio-tracked was seen to kill and eat a small oystercatcher chick. The analysis of hedgehog scats from South Uist by Watt (1995) indicated that wader chicks were occasionally taken by hedgehogs. Remains of chick down not in association with egg shell were found in 3% ( $n = 242$ ) of the scats.

#### 5.7. Hedgehog predation as a cause of wader population declines

The large declines in most species of waders recorded on the three study sites between 1983 and 1995 resemble the wider picture for the South Uist and Benbecula (Whyte and O'Brien, 1995). The drastic decline in the nest success of some species over the same period suggests that poor hatching success, caused by hedgehog predation, is the cause of the population changes. Loss of eggs to hedgehogs is a new and important cause of breeding failure for dunlin, redshank, lapwing and snipe. Comparison of estimates of dunlin, redshank and ringed plover chick survival made on South Uist in the 1980s and 1990s show that there were no significant changes. Chick survival was generally high in both periods (Jackson, 1988; RSPB, unpublished data). The level of hedgehog predation on ringed plover nests seems too low to explain the decline of this species, and the failure rate of ringed plover nests to all causes was found not to be significantly higher in the 1990s than in the 1980s.

#### 5.8. Impact of hedgehog introductions on bird populations of other islands

Hedgehogs have been introduced to many other islands besides the Uists, and are reported to be serious

predators of bird eggs at some of these. The breeding success and populations of Arctic terns and ringed plovers are reported to have declined on island of North Ronaldsay Orkney following the introduction of hedgehogs (H. Warwick, *pers comm*). Similarly, on the island of Wangerooge in the German Waddensee hedgehogs were introduced around 1960 and soon afterwards redshank and tern populations declined markedly (Grosskopf, 1989). Introduced hedgehogs also pose a risk to endemic ground-nesting birds in New Zealand where they were responsible for significant losses of banded dotterel (*Charadrius bicinctus*) clutches (Sanders, 1997). Heavy hedgehog predation on the eggs of colonial birds, e.g. black-headed gulls (Kruuk, 1964), and little terns (*Sterna albifrons*) (R. Cryer *pers comm*), has been identified previously at several sites. However, there are no previous studies that quantify the impact of hedgehog predation.

#### 5.9. Prospects for the conservation of wader populations in the Outer Hebrides

The small contribution of wader eggs to the diet of hedgehogs is a guide to the likely intensity of predation by hedgehogs on wader nests in the future. If wader eggs had been found to be an important component of hedgehog diet, it would be expected that the population density of hedgehogs on machair would fall if wader numbers and the availability of eggs continued to decline. If this was the case, then the risk of hedgehog predation might fall as wader density declined. The consequent higher nest success might lead to stabilisation of wader populations, though at a lower level. However, it seems more likely that the density of hedgehogs on the machair is not determined by the abundance of waders and that high levels of hedgehog predation will continue and may result in the local extinction of the more susceptible wader species. Hedgehogs are now widespread on South Uist and Benbecula and are in the process of colonising North Uist. It seems probable that populations of susceptible waders in North Uist will decline if hedgehogs spread throughout the island.

An important gap in our study is that we did not measure hedgehog density and wader nest success on blackland. This habitat, a mixed shell sand/peat zone inland from the machair, is known to hold significant numbers of breeding waders, especially redshank and snipe. Work on blackland study areas is now in progress and will be reported elsewhere. The impact of hedgehog predation on the nesting success of other ground-nesting birds in the Uists has not been studied. The islands hold one-third of the UK population of the corncrake (*Crex crex*) (Green, 1995). However, studies on the island of Coll (Argyll, Scotland), where introduced hedgehogs are present, did not find evidence of hedgehog predation on their eggs (Green et al., 1997).

The decline of the Uist wader population is a major conservation problem. This paper provides strong, though circumstantial evidence that hedgehog predation has been at least a partial cause. Studies in progress on the effects upon wader nesting success of hedgehog exclusion suggest that wader productivity would improve substantially if hedgehog predation could be prevented (D.B. Jackson, unpublished data). This appears to be the first documented case of hedgehogs threatening an internationally important bird population with regional extinction. The result of hedgehog introductions on island bird populations elsewhere needs to be more widely appreciated and legislative and practical measures taken to prevent the introduction of hedgehogs to the few remaining hedgehog-free islands in north-west Europe.

## Acknowledgements

This study would not have been possible without the help and co-operation of the many people who live and work on the Uists. Particular thanks are due to thecrofting townships, South Uist Estate, MoD Hebrides Royal Artillery Range, Norman MacAskill, David Buckland and John Love. Alex Turner and Lucy Gilbert are thanked for all their hard work and long hours collecting field data. The numerous people who gave up spare nights to help with the hedgehog surveys are thanked, in particular Gill Key. Karin Klauss is thanked for translating one of the cited German papers. Nigel Reeve is thanked for providing data on hedgehog density and his general advice on studying hedgehogs. Many colleagues in RSPB are thanked for their help behind the scenes in many ways, in particular, Gwen Evans, Ian Bainbridge, Anita McClune and Ellen Kelly and her team. Ian Bainbridge and David Gibbons are thanked for their helpful comments on an earlier draft of this paper. RSPB gratefully acknowledges the financial assistance from Scottish Natural Heritage towards the 1997 hedgehog research.

## Appendix A

### *Hedgehog mark-recapture models and population estimates*

Analyses of combined data from recapture searches and radio-tag checks were carried out to estimate the parameters of a model describing the chance that a marked animal would be alive and present in the study area and that it would be identified during a search. The daily probability of survival of marked animals  $s$  was treated as being constant through the study period. Survival between two searches on dates  $t_1$  and  $t_2$  was given by  $s^{t_2-t_1}$ . The

conditional probability  $w$  of a marked animal being detected during the search, given that it was alive and present in the study area, was modelled as;

$$w = m^*(1 - \exp(-c^*F)),$$

where  $F$  is searching effort in person-minutes and  $c$  and  $m$  are constants.

This formula assumes that  $w$  increases with increasing search effort; the difference between  $m$  and  $w$  declining exponentially with effort. Such a relationship, with  $m < 1$ , might be expected if a proportion  $1-m$  of animals remain hidden during the search period. The relationship between recapture probability and effort was treated as being constant through the study period.

It was assumed that there was a probability  $k$ , which did not vary over time, that an animal was within the study plot during the search and not temporarily in part of its home range outside the plot. Hence, the overall probability  $p$  that a marked animal with at least part of its home range in the study area was recaptured during a search was given by;

$$p = k*m^*(1 - \exp(-c^*F)).$$

The probability of the recapture history of each animal was specified as described in the statistical appendix of Clobert et al. (1985) in terms of the parameters  $s$ ,  $c$ ,  $m$  and  $k$ . Logarithms of these probabilities were summed over individuals to obtain the log-likelihood of the observed histories. Maximum-likelihood estimates of  $s$ ,  $c$ ,  $m$  and  $k$  were obtained numerically by iteratively maximising the log-likelihood of the data under the assumed model using a quasi-Newton method. The information from radio-marked animals allowed  $k$  and  $m$  to be estimated separately; otherwise only the product  $k*m$  would have been identifiable.

Models were fitted which assumed either that a particular parameter took the same value across all study areas, or that there was a value specific to each area. The possibility that some parameters differed between the sexes was also considered. When the model included effects on the same parameter of both area and sex, they were combined by assuming that the effect of sex was additive after logit transformation, e.g.

$$\text{logit}(m_{lf}) = \text{logit}(m_{lm}) + g$$

Where  $m_{lm}$  and  $m_{lf}$  are values of  $m$  for Ormiclate (study area 1) for males and females respectively and  $g$  is a constant.

A range of mark-recapture models with different plausible assumptions about variation in parameters between sexes and among plots were compared were compared by likelihood-ratio tests (Clobert et al., 1985) on the associated deviances  $[-2*\log_e(\text{likelihood})]$  and

the Akaike Information Criterion (AIC) (Akaike, 1974). This index penalises models with large numbers of fitted parameters by adding twice the number of parameters to the deviance. The model with the smallest AIC value is preferred. Comparison of models (Table 8) gave no indication of variation among plots in survival  $s$  or the slope  $c$  of the relationship between conditional recapture probability and search effort (likelihood-ratio tests; Models B vs A,  $\chi^2_{(2)} = 0.02$ ,  $p > 0.90$ ; Models C vs A,  $\chi^2_{(2)} = 0.58$ ,  $p > 0.70$  respectively). However, there was significant variation among plots in the asymptote  $m$  of the relationship between conditional recapture probability and search effort and the probability  $k$  of a surviving animal being present within the plot (Models D vs A,  $\chi^2_{(2)} = 6.64$ ,  $p < 0.05$ ; Models E vs A,  $\chi^2_{(2)} = 8.05$ ,  $P < 0.02$ ). The reduction in deviance resulting from the inclusion of differences between the sexes in  $m$  and  $k$  was not significant by a likelihood-ratio test (Models J vs F,  $\chi^2_{(2)} = 4.25$ ,  $p = 0.13$ ). However, the model that included sex differences (J) had the lowest value of the Akaike Information Criterion and was therefore selected as the most appropriate model.

The estimates of the parameters of Model J are shown in Table 9. The estimate of  $s$  indicated that no mortality occurred during the study period. A similar conclusion was reached when other models were fitted. The lowest estimated value of  $s$  (from Model G) was 0.999983 which would result in an expected mortality of only 0.2% during the period May–August inclusive (123 days; the 4-month

period spanning most of the study). The conclusion is supported by the results from radio-tagging. A total of 18 animals (nine males and nine females) was radio-tagged, including some outside the study plots, and monitored for a total of 1,005 animal-days. No tagged animals were found dead, so this approach also yields an estimate of  $s = 1$ . This excludes one male that died within one day of tagging. The lower exact binomial 95% confidence limit for this estimate of  $s$  is 0.9963 [p.103 of Diem (1962)], equivalent to 37% mortality during May–August.

A potential source of bias in studies of survival using radio-tagging is that the signals from some tagged animals are lost. This may be due to a defective tag, detachment of a tag underground where a signal is difficult to detect or emigration from the area searched. However, if the animal is not seen again the possibility that it died underground or was killed by a predator that also damaged the tag cannot be excluded. Most tags were still attached and operating at the end of the study (8), found detached in circumstances that did not suggest predation (4) or removed by the researchers during a recapture (3). Only three tagged animals were lost to follow-up during the study period because a signal could not be found. These could easily be cases of tag failure or migration, but even if they were all associated with death of the tagged animal, the estimate of  $s$  would be 0.99701, equivalent to 31% mortality during May–August.

According to Model J, the asymptotic probability of an animal present in the study area being captured during a search was lower for females than males, the odds being a factor of 2.7 lower. However, females were more likely than males to be inside the study area rather than temporarily absent; the odds of a female being present being 3.9 times higher than for a male (Table 9).

The mean number of animals of each sex present in a study area during a search was calculated by dividing the total number of records, summed over all searches, by the sum over all searches of the expected values of  $w$  for that sex and study area calculated from Model J. Allowance

Table 8  
Comparison of mark-recapture models used to describe observations of marked and radio-tagged hedgehogs during searches of three study areas<sup>a</sup>

Model	Model specification				Number of parameters	Deviance	AIC
	$s$	$c$	$m$	$k$			
A	C	C	C	C	4	319.55	327.55
B	A	C	C	C	6	319.53	331.53
C	C	A	C	C	6	318.97	330.97
D	C	C	A	C	6	312.91	324.91
E	C	C	C	A	6	311.50	323.50
F	C	C	A	A	8	305.67	321.67
G	C	A	C	A	8	310.70	326.70
H	C	C	A&S	A	9	304.98	322.98
I	C	C	A	A&S	9	304.41	322.41
J	C	C	A&S	A&S	10	301.42	321.42

<sup>a</sup> Each model is specified according to the treatment of the parameters  $s$  (daily survival),  $c$  (slope of the relationship of recapture probability to search effort),  $m$  (asymptotic recapture probability) and  $k$  (probability of surviving animal being within the study area during a search). Where a parameter was assumed not to vary among study areas or between sexes it is labelled C. Variation among plots is indicated by A. A&S indicates that a parameter was assumed to vary among study areas and that there was also a difference between sexes which was the same in all plots after logit transformation. The number of fitted parameters, the deviance and the Akaike Information Criterion are also shown.

Table 9  
Estimates of the parameters of the mark-recapture Model J (see text and Table 8)

Parameter	Plot	Symbol	Estimate		
			Male	Common	Female
Daily survival		$s$	1.0000		
Slope of recapture prob vs effort		$c$	0.0131		
Asymptotic recapture probabilities for plots	Ormiclate	$m_1$	0.523		0.288
	Drimore	$m_2$	0.154		0.063
	Loch Bee	$m_3$	0.365		0.175
Probabilities of animals being within plots	Ormiclate	$k_1$	0.491		0.791
	Drimore	$k_2$	0.851		0.957
	Loch Bee	$k_3$	0.324		0.654

was made for a male which died as a consequence of being radio-tagged during the first search at Ormiclate by adding  $\Sigma(k_s * t_i - t_1)$ , summed over visits  $i = 2$  to  $i = 11$ , to the total number of records of males on that study area. The method assumes that the probability of capture of an unmarked animal was the same as for a marked individual that had been captured previously. The estimates of mean numbers present per visit were converted to population densities by dividing them by the area of each plot. The average population density in all plots was obtained by dividing the sum of the estimates of the mean number of animals present per visit by the combined area of the three plots. The 95% confidence interval for a density estimate was taken to be the range of the central 950 of 1000 estimates derived from bootstrap samples. The recapture histories of individual animals were resampled, with the number of times a particular history was included in the bootstrap sample being generated by a random Poisson variable with a mean value of 1. This method allowed the total number of animals captured to be subject to sampling variation. The mark-recapture model was then fitted to the bootstrap sample and the parameter estimates used to calculate the population density as described above. The bootstrap procedure failed for females at Drimore because the small number of recaptures available for this plot led to unrealistically low recapture probabilities and high population estimates for some bootstrap samples. Hence no confidence limits for the density of females or both sexes combined are available for this plot.

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