Waders, hedgehogs and machair: research and conservation lessons from the Outer Hebrides

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In 1974, the hedgehog, a medium-sized insectivore native to the UK mainland and most of Europe, was deliberately introduced to one of the islands in the Outer Hebrides, Scotland. The impact of these animals on the island's internationally important breeding waders was studied by monitoring wader populations, measuring nesting success, identifying causes of nest failure and through a predator removal experiment. It was concluded that egg-predation by hedgehogs had caused large population declines in four wader species.

Studies of the hedgehogs suggested that they find nests incidentally whilst foraging for invertebrates and that there is unlikely to be a density-dependent relationship between nest density and the risk of hedgehog predation. There are considerable practical difficulties in tackling the hedgehog problem and achieving successful long-term wader conservation. Challenges include preventing hedgehogs from spreading to parts of the islands they have not yet colonised and, where they are present, reducing their density to levels that allow wader productivity to increase sufficiently to allow population recovery.

The story of waders and hedgehogs in the Outer Hebrides contains a number of lessons of wide application. In particular, it underlines the dangers of introducing to islands species that may be native on the nearby mainland and which, at first sight, appear to pose no serious risk to island wildlife.

INTRODUCTION

The negative impacts of introduced mammal predators to island bird communities presents a major world-wide challenge to bird conservation. Although the most celebrated losers in this process are island endemics and seabirds (Atkinson 1996), serious impacts to breeding waders are being increasingly demonstrated (Jackson & Green 2000, Dowding & Murphy 2001). Given that some Southern Hemisphere wader species are confined to islands, and that large numbers of widespread Northern Hemisphere species breed on islands, the issue of predator introductions to islands should be considered as one of the "big issues" facing wader conservation in the 21st century.

This paper summarises the main results of research into the impact of a recently introduced mammal predator, the hedgehog *Erinaceus europaeus*, on the internationally important wader populations breeding on the Uists in the Outer Hebrides of Scotland. The stories of the Uist waders and hedgehogs and the ongoing attempts to address the birds' conservation needs, provide some valuable lessons. These should be particularly helpful in assessing the threats to waders from introduced mammals and finding solutions elsewhere.

BACKGROUND: LIFE BEFORE HEDGEHOGS

One of the largest concentrations of breeding waders in Europe occurs on the 250 km^2 coastal plain lying along the west side of the islands known as the Uists. The Uists comprise South Uist, Benbecula and North Uist and certain adjacent smaller islands and are linked by tidal strands and man-made causeways. On these islands, the combination of soils derived from wind-blown shell sand, a cool, wet, windy climate and low-intensity crofting agriculture has resulted in the development of the habitat known as "machair". This consists of a mosaic of dry and damp semi-natural grasslands, marshes and standing water and is ideal breeding habitat for six wader species. These are dunlin *Calidris alpina*, ringed plover *Charadrius hiaticula*, common redshank *Tringa totanus*, common snipe *Gallinago gallinago*, Eurasian oystercatcher *Haematopus ostralegus* and northern lapwing *Vanellus vanellus*. The first full wader survey of the Uists in 1983 estimated that these six species totalled at least 17,000 pairs (Fuller *et al.* 1986), including about 25% of the total UK populations of ringed plover and dunlin.

The Uist breeding grounds are of very high conservation value, in particular because wader densities are exceptionally high compared to those reported from other areas (densities frequently exceed 100 pairs km^{-2}). Apart from the otter *Lutra lutra* (a species that forages almost exclusively in water and poses no threat to waders), the Uists have no native mammal predators, and this is probably one of the key factors allowing high breeding wader densities to be achieved. Over the years, humans have introduced several mammal predators, namely rat *Rattus norvegicus*, cat *Felix domesticus*, polecat ferret *Mustelo furo*, European hedgehog and American mink *Mustela vison*. Most of these introduced predators have been present on the Uists for a long time, but two are recent arrivals. The hedgehog was introduced to South Uist in 1974 and mink were first noted on North Uist in 2000, having colonised from islands to the north where they escaped from

Table 1. The estimated change in wader populations between 1983 and 2000.

Species	South Uist and Benbecula	North Uist and adjacent islands
Redshank	–41%	+51%
Lapwing	–31%	+24%
Snipe	–57%	– 2%
Dunlin	–56%	–30%
Ringed plover	–56%	–49%
Oystercatcher	+21%	+55%

fur farms in the 1950s. A study of the breeding biology of dunlin, redshank and ringed plover made on South Uist in the mid-1980s showed that these waders generally enjoyed high breeding success and that the populations were flourishing (Jackson 1988, 1994). This study took place before hedgehogs became properly established and has since been invaluable in providing baseline information against which later changes could be assessed. The study was also important because it showed that the waders were thriving alongside rats, feral cats, and polecat ferrets.

THE SPREAD OF HEDGEHOGS

For about ten years after their deliberate introduction to the south end of South Uist in 1974, hedgehogs were restricted to within a few kilometres of the release site and they were relatively few in number (Morton 1982, Jackson *et al.* in press). This means that the 1983 wader survey took place before hedgehogs could have had any significant effect on wader populations. After this, hedgehogs spread north relatively rapidly and by the early 1990s they were present along the length of South Uist and Benbecula and had even colonised the southern part of North Uist (Angus 1993). This rapid spread was almost certainly aided by humans, particularly the colonisation of southern North Uist (Jackson *et al.* in press). Today, ten years later, the distribution of hedgehogs on the Uists is little changed. They are common throughout South Uist and Benbecula, particularly in machair habitats, but, apart from a small and somewhat isolated area in the south, they are absent from North Uist and its adjacent islands (Jackson *et al.* in press).

WADER DECLINES

The first evidence that all was not well for the Uist's waders, came from the results of routine monitoring undertaken by the Royal Society for the Protection of Birds (RSPB) in 1995 (Whyte & O'Brien, 1995). This showed that numbers of some species on South Uist and Benbecula had declined by 30–60% since the 1983 survey. This result came as a surprise. At this stage, the reason for the decline was unknown and so research was started by the RSPB the following year.

A comprehensive wader survey in 2000 allowed a detailed assessment to be made for each species of the spatial pattern of population change since 1983 (Jackson *et al.* in press). The most striking aspect of this analysis is the marked north–south divide in how wader numbers have changed (Table 1). Overall, waders in the northern part of the breeding grounds (North Uist and adjacent small islands) have fared much better than those in the southern part (South Uist and Benbecula). Numbers of dunlin, redshank, snipe and lapwing have each undergone large to moderate declines in the south, whereas in the north their numbers have either increased (lapwing and redshank) or declined by much less (dunlin and snipe). Ringed plover show a different pattern, having undergone large declines everywhere although slightly more so in the south. Oystercatchers also show a different pattern, with the species increasing in all areas. However, the size of the increase has been nearly three times greater in the north.

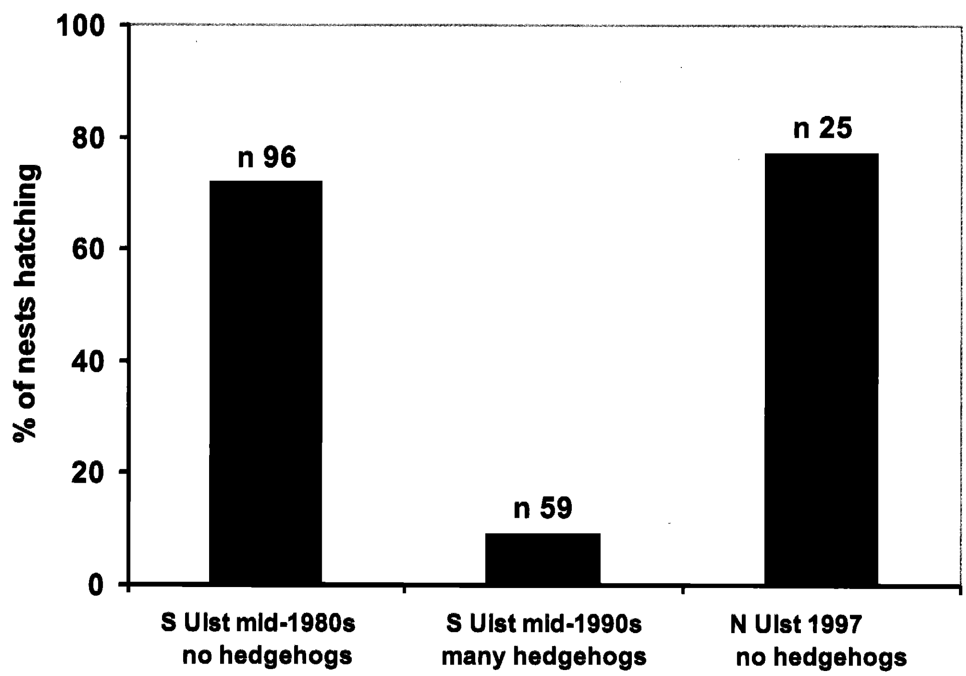

Fig. 1. Dunlin hatching rates in the Uists in relation to the presence of hedgehogs. Nest survival rates were calculated using the Mayfield Method.

Plate 1. Hedgehog eating lapwing eggs. Introduced in 1974, the hedgehog is now common across large parts of the Outer Hebrides and a major predator of wader eggs.

Plate 2. Colour-ringed *schinzii* race dunlin breeding in machair habitat in the Outer Hebrides. Dunlin are one of the species that that has undergone large declines because of egg predation by hedgehogs.

The north–south difference in the way wader numbers have changed reflects the distribution of hedgehogs, i.e. hedgehogs are present throughout the southern areas and absent in the northern areas (Jackson *et al.* in press). However, by itself, this is purely circumstantial evidence that the two may be connected.

DECLINE IN NEST SUCCESS

A pilot study by Scottish Natural Heritage (SNH) in 1995 into the possible impacts of hedgehogs found that some hedgehog scats contained fragments of wader eggshell (Watt 1995). Of course, showing that hedgehogs sometimes eat wader eggs did not mean hedgehogs were the cause of the wader declines. Far more evidence was required to quantify what impact, if any, hedgehogs were having.

Large numbers of wader nests were monitored in 1996/97 at sites on South Uist (where hedgehogs were common) and North Uist (where hedgehogs were absent) and nest survival rates calculated. For three species (dunlin, redshank, and ringed plover) it was possible to compare these values to corresponding measures made on the same South Uist sites in the mid-1980s, before hedgehogs established.

The 1990s nest survival rates for three species that had undergone large declines on South Uist (dunlin, redshank and snipe) were very low (10–20%) in South Uist and relatively high in North Uist. Furthermore, for the three species where a comparison could be made, the mid-1990s South Uist nest survival rates were much lower than they had been in the mid-1980s (Jackson & Green 2000). These differences are well illustrated by the nest survival rates for dunlin (Fig. 1).

Mid-1990s nest survival rates for oystercatcher, the only species that has not declined in South Uist were high on both South Uist and North Uist. Lapwing nest survival in the mid-1990s was moderate on South Uist, where this species had undergone moderate population decline, and high on North Uist, where numbers had increased. Finally, mid-1990s nest survival rates for ringed plover, the species that had declined throughout the islands, were low in both North Uist and South Uist. They also show that for all six species there is a strong positive correlation between recent population change and nest survival (Jackson & Green 2000).

CAUSE OF DECLINE IN NEST SUCCESS

Accurate identification of the cause of nest failure was essential to determine the relative importance of different nest predators and other causes of failure. On the South Uist study sites, observations during daylight and spot-lamp surveys at night showed that there were few candidate predators present, and that two species were much more frequently seen than others, namely common gulls *Larus canus* (during daytime) and hedgehogs (at night). Nest predation events by gulls and hedgehogs were witnessed on several occasions and signs remaining at the nest sites were examined (Jackson & Green 2000). It was found that the signs left by these two predators are very different and distinctive. Gulls leave behind an empty undisturbed nest, whereas nests taken by hedgehogs have a very disturbed lining and there are always remains of eggshells in the vicinity. Furthermore, these shell fragments are always licked clean, typically have chewed edges or teeth holes and sometimes two or three half-eggshells are stacked inside one another. Additional evidence linking the signs left behind with the exact time of nest failure was obtained using data-loggers set up to record nest temperature every few minutes. The loggers showed that all but one of the nine losses ascribed to gulls occurred during daylight and all 17 of the losses ascribed to hedgehogs occurred at night (Jackson & Green 2000). It was possible, therefore, to identify the cause of almost all nest failure events with confidence.

On the basis of the signs left at failed nests, it was estimated that on South Uist in the mid-1990s, hedgehogs were responsible for at least 60 % of the nest failures of dunlin, redshank and snipe and 35% of lapwing nest failures. However, hedgehogs appeared to be the cause of only about 10% of ringed plover and oystercatcher nest failures (Jackson & Green 2000, RSPB unpublished data).

HEDGEHOG REMOVAL EXPERIMENT

A predator removal experiment was conducted on South Uist in 1998 (Jackson 2001). The main purpose of this was to test the results of the nest-monitoring studies and to show that conservation measures could be worthwhile. The experiment consisted of making two large exclosures using hedgehog-proof fencing before the start of the wader nesting season and removing all hedgehogs from within. Dunlin and lapwing nest hatching rates inside the exclosures were then compared with those in adjacent control areas and also with rates for the previous year at the same sites. The experiment showed that hatching rates were approximately 2.4 times higher in the absence of hedgehogs (Jackson 2001).

HEDGEHOG FEEDING ECOLOGY

The nature of the predator–prey relationship between hedgehogs and waders has important implications for predicting how waders may fare in the future and for designing effective conservation measures. The observed high rate of egg loss to hedgehogs, superficially suggests that hedgehogs are capable nest-finders and that eggs are an important part of their diet. However, research into the feeding ecology of Uist hedgehogs indicates otherwise. Based on the estimated number of eggs lost and the density of hedgehogs present, Jackson and Green (2000) calculated that wader eggs contributed only 2–5% of the energy intake of hedgehogs during the wader nesting-season. Similarly, eggshell fragments were found in about 2% of hedgehog droppings at this time of year. Thus, wader eggs are of little importance to hedgehogs and there is no expectation that hedgehogs will be short of food without eggs.

There are two methods that hedgehogs could use to locate nests: on the one hand they could actively look for nests; alternatively they could come across them passively during their normal foraging for invertebrates. To discover which method they use, Uist hedgehogs (n=18) were fitted with radio tags and beta-lights (a small dimly glowing phosphorous light) so that they could be followed all night without disturbing them. This study found no evidence of hedgehogs searching for eggs, but on several occasions hedgehogs that were foraging normally for invertebrates were observed encountering a nest and then eating the eggs (RSPB unpublished data). A small sample of hedgehogs tracked, using the "line-and-spool" technique, was observed to pass by nests only a few metres from their routes (RSPB unpublished data). Therefore, it appears that hedgehogs need to be very close to a nest before they can detect it. Exactly how close is not known (and it is probably influenced by wind and humidity), but it is probably less than one metre. Thus it seems that hedgehogs are not expert nest finders. So why are so many nests lost to hedgehogs?

Three factors combine to explain why so many wader nests are found by hedgehogs. These are the relatively large distance travelled each night by hedgehogs, high hedgehog densities and the relatively long period that eggs are at risk (the laying and incubation periods combined for these waders is about 27 days). The all-night tracking of Uist hedgehogs showed that, on average, males travel about four kilometres each night during their foraging and females about two kilometres (RSPB unpublished data). If, on average, a hedgehog can only detect nests within 0.5 m of its foraging route then males would effectively "search" an area 4 km × 1 m, and females half this. Survey work has shown that the instantaneous hedgehog density on the Uist machair is typically around 30 animals km^{-2} and that the sex ratio is approximately 1:1 (Jackson & Green 2000, RSPB unpublished data). Based on these figures, the accumulated distance travelled by foraging hedgehogs each night in a hypothetical 1-km square of the wader nesting grounds would be 90 km. If each animal's route is random relative to the routes of others (which appears to be the case) then 8.6 % of the ground would be effectively "searched" each night.

This calculation of the theoretical daily risk of nest detection is similar to the *ca.* 5–7% daily loss rates to hedgehogs observed on South Uist for nests of dunlin, redshank, and snipe (Jackson & Green 2000). The above calculation, however, is simplistic because it does not take into account habitat selection by hedgehogs and birds and relies on a number of uncertain assumptions, for example the effective search with of hedgehog routes. Nevertheless, it is probable that it correctly describes the basis of the risk and its approximate magnitude. Habitat selection very likely explains why ringed plovers suffer fewer losses to hedgehogs than the other small wader species. In the Uists, ringed plovers nest mainly on bare sandy habitats such as ploughed ground and recent fallow (last season's cereal stubble), habitats that hedgehogs generally avoid when foraging (RSPB unpublished data).

If, as is almost certainly the case, hedgehogs come across wader eggs by accident and eggs are of trivial importance to them, then density-dependent negative feedback is not to be expected in this predator–prey relationship. Unlike the risk posed by a predator that hunts for prey and switches to alternative prey when low density makes hunting unprofitable (as, for example, in the case of gulls feeding on wader eggs) the theoretical risk posed to wader eggs by hedgehogs will not diminish as wader nest density declines. The risk is purely a function of hedgehog density and how far they travel. This has important implications for conservation. First, it is theoretically likely that hedgehogs will cause continuing wader declines and could possibly cause the local extinction of some species (Jackson & Green 2000). Second, to be effective, conservation measures will need to greatly reduce hedgehog density on the wader breeding grounds.

TOWARDS A SOLUTION

It is beyond the scope of this paper to describe in full the process and ongoing work aimed at wader conservation on the Uists. The Uist Wader Project, a partnership between The Scottish Executive, Scottish Natural Heritage (the government conservation agency) and RSPB was formed in 2000 to develop and deliver conservation measures. Large areas of the Uists are designated as Special Protection Areas for breeding waders under the European Union's Birds Directive, and the UK Government is obliged to maintain populations within these areas in a "favourable conservation status".

Preventing further hedgehog spread in North Uist is the top priority and this is being attempted by erecting barrier fences and trapping and removing hedgehogs. Ultimately, the objective is to achieve wader population recovery throughout the Uists. The feasibility of reducing hedgehog densities, and of total removal, will be investigated through practical trials and continued detailed research into Uist hedgehog demography, habitat use and dispersal.

Conservation work is still at an early stage and it will be some years before the likelihood of success of different options can be fully evaluated. It is already clear that the sheer size of the islands (750 km^2), the difficulty of detecting and catching hedgehogs when at low density and their high fecundity and dispersal rates make it unlikely that total removal can be achieved with current technology. However, reducing hedgehog densities to levels compatible with waders (say an 80% reduction) should be relatively straightforward. The drawback of this approach is that it requires a perpetual effort and will therefore become very expensive in the long run. Furthermore, any conservation gains would soon be lost if (as is likely) this effort ceased in the future. Perpetual control could help "buy time" whilst new techniques that make total removal feasible are developed, such as immuno-sterilization.

In the UK, hedgehogs have a high positive public profile. As a result, the issue of hedgehogs and waders has attracted considerable media attention and there is significant public concern for the welfare and fate of Uist hedgehogs. These concerns, together with the partial legal protection afforded to hedgehogs, significantly constrain the range of techniques available for controlling them and have caused delays in starting conservation work. (At the time of writing, six years after it was shown that hedgehogs are a major problem, no hedgehog control has yet taken place although work will commence on North Uist in 2003.) This contrasts to the situation for American mink, a species that has been demonised by the media. Large-scale lethal control of mink started on the Uists within a few months of their first detection.

CONCLUSIONS

The spatial and temporal coincidence between hedgehog colonisation and wader declines, together with the data on the extent and causes of nest failure and the results of the hedgehog removal experiment show that the introduction of hedgehogs has had a large negative impact on four wader species. However, hedgehogs do not appear to be a major direct factor in the decline of the ringed plover. The reasons for the decline in this species are not fully understood but are probably linked to land management and changes in the severity of egg-predation by gulls (see Jackson *et al.* in press).

The nature of the predator–prey relationship between hedgehogs and waders suggests that the risk of egg-predation by hedgehogs is unlikely to be modulated by direct density-dependence and that the risk is simply a function of hedgehog density. If this is so, there is a high likelihood that, without conservation measures, some wader species will decline further and may even become locally extinct. Contrary to this rather pessimistic forecast, there is some evidence that in recent years the rates of decline on South Uist and Benbecula have slowed and some species may have even stabilised (Jackson *et al.* in press). This may be because egg predation risk is locally modulated by habitat composition and scale (in ways that are not yet fully understood) or because density-dependent effects are acting on other egg predators or at other stages of the waders' life cycle.

Apart from oystercatcher, Uist breeding waders do not presently have a favourable conservation status. Large-scale, long-term conservation work will be required to restore and safeguard these populations. Although tackling the hedgehog problem is a top priority, this alone will not be sufficient. Of equal importance is making sure that the unique machair habitat mosaic of the Uists is maintained and appropriately managed by traditional crofting.

The story of the Uist waders contains a number of useful lessons:

1. The value of baseline information. Without the 1983 surveys and mid-1980s data on wader breeding success, it would have been much harder to demonstrate the impact of hedgehogs on waders and make the case for conservation action. It is likely that many of the effects of predator introductions go unnoticed because there are no baseline data.
2. The value of routine monitoring. At the time of the 1995 surveys, no one suspected there was a problem, despite considerable bird watching activity on the islands and some areas being nature reserves.
3. The benefits of multiple evidence. The case that introduced hedgehogs have caused large deleterious impacts to Uist waders is compelling because it is based on several lines of evidence: the timing of hedgehog spread, the spatial and temporal changes in wader populations, the declines in wader hatching rates, the proportion of nests lost to hedgehogs, a predator removal experiment and studies of the predator's feeding ecology. Initially many people were sceptical that hedgehogs, a species with the reputation of a "harmless insectivore", could cause such a large impact. The removal experiment has been particularly valuable, as it tested the conclusions of the nest survival study and practically demonstrated the value of hedgehog removal. The multiple evidence was also important in demonstrating that hedgehogs are not the direct cause of declines in ringed plover.
4. The importance of understanding the nature of the relationship between predator and prey. The expected lack of direct density-dependent effects between nest density and predation risk has important implications.
5. The importance of knowing the "enemy". A thorough understanding of Uist hedgehog biology is a key element underpinning the current development of conservation solutions.
6. The importance of public opinion. Public concern for the welfare of well-liked "problem" species, like the hedgehog, can constrain and delay control measures.
7. The dangers of introducing to islands, mammals from the nearby mainland. Hedgehogs are native on the UK mainland and there is no legislation prohibiting their introduction to parts of the UK where they are not native, such as islands.

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REFERENCES

Angus, S., 1993. Hedgehogs in the Western Isles in 1991. *Hebridean Naturalist* 11: 73–76.

Atkinson, I.A.E., 1996. Introductions of wildlife as a cause of species extinctions. *Wildlife Biology* 2: 135–141.

Dowding, J.E. and Murphy, E.C., 2001. The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. *Biol. Cons.* 99: 47–64.

Fuller, R. J., Reed, T. M., Buxton, N. E., Webb, A., Williams, T. D. and Pienkowski, M. W., 1986. Populations of breeding waders Charadrii and their habitats on the crofting lands of the Outer Hebrides, Scotland. *Biol. Cons.* 37: 333–361.

Jackson, D.B., 1988. Habitat selection and breeding biology of three species of wader in the Western Isles of Scotland. Unpublished Ph.D. thesis, University of Durham.

Jackson, D. B., 1994. Breeding dispersal and site-fidelity in three monogamous wader species in the Western Isles, UK. *Ibis* 146: 463–473.

Jackson, D.B., 2001. Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *J. App. Ecol.* 38: 802–812.

Jackson, D.B. and Green, R. E., 2000. The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on the machair in South Uist, Scotland. *Biol. Cons.* 93: 33–348.

Jackson, D.B., Fuller, R.J. and Campbell, S.T., *in press*. Long-term population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to an introduced mammalian predator. *Biol. Cons.*

Morton, E., 1982. Hedgehogs in South Uist. *Hebridean Naturalist* 6: 46–47.

Watt, J., 1995. *Hedgehogs and ferrets on the South Uist machairs; a pilot study of predation on ground nesting birds.* Unpublished report, Scottish Natural Heritage, Inverness, UK.

Whyte, C. and O'Brien, M., 1995. *Changes in the number of waders breeding on machair habitats on the Uists and Benbecula, 1983–1995.* Unpublished report, Royal Society for the Protection of Birds, Edinburgh.