

Predation studies on breeding waders of the Uist machair: Final report covering fieldwork undertaken in 2012-14





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COMMISSIONED REPORT

Commissioned Report No. 811

Predation studies on breeding waders of the Uist machair: Final report covering fieldwork undertaken in 2012-14

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COMMISSIONED REPORT

Summary

Predation studies on breeding waders of the Uist machair: Final report covering fieldwork undertaken in 2012-14

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Breeding waders; hedgehog predation; Uist Machair; dunlin; redshank; ringed plover; lapwing.

Background

The west coast habitats of the Uists hold concentrations of breeding waders that are exceptional in Scottish, British and wider European contexts. Observed declines in wader populations on South Uist and Benbecula since the 1980s were argued to be largely due to predation of clutches by hedgehogs, which were first introduced to the islands in 1974. This argument, supported by evidence derived from experimental and observational studies, led to an ongoing programme of hedgehog removal.

Concern remained however that breeding populations of some waders did not show the signs of recovery that might be expected in response to hedgehog control. In 2011, SNH commissioned a consortium (British Trust for Ornithology, the James Hutton Institute and MacArthur Green Ltd) to provide specialist scientific advice to SNH's Uist Wader Research (UWR). The consortium produced a scoping document with prioritised modular options for a 2012-14 research programme to assess the influence of a range of factors (including predation, habitat, land use, invertebrate availability) on the breeding waders on the Uists' machair. UWR decided to focus on predation-related measures using fixed point observations, nest temperature loggers, nest cameras and, in 2014 only, transects recording wader behaviour. Fieldwork, undertaken and managed by SNH, was in two broad study areas selected to represent the extremes of hedgehog abundance on the Uists: North Uist (Baleshare, Balranald and Berneray) where hedgehogs were absent or at low density and South Uist (Cill Donnain to Aird a' Mhachair) where hedgehogs were abundant. The principal aims of the study was to quantify the importance of predation by hedgehogs relative to that by other predators which would assist a consideration of the likely effectiveness of continued and enhanced removal of hedgehogs in maintaining and restoring the breeding wader populations.

Main findings

- The study provides further evidence for an ongoing impact on breeding success of wader nest predation by introduced hedgehogs on the Uist machair, at least some of which is additional to that of gulls on wader chicks.

- In North Uist (low density of hedgehogs) clutch survival rates were higher than on South Uist (high density of hedgehogs): Dunlin, 0.73 compared to 0.32; Lapwing 0.55 compared to 0.32; Redshank 0.44 compared to 0.11; Ringed Plover 0.37 compared to 0.26. Overall, in North Uist, 74% of wader nests (n = 117) where outcome was confirmed, successfully hatched chicks. In South Uist only 45% of nests (n = 174) where outcome was confirmed successfully hatched chicks. Most observed losses in both areas were due to predators.
- Hedgehogs were the most numerous nest predator identified using nest cameras and other evidence (32 confirmed instances compared to 29 by all other predators combined) with all confirmed instances of predation by hedgehogs occurring in the 'high hedgehog density' areas. In the high hedgehog density areas, hedgehogs were responsible for 35% of nest failures.
- 45% of clutch incubations ended during darkness in high hedgehog density areas compared to 29% in low density areas which is consistent with a hypothesis that nocturnal predation by mammals is more prevalent in high hedgehog density areas.
- Wader clutches in low hedgehog density areas tended to be laid earlier than in high density areas, as indicated by egg flotation to gauge stages of incubation at the start of nest monitoring. This could be indicative of more replacement clutches (and therefore higher levels of predation) in high hedgehog density areas and/or flexible behavioural responses by the birds in which individuals capable of nesting earlier can select to breed in areas of lower predation risk.
- Despite this, measured wader clutch incubation durations (using nest temperature loggers) were on average 57 hours longer in low hedgehog density areas than in high hedgehog density areas which is suggestive of higher clutch predation levels in areas of high hedgehog density.
- Although avian predators (gulls, raptors and corvids, which are diurnal predators) were recorded most frequently in the high hedgehog density areas (potentially confounding any assumptions that higher predation levels were directly associated with hedgehogs) there were no differences detected in the frequency of predation attempts by avian predators (measured by fixed point observations throughout the season) between the areas.
- The number of successful attacks by avian predators witnessed during fixed point observations was small (24 in three years) compared to the number of avian predator observed (22,860 discrete observations) but crude extrapolations suggest they could be important predators of breeding waders. More successful avian predation events were recorded in low hedgehog density areas (n = 15) than in high hedgehog density areas (n = 9), despite lower abundance of avian predators in the low hedgehog density areas.
- A lower proportion of waders (redshank, ringed plover and dunlin) showed behaviour indicative of having dependent young in low hedgehog density areas (15%) than in high hedgehog density areas (38%) in June and early July and the average rate of change in that proportion over a six-week period suggested a more rapid decline in the low hedgehog density areas. This, if representative of an index of chick survival, along with a higher number of attacks by avian predators (mostly gulls) directly observed, could be consistent with a hypothesis that predation by hedgehogs and other (predominantly avian) predators is to some degree complementary rather than being completely additive. Such an interpretation should be treated with caution however, because of a low sample size of direct observations and a difference in the pattern of changes in proportions of recorded behaviour which could be associated with differences in laying dates between study areas.
- Population models (which included quite a few uncertainties) suggested a greater influence of chick predation (which was principally by gulls) than of egg predation on predicted population changes. However, reducing clutch predation levels to those recorded in low hedgehog density areas did result in a positive change in the modelled predicted population trajectory.

- Modelling suggests that clutch and brood survival both need to be greater than 33% for wader populations to increase. Amongst the four principal study species, this was achieved by redshank only under a low hedgehog density scenario; the only species that has generally increased on the Uists over recent decades.

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Table of Contents	Page
1. INTRODUCTION	1
1.1 General background	1
1.2 Developing the research programme for 2012-14	2
2. METHODS	4
2.1 Study sites and species priorities	4
2.2 Measuring clutch survival	5
2.3 Identification of clutch predators and successful hatching	6
2.3.1 Diurnal distribution of incubation termination	6
2.3.2 Evidence for clutch predators and hatching	6
2.4 Fixed point observations: daylight predators and disturbance	7
2.5 Behaviour recording transects: a chick survival index	9
2.6 Habitat recording	10
2.7 Population modelling	11
3. RESULTS	13
3.1 Hatching success of study nests	13
3.2 Clutch survival assessed using temperature loggers	13
3.3 Identification of clutch predators	14
3.4 Occurrence of daylight predators and other disturbance	14
3.4.1 Daylight predator occurrence rates	14
3.4.2 Predation rates	14
3.4.3 Human disturbance rates	15
3.5 Changes in agitation behaviour by breeding waders: chick survival index	15
3.6 Population models	15
4. DISCUSSION	17
4.1 Relative importance of hedgehogs as nest predators	17
4.2 Relationships between clutch and brood predation	17
4.3 Predation as a driver of population change	19
4.4 Potential further research	20
REFERENCES	21
ANNEX 1: TABLES	23
ANNEX 2: FIGURES	34

1. INTRODUCTION

1.1 General background

The west coast habitats of the Uists, Benbecula and islands in the Sound of Harris, hold concentrations of breeding waders that are exceptional in Scottish, UK and wider European contexts. In 1983 this region (hereafter referred to as ‘the Uists’) was estimated to hold approximately a third and a quarter of the UK breeding populations of dunlin *Calidris alpina* and ringed plover *Charadrius hiaticula* respectively (Fuller *et al.*, 1986). By 2000, however, overall and widespread losses of approximately 50% in both the ringed plover and dunlin populations had occurred. By contrast, oystercatcher *Haematopus ostralegus* numbers had increased in all areas, showing an overall rise of nearly 40%. Other species did not show such uniform trends across all the islands. Redshank *Tringa totanus* and lapwing *Vanellus vanellus* both declined on South Uist but increased on North Uist. Snipe *Gallinago gallinago* also declined on South Uist and Benbecula but showed no change on much of North Uist (Jackson *et al.*, 2004).

A repeat survey of the Uists’ breeding wader populations in 2007 showed that, overall, the decline of ringed plover had levelled off and the rate of decline in dunlin numbers had also slowed to some extent (Fuller *et al.*, 2010). However, the latest repeat survey in 2014 suggests a continued decline for both species (unpublished data). In addition, redshank numbers have increased since 2000, notably on North Uist and even on South Uist and Benbecula, thus partially reversing the previously reported declines on the latter two islands. Lapwing also increased on South Uist and Benbecula between 2000 and 2007, again at least partly reversing the decline there between 1983 and 2000. The most recent 2014 survey suggests a subsequent decline in lapwing that was most marked on South Uist and Benbecula.

Causes of these changes in breeding numbers are unclear, but strong evidence based on a combination of hedgehog exclusion experiments and large-scale surveys of waders implicated hedgehog *Erinaceus europaeus* depredations of wader eggs as an important factor in declines. Hedgehogs were first introduced to South Uist in 1974 (Jackson, 2007) but by the mid 1990s they had extended their range to the southern end of North Uist (Jackson *et al.*, 2004). Experimental work carried out in 1998 on South Uist demonstrated that in areas where hedgehog densities were manipulated to virtually zero, the hatching success of the combined suite of species dunlin, lapwing, redshank and snipe – these species being especially vulnerable to hedgehogs – was 2.4 times higher than in comparable areas where hedgehog densities remained high (Jackson, 2001). Consequently the observed declines in populations of these species between 1983 and 2000 on South Uist and Benbecula were argued to be largely due to predation of clutches by hedgehogs (Jackson and Green, 2000; Jackson *et al.*, 2004). The spatial patterns of change in wader populations between 1983 and 2000, as reported by Jackson *et al.* (2004), were broadly consistent with the hypothesis that predation by hedgehogs was a major factor causing declines in some populations of some wader species.

In response to the declines in wader populations, SNH established the ‘Uist Wader Project’ in 2000 (renamed ‘Uist Wader Research’, UWR, in 2011), with the aim of “reducing the hedgehog population across the Uists to a level that allows waders to fully recover”. By 2003 a programme of hedgehog removal on North Uist had begun, which was extended in 2004 to include Benbecula; and work continues to date. There is concern, however, that the numbers of some of the species of waders have not returned to the levels recorded during earlier periods when hedgehog densities are likely to have been relatively low. While a possible reason could be lack of enough time for population recovery, other factors, in addition to predation by hedgehogs, may also be limiting wader numbers and slowing or even preventing recovery.

Although the evidence for the negative impacts of hedgehog predation appeared compelling, attributing declines in the numbers of breeding waders on the Uists to a sole cause is acknowledged to be an oversimplification of a complex system where a range of factors is likely to be operating (Fuller and Jackson, 1999; Calladine *et al.*, 2014). For example, numbers of both redshank and lapwing on South Uist were higher in 2007 compared to 2000, despite the lack of a formal hedgehog trapping programme during that period (although a bounty scheme to encourage hedgehog removal did operate from 2003-2006). Both redshank and lapwing subsequently declined again by 2014, though they were still present at higher numbers than in the 2000 survey (unpublished data). Furthermore, several locations in the Sound of Harris and North Uist, which have never supported hedgehogs, have experienced declines in lapwing, ringed plover and dunlin (Fuller and Jackson, 1999; Calladine *et al.*, 2014).

Immediately preceding and concurrent to the removal of hedgehogs, was a programme to remove American mink *Neovison vison*, another non-native predator, from Uist (Iain Macleod *pers. comm.*). Thought to have been both more widespread and present at higher densities on North Uist than on South Uist, an eradication programme removed the majority of mink between 2001 and 2003 (Iain Macleod *pers. comm.*). Any apparent response by breeding waders to the control of hedgehogs after 2003 could also have included an influence of the removal of mink. However, because of the timing of mink removal relative to that of the hedgehog control programme, it is unlikely that mink would have been responsible for any absence of response in wader numbers to the hedgehog removal.

In 2011, SNH commissioned a consortium (British Trust for Ornithology (BTO), the James Hutton Institute (JHI) and MacArthur Green Ltd) to provide specialist scientific advice to UWR. The consortium produced a scoping document suggesting options for a research programme during 2012 – 2014 to assess the influence of a range of factors on the breeding wader populations on the Uists' machair (Humphreys *et al.* 2012).

1.2 Developing the research programme for 2012-14

Humphreys *et al.* (2012) proposed a number of modular research options designed to assess a range of factors that were likely to influence breeding waders on the Uists' machair. For the 2012 breeding season, each module was prioritised according to the practical likelihood of delivery of applicable outputs for UWR. Provisional future options were also presented with the caveat that these would need to be further refined to take account of the findings, both biological and practical, of the initial 2012 season.

High priority options for the 2012 season included the use of nest cameras, temperature loggers and fixed point daytime observations to record predation events directly, plus associated recording of vegetation structure, land use and habitat classification. Medium priority options included the use of counts of adult to young ratios at the end of the breeding season (as a proxy of breeding success) and invertebrate sampling (as a measure of food availability). Options ranked as low priority included radio-tracking chicks (as a measure of breeding success), checks of bird predator nest contents and wader chick growth measurements (the latter as a proxy of habitat quality).

UWR chose to undertake the high priority options (nest cameras, temperature loggers and fixed point observations) in the 2012 breeding season, together with some land use and habitat recording associated with those direct measures of predation. However, fieldwork in 2012 failed to meet intended sample sizes for any of the three priority options, and so interpretation of the data from that year was compromised (Calladine *et al.*, 2012). The same suite of fieldwork and data collection was undertaken in the 2013 season with increased manpower to overcome logistical issues encountered in 2012 (Calladine *et al.*, 2013). Following a successful season of data collection in 2013, a similar fieldwork

programme was repeated in 2014 with the primary aim of increasing sample sizes with the potential to assess inter-annual differences.

This final report describes the fieldwork undertaken in the three breeding seasons, 2012-14, and presents analyses and interpretation of the data to assess the role of all predators in influencing the breeding success of waders on machair and associated habitats. In particular, this study aimed to assess:

- a) The relative importance of wader nest losses to hedgehogs and other predators;
- b) How predation rates on waders differ between areas with high hedgehog densities and areas with low hedgehog densities;
- c) The evidence as to whether predation by hedgehogs was additive or compensatory to that by other predators;
- d) Likely impacts of different levels of predation on wader population changes.

2. METHODS

2.1 Study sites and species priorities

Given that the role of nest predation by hedgehogs had already been established (e.g. Jackson & Green, 2000), two study areas were selected: (i) one at each of the two presumed extremes of the gradient of hedgehog densities found within the Uists (see below); (ii) each supporting a representative range of machair and associated habitats; and (iii) each supporting densities of waders sufficient to achieve target numbers of nests to be monitored.

Priority nests for study were those of dunlin, ringed plover, redshank, and lapwing. The decision was made to also include any snipe nests that were found but not to deploy nest cameras (see Section 2.3) on them (principally because sample sizes were always likely to be low and also because their recent population trends in the Uists are least well known because of inherent difficulties in monitoring them; Fuller & Jackson, 1999). Although oystercatcher nests were included in the 2012 sample, they were excluded in 2013-14 because of their lesser status of conservation concern (British populations, including those on the Uists, generally having increased), the lesser relative importance of their machair breeding populations in national and international terms, their somewhat different breeding behaviour (adults actively feed the young), and the observations from previous work that hedgehogs rarely take oystercatcher eggs.

Dunlin and ringed plover were given the highest priority amongst the study species (in terms of effort allocated to find their nests) because their populations on the Uists have declined most markedly and due to their relative (national and international) importance. Redshank nests were included to potentially provide an interesting 'control' for dunlin in that they have similarly concealed nests but their populations on the Uists have increased. Further, given widespread declines in numbers of breeding redshank in Britain (Balmer *et al.*, 2013; Malpas *et al.*, 2013), the relative importance of the population on the Uists will have increased. Lapwings were also included to ensure sufficient sample sizes to study predation; that species being the most numerous and their nests being the easiest to find.

In 2012, two initial study areas were selected: (1) Baleshare (ca. 364 ha of an island off the west of North Uist), as an area with no (or extremely low densities of) hedgehogs; and (2) Bornish (ca. 996 ha on South Uist between the townships of Staoinebrig and Cill Donnain), as an area where hedgehogs have not been controlled and their densities are expected to be high (Figure 1). To increase sample sizes of the higher priority species, an additional 787 ha around Balranald were included in 2013-14 and 550 ha of Berneray in 2014 (no or low hedgehog density on North Uist/Sound of Harris), and the Baleshare study area was extended to 785 ha in 2013-14. The high hedgehog density South Uist study area was also increased (to 2225 ha) in 2013-14 by northward extension to Aird a' Mhachair (Figure 1).

Within all study areas, three complementary methods were employed to record predation events: nest temperature loggers; nest cameras; and fixed point daytime observations. In 2014, behaviour-recording transects were introduced as an additional attempt to quantify differences in losses during the chick-rearing period. Written protocols for field methods for the SNH employed fieldworkers were produced for the start of the field season.

The presumption of contrasting hedgehog densities was tested in late 2013 using a combination of footprint monitoring tunnels, camera traps and searches using sniffer dogs at Balranald, Baleshare and South Uist. Although hedgehogs were detected (and removed) from the Balranald area, encounters by all methods were lower there and at Baleshare than at South Uist confirming the original assumption (Charles Thompson unpublished data).

2.2 Measuring clutch survival

Temperature loggers (commercially available ThermoChron iButtons) were placed in 1233 nests (56 in 2012, 466 in 2013 and 711 in 2014). Each logger was programmed to record temperature every 30 minutes (or 15 minutes for 41 loggers in 2012), sealed in plastic and placed below the eggs within the nests. All loggers were anchored by wire threads into the soil at the base of the nests in 2013-14, to reduce incidence of displacement from nests. Data and loggers were retrieved from 1018 nests (29 in 2012, 394 in 2013 and 594 in 2014; Table 1). Most loggers were retrieved in July to minimise disturbance to waders during the sensitive breeding season. The relocation of loggers was facilitated by use of high-precision hand-held GPS units and, where necessary, a metal detector. The temperature traces downloaded from the loggers were used to identify the date and time when incubation ceased, thereby recording either when eggs hatched or were taken by predators. The point of incubation ending was taken as when a clear diurnal cycle of temperature variation commenced (see Figure 2).

Generalised Linear Models (GLMs; all statistical analyses used the program SAS v9.2 unless otherwise stated) were used to test for any differences in the duration of incubation between the two study areas. Two approaches were used: (a) a comparison of measured incubation durations that permits the inclusion of all usable data collected from the temperature loggers; and (b) a comparison of clutch survival rates that was restricted to nests with known clutch outcomes (hatched or failed).

For approach (a) we hypothesized that if a higher proportion of clutches was lost, for example due to predation, at one site relative to the other, then the recorded duration of incubation would be less. In the model, incubation duration (in hours) was the dependent variable. Independent factors were: study area ($n = 2$, as a proxy of hedgehog density); wader species ($n = 6$); the first tier habitat classification ($n = 3$, see Section 2.6); distance to the nearest neighbouring habitat type (as a continuous variable); the start date of nest monitoring (annual Julian date as a continuous variable); year ($n = 3$); and whether the nests were monitored using cameras or not ($n = 2$). The original models included the four interaction terms: (i) habitat * site; (ii) species * habitat; (iii) start date * site; and (iv) camera * start date. The models used a normal distribution and identity link function (Kolmogorov-Smirnov test for normality $D = 0.08$, $P < 0.01$).

Although the data included in the analysis that considered all incubation data did not appear to violate the assumption of a normal distribution (see above), this is effectively a 'time to survival analysis' and the use of a normal distribution may be considered inappropriate. As an alternative approach we used a Mayfield binomial GLM (Aebischer, 1999) restricted to clutches of known outcome. Success or failure to hatch (a binomial variable), with the number of hours for which a clutch was monitored as the binomial denominator, was the dependent variable. The same explanatory variables as in the more inclusive model (approach (a)) were included and the model used a binomial distribution and logit link function.

Wader species was included in the models to account for inter-specific differences in the incubation periods. As well as habitat classification (to assess any associations of clutch survival with the habitat supporting the nest), the nearest distance to a neighbouring habitat was included as a proxy for habitat heterogeneity within the vicinity of a nest (though it should be acknowledged that this may not necessarily be representative of how waders perceive habitat heterogeneity). Distances to neighbouring habitats were determined using GIS as the nearest distance between the plotted location of a nest (determined in the field using hand-held GPS) and the boundary of the plotted polygon representing wader habitats (see Section 2.6). The measured incubation period would be influenced by the date when the loggers were first placed in nests. If placed later during incubation, then the recorded

period would be less. Inclusion of the start date within the models would account for such variation and the start date * site interaction terms would suggest if there was any systematic bias in logger deployment. Inclusion of whether or not nest cameras were deployed aimed to assess whether the additional disturbance or marking of nests (with a visible camera) could have had a measurable influence on clutch survival, with the associated interaction recognising that cameras would have been deployed on the earlier nests of target species that were found.

Nest contents were recorded at the time of logger deployment and the stage of incubation was categorised using the egg floatation method (Mabee *et al.* 2006). An egg was placed into a container of water and its buoyancy and float angle recorded. Early incubation (category A) was recorded if the egg rested on the bottom of the container. Late incubation (category C) was recorded if the egg floated and partly rose above the water surface. Mid incubation (category B) was recorded if the floatation was intermediate between the two extremes (after Mabee *et al.* 2006). Contingency (Chi-square) tests were used to identify any systematic differences in the stages of incubation at the start of nest monitoring between study areas that might confound the incubation durations recorded by data loggers.

2.3 Identification of clutch predators and successful hatching

2.3.1 Diurnal distribution of incubation termination

It was expected that most predation of clutches by mammals would occur at night. If predation by mammals was more prevalent at one site than at the other, then one expected consequence would be that a greater proportion of incubations would terminate at night. Contingency (Chi-square) tests were used to test for differences between the two study areas in the incidence of incubation termination during darkness.

2.3.2 Evidence for clutch predators and hatching

Motion-triggered video cameras (most, and the most successfully deployed, were commercially available Bushnell Trophycams), each with night and day-vision capabilities, were placed overlooking 283 wader nests (6 in 2012, 134 in 2013 and 143 in 2014) across both study areas (Table 2); 32 camera units were available and these were redeployed to different nests after outcomes were known. The video images captured were used to specifically identify nest predators and also to confirm successful hatching. These were also used to confirm the assumption that most predation by mammals occurred at night (see Section 2.3.1).

Using one or more of: (a) captured video images; (b) the examination of nest contents when retrieving temperature loggers; and (c) direct observations, the outcomes of monitored clutches were recorded as: (i) hatched; (ii) predated; (iii) lost to cultivation; (iv) otherwise failed; or (v) unknown. For each of the first four categories, the outcomes were defined as either confirmed or probable depending on the quality of evidence. Outcomes were classed as confirmed in cases where there was supporting video or direct observational evidence and also where any remaining nest contents provided irrefutable evidence of an outcome (e.g. remains of predated eggs or clear remains of egg membranes after hatching). Probable outcomes were classed as those where the evidence was less clear but still suggestive. Probable outcomes included video images where predators were seen at nests but not actually taking eggs, and less conclusive remains of nest contents. Note that many nests were not examined until July (when temperature loggers were retrieved) and therefore contents could have remained exposed for two months or more. All other nest outcomes were classified as unknown.

2.4 Fixed point observations: daylight predators and disturbance

Temperature loggers and nest cameras were restricted to the monitoring of nests with eggs. Fixed point observations were undertaken to collect further information on: the suite of predators affecting breeding waders; interactions between predators and other events such as disturbance; and on predation of chicks.

Five fixed points were selected in each hedgehog density stratum in each year 2012 – 14 with an additional point in the low hedgehog density areas in 2014 (Figure 3) from which systematic visual observations of predation events were made during the three months, April to June inclusive. Observations were undertaken from a vehicle, hide or against a building (as appropriate for the point and in all cases to minimise an observer influence on the behaviour of potential predators). Each watch from any one point lasted for two hours, unless curtailed by changing weather that restricted visibility. Observations sampled an arc of 180° centred on a fixed direction for each point and aimed to sample each of six diurnal time periods (n = 6, see Table 3) within each month (April – June, n = 3) for a single two-hour observation period (Table 3).

Recorded during fixed point observations were:

i) *Daylight predator occurrence* – the total number of ‘predator-visits’ seen per half hour. A predator visit was a gull, corvid, raptor or other predator passing through (irrespective of height) the observation area within 500m of the fixed point (the distance at which flying predators could be reliably detected). All predators were identified to species;

ii) *Wader occurrence* – the number of waders (identified to species) visible within an arc of 300 m (the distance to which it was judged that a representative proportion of waders on the ground could be seen reliably). These were counted three times per 2-hour watch, once at the start of the watch, once at the mid-point and again at the end. Although there would be differences of detectability between wader species (associated with size, behaviour and preferred habitats) and between observation points (associated with topography and habitats) these counts would provide a crude index of relative wader abundance;

iii) *Predation events* – most occurrences of predators elicited responses from the breeding waders (flying towards the predator to drive it away or draw attention to it). An actual predation event was identified when the predator made clear manoeuvres in attempts to take either young or eggs from the ground. For each predation event the following were recorded:

- a) Time and date;
- b) Predator species;
- c) Prey species;
- d) Successful predation – Yes or No;
- e) Target – Adult, Young or Eggs;
- f) Whether associated with a human disturbance event (Yes / No; see below);
- g) Habitat at the point of predation (see Section 2.6);
- h) Other notes that may be relevant.

The locations of all predation events were plotted onto large scale field maps and the distance from the observation point was thus measured.

iv) *Human disturbance events* – all movements of people through and within the observation area within a 500 m arc were recorded. For each such disturbance event the following were recorded:

- a) Time and date;
- b) Number of people;
- c) Whether on foot or in a vehicle (excluding vehicles if on a frequently used public road);
- d) Whether the disturbance event was associated with agricultural activities, recreational activities or other and unknown activities;
- e) With dog(s) – Yes or No;
- f) Whether the disturbance event was associated with any predation events (Yes or No; see above).

Note that because of the density and distribution of breeding waders, movements of people within the recorded areas from the observation points will have all resulted in disturbance.

Each predation and disturbance event was given a unique code to permit cross-referencing.

For analyses, avian predators recorded during the fixed point observations were classed into two groups: (i) 'Gulls', which included all gull species as well as the small numbers of skuas that were seen; and (ii) 'Raptors', which included all raptors as well as short-eared owl *Asio flammeus* and corvids (predominantly raven *Corvus corax*). Three separate analyses were conducted, primarily to test for differences in avian predation rates and human disturbance rates between sites, and to identify which factors influenced avian predation attempt rates as follows:

Generalised Linear Mixed Models (GLMMs) were used to assess if and how the occurrence rates of the two classes of predators (separate analyses for the two predator groups) differed between the two study sites and between times of day and season. Within these models, the total number of individual 'gulls' or 'raptors' recorded within 500 m of the observation point during a two-hour watch (or less if necessarily truncated) was the dependent variable. Fixed factors were: Study area ($n = 2$); Month ($n = 3$); Time of day ($n = 6$); Year ($n = 3$); Observer ($n = 12$, to account for different detection abilities between observers); and the sum of the three counts of waders visible within 300 m (a continuous variable, log-transformed); appropriate interaction terms were included in the models. The fixed vantage points at each study site were entered into the models (nested within the Study area variable) as random repeated variables to account for the high likelihood that the same individual birds will be recorded repeatedly from each fixed point. The models used a Poisson error distribution and a log-link function. The duration of each watch (log-transformed hours) was entered into the models as an offset. This effectively turned the counts of avian predators into occurrence rates (birds per hour) without compromising the assumptions of the Poisson error distribution (data have to be integers) and also accounted for the occasions when watches were truncated because of deteriorating weather conditions. Post-hoc pair-wise comparisons were used to identify the sources of any significant influences on the dependent variable (effectively the occurrence rate).

A Generalised Linear Model (GLM) was used to investigate potential influences on rates of observed predation attempts. The sum of all avian predation attempts (gulls and raptors combined) per watch was the dependent variable. Independent factors were: Study area ($n = 2$); Month ($n = 3$); Time of day ($n = 6$); Year ($n = 2$); and the interaction terms with Year. The model used a Poisson distribution and log-link function and the duration of the watch (log transformed) was introduced into the model as an offset for the reasons outlined above. Note that the data for models that included observer, counts of waders and habitat types were too sparse to allow convergence, and the influence of these factors could therefore not be tested.

Another GLM was used to test if there were any differences in human disturbance rates between study areas, months, time of day and year. The cumulative duration of any disturbance within a timed observation period was the dependent variable and the duration

of the watch (log-transformed) was included in the models as an offset, effectively making the disturbance duration a rate (minutes of disturbance per hour). The models assumed a Negative binomial distribution and log-link function. Post-hoc pair-wise comparisons were used to identify the sources of any significant influences on the dependent variable (effectively the disturbance rate).

2.5 Behaviour recording transects: a chick survival index

The objective of the behaviour recording surveys was to assess any differences in the proportions of waders that were present and showing behaviour indicative of having dependent young between areas of contrasting hedgehog densities and whether the changes in those proportions differ between areas as the main chick rearing period progressed. The proportions were expected to provide an index for the survival of dependent young.

In 2014, ten 1-km transects were walked 6 times, weekly between 4th June and 10th July (Fig. 4). All behaviour transect surveys were carried out within the times of 11:00 – 15:30. Single observers walked each transect and recorded (by plotting onto large scale maps) the locations of redshank, dunlin and ringed plover and recorded whether they were showing alarming or other agitated behaviour indicative of the presence of dependent young. For redshank such agitated behaviour primarily included persistent alarm calling while flying around and/or calling from fence posts. For dunlin, this primarily included ‘crawling mouse’ distraction displays and similarly for ringed plover which also included feigned broken-wing displays. Where two birds were thought to represent a pair, these were identified as such.

Poisson GLMMs were used to assess differences in proportions, and rates of change of those proportions, of the ‘apparent pairs’ appearing to have dependent young between areas of contrasting hedgehog densities. The dependent variable was the number of alarming apparent pairs of each wader species recorded on a single transect during a single survey visit. The number of apparent pairs was the sum of assumed pairs recorded as such on the transect plus the sum of the number of individuals not assigned to a pair (and assumed that their mates were away from the areas at the times of survey). Only birds recorded within 100 m of the transects were included; birds were initially assigned to within distance bands of 25 m, 50 m, 100 m and 500 m, however some initial trial analyses found common results between data truncated at all distances but with lower statistical power associated with those with smaller sample sizes. Given the mobility of the birds (difficult to accurately assign many to say 25 or 50 m distance bands), the small numbers that were recorded as between 100 – 500 m from the transects and no evidence or reason for differences in detection functions with distance between areas of different hedgehog densities (similar habitats and topographies), data included in analyses are simply truncated to those birds recorded within 100 m of the transects.

Factors included in the GLMMs were ‘Week’ (1 – 6 as a continuous variable), ‘Hedgehog density’ (n = 2 classes), and ‘Species’ (n = 3 waders) and the three two-way interaction terms. The total number of apparent pairs of each species was introduced into the models as an offset, after log-transformation, effectively making the dependent variable a proportion of the pairs that were showing agitated behaviour without violating the assumptions of a Poisson distribution (requiring integers). The transects (n = 10) were included in the models as random repeated variables to account for: (a) individual site specific differences between transects; and (b) repeated counts of the same transects will include a high proportion of the same individual birds.

A statistically significant influence of the ‘Hedgehog density’ term would suggest an overall difference in the proportions of pairs successfully retaining young. A significant influence of the ‘Hedgehog density’ * ‘Week’ interaction term would suggest that the rates of change in

the proportions of pairs retaining young differ between areas of contrasting hedgehog density during the survey period. Both would be indicative of differences in chick survival and potentially inform the possibilities of either compensatory or additive associations between clutch and chick survival rates.

2.6 Habitat recording

Habitat and land use types were recorded for each of the monitored nests or recorded predation events at the time of observing a predation event, putting a temperature logger in a nest or starting a camera recording the activities at a nest. Machair habitats do not fit easily into the 'standard' classification systems such as the National Vegetation Classification or Phase 1 habitat classifications (Humphreys *et al.* 2012). The classification adopted for this work is based on those used during ESA and Stewardship agri-environment survey work and is modified into a two-tier system to permit analyses and interpretation at different scales. Below, the more detailed 'second tier' categories are listed under the four 'first tier' habitats:

Cultivated machair

Second tiers:

- Stubble (sometimes under-sown with grass);
- First year fallow;
- Second year fallow;
- Third year and older fallow;
- Arable in crop;
- Arable recently ploughed (< 10% vegetation cover);
- Strips of fallow and arable (but only where this can not be clearly defined into a combination of the above).

Pasture machair

Second tiers:

- 'Unimproved' plain grassland (damp machair grassland, stable dunes and slacks);
- Improved pasture, sown grassland;
- Marram dunes (marram grass present at >10%);
- Bare dunes (< 10% vegetation cover);
- Saltmarsh and its machair transition.

Blackland (the mineral interface between machair and peatlands)

Second tiers:

- Improved pasture, sown grassland;
- Rush pasture – contains rushes. Reverting from previously improved land with *Juncus effusus* establishing or dominating;
- Tall herb/marshland – waterlogged marsh ground characterised by iris *Iris pseudacorus* and usually rushes (also includes some loch sides);
- *Eriophorum* bog (also includes some loch sides);
- Rocky pasture - pasture with rocky outcrops, typically uneven ground.

Peatland/Moorland

Second tiers:

- Moorland (>25% ericaceous heath species);
- Wet heath – Contains at least one of the following: *Erica tetralix*, *Myrica gale*, *Sphagnum* spp. or *Narthecium ossifragum*;
- *Rocky moorland* – with rocky outcrops, typically uneven ground.

The above habitat categories were recorded in the field at the point of recording information about nest contents and nest recording. Habitats and their extent were not plotted or otherwise mapped because of time constraints. To derive information on habitat mosaics (included in some analyses; see Section 2.2) an 'Uist Wader Habitat Map' was produced by combining the Land Cover Map 2007 (Morton *et al.* 2011) and the Sand Dune Survey of Scotland (Dargy 1998). Analyses of associations of predation with habitats in the first instances considered the first tier habitats as recorded at the point of the nests (or predation event). In the event of statistically significant associations being identified, second tier habitats and potentially those from the Uist Wader Map would have been included.

2.7 Population modelling

To determine the likely relative sensitivities of breeding wader populations to contrasting rates of hatching and fledging successes, simple density-independent population models were constructed for dunlin, lapwing, redshank and ringed plover. The models used two age classes of full grown birds (birds in their second calendar year and older birds) in a Leslie matrix model using the package ULM (Legendre & Clobert 1995) where the number of eggs reaching the first breeding season per pair is:

$$\text{Breeding population (pairs)} * \text{Number of clutches per pair} * \text{Clutch size} * \text{Clutch survival} * \text{Brood survival} * \text{1st year survival}$$

Single clutches laid per pair were assumed for dunlin, lapwing and redshank and two per pair for ringed plover (after Robinson, 2005) and average clutch sizes used in models were 3.71 for dunlin, 3.76 for lapwing, 3.87 for redshank and 3.72 for ringed plover (after Robinson 2005). In the absence of other information it was assumed that any clutch surviving through to fledging produced 0.75 chicks fledged per egg.

Survival parameters were modelled using a beta distribution (to keep values between 0 and 1; Legendre & Clobert, 1995) with a standard deviation of 10% of the mean to simulate the effects of environmental variation (though the extent of this variation made little difference to the models). Breeding population sizes were those of the four extensive surveys of the Uist machair in 1983 (Fuller *et al.*, 1986), 2000 (Jackson *et al.*, 2004), 2007 (Fuller *et al.*, 2010) and 2014 (unpublished data). Raw uncorrected counts were used throughout. All models assumed a population with no net immigration or emigration.

Clutch and brood survival rates used in the models were specific to the Uists and estimated using data collected in the present study. Clutch mortality was estimated using a standard Mayfield method (Mayfield, 1975). For each species, a daily clutch mortality rate was calculated by dividing the total number of clutches that were known or were likely to have failed (see Section 2.3.2) by the cumulative total number of days that all nest were monitored. A daily survival rate was then calculated (1 – daily mortality rate) which when raised to the power of the incubation period (in days) gave the overall hatching rate. The incubation periods were assumed to be 21.5 days for dunlin, 24 days for redshank and ringed plover and 30 days for lapwing (after Robinson, 2005).

Brood survivals were more crudely estimated from the behaviour recording transects (Section 2.5). For dunlin, ringed plover and redshank, these were taken as the mean of the proportion of apparent pairs (assumed pairs plus apparent singles) that showed agitated behaviour during all of the transect surveys. The proportions were arcsin square-root transformed, the means calculated and then back-transformed. Lapwing were not recorded during the behaviour transects (because mobbing birds tend to be drawn from a large area and include ones with eggs as well as chicks) and in the absence of site-specific information, the figure for brood survival used was the mean for the other three species.

First-year (from fledging to the following spring) survival rates (dunlin 0.46; lapwing 0.67; redshank 0.43; ringed plover 0.57) and adult (subsequent annual) survival rates (dunlin 0.80; lapwing 0.84; redshank 0.82; ringed plover 0.85) that were included in the models were sourced from the literature (Robinson *et al.*, 2007; Burton, 2010; Robinson *et al.*, 2014; Pienkowski, 1984; Wallander & Anderson, 2003). The models assumed that all surviving dunlin, redshank and ringed plover bred in their first year after hatching while two-thirds of lapwing did so with all surviving adults breeding in subsequent years (after Thompson *et al.*, 1994).

Clutch and brood survival rates were calculated separately for high hedgehog density areas (South Uist) and low hedgehog density areas (North Uist). To assess the relative sensitivities of population change rates to the different survival rates recorded, alternative models were run for each species, each with combinations of clutch and brood survival rates from both study areas (making four models for each species).

Population growth rates derived from deterministic models (i.e. those that do not incorporate annual variability in demographic parameters resulting from variation in environmental conditions) consistently overestimate the true population trajectory (Saether, 1997). In order to account for such variation we conducted simulations that allowed each variable to vary with a standard deviation of 10% of the mean value, which represents a moderate degree of variability (and is broadly typical, for instance, of the variability about annual survival estimates, R.A. Robinson pers. obs.). We used the default settings of ULM to do simulations, i.e. calculating the mean over 100 simulated trajectories of 50 time-steps each. In practice, differing levels of variability did not seem to have a large impact on the conclusions drawn.

3. RESULTS

3.1 Hatching success of study nests

Study nests showed significant differences in hatching success between the two study areas. From nests where the outcome was confirmed, 74% hatched successfully in North Uist, whereas only 45% hatched successfully in South Uist (Table 4). Most of the failures to hatch were due to predation, although some nests at both sites were lost to ploughing operations (Table 4). Considering a larger sample size including nests where the outcome was probable in addition to those that were confirmed, the proportions hatching and failing were little altered (Table 4), also indicating higher hatching success of nests in North Uist.

3.2 Clutch survival assessed using temperature loggers

Analyses which included all the valid temperature logger data (and assumed a normal distribution) identified statistically significant associations of clutch survival with study area (as a proxy for hedgehog density), species and start date of nest monitoring on the incubation duration recorded by the nest temperature loggers. No apparent differences were identified between years or first tier habitat classifications and none of the interaction terms was statistically significant (Table 5). Similarly, there was no detected effect of whether a nest was monitored by a camera or not. Post-hoc, pair-wise comparisons showed that wader clutches survived for longer on North Uist (back-transformed mean of 320 hours, 95% confidence interval 287 – 353 hours) than on South Uist (mean 263 hours, CI 230 – 295); on average, monitored clutches on North Uist survived for 57 hours longer than on South Uist.

There was a statistically significant negative association between measured incubation duration and the start date of nest monitoring, that is shorter incubation periods were recorded at nests where monitoring started later. This was expected because later deployment of temperature loggers meant that there would be a tendency for the monitoring of nests to have been started later during the incubation period while an earlier starting of monitoring would tend towards incubation being measured for a longer period.

An absence of significant interaction terms suggested an absence of any systematic difference in the dates when loggers were deployed in nests between the two study sites. There was, however, a significant difference in the stage of incubation recorded between the two study areas ($X^2 = 12.4$, $P = 0.002$) suggesting a systematic difference in laying dates and therefore a potentially confounding influence on the recorded incubation duration. In the three categories of incubation stage at the start of recording, on North Uist 44% of tested eggs were in the earliest stage and 56% in the mid and late stages ($n = 408$ eggs). On South Uist, 48% were in the earliest and 51% in the mid and late stages ($n = 561$ eggs). Therefore, there was a general tendency for the monitored clutches to have been laid earlier on North Uist than on South Uist. Given the generally more advanced stage of incubation recorded at the start of monitoring on North Uist, all factors being equal (and given the negative relationship between recorded incubation duration and laying date, see above), we can predict that they would be monitored for a shorter period (until hatching or otherwise). However, this study found that recorded incubation periods tended to be longer which is counter to expectations based on incubation stage alone (clutches on North Uist tended to be at a more advanced state of incubation at the start of their monitoring). Therefore, in reality the difference in incubation duration (as an index of clutch survival) would have been greater than the 57 hours recorded if the systematic difference in laying dates were taken into account.

There were no apparent differences in the stages of incubation at the start of nest monitoring between the three first-tier habitat categories ($X^2 = 1.40$, $P = 0.84$).

The alternative Mayfield binomial GLM (restricted to data from loggers placed in nest that were known to have definitely hatched or otherwise failed to hatch) similarly found that the survival of clutches tended to be greater on North Uist than on South Uist and a negative association with the start date of monitoring (Table 5).

3.3 Identification of clutch predators

On North Uist 29% of recorded incubations ended during darkness while the comparable figure for South Uist was 45% ($X^2 = 25.8$, $P < 0.001$) which is consistent with the hypothesis of a greater incidence of nocturnal predation on South Uist. The proportion of nests that were lost to predation on South Uist was greater than that on North Uist (51% compared to 29% of nests for which there was evidence to indicate that loss to predation was at least probable; Table 4). Amongst the monitored nests where hatching was confirmed, just one hatched during darkness, compared to 111 in daylight (though the latter figure will include eggs that hatched during darkness but the young continued to be brooded until daylight). Where nests were confirmed to have been predated, 72 were during darkness compared to 36 in daylight.

Hedgehogs were by far the most numerous identified predators of wader clutches on the Uists, with all confirmed occurrences on South Uist (Table 6). Although instances of nest predation by birds were also recorded more frequently on South Uist, the sample sizes were too small to allow generalisation. There were no apparent patterns of predator prevalence by habitat type (Table 7).

3.4 Occurrence of daylight predators and other disturbance

3.4.1 Daylight predator occurrence rates

A total of 22,860 discrete observations of 22 species of avian predator were recorded within 500 m of the fixed observation points during systematic watches. Common gull *Larus canus* was by far the most abundant and, in addition, four species of mammal were also recorded (Table 8).

Both gulls and raptors were recorded more frequently on South Uist than on North Uist (Table 9). On South Uist the back-transformed mean from the GLMM was for a rate of 34 gulls per hour (95% confidence limits 25 – 47 per hour) compared to 17 gulls per hour (13 – 24) on North Uist. Back-transformed means of raptors were 1.5 per hour (0.7 – 2.3) on South Uist and 1.1 per hour (0.4 – 1.9) on North Uist. Both gulls and raptors also tended to be recorded more frequently in April (30 gulls per hour (21 - 42) and 2.5 raptors per hour (1.7 – 3.5)) than in either May (24 gulls (18 – 37) and 0.7 raptors (0 – 1.5) per hour) or June (20 gulls (15 – 27) and 0.7 raptors (0 – 1.4) per hour).

3.4.2 Predation rates

A total of 124 predation attempts were recorded during fixed point observations in 2012 - 2014 of which 24 were successful (Table 10). No difference in predation rates by avian predators (all combined) between the two study areas was detected, however there were differences in predation rates between months and years (Table 11). Predation attempts were less frequent in May (back-transformed mean of 0.06 per hour, 95% confidence interval 0.04 – 0.09) than in either April (0.14 per hour, 0.10 – 0.29) or June (0.15 per hour, 0.12 – 0.20). They were also more frequent in 2013 (0.25 per hour, 0.20 – 0.31) than in 2012 (0.06 per hour, 0.03 – 0.11) or 2014 (0.09 per hour, 0.06 – 0.12).

3.4.3 Human disturbance rates

Incidences of human disturbance of breeding waders were recorded 340 times during the fixed point observations over three years (Table 12). Rates of disturbance differed between the two study areas and varied with time of day (Table 13). Disturbance rates were greater on South Uist (mean of 0.37 instances per hour, 95% confidence interval 0.32 – 0.43) than on North Uist (0.22, 0.18 – 0.27). Statistically significant differences were for the early morning period (0.08 per hour, 0.05 – 0.14) to be lower than all others and for the mid morning (0.29, 0.21 – 0.37) and late evening periods (0.33, 0.26 – 0.43) to be less than the period with most disturbances, mid afternoon (0.50, 0.39 – 0.64). The confidence intervals of the other two periods were within the ranges of 0.28 – 0.48 instances per hour.

Four out of 24 (17%) observed successful predation events were associated with human disturbance in the three years (Table 10). Nine of the 340 (2.6%) events of human disturbance recorded during the three years were associated with a predation attempt (Table 10).

3.5 Changes in agitation behaviour by breeding waders: chick survival index

The rate of change during June and into early July in the proportion of waders (dunlin, redshank and ringed plover) that showed behaviour indicative of having dependent young differed between North Uist and South Uist (a statistically significant Week : Site interaction term; Table 14). Relative to that for South Uist, the model (GLMM) estimate of 'Week' as a continuous factor (the untransformed slope of rate of change) for North Uist was -0.68 (SE = 0.13) suggesting that the proportion of waders with dependent young declined more rapidly on North Uist than it did on South Uist. The back-transformed model means shows the proportion of waders apparently retaining dependent young was 0.15 (95% confidence limits 0.09 – 0.26) on North Uist and 0.38 (0.30 – 0.48) on South Uist. This suggests that the loss of broods could be 61% greater on North Uist than on South Uist during June and early July. However, we cannot exclude the possibility that different behaviours of waders in response to the presence or absence of hedgehogs might also have contributed to the observed differences in exhibiting apparent agitation in response to a human intruder (the surveyor recording the behaviours).

To examine the nature of the contrasting patterns between the two areas, separate models were run for each site but with week included as a categorical term ($n = 6$) and the back-transformed mean proportions for each week plotted (Fig. 5). The decline started somewhat later (by about two weeks) on South Uist than on North Uist (Fig. 5), rather than the difference in apparent rates of chick survival being constant through the monitored period.

3.6 Population models

To assess the relative sensitivities of predicted changes in wader populations to the different clutch and brood survival rates, alternative models were used that included the contrasting rates that were measured in areas of low and high hedgehog density. When clutch survival rates were changed (lowered) from those recorded in low hedgehog density areas to the reduced levels that were recorded in high hedgehog density areas, the projected annual population growth rates decreased by 1% (for ringed plover from 0.898 to 0.885; Table 15), 4% (dunlin and lapwing) and 8% (redshank) (Table 15). These alternative models assumed the higher brood survival rates that were found in high hedgehog density areas.

When brood survival rates were changed (raised) from those recorded in low hedgehog density areas to the increased rates that were found in high hedgehog density areas, the projected annual population growth rates increased by 12% (dunlin), 15% (redshank) and 20% (lapwing and ringed plover). These alternative models assumed the higher clutch survival rates that were found in low hedgehog density areas.

The population models did not capture well the observed population dynamics, however, probably because of inadequacies in measuring chick survival, which in turn is probably because of the inherent difficulties associated with collection of those data and the indirect approach that was employed on the Uists. If the observed population growth rates between 2007 and 2014 (concurrent with the present study) in the high hedgehog density areas are accurate, and assuming that clutch survival rates (as measured in the present study) are reasonable, the predicted brood survival for dunlin would need to be higher (at 67.5%) than was observed (41%) but lower than was observed for ringed plover (7.5% compared to the observed 40%). The assumed brood survival rate would also need to be lower than the figure used for lapwing (39% compared to 60%), but note that brood survival rates were not estimated by direct observations of lapwing, rather a mean estimate from the other three species was used. For redshank, with a clutch survival rate of 11% in high hedgehog density areas, there was no value of brood survival that would have produced the observed change (the models indicated that the best that could be achieved was an annual decline of about 10%).

4. DISCUSSION

4.1 Relative importance of hedgehogs as nest predators

Three years of data collection has provided some interesting evidence for the relative contribution of wader nest predation by hedgehogs on the Uist machair. Clutch survival was generally lower on South Uist (an area with high hedgehog densities) than on North Uist (an area with low hedgehog densities). No influences on clutch survival of habitat or of position of a nest within a habitat mosaic were identified. Hedgehogs were the most numerous predator recorded by nest cameras or for which there was reasonable evidence to record them as at least probable predators of nests of all five wader species that were monitored (Table 16). Avian predators of eggs could have been under-sampled however; where video recordings of predation by gulls were captured, they were usually of birds flying away while hedgehogs remained at the nests typically for several minutes. Although behavioural differences between the predators could bias their detection by nest cameras, the greater incidence of nocturnal predation (as suggested by the nest temperature loggers) in the study area with a high density of hedgehogs provides strong evidence of their greater importance as nest predators.

Exclusion of hedgehogs from experimental plots on South Uist in 1998 was associated with a 2.4 times higher hatching success across four wader species combined, mostly dunlin and lapwing but also redshank and snipe (Jackson 2001). In the present study, mean hatching success was greater in low hedgehog density areas than in high hedgehog density areas, by 2.3 times for dunlin, 1.4 times for ringed plover, 4.0 times for redshank and 1.7 times for lapwing (based on non-overlapping 95% confidence intervals, a statistically significant difference for all except ringed plover; after Table 15). Although current mean differences are within the expected ranges reported for the enclosure experiment, their tendency to be slightly less than in 1998 could be explained by the exclusion of all ground predators from the experimental plots of the earlier study; nests in the present study were still predated by rats and otters on North Uist, for example. In the late 1990s, hedgehogs accounted for 55% of nest failures ($n = 131$ over three years) on South Uist outside of enclosures (Jackson 2001). In the present study 51% of nests on South Uist were predated, or else there was strong evidence that they were predated (Table 4). Of those, 69% of nest predations were attributed to hedgehogs (Table 7) suggesting that they accounted for 35% of all nest failures ($n = 521$) on South Uist during 2012 – 14. Although hedgehogs, where they occurred, remained a major predator of wader nests in the present study, they appeared to be responsible for a lower proportion of all nest failures compared to the 1990s study.

4.2 Relationships between clutch and brood predation

Avian predators and human disturbance were both more frequent on South Uist than on North Uist. Both are potentially confounding factors when assessing the relative importance of nest predation by hedgehogs. If predation by hedgehogs was additive to that by avian predators (on the Uists predominantly by gulls), then it might be expected that predation by gulls would be more frequent on North Uist (where predation by hedgehogs is less). This was not apparent from the frequency of observed predation attempts within the three years of study, despite the differences in their occurrence and also differences in levels of human disturbance between the two areas. However, the number of successful attacks by avian predators that were recorded during fixed point observations was greater on North Uist (15) than on South Uist (9), despite fewer avian predator occurrences on North Uist. Although only 24 successful predation events by avian predators were observed directly during the fixed point observations in 2012-14, this was during 10% of available daylight hours only (assuming an average of 18 hours per day for the full three months April to June, making a total of 1638 hours of available daylight in each of the three years). Further assuming that all predation events during the observations were detected within a 750 m radius (the most distant predation event observed) semi-circle from the observation point (an area 0.88 km²)

and that those areas under observation were representative of the wider areas, a crude extrapolation suggests that there could have been 83 successful attacks per km² during a single three-month breeding season. With 30 – 80 breeding wader ‘pairs’ per km² (e.g. Calladine *et al.* 2014), this suggests that a reasonably high proportion of nesting attempts could be subject to successful attacks from avian predators. However, it should also be emphasised that not all successful avian predator attacks result in complete failure of a breeding attempt, as only single eggs or young will be taken during many attacks. Taking this crude extrapolation further leads to estimates of 109 and 71 successful attacks by avian predators per km² per season on North Uist and South Uist respectively. However such figures are derived from very few actual observations so should be treated with caution though they might indicate a potential scale of predation.

Interestingly, just 15% of the observed successful attacks by avian predators were associated with human disturbance; four on North Uist and one on South Uist (Table 10). Again, any interpretation on the importance of human disturbance related predation should be treated with extreme caution because of the very small size sample size of observations.

Contrasting rates of change in the behaviour of waders during the chick rearing period provide some further evidence that avian predation of chicks could be greater on North Uist (low hedgehog density) than on South Uist (high hedgehog density). However, there is a potentially confounding effect of differences in laying dates and potentially a difference in how the birds respond to any perceived threat in the presence or (relative) absence of mammalian predators. Reasons for an apparent difference in laying dates (deduced from egg flotation) for waders between the two areas could include: (i) the inclusion of more replacement clutches on South Uist (evidence of a higher incidence of clutch predations); and (ii) a systematic difference in initial clutch laying dates with potentially ‘better quality’ or behaviourally more flexible birds laying earlier on North Uist (evidence of a difference of overall breeding success). Both of these potential reasons are, or could be, associated with different levels of predation, the first directly, and the second through a longer term behavioural response by the waders with ‘higher quality’ birds able to recruit or otherwise select to breed in areas with lower risks of predation. The selection process driving the latter could be associated with hedgehogs, avian predator abundance, levels of disturbance or a combination of factors. Previous work on the Uists has shown a negative association between adult dispersal and breeding success in the previous year for dunlin, ringed plover and redshank, with dispersal distances of up to 40 km being recorded (Jackson 1994). Therefore redistribution of waders between South Uist and North Uist in response to differential predation risks could be a feasible mechanism.

Modelling of different scenarios of clutch and brood mortalities suggest a potentially greater influence of chick survival on predicted population trends than of egg survival (inclusion of the lower value for brood mortality resulted in a greater positive change in the predicted rate of population change). This could be interpreted as chick predation (which was principally by gulls) as having a greater impact on breeding wader populations than egg predation (which was principally by hedgehogs). If this was the case, then there is a need to consider the foraging behaviour of gulls. As eggs have to survive to full term for chicks to be produced, they will be more available in areas where egg mortality is comparatively low (on the Uists this is in low hedgehog density areas such as North Uist) and therefore foraging on wader chicks could prove to be more efficient where hatching success is higher. The implication is that if hedgehog densities were to be reduced on South Uist then, although more eggs are able to hatch, a comparative increase in chick losses might be expected. Gull predation of chicks therefore may appear to be compensatory to some degree with that of eggs by hedgehogs. However it should be noted that the estimated chick survival rates did not give a particularly good prediction of the observed changes in breeding wader populations and so should be treated with caution. In the population models, for simplicity, we included a single value for chick survival from any surviving clutches. In reality, it is

perhaps more likely that brood attrition through the loss of individual chicks might be more realistic and our simple assumption could exaggerate the model's sensitivity of the influence of chick survival on predicted population trajectory. Furthermore data on chick survival were derived from a single year collection (2014) whereas the data on clutch survival (which is also inherently less difficult to collect and likely to be more robust) were derived from three years of data. It is also important to note that the models also predicted an influence of clutch mortality (for which we have more confidence in the robustness of data) on the predicted population trajectories and so it is most likely that at least some of the impact of hedgehog predation on wader clutches will be additional to that of gulls on wader chicks.

For a wader with an adult annual survival rate of about 80% and a first year survival (between fledging to recruitment into the breeding population) of about 45% (as is assumed for machair waders in the population models), modelling suggests that clutch and brood survival combined needs to be greater than about 33% for a population to increase (Fig. 6). Amongst the four principal study species, this was achieved by redshank only and only under a low hedgehog density scenario (after Table 15); the only species that had generally increased over recent decades.

4.3 Predation as a driver of population change

The factors influencing population sizes of breeding waders on the Uist machair will be complex and unlikely to be attributable to the sole cause of predation or by a single species of predator (Fuller & Jackson, 1999). Although a number of associations between breeding wader densities with machair habitats types and land uses have been identified, rather few associations with changes in machair and associated habitats were found over the three decade period 1980s – 2000s (Calladine *et al.*, 2014). This implies either there had been relatively little change in the habitats that are associated with changes in breeding wader densities or else there is a low power to detect those changes and associations. In either case the implication is that there is likely to have been other drivers (some possibly interacting with changes in habitats) of population changes than that of habitat change.

One marked change on the Uist machair in the period has been the introduction of hedgehogs. This study has added to the evidence base highlighting hedgehogs, where they occur, as an important and continuing influence on breeding waders of the Uist machair. The proportion of nests predated by hedgehogs was greatest for redshank and dunlin and least for lapwing and ringed plover amongst the four species prioritised in this study (Table 16). The differences between species are in line with those reported for the late 1990s (Jackson & Green, 2000) but with the notable difference that hedgehogs were as important a predator of ringed plover nests as they were of lapwings in this current study. Based on low predation rates and observed behaviours of hedgehogs in tending to avoid areas favoured by nesting ringed plovers, previously it had been assumed that nesting ringed plovers were relatively unsusceptible to hedgehogs (Jackson & Green, 2000). A comparable decline in ringed plover and dunlin breeding populations on the Uists, despite what had been assumed to be contrasting susceptibility to nest predation by hedgehogs, had understandably led to some uncertainty over the importance of hedgehogs in relation to other potential factors determining population trends. This current study suggests that the difference in nest susceptibility between dunlin and ringed plover may be as great as previously suggested, or else other (as yet unidentified) conditions have changed that now make ringed plovers more susceptible. For the other three species, however, the proportion of all nests lost to hedgehogs was lower than reported in the late 1990s (outside of exclosures). Potentially, this could be a result of selection against the most susceptible individuals in the four decades that hedgehogs have been present on the Uists.

Direct observations of attacks by avian predators (possibly higher in areas of low hedgehog density but with the caveat that this is based on a low number of observations) and

assumptions from changes in agitated behaviour during the chick rearing period (possibly higher rates of chick loss in areas of low hedgehog density but with the important caveats that (a) there are more chicks to predate in North Uist, and (b) that this field method would benefit from further development) are consistent with hypotheses that predation by hedgehogs and avian predators are to some extent complementary. However models of population change in response to different levels of clutch and brood predation predict that although predation of chicks might have a greater influence on rates of population change, lower levels of clutch predation by hedgehogs should lead to more positive rates of wader population change.

Different wader species have differing vulnerability to predation which can be positively related to breeding densities (Dyrz *et al.*, 1981, Kis *et al.*, 2000, Šálek & Šmilauer, 2002). Qualitative observations during the course of fieldwork on the Uists suggest that current densities, in particular of lapwing and redshank can be quite effective at driving away avian predators. Video evidence suggests that they may be less effective at driving away mammalian predators, even during daylight, though this has not been formally analysed. A potential future scenario is that some increase in predation levels (mammalian, avian or both) could reduce wader population densities to a particular threshold below which they will become increasingly vulnerable to avian predation with resultant accelerated population declines.

4.4 Potential further research

A number of key questions for the future conservation of the important machair wader assemblages remain. Potential further work and studies include:

- a) The behaviour recording transects were undertaken in just a single season but showed an interesting difference in both proportions of birds behaving as if they had dependent young and the pattern of change between areas. Repeats of these transects in further years would be needed to see if such differences are usual and to add confidence to their interpretation. The field method has real potential but more work is needed to verify this approach and to develop it maximum effect;
- b) The role of the wader assemblage in deterring predators to identify thresholds below which the waders may become increasingly susceptible to predators. The extensive video images collected during the course of the present study would provide a good start to look at wader responses to different predators;
- c) The importance of vegetation changes and invertebrate availability relative to, and interacting with, predation. Experimental manipulations that simulate different management scenarios for machair habitats would elucidate some of the mechanisms and interactions that influence breeding wader numbers;
- d) Continuing of periodic wader population surveys including both sample sites repeated in blocks of ideally 3-4 years and less frequent extensive surveys is essential to monitor and record ongoing changes in machair breeding wader assemblages. Periodic monitoring of the impacts of all predators on breeding waders would identify future changes in predation pressure and associations with changes in wader numbers;
- e) This study has accumulated a considerable amount of data, particularly temperature logger data and video images that to date have been used only to ascertain outcomes of wader nests. Further analyses would provide new information on, for example, incubation behaviours which would be directly relevant to wader management issues on the Uists as well as contributing more widely to knowledge of wader biology.

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ANNEX 1: TABLES

Table 1. The numbers of temperature loggers with interpretable data retrieved from nests of waders in 2012-14 by (a) Study Area and (b) Principal habitat classification.

	North Uist				South Uist			
	2012	2013	2014	Total	2012	2013	2014	Total
a) Species								
Lapwing	11	84	171	266	4	133	208	345
Oystercatcher	7	0	0	7	4	0	0	4
Redshank	1	24	52	77	0	39	41	80
Dunlin	0	21	26	47	0	38	25	63
Ringed Plover	0	9	17	26	0	34	35	69
Snipe	2	3	10	15	0	9	10	19
b) Principal habitat class (defined in Section 2.6)								
Blackland		12	23	82	0	53	47	
Cultivated machair ¹		3	12	56	0	101	158	
Pasture machair		6	107	138	8	99	114	

¹ Includes fallow

Table 2. Wader nests monitored by cameras in 2012 - 2014.

	North Uist				South Uist			
	2012	2013	2014	Total	2012	2013	2014	Total
Lapwing	3	9	20	32	0	35	26	61
Oystercatcher	1	0	0	1	1	0	0	1
Redshank	0	9	15	24	0	16	16	32
Dunlin	0	4	17	21	0	27	14	41
Ringed Plover	0	6	10	16	0	26	22	48
Snipe	1	1	3	5	0	1	0	1

Table 3. The number of 2-hour fixed point observation watches completed during April – June 2012 – 2014: (a) The distribution of watches by Month; and (b) the distribution of watches by time of day.

	North Uist			South Uist		
	2012	2013	2014	2012	2013	2014
<i>a) Month</i>						
April	10	30	36	7	30	30
May	18	30	36	19	30	30
June	28	30	36	29	30	30
<i>b) Time of day¹</i>						
Early morning	9	15	18	9	15	15
Late morning	13	15	18	17	15	15
Mid day	9	15	18	10	15	15
Mid afternoon	2	15	18	1	15	15
Early evening	14	15	18	9	15	15
Late evening	9	15	18	9	15	15

¹ The broad timings for the diurnal periods are listed below:

Sampling Period	APRIL	MAY	JUNE
Early morning	05:30 – 07:30	05:00 – 07:00	04:00 – 06:00
Late morning	08:00 – 10:00	08:00 – 10:00	06:30 – 08:30
Mid day	10:30 – 12:30	11:00 – 13:00	09:00 – 11:00
Mid afternoon	13:00 – 15:00	13:30 – 15:30	11:30 – 13:30
Early afternoon	15:30 – 17:30	16:00 – 18:00	17:30 – 19:30
Late evening	18:00 – 20:00	19:00 – 21:00	20:00 – 22:00

Table 4. Outcomes of wader nests within the two study areas for 2012-14 combined, based on the evidence of captured video images, the examination of nest contents and direct observations. The left part of the table includes only nests where the outcome was definitely known ('confirmed'), while the right hand columns additionally include nests where the outcome was probably correctly allocated to each category, but not confirmed.

	Confirmed outcome		Confirmed and probable outcomes	
	North Uist	South Uist	North Uist	South Uist
Hatched	74%	45%	69%	47%
Predated	18%	50%	29%	51%
Cultivation ¹	8%	5%	2%	2%
Sample size	117	174	371	521
Difference	$X^2_2 = 30.6, P < 0.001$		$X^2_2 = 42.9, P < 0.001$	

¹ Nest lost to cultivation by ploughing or rolling.

Table 5. Effects of different factors on the recorded duration of incubation using nest temperature loggers. A summary of the GLM outputs for the main effects (Species, Study site [as a proxy for hedgehog density], Start date of nest monitoring, First tier habitat classification) and their interaction terms. Outputs are presented from two models: (a) Normal GLM that includes all retrieved data loggers: and (b) Mayfield binomial GLM that includes data restricted to clutches that were known to have hatched or not.

Effect	Model (a)			Model (b)		
	df	X ²	P	X ²	P	
Species	4	19.44	0.002	5.20	0.27	
Study site	1	16.95	<0.001	4.99	0.02	
Start date	1	35.25	<0.001	6.76	0.01	
Habitat	2	2.46	0.29	0.18	0.91	
Distance (to neighbouring habitat)	1	0.38	0.54	0.61	0.44	
Year	2	3.59	0.17	0.17	0.68	
Camera	1	0.05	0.83	1.03	0.32	
Study site * Habitat	2	0.38	0.83	0.76	0.68	
Species * Habitat	8	6.28	0.62	4.10	0.77	
Start date * Study site	1	0.05	0.83	1.17	0.28	
Distance * Study site	1	1.84	0.17	0.05	0.83	
Camera * Start date	1	0.15	0.70	2.05	0.15	
Species * Study site	5	3.25	0.66	0.76	0.94	
Year * Study site	2	0.64	0.73	0.05	0.83	

Direction of effects where they were statistically significant:

Study site (both models): North Uist > South Uist (by 57 hours from model a).

Start date (both models): Estimate of slope -0.77 (Std. Err. 0.98), from model a.

Species (model a only): Dunlin > Redshank (by 93 hours); Dunlin > Ringed Plover (by 64 hours); Dunlin > Snipe (by 106 hours); Lapwing > Redshank (by 54 hours).

Table 6. The percentage of monitored wader nests that failed due to different predators on North Uist (n = 303) and South Uist (n = 272) in 2013 and 2014. Predator identification was confirmed from captured video images, direct observation and examination of nests contents. The right hand columns also include nests where the outcome was probably correctly allocated to each predator, in addition to those that were confirmed.

	Confirmed %		Circumstantial and confirmed %	
	North Uist	South Uist	North Uist	South Uist
Hedgehog	0	12	0.7	23
Otter	0	0.7	0	0.7
Cat	0	0.4	0	0.4
Rat	2.6	0	3.6	0
Common Gull	1.0	3.0	1.0	3.3
Black-headed Gull	0	0	0	0.4
Great Black-backed Gull	0.3	0	0.3	0
Herring Gull	0	0.4	0	1.1
Raven	0	0.4	0	0.4
Unknown avian	0	1.5	2	3.7

Table 7. The number of wader nests that failed due to different predators in the three first-tier habitat types (BL = Blackland; CM = Cultivated machair; PM = Pasture machair) on the Uists in 2013-14. Predator identification was confirmed from captured video images, direct observation and examination of nests contents. The right hand columns also include nests where the outcome was probably correctly allocated to each predator, in addition to those that were confirmed.

	Confirmed			Circumstantial and confirmed		
	BL	CM	PM	BL	CM	PM
Hedgehog	7	14	11	16	24	25
Otter	0	2	0	0	2	0
Cat	1	0	0	1	0	0
Rat	5	0	3	6	0	5
Common Gull	2	6	3	2	6	4
Black-headed Gull	0	0	0	0	1	0
GBB Gull	0	0	1	0	0	1
Herring Gull	0	1	0	0	3	0
Raven	1	0	0	1	0	0
Unknown avian	0	1	3	0	4	10

Table 8. The number of discrete observations of potential predators recorded within 500 m of fixed observation points within the two study areas during daylight hours April – June 2012-14.

<i>Hours of observation</i>	North Uist			South Uist		
	2012	2013	2014	2012	2013	2014
	55	90	90	56	90	108
SPECIES						
Grey Heron	9	16	3	1	4	3
White-tailed Eagle	0	0	1	2	3	0
Hen Harrier	13	12	7	6	5	1
Sparrowhawk	0	0	0	0	1	0
Buzzard	17	71	28	50	38	15
Golden Eagle	0	1	0	10	8	0
Kestrel	1	0	0	0	0	0
Merlin	2	11	5	1	3	0
Peregrine	1	1	2	1	2	2
Pomarine Skua	0	0	0	0	0	1
Arctic Skua	5	3	7	3	3	4
Great Skua	1	2	3	1	0	0
Black-headed Gull	195	465	378	240	1274	728
Common Gull	1648	1285	2370	1137	4166	4707
Lesser Black-backed Gull	18	67	72	31	212	82
Herring Gull	137	393	227	283	748	784
Iceland Gull	0	0	1	4	0	1
Glaucous Gull	0	2	0	0	0	2
Great Black-backed Gull	32	106	89	26	51	48
Short-eared Owl	2	3	1	4	0	0
Hooded Crow	0	22	7	0	1	6
Raven	11	47	82	47	192	36
Cat	1	0	1	0	0	0
Hedgehog	0	0	0	1	0	0
Otter	0	0	0	2	1	0
Rat	1	0	0	0	0	0

Table 9. The statistical significance of the main effects (study site, observer, wader abundance, month, time of day and year) and their relevant interaction terms on the frequency of (a) gulls and (b) raptors recorded passing over the study areas assessed using GLMMs.

Effect	Degrees of freedom	F	P
a) Gulls			
Study area ¹	1, 19	47.9	<0.001
Observer	11, 78	4.0	<0.001
Wader count ¹	1, 438	0.2	0.70
Month	2, 38	4.3	0.02
Time of day	5, 87	1.4	0.22
Year ¹	2, 6	2.7	0.12
Study area*Time of day	5, 87	0.2	0.97
Study area*Month	2, 36	1.5	0.23
Time of day*Month	10, 123	0.6	0.83
Wader count*Study area	1, 416	0.03	0.86
Study area*Year	2, 6	12.6	0.01
Wader count*Year	2, 416	3.7	0.03
Observer*Study area	9, 69	1.15	0.34
b) Raptors			
Study area ¹	1, 19	48.0	<0.001
Observer	11, 78	3.8	<0.001
Wader count	1, 416	0.2	0.70
Month ¹	2, 38	4.3	0.02
Time of day	5, 87	1.4	0.22
Year	2, 6	2.7	0.12
Study area*Time of day	5, 87	0.2	0.97
Study area*Month	2, 36	1.5	0.23
Time of day*Month	10, 123	0.58	0.83
Wader count*Study area	1, 416	0.1	0.86
Study area*Year	2, 6	2.6	0.13
Wader count*Year	2, 416	3.7	0.03
Observer*Study area	9, 69	0.73	0.68

¹ As relevant interaction terms were statistically significant, the significance values of these main effects are those without the interaction terms included in the model.

Table 10. The number of observed predation attempts on breeding waders on North Uist and South Uist in 2012 – 2014. The numbers of attempts that were associated with human disturbance are given in parentheses.

	BY GULLS			BY RAPTORS		
	2012	2013	2014	2012	2013	2014
NORTH UIST						
<i>Hours of observation</i>	56	90	108	56	90	108
All attempts	9 (3)	34 (3)	22 (2)	0	3	3
Successful predation of eggs	2 (1)	4 (1)	0	0	0	0
Successful predation of young	5 (2)	1	1	0	1	0
Successful predation of adults	0	0	0	0	1	0
SOUTH UIST						
<i>Hours of observation</i>	55	90	90	55	90	90
All attempts	3 (1)	30	10	0	7	3
Successful predation of eggs	2	0	0	0	0	0
Successful predation of young	0	4	1	0	1	0
Successful predation of adults	0	0	0	0	1	0

Table 11. The statistical significance, assessed using a GLM, of the main effects (study site, month, time of day and year) and their relevant interaction terms on the frequency of daylight predation attempts on breeding waders.

Effect	df	X ²	P
Study area	1	0.30	0.58
Month	2	15.95	<0.001
Time of day	5	3.21	0.67
Year	2	44.06	<0.001
Study area*Year	2	5.57	0.06
Month*Year	4	3.10	0.54

Direction of effects where they were statistically significant:

Month: May < April ; May < June

Year: 2012 < 2013 ; 2013 > 2014

Table 12. The number of observed incidences of human disturbance of breeding waders on North Uist and South Uist in 2012 and 2013.

		DISTURBANCE TYPE		
		Agricultural	Recreational	Other
NORTH UIST	2012	17	14	0
	2013	17	19	7
	2014	28	19	6
SOUTH UIST	2012	19	14	1
	2013	30	65	11
	2014	24	39	10

Table 13. The statistical significance, assessed using a GLM, of the main effects (study site, month, time of day and year) and their relevant interaction terms on the frequency of human disturbance events on breeding waders.

Effect	df	X ²	P
Study area	1	14.22	<0.001
Month	2	1.89	0.39
Time of day	5	56.55	<0.001
Year	2	2.01	0.37
Study area*Year	2	5.39	0.07
Month*Year	4	4.41	0.35

Table 14. The statistical significance, assessed using a GLMM of the main effects (Week, Study area and Species) and their two-way interaction terms on the proportion of waders (dunlin, redshank and ringed plover only) showing behaviour indicating the presence of dependent young.

Effect	Degrees of freedom	F	P
Week	1, 187	6.98	0.009
Study area	1, 8	0.23	0.64
Species	2, 12	2.63	0.11
Week * Study area	1, 187	6.90	0.001
Study area * Species	2, 12	1.23	0.33
Week * Species	2, 187	0.18	0.84

Table 15. Annual rates of change estimated by population models using clutch and brood survival rates estimated from fieldwork on the Uist machair 2012-14 in areas of contrasting hedgehog densities. Presented in bold are the model predictions for actual scenarios. Presented in normal font are the model predictions with alternative clutch or brood survival rates. Observed rates of change based on four extensive surveys in 1983, 2000, 2007 and 2014 are also shown.

DUNLIN	Clutch survival (mean and 95% CLs)	
	Low hedgehogs	High hedgehogs
	0.73 (0.67 – 0.76)	0.32 (0.23 – 0.39)
Brood survival		
Low hedgehogs (0.14)	0.859	0.824
High hedgehogs (0.41)	0.958	0.875
Actual change		
1983 – 2014	0.982	0.952
2000 – 2014	0.961	0.947
2007 – 2014	0.944	0.918
LAPWING	Clutch survival (mean and 95% CLs)	
	Low hedgehogs	High hedgehogs
	0.55 (0.52 – 0.57)	0.32 (0.29 – 0.34)
Brood survival		
Low hedgehogs (0.21)	0.941	0.900
High hedgehogs (0.60)	1.121	1.008
Actual change		
1983 – 2014	0.992	0.990
2000 – 2014	0.972	1.003
2007 – 2014	0.966	0.950
REDSHANK	Clutch survival (mean and 95% CLs)	
	Low hedgehogs	High hedgehogs
	0.44 (0.35 – 0.50)	0.11 (0.05 – 0.16)
Brood survival		
Low hedgehogs (0.33)	0.908	0.840
High hedgehogs (0.84)	1.046	0.875
Actual change		
1983 – 2014	1.023	0.995
2000 – 2014	1.021	1.026
2007 – 2014	1.026	1.000
RINGED PLOVER	Clutch survival (mean and 95% CLs)	
	Low hedgehogs	High hedgehogs
	0.37 (0.24 – 0.47)	0.26 (0.18 – 0.33)
Brood survival		
Low hedgehogs (0.07)	0.898	0.885
High hedgehogs (0.40)	1.092	1.023
Actual change		
1983 – 2014	0.954	0.975
2000 – 2014	0.929	0.999
2007 – 2014	0.862	0.899

Table 16. The percentage of monitored nests of each wader species that were either confirmed or probably predated by known predator species.

	PREDATOR									
	Hedgehog	Otter	Cat	Rat	Common Gull	Black-headed Gull	Great Black-backed Gull	Herring Gull	Raven	Other avian
Lapwing	5	<1	0	1	<1	<1	<1	<1	<1	1
Redshank	21	<1	0.6	3	1	<1	<1	<1	<1	4
Dunlin	9	0	0	2	2	0	0	0	0	0
Ringed Plover	7	1	0	0	5	0	0	1	0	3
Snipe	3	0	0	3	0	0	0	0	0	3

ANNEX 2: FIGURES

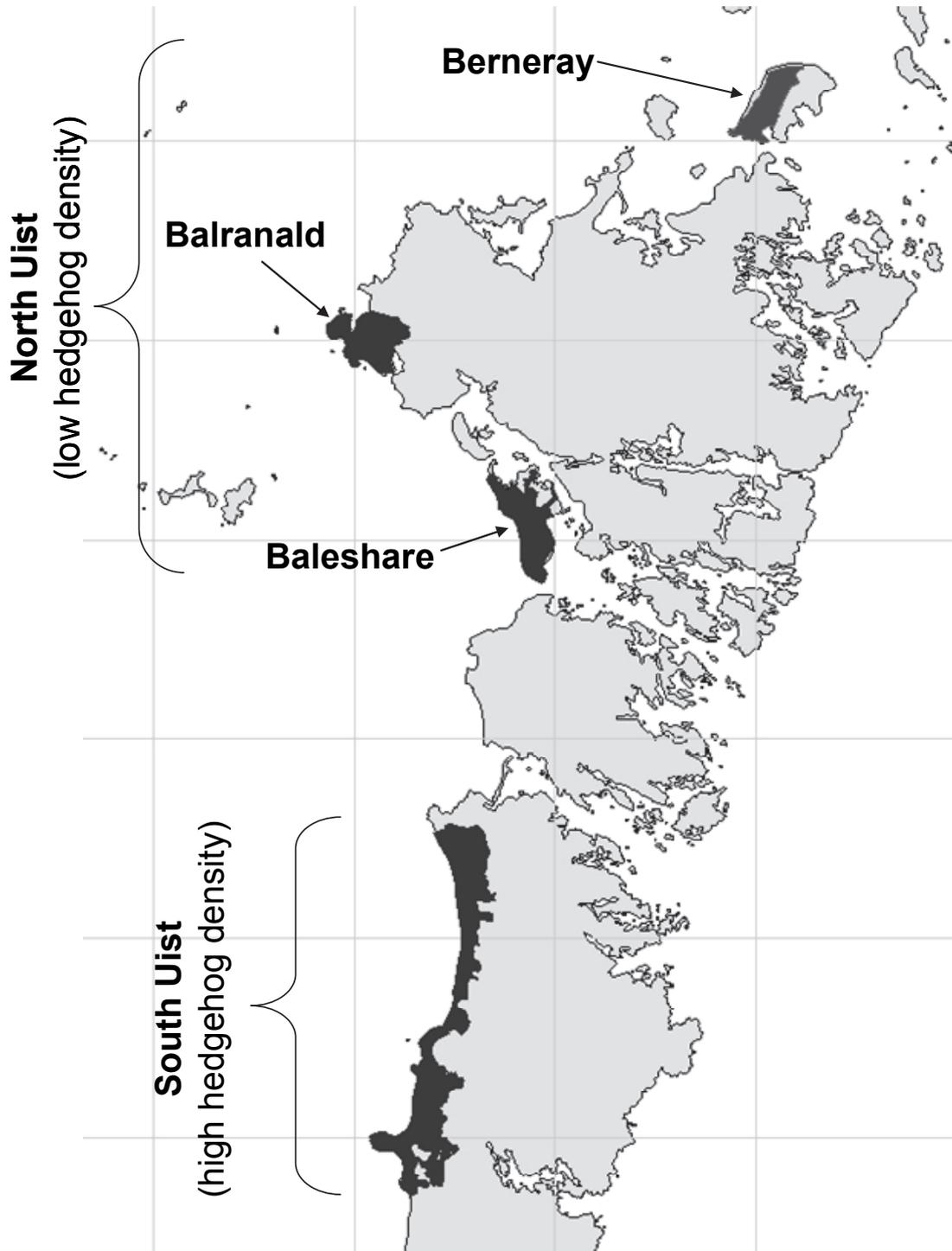


Figure 1. The locations of the Uist study areas used in 2012 – 2014. The grid lines represent the 10-km divisions of the Ordnance Survey national grid. © Crown copyright and database rights 2015 Ordnance Survey 100017908.

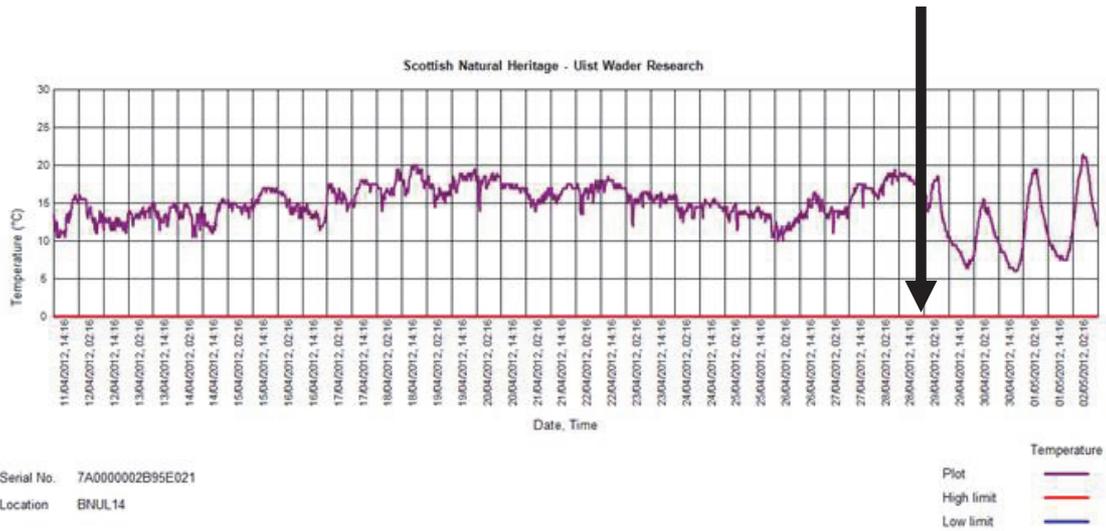


Figure 2. An example of a temperature trace from nest temperature loggers (a lapwing at Baleshare in 2012). The arrow marks the point where a clear diurnal cycle of ambient temperature commences and is taken as when incubation finished.

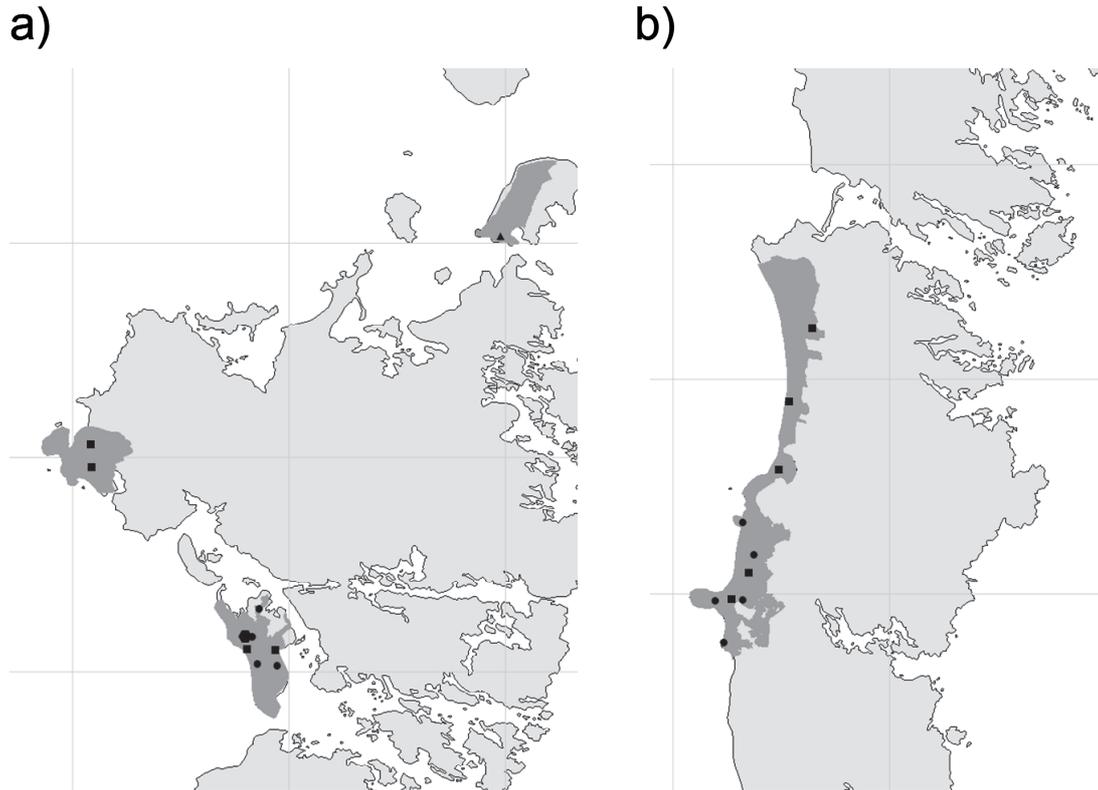


Figure 3. Locations of fixed points for visually recording predator occurrence and predation and disturbance events on (a) North Uist and (b) South Uist. Round mark points (●) used in 2012 and squares mark points (■) used in 2013 and 2014. The hexagonal point on Baleshare (North Uist) was used in all three years. The triangle (▲) on Berneray was in 2014 only. © Crown copyright and database rights 2015 Ordnance Survey 100017908.

a)



b)

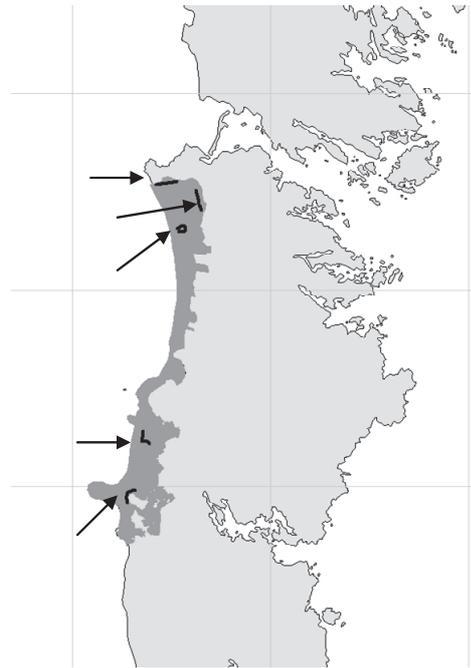


Figure 4. Locations of behaviour recording transects on (a) North Uist and (b) South Uist in 2014. © Crown copyright and database rights 2015 Ordnance Survey 100017908.

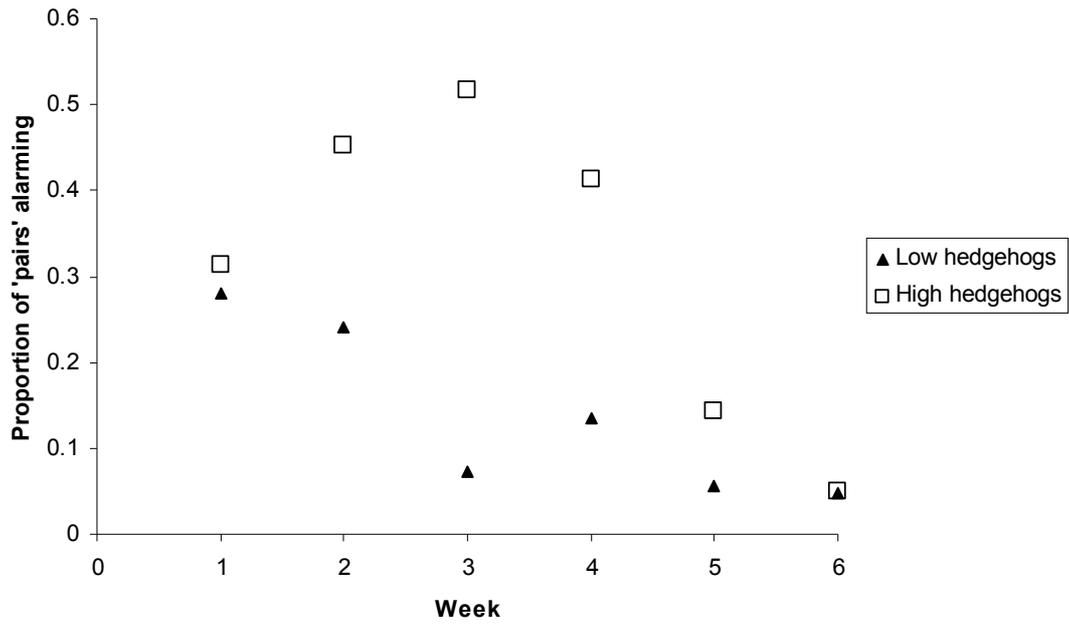


Figure 5. The proportions of assumed pairs (redshank, dunlin and ringed plover combined) showing behaviour indicative of having dependent young between 4 June – 10 July 2014 (six weeks).

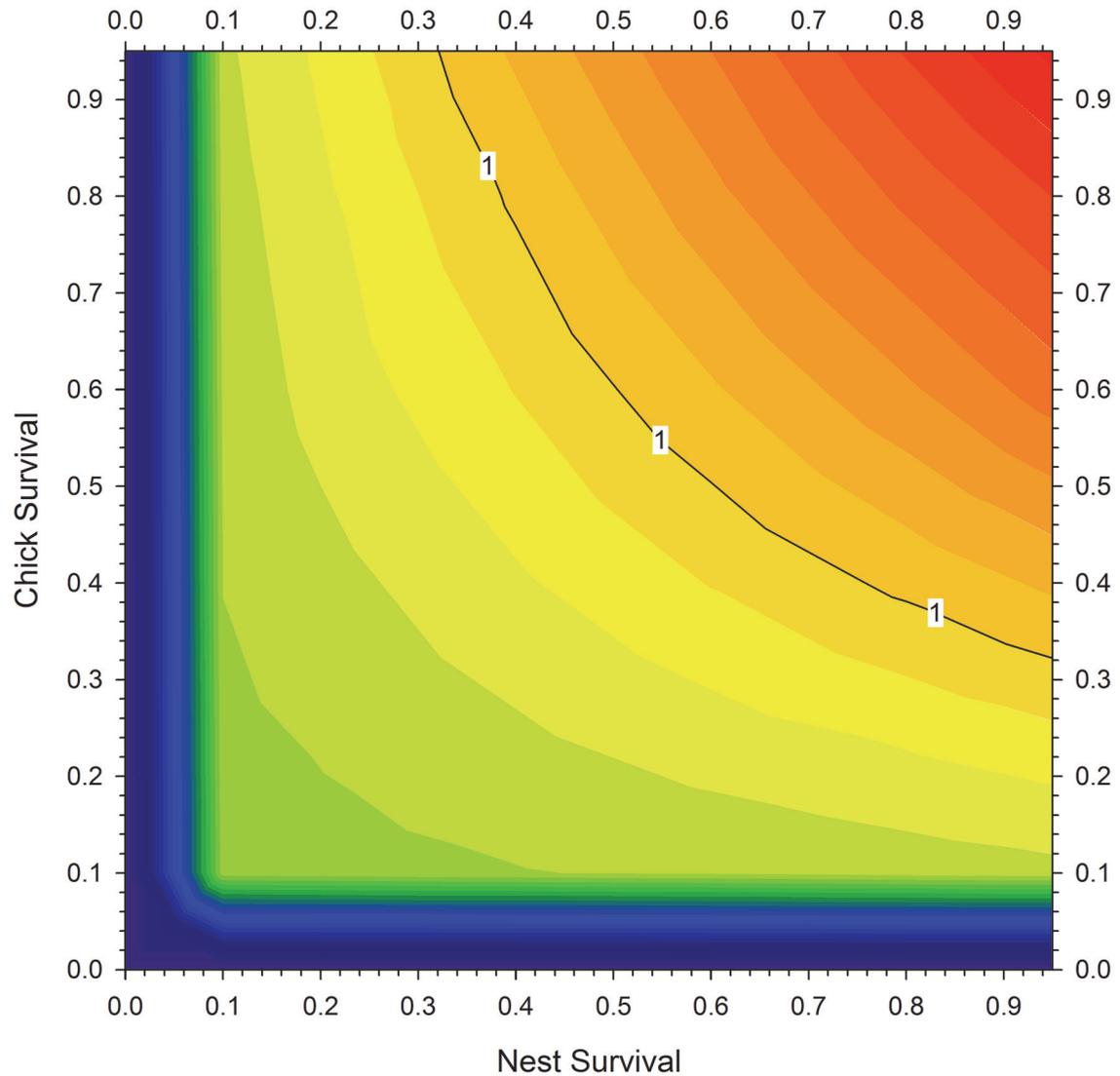


Figure 6. Modelled population growth rates of a machair breeding wader with adult annual survival of 80% and first-year survival of 45% under different combinations of nest survival (clutch survival as the x axis) and Chick survival (y axis). Combinations below and left of the line (yellows and greens) represent declining populations, those right and above (oranges and reds) increasing populations.

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