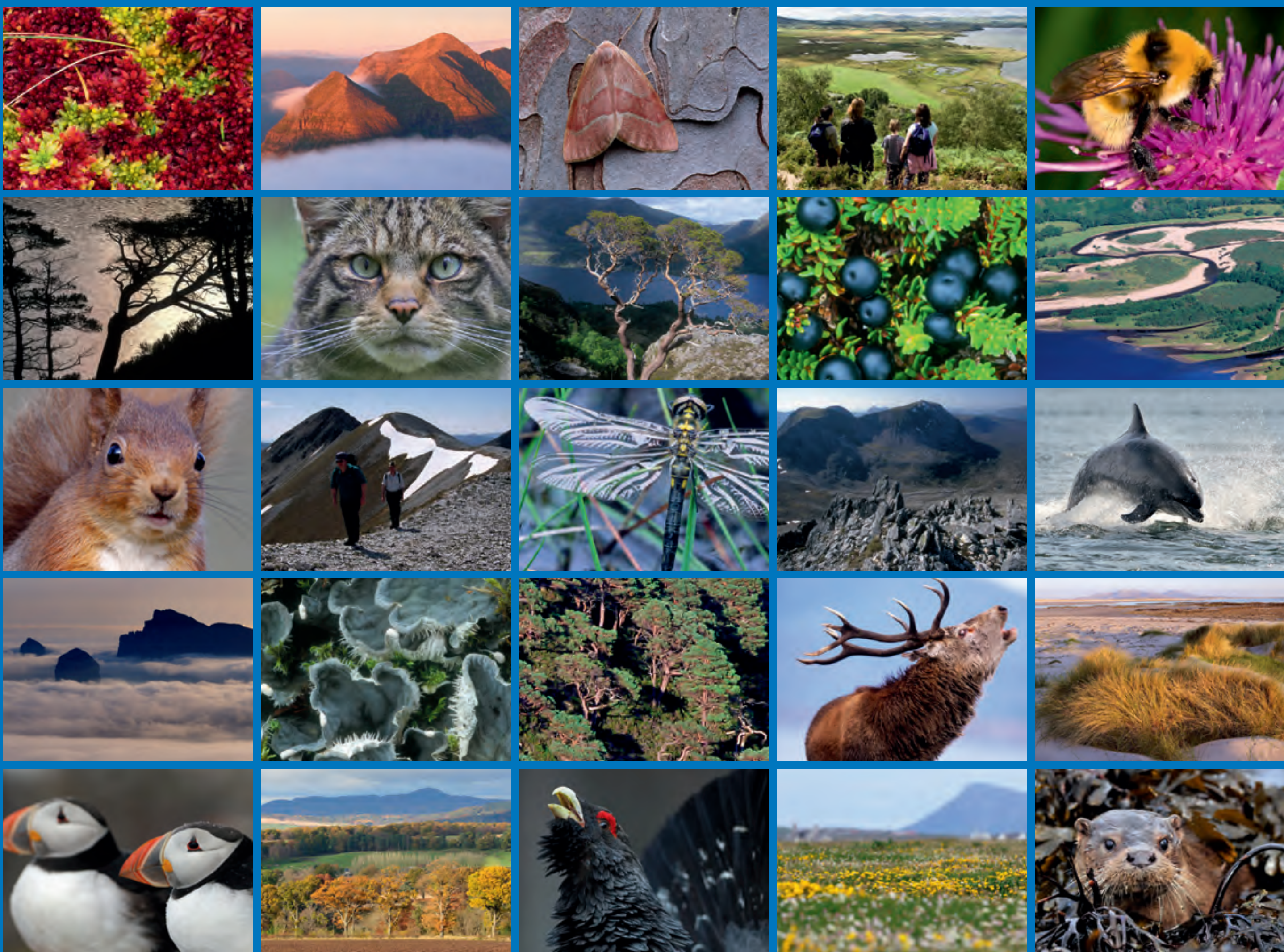
Scottish Natural Heritage
Commissioned Report No. 411

Population changes in breeding waders on machair in North Uist and Benbecula and their associations with vegetation and landuse



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C O M M I S S I O N E D R E P O R T

Commissioned Report No. 411

Population changes in breeding waders on machair in North Uist and Benbecula and their associations with vegetation and land use

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COMMISSIONED REPORT

Summary

Population changes in breeding waders on machair in North Uist and Benbecula and their associations with vegetation and land use

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Keywords

Breeding waders; machair; hedgehog; vegetation; Uist; BTO; James Hutton Institute.

Background

The west coast habitats of the Uists are internationally important for their populations of breeding waders. Recent changes in numbers have been mainly linked with impacts of predation by hedgehogs which were introduced to South Uist in 1974. However, changes in agriculture, other predation pressures and other factors may also contribute to the changing status of these birds. This report presents joint analyses of two independently-collected data sets, one on breeding waders (sampled in the 1980s, 1990s and 2000s) and one on vegetation (sampled in 1976 and 2009) from four machair sites in North Uist and Benbecula, sites where hedgehogs have either been absent (North Uist) or are currently present at low densities (Benbecula). Relationships between the abundance of breeding waders and machair vegetation characteristics (in the relative absence of hedgehogs), and how both have changed over the past three decades are examined. These relationships are presented in the context of changes in land use as determined from interviews with the Grazing Clerks for those machair study areas. Note that this study primarily concentrates on machair habitats and not the adjacent 'blackland' and meadows, both of which also support important concentrations of breeding waders.

Main findings

- These analyses have increased our understanding of habitat associations and point towards some interesting changes in machair systems that may have affected breeding waders, notably agricultural intensification and changing soil chemistry (reaction and salinity). Many of the effects are species-specific.
- Breeding ringed plovers and dunlins have declined across all four study areas (by 67% and 53% respectively) between the 1980s and 2000s. Redshanks increased by 42% across all sites. Oystercatchers increased by 67% at two sites and remained stable at the others. Lapwings possibly decreased by 21% at two sites and remained stable at the other two.
- Indices (Detrended Correspondence Analyses, Ellenberg Indicator Values and structural data) derived from the vegetation survey data indicated decreased soil fertility and increased salinity across all sites between 1976 and 2009. There was an overall reduction in vegetation cover at two sites and also in vegetation height at one of them.

- Common relationships amongst the breeding waders were a tendency to avoid areas of young dunes and to be more concentrated into areas with more basic and also wetter soils. Ringed plovers were the exception as they did not show a relationship with soil moisture.
- Oystercatchers, lapwings and ringed plovers tended to be concentrated in the more fertile machair grassland.
- Oystercatchers and lapwings avoided the more saline areas.
- Ringed plovers, dunlins and redshanks tended to avoid vegetation characterised by the most shade intolerant species, however some contradictions particularly for ringed plovers (preferences for sparsely vegetated areas) and the narrow range of that index, suggests that the derived indicator for site illumination may not be particularly reliable or appropriate for use in machair habitats.
- Lapwings tended to be concentrated into areas of relatively dense vegetation (though possibly avoiding the densest areas). Oystercatchers avoided taller vegetation which is where redshanks tended to be more concentrated.
- Oystercatchers and ringed plovers preferred areas with arable activity, while both redshanks and snipe tended to avoid those areas.
- Associations between locally measured changes in habitat indices and breeding wader abundance were relatively few and sometimes contradicted the general habitat – bird relationships that were otherwise apparent. The greatest measured changes were probably confounded with the greatest agricultural changes which otherwise reduced the habitat quality for some breeding waders (e.g. invertebrate availability).

A better understanding of how waders use the mosaic of machair habitats at multiple scales for different functions and the interactions of habitat use with predation risks would be extremely valuable in understanding the processes underpinning changes in these wader populations.

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Acknowledgements

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1. INTRODUCTION

The Uists are internationally important for their populations of breeding waders (*Charadrii*) where machair and adjacent habitats support the largest concentrations in the UK (Fuller *et al.* 1986, 2010). Machair is a vegetated plain of calcareous shell-sand formed on the western side of the islands which grades into acidic peat-based moorlands of the interior (Ritchie 1976). A complex of habitats is associated with the machair, including young dunes, more mature dunes with slacks, stable dune pasture, cultivated sandy plain, damp grassland, permanently wet marsh and emergent loch-edge vegetation. This suite of machair habitats, therefore, shows great variation in dampness and topography.

Recent declines in the numbers of breeding waders in parts of the islands have been linked mainly with impacts of predation by hedgehogs *Erinaceus europaeus* which were introduced to South Uist in 1974 (Jackson and Green 2000, Jackson 2001, 2007, Jackson *et al.* 2004). However, there have been declines in some species (lapwing *Vanellus vanellus*, ringed plover *Charadrius hiaticula* and dunlin *Calidris alpina*) on North Uist at sites where there have been no hedgehogs (Fuller and Jackson 1999, Fuller *et al.* 2010). Therefore, other factors such as changes in agriculture, other predators and potentially other factors such as local disturbance will also have contributed to the changing status of these birds.

Long-term data on breeding waders are available for four sites (Berneray, *ca.* 550 ha; Sollas, *ca.* 522 ha; Baleshare, *ca* 953 ha; and Benbecula, *ca.* 1527 ha) for three time periods from surveys conducted by the Wader Study Group, BTO and RSPB in 1983-87, 1998-2000 and 2007-10 (Fuller *et al.* 1986, 2010, Fuller and Jackson 1999, Conway *et al.* 2008, Calladine *et al.* 2010). Quantitative data on vegetation composition, structure, and land use are available for machair habitat in those same study areas from the Nature Conservancy Council in 1976 (Shaw *et al.* 1983), which were resurveyed by the Macaulay Land Use Research Institute (MLURI) in 2009. The geographic overlap of the long-term bird and vegetation studies provided an opportunity to assess relationships between wader numbers and vegetation characteristics for machair habitat.

This report describes spatial relationships between the abundance of breeding waders and vegetation attributes. Relationships are also examined between measured changes in birds and vegetation since the 1970s. In addition, reported changes in the agricultural use of the machair since the 1970s are assessed from interviews with Grazing Clerks and crofters. Inter-relationships between reported changes in land use, vegetation composition and breeding waders are discussed. Based on the same 1970s vegetation dataset, most of the major machair sites along the Western Isles were resurveyed in 2010, and crofters and Township Clerks interviewed with respect to changes in land use. The results of these analyses will become available during 2011.

2. METHODS

2.1 Surveys of breeding birds

The breeding waders of four study areas (Figure 1) were surveyed around the end of May and the first week of June in 1983 (Benbecula only), 1984-87 (Baleshare, Sollas and Berneray), 1998-99 (Sollas and Berneray), 1998-2000 (Baleshare), 2000 (Benbecula), 2007-09 (Benbecula) and 2007-10 (Baleshare and Sollas), and 2007-08 and 2010 (Berneray). In each year, single survey visits covered the entirety of the study areas and employed the same field and analytical methods (Reed and Fuller 1983). On open machair, a team of two to four surveyors walked transects 100 m or 150 m apart recording all registrations of waders on 1:10,000 field maps. Where walking transects was impractical, because of field boundaries, ditches and water bodies, a 'constant-effort-search-approach' was adopted whereby all parts of a field were approached to within at least 50 m. Observations from neighbouring observers were integrated in order to remove duplicate observations.

Field maps were summarised into 'pair summary' maps where a single registration represented an apparent pair of breeding birds. The following rules were applied to identify 'pairs' and to ensure direct comparability between surveys (after Reed and Fuller 1983):

a) 1 bird recorded alone 50 m or more (for ringed plover and dunlin), 75 m or more (for redshank *Tringa totanus* and lapwing) and 125 m or more (for oystercatcher *Haematopus ostralegus*) from other birds were defined as a pair;
b) 2 individual birds within 50 m (for ringed plover and dunlin), 75 m (for redshank and lapwing) and 125 m (for oystercatcher) of each other were defined as a pair;
c) 2 birds together, or 2 birds recorded as a pair were defined as a pair;
d) 3 or 4 birds together were defined as 2 pairs;
e) 1 – 4 birds flying into, out of or through the area, or into the site were defined as 1 – 4 pairs as appropriate;
f) 5 or more birds remaining in the area, either on the ground or circling around (vocal birds only) were defined as 3+ pairs as appropriate;
g) 3 or more oystercatchers remaining in the area either on the ground or circling around (vocal birds only) were defined as 2+ pairs as appropriate;
h) Drumming, chipping or alarming snipe *Gallinago gallinago* were defined as a pair.

The following were rules were applied to identify non-breeders to be excluded from the pair summary maps:

i) 5 or more birds in a flock on the ground without vocal registration;
ii) Any bird(s) which flew out of or through the area in one direction for more than 150 m without landing;
iii) Nests were not included in the estimates of numbers of breeding pairs;
iv) Ringed plovers identified by plumage and morphological characteristics as being of a race that breeds at more northerly latitudes (usually supplemented by the above behavioural observations).

The pair summary maps were subsequently digitised (ArcGIS 9.2; ESRI 2006) to facilitate spatial association with the vegetation data (Section 2.2).

Variation in the detection of birds is a function of their actual abundance and the probability of their detection by observers. Factors that influence detectability include species, behaviour, habitat, weather and the times of day and year, the distance from the observer and also the ability of observers themselves (Sauer *et al.* 1994, Buckland *et al.* 2001, Buchanan *et al.* 2006, Alldredge *et al.* 2007). By surveying using the same methods and at the same time of year, the influence of some of these factors will be minimised, however population estimates derived from single survey visits will always be subject to these biases and in particular, to biases associated with variations in the timing of breeding and of breeding success. Most surveys of breeding birds require multiple survey visits to establish indices of population size, or population estimates, which are both accurate and precise (Bibby *et al.* 2000, Calladine *et al*. 2009). For a species-specific discussion of the limitations of the method used in surveying the machair waders see Fuller and Jackson (1999). Therefore, in assessing changes of population size and for deriving indices of population density of breeding waders, single estimates (either means or medians for individual sites or sampling points as appropriate, see Section 2.4.2) are derived for each of the three periods of surveys (1983-87, 1998-2000 and 2007-10). Given the high densities of breeding waders on the machair of the Uists, the potential impact of their disturbance by repeated surveys within a season is a major concern. In particular predatory common gulls *Larus canus* can be attracted by both surveyors and the associated disturbed breeding waders (Fuller and Jackson, 1999, personal observations). Repeated annual single-visit surveys offer a practical compromise between the need to increase the accuracy of population estimates through multiple survey visits and the need to reduce the risks associated with disturbance-related predation.

2.2 Surveys of vegetation

Sample vegetation surveys were undertaken in June and July 2009 using identical methods and sampling locations as in 1976 (a density of *ca.* 15 locations km^{-2}; Figure 1) (Shaw *et al.* 1983). Sampling locations plotted onto 1:10 000 Ordnance Survey maps for the 1976 surveys were relocated in 2009 using hand-held GPS. However, the heterogeneity of the habitat can be at a finer scale than the accuracy of this process, as a result of location and plotting errors in 1976, and errors in the digitisation process. To avoid misrepresentation of changes in habitats, the vegetation at each sampling point was compared in the field with that from the 1976 survey. If it was considered that there was no ecological or practical possibility of the apparent transition having taken place (e.g. through erosion, seral development or agricultural management) the plot location was then moved to a random point within the nearest likely area of vegetation that was comparable to the 1976 survey (or to where any changes were considered to be realistic). This process prevented the recording of spurious changes within the vegetation data, but is necessarily somewhat conservative in that there remains a possibility, however slight, that some actual change may go unrecorded. For those sampling points on Benbecula, for which there was no previous survey in 1976 (i.e. all those away from the area at Borve (Borgh), Figure 1), four points were randomly located within each 500 m x 500 m area surveyed to achieve a similar density to the 1976 survey.

At each sampling location a 5 m x 5 m quadrat was laid out within which all species were recorded and a visual estimate of cover was made for each species. Land use and structure data for each quadrat were also recorded (see (c) and (d) below). To summarise the vegetation data in order to relate it to breeding wader abundance, and changes thereof, the following indices were derived:

a) *Detrended Correspondence Analysis (DCA) axes* – Vegetation cover data were subject to Detrended Correspondence Analysis (Hill and Gauch 1980) as a means of data reduction. In this case, this permitted the reduction of data on 238 plant species to up to 4 axes (using CANOCO 4.5; ter Braak and Šmilauer 2002) which describe the main variation between the plots. For this analysis, only Axes 1 and 2 captured substantial and identifiable variation in the vegetation data, and hence Axes 3 and 4 were not considered further;

b) *Ellenberg Indicator Values (EIV)* – A set of Ellenberg Indicator Values (scores between 1 and 9; Ellenberg 1988) were computed for each plot based upon the weighted (by cover) mean of the Ellenberg Indicator Values (EIV) for each species within the plot. EIVs were based upon the recalculated values for the UK by Hill *et al*. (1999) and weighted means were calculated for (i) Light (an indicator of the exposure to direct sunlight of the ground vegetation), (ii) Water (an indicator of soil moisture), (iii) Reaction (an indicator of soil pH), (iv) Nitrogen (in effect an indicator of soil fertility) and (v) Salt (an indicator of soil salinity);
c) *Agricultural activity* – The presence or absence of grazing (and its approximate seasonality) and arable cultivation (i.e. active cultivation or fallow) were recorded for each plot;
d) *Height and density* – The height and density of each of three functional groups of plants (herbs, grasses, shrubs) were recorded in three height classes (0-20 cm, 20–50 cm and 50–100 cm above the ground). For analysis, these were condensed into two measures: a measure of density – taken as the maximum score for the lowest height class (0–20 cm) across all three functional groups, and a measure of height – taken as the highest height class recorded for any of the three functional groups;
e) *Cover* – A summation of the estimated cover (% of ground cover) by all plant species. Note that because of overlapping cover, this can exceed 100%.

2.3 Land use

In the Uists, the areas of machair are divided into 'townships' within which common grazing rights are shared among the group of crofters. The Grazings Clerks administer township rules in relation to use of the machair shares. To gather information on current machair land-use practices, and changes in these practices since the 1970s, face-to-face interviews were sought with the Grazing Clerk of each township covering areas of machair subject to bird and vegetation surveys. Grazing Clerks of the following townships were interviewed in 2009: Rushgarry and Borve (Berneray); Grenitote, Sollas, Middlequarter, Baleshare, Illeray and Claddach Illeray (North Uist); Uachdar, Aird, Torlum and Liniclate (Benbecula). In the interviews the term '1970s' was used as a more practical reference point rather than the specific date of the original vegetation surveys, 1976. Where time allowed, the interviewers also collected information on the current and past use of both croft in-bye (usually situated just inland from the machair on the 'blackland') and hill common grazings as changes in the use of these might have had subsequent implications for the use of the machair.

Although Grazing Clerks were generous in their offer to help, they were often limited in the time that they had available. Some were too young to recall detailed information from the 1970s, or were not crofting at that time. Similarly, some Clerks could recall much detail for their own land but were less sure of other crofters' land management practices. It is also important to note that machair use may vary not only between townships but also within townships. For this reason, caution is needed when generalising current land use practices to the level of the township.

2.4 Analyses of bird – vegetation relationships

Relationships between the indices derived from the vegetation sampling surveys and the recorded abundances of breeding waders were investigated using two approaches. The first investigated their current spatial associations using the vegetation data collected in 2009 and the breeding wader data collected in 2007-10. The second investigated relationships between recorded changes in the vegetation (1976 to 2009) with recorded changes in breeding wader densities (1983-87 to 2007-10).

2.4.1 Current relationships

From the digitised breeding wader data (Section 2.1), all apparent territories within 100m of the vegetation sampling locations (central grid reference) were selected. Where there was an overlap of bird data (where the distance between vegetation sampling points was less than 100m), data from one point was selected at random and included within the analyses. For each species, the sum of apparent territories within 100m of each vegetation sampling point for each of the years 2007-10 was the dependent variable or 'Count' in the Generalised Linear Mixed Models (GLMMs, Proc Glimmix in SAS 9.2; SAS Institute Inc. 2008). This was used to examine the relationship of species abundance with the indices derived from the vegetation surveys (Section 2.2). Not unexpectedly there were significant correlations (Proc Corr in SAS 9.2, $P < 0.05$) between some of the vegetation indices, notably between the DCA axes and some of the EIVs. For example, the Pearson Correlation Coefficients (r) exceeded 0.7 between the first DCA axis and EIVs for light, moisture and salt and between the second DCA axis and the EIV for nitrogen. Because of these correlations and the independent derivation of the two sets of indices, separate models were run with the DCA values and the EIVs as the independent variables.

The model investigating the relationships between breeding wader abundance and the DCA axes only considered the first two axes. DCA axis 1 reflected the change in the physical structure from young dunes (a high score) through to the machair plain with fixed vegetation (a low score). DCA axis 2 reflected a gradation of machair grassland from uncultivated (a high score) through to more cultivated and more fertile ground (a low score). There was much less variation in the other two derived DCA axes and as they did not appear to be identifying any variables other than those driving the first two axes (largely separating out on fertility), they were hence excluded from the models.

The model investigating the relationships between breeding wader abundance and EIVs also included the structural and agricultural use information. The recorded scores for winter grazing and summer grazing were mutually exclusive and both were correlated with the presence of arable ($r = 0.75$, $P < 0.0001$). Therefore, in addition to the five EIVs (light, water, reaction, nitrogen and salt), height and density, only the score of arable activity was included as an independent fixed variable in the models.

The models assumed a Poisson error distribution and a log-link function (to best fit the overdispersed nature of the bird count data with its many 'zeros') and study site ($n = 4$) was included as a random term. In order to account for incomplete coverage across all four years (Section 2.1), the number of years in which the waders were surveyed was included as an offset. The use of this offset effectively turns the dependent variable (count) into the mean for the number of years of survey data while not violating the assumptions of a Poisson distribution by retaining the dependent variable (counts of birds) as an integer.

Initial analyses using multi-species models identified differences between species of breeding wader, as regards the nature of the relationships between each species and the vegetation indices. These models included species and its interaction term with each vegetation index as independent variables. These initial models identified which waders showed similar relationships of abundance with the vegetation indices.

2.4.2 Changes in vegetation, wader abundance and their relationships

Changes in breeding wader population sizes were assessed by comparing the median estimates for each of the four sites from each of the three time periods for which there are directly comparable data (1983-87, 1998-2000 and 2007-10). Data from some partial surveys of Sollas in 2009 and Benbecula in 2010 are excluded from the derivation of median counts for the period 2007-10 (Calladine *et al.* 2010) and to be consistent with reporting count data across all years, correction factors have not been applied (these were used as a correction for low detectability for some species in earlier analyses e.g. Fuller *et al*. 1986). Therefore some figures will differ slightly from those given in some other published sources.

Changes in the vegetation indices were assessed by comparing the DCA scores, EIV indices and scores for other measures of structure and features derived from the surveys in 1976 and those from 2009. Comparisons of both breeding wader and vegetation data used Generalised Linear Models (GLM; Proc Genmod in SAS 9.2) where the dependent variable was either the median count (for breeding waders) or the derived vegetation index. The independent variables in the models were Site (n = 4), Year (n = 2 for the vegetation data and n = 3 blocks for the wader data) and their interaction term. For the breeding wader models, the areas of the study sites (km^2) were entered as an offset, so the models were effectively comparing wader densities. All models for breeding waders assumed a Poisson error distribution and log-link function. The error distributions for the models comparing vegetation indices were those that best fitted the data: a) Normal with an identity link function for DCA axis 1 and the EIVs for Light, Water, Reaction and Nitrogen; b) Poisson with a log link function for DCA axis 2, EIV for Salt, and the scores for Density, Height and Cover; and c) Binomial with a logit link function for the presence of arable). *Post hoc* pair-wise comparisons were used to identify the sources of statistically significant differences.

Relationships between the changes in breeding wader abundance and in vegetation were assessed by modelling the changes in wader numbers between 1983-87 and 2007-10 with the vegetation changes between 1976 and 2009. Although the early time period is not coincident, the wader data from the 1980s are the closest that are available and they can be spatially referenced with the vegetation data from 1976. The dependent (or response) variable was the difference between the mean of the counts of apparent wader territories, for each species, within 100m of the vegetation sampling points within the two time periods (1980s and 2000s). Independent variables (or factors) were the indices derived from the vegetation measures. As was done for modelling the current relationships (Section 2.4.1), two separate GLMMs were employed, one for the DCA scores and one for the EIVs, the latter also including the structural and agricultural use data. The models assumed a normal distribution (as best fitted the dependent data) and site was introduced as a random variable. As with the models investigating current relationships, initial multi-species modelling identified the similarities and differences between species in their relationships. As most of Benbecula was not surveyed in 1976, that site does not form part of the analysis of changes in wader abundance and vegetation.

3. RESULTS

3.1 Changes in breeding waders

There were marked contrasts in the changes of population density between species of breeding waders since the 1980s (Figure 2–7). Lapwing was the only species not to show a statistically significant difference in breeding density across all sites between data collected from the three decades (1980s, 1990s and 2000s): the Year term in the models was statistically significant ($P < 0.0001$) for all species apart from lapwing ($P = 0.30$) and snipe (data too sparse for model convergence). The Site*Year interaction term was also statistically significant ($P < 0.01$) for all species apart from redshank ($P = 0.08$) and snipe (data too sparse) showing that there have been contrasting trends for most species between the four study areas (Figure 2–7). Details of the actual counts are reported elsewhere (Calladine *et al.* 2010), but in summary:

- Breeding **oystercatchers** have increased by *ca.* 67% at two sites (Berneray and Sollas), with most of that increase between the 1980s and 1990s. At both sites, breeding densities increased to levels similar to those which have been recorded at Baleshare throughout the three decades (Figure 2). Little change was noted at Benbecula where densities have remained at relatively low levels, similar to those found at Berneray and Sollas in the 1980s. The median population estimate (2007-10) across the four study areas was 798 pairs.

- **Lapwings** have decreased by *ca.* 21% at Baleshare and Sollas since the 1980s though the apparent difference is close to that which might be attributable as a count artefact associated with the survey methods (Fuller and Jackson 1999). There has been little change at Berneray (a site with relatively high breeding density throughout the study period) and Benbecula (a site with a relatively low breeding density through the study period) (Figure 3). The combined median population estimate (2007-10) was 852 pairs.

- **Ringed plovers** have declined by *ca.* 67% across the four study areas since the 1980s. Two sites that supported high breeding densities in the 1980s (Berneray and Sollas) have experienced the most marked declines with current densities approaching those found at the other two study sites (Figure 4). The combined median population estimate (2007-10) was 210 pairs.

- **Dunlins** have declined by *ca.* 53% across the four study areas since the 1980s. At Berneray, which formerly supported a particularly high density of breeding birds, the decline appears to have stabilised since the 1990s, while at Sollas, the decline may have only occurred since the 1990s (Figure 5). The combined median population estimate (2007-10) was 258 pairs.

- **Redshanks** have increased by *ca.* 42% across the four study areas. The increases at Berneray and Benbecula were not apparent until after the 1990s (Figure 6). The median population estimate (2007-10) across the four study areas was 755 pairs.

- Although difficult to survey and in relatively low numbers, there appears to have been a decrease (*ca.* 75%) in breeding **snipe** on Benbecula since the 1980s (Figure 7).

3.2 Changes in vegetation indices

In the indices derived from the vegetation data, there was greater variation between sites than there was between the two study years, 1976 and 2009 (Table 1). Significant temporal changes that were apparent across the study areas were an increase in the scores associated with DCA axis 2, a decrease in the EIV for Nitrogen, an increase in the EIV for salt and a decrease in overall vegetation cover (Table 1). Changes in both the DCA axis 2 score and the EIV for Nitrogen both suggest reduced fertility and/or management influences on soil fertility. The absence of any statistically significant differences of the interaction term (Table 1) suggests that the increase in the index of soil salinity, and those for reduced fertility occurred similarly across all study areas (Tables 2 and 3). The reduced index of vegetation cover was largely driven by changes at Baleshare and Berneray (significant interaction term; Table 1). At Berneray alone, there was a statistically significant reduction in the index for vegetation height (Table 1).

In all cases, the changes were arguably subtle in term of the broad vegetation communities and represented fairly small shifts within the respective values of the indices (Tables 2 and 3). For example, the mean EIVs for Nitrogen remained within the 'indicators of intermediate fertility' categories between the two surveys, despite there being a statistically significant change to a lower value. Similarly, the mean EIVs for Salt remained within the categories indicative of 'slight salt tolerance' between the surveys despite a slight but measurable shift towards a more saline indicator.

Although there was no apparent change in the proportion of sampling points where the vegetation was measured showing signs of agricultural activity, there had been a 58% drop across all sites in the number of points that fell on active arable ground and therefore could not be sampled (at Borve from 5 in 1976 to 1 in 2009, at Baleshare from 8 to 6, at Sollas from 18 to 7 and at Berneray from 9 to 3).

3.3 Relationships between breeding wader abundance and indices of vegetation

Common relationships amongst the breeding wader species were tendencies to avoid areas of young dunes (a negative relationship with the DCA axis 1 for all species) and to be more concentrated in areas of more basic and also wetter soils (a positive relationship with the EIVs for Reaction and Water within the ranges found in the study areas) (Table 5). Exceptions to these general trends were for ringed plovers which did not show any significant association with soil moisture (in any direction) and for snipe, an absence of relationships for either of those EIVs (Table 5). In the case of snipe, an absence of relationships may be a function of the limited power to detect any relationships as a result of their low densities compared to the other species.

Three species (oystercatcher, lapwing and ringed plover) showed a significant negative relationship with the DCA axis 2, suggesting a tendency to concentrate in the more fertile and more cultivated machair grassland (Table 5). Redshanks showed an opposite tendency, to concentrate on the less-fertile and less-cultivated grassland (a significant positive relationship with the DCA axis 2; Table 5). In contrast, no species showed a statistically significant relationship with the other index of fertility, the EIV for nitrogen (Table 5). However, redshanks demonstrated a marginally non-significant ($0.05 > P > 0.10$) negative relationship with the indicator for nitrogen which contrasts with the apparently positive association with more intensively managed machair (with possibly more fertile soil) associated with DCA axis 2 . Dunlins and snipe showed no significant relationships with either index of soil fertility, though for the latter species again there was limited power to detect such relationships.

Significant negative relationships with the EIV indicators of soil salinity show that two species (oystercatcher and lapwing) tended to avoid the more saline areas, within the range of those sampled areas (Table 5). Three species, ringed plover, dunlin and redshank showed a negative response with the EIV for light suggesting a tendency for them to avoid habitats characterised by the most shade-intolerant species such as those characteristic of disturbed areas (Table 5). Ringed plovers, however, show a preference for the more sparsely-vegetated areas as indicated by their negative relationships with measures of both vegetation density and overall cover (Table 5). For ringed plover in particular, this could potentially contradict their apparent tendency to avoid vegetation indicative of the most shade-intolerant species. But it must be stressed that the weighted mean indicator for light varied over a narrow range (mostly 7.08 – 8.91, out of a range of 0 – 9) so almost all plant species recorded were characteristic of open conditions. Given the narrow range of this indicator, it is possible that the presence and abundance of the dominant plant species within the sampling points is driven more by the breadth of these species' niches rather than their general preferences for high levels of illumination. The other measures and indicators of vegetation structure may therefore be more informative.

The distribution of lapwings, oystercatchers and redshanks were associated with variations vegetation structure, with lapwings more concentrated where the vegetation density score was greater, oystercatchers avoiding taller vegetation and conversely redshanks concentrated within taller vegetation (Table 5). Oystercatchers and ringed plovers showed preferences for areas with arable activity, while both redshanks and snipe tended to avoid those areas (Table 5).

3.4 Relationships between changes in breeding wader abundance and changes in indices of vegetation

Recorded changes in the scores associated with the DCA axis 2 were associated with changes in the breeding density of three species of waders. Lapwings and dunlins both declined the most where the changes in vegetation which indicate increased levels of management were the greatest (Table 6). This, however, could contradict the general relationship whereby all wader species tended to be more abundant where that index suggested the machair grassland was more managed and fertile (Table 5). It is possible that sites where the change has been greatest are actually areas where the machair has been most 'improved' agriculturally and conditions have actually become less suitable, in terms of structure and/or food availability. Relationships between recorded changes in vegetation and in breeding wader densities were otherwise relatively few. Ringed plovers appeared to have experienced the least declines (or even increased) where indicators of light increased, and the soil became more basic, more fertile and less saline (Table 6). Redshanks had increased least (or declined) where the DCA axis 1 scores had increased (suggestive of encroaching dunes or otherwise unstable vegetation) and where the vegetation height had also increased. The latter association of reduced numbers of redshanks where vegetation height had increased contradicts the general relationship for that species (i.e. more concentrated where the vegetation was taller). Again, the measure of change could indicate the greatest 'agricultural' improvement with those areas becoming less suitable for other reasons or in some cases where marram grass *Ammophila arenaria* had encroached onto the less-used agricultural areas.

3.5 Changes in land use since the 1970s reported by Grazing Clerks

Interviews with the eleven Grazing Clerks did reveal a range of changes in land management since the 1970s that may have contributed towards some of the changes in machair habitats and their breeding waders, although in the most part detailed or quantitative data were not available. In the Clerks' views:

- There has been a reduction in the number of people cultivating the machair, a trend that started prior to the 1970s. However, this was not always perceived as being associated with a reduced area of cultivation. In some cases, Grazing Clerks suggested that the same area of machair is cultivated now as would have been in the 1970s but by fewer people. In Borve (Berneray) for example, the clerk suggested that all 24 machair shares are now cultivated by seven people compared to the 1970s when 17-20 people would have cultivated the same area. In the neighbouring township of Rushgarry, only two people are now cultivating cereals on the 22 machair shares (although nine people still grow potatoes in relatively small patches). In Liniclate (Benbecula), there are 34 shareholders, and probably all of these would formerly have cultivated this township's machair; currently, ten people cultivate that same area. These comments contradict the observed decline in the area of active cultivation recorded by the decline in the number of points where the vegetation could not be sampled because of growing crops (Section 3.2).

- In general, the number of grazing cattle has decreased while sheep numbers have increased. For example in Liniclate, interview responses suggested that cattle numbers had decreased from 100 in the 1970s to approximately 20 in 2009. In contrast, responses indicated that sheep numbers greatly increased in the 1980s, partly due to policy incentives, and there were approximately 1000 in 2009. Prior to the 1970s, most households would have kept only ten or so sheep and so total numbers may have been 300 or less. There has also been a tendency for a change in sheep breeds towards heavier breeds [that have higher intake rates]. Blackface sheep were formerly the principal breed, however Cheviots, Suffolks, Texels and crosses of these now graze the machair. [Note that Agricultural Census figures are available at the parish level only, and hence specific changes at the township level cannot be verified.]

- Fertilisers applied to the machair have changed with less seaweed and little farm yard manure (both formerly important) now applied. As well as issues with the labour required to collect seaweed, it is considered (by some) to be unsuitable for fertilising grass silage as litter in the bales can cause rotting. Even where seaweed application is part of an agri-environment agreement (for example at Illeray), there are now reported problems associated with poor deposition on the shore and therefore insufficient availability. Compound fertilisers are now widely used with reported application rates ranging from 300 – 500 kg ha^{-1}. Reported recent changes were for compound fertilisers richer in phosphorous and potassium to be applied, attributed to the requirements of grass silage.

- Silaging began during the mid-1980s, replacing hay production and other crops, but was initially only adopted by some crofters and in some townships. Nowadays most crofters grow arable silage.

- Changes in ploughing equipment and also the increased use of contractors for ploughing are reported to be responsible for an increase in ploughing depths. In the 1970s plough depths were in the region of 7.5 – 10 cm which has increased to the current 10 – 15 cm. There were mixed reports as to whether machair soils were too unstable to sustain deeper ploughing.

- Although little supporting information was presented, there was also a general impression that drains were kept 'cleaner' in the 1970s than is currently practiced. [This practice may have been supported by the Integrated Development Programme.]

- The extent of fallow and the longevity of individual fallow patches vary and reports on their changes were mixed. One Grazing Clerk suggested that there may have been less fallow land at any one time on the machair prior to the 1970s (in response to pressure to produce more crops), however that perception was not reported widely (perhaps because many people interviewed were too young to have known whether or not this would have been the case). Current management is for ploughing for two consecutive years (a maximum of three) with land then being put to fallow or grass for 'as long as it grows well or until it starts to give bad cover', which is usually two or three years.

- In-bye (the enclosed ‘blackland’ that is the transitional area between the machair plain and peat moorland) is now used almost exclusively as pasture. Hay production on the in-bye is now much reduced compared to the 1970s while other crop production had probably almost ceased on that ground by the 1970s.

4. DISCUSSION

4.1 Breeding wader – machair habitat relationships

The machairs of North Uist and Benbecula continue to support an internationally important concentration of breeding waders. However, the composition of that community has changed over the past three decades, most notably with a decline in the populations of ringed plovers and dunlins and increases in oystercatchers and redshanks. As well as the machair itself, the adjacent 'blackland' (the transitional in-bye area between the machair plain and peat moorlands, areas which are now almost exclusively pastoral) and the neighbouring salt and freshwater marshes (although restricted in area) can support high densities of breeding waders. This study considers data collected from two independent studies, one monitoring population sizes of breeding waders, principally in machair habitats but also including adjacent blackland, loch-sides, freshwater and salt marshes and the other assessing vegetation composition and structure on machair. Fortuitously, there has been a considerable geographic overlap between these studies. Unfortunately, the blackland was not sampled during the vegetation surveys in 1976 (though areas on Benbecula were included in 2009; Fig. 1) and salt marsh was not sampled in either of the vegetation surveys. Therefore the relationships between changes in vegetation and breeding wader populations are largely restricted to the (albeit important) machair habitats.

Amongst the measures of habitat composition and structure that appear to be related to breeding wader densities are the general structure of the sandy substrates (young dunes to fixed machair plain), soil moisture, pH, fertility and salinity, vegetation structure (height and density) and arable cultivation. Although all wader species showed a tendency to avoid young dunes and to be concentrated in areas of more basic soils, the relationships with the suite of other habitat variables tended to be more species-specific. Relatively few measured changes in the habitat appeared to be related to the changes in breeding wader densities. Notable exceptions were as follows:

- First, indices of soil fertility, where declines in fertility were associated with declines in lapwings and dunlins, but increases in oystercatchers. However these might be confounded with measures of the greatest agricultural change in that changes in breeding wader densities were not necessarily in the direction that might be predicted by the their general relationships with those particular habitat variables (see Section 3.4). Oystercatchers however might be expected to benefit from an increase in earthworms that may follow from higher fertiliser inputs (Beintema *et al.* 1991).

- Secondly ringed plovers showed the greatest declines where measures of soil acidity and salinity had increased and most stability where measures of light and fertility had decreased the least. However, the range of indices found within the sampled areas was quite narrow in some cases. For example that for light suggested that plants occurred in 'well lit' to 'full sun' conditions only and for pH between 'moderately acidic' to 'weakly acidic'. Therefore the apparent associations with these two indicators at least (negative with the light indicator value for ringed plover, dunlin and redshank and the concentration towards the more basic soils for all species), either suggest that these species are very sensitive to relatively small variations (in light and pH) or that the derived EIVs may also represent other factors that determine the abundance of indicator plant species.

Other indices suggest a broader range of variability in those conditions, for example that for moisture ranged from 'dry' through to 'water-saturated' sites, for nitrogen from 'less' fertile through to approaching richly fertile sites and for salinity from an absence of salt-tolerant species through to communities that can occur in saline situations. Arguably, more confidence can be given to those relationships with habitat variables where the range of variation is greater. Soil fertility declined across all sites between 1976 and 2009 (suggested by both DCA scores and EIVs for nitrogen). The DCA score (which decreases with greater soil fertility) is negatively related (i.e. positively related to fertility) with breeding densities of ringed plovers (a species that has declined) and lapwings (for which there is strong evidence of some local declines). However, oystercatchers also have a negative relationship between breeding density and the relevant DCA axis but that species has generally increased which is counter to what might be expected on that relationship alone. The general increase in breeding redshanks could arguably be expected, given their negative relationships with increasing soil fertility. There has been a general increase in soil salinity, a measure with which two species show a negative relationship; lapwing (local declines) and oystercatcher (a species that has increased). For lapwing, declines have been most apparent at Sollas (evidence of a continued decline) and at Baleshare (a decline since the 1990s). Both these sites have experienced the greatest proportional increases in salinity indices. Although the measure of cover decreased between the years 1976 and 2009, ringed plover was the only species to show a statistically significant relationship with this variable (strongly negative). Ringed plover populations have declined markedly in the study areas which again is counter to what might be expected from that relationship and the measured reduction in vegetation cover if that relationship alone were driving changes in their breeding populations.

These analyses have increased our understanding of the habitat associations of breeding waders on machair. They point to some interesting changes in machair systems that may have affected breeding waders, for example agricultural intensification (as measured by change in the DCA axis 2 scores) and changing soil chemistry (reaction and salinity). The latter is likely to have affected the invertebrate food sources for those breeding waders. The relationships between wader breeding densities and habitat variables are clearly complex and often species-specific. The interpretation of these relationships would benefit from a more complete understanding of how breeding waders use the mosaic of machair habitats at a range of scales.

4.2 Other potential drivers of change – land use and habitat mosaics

The nature and 'grain' of the habitat mosaic on the machair will certainly influence how breeding waders utilise the available resources (Wilson 1978). Unfortunately, the density of vegetation sampling points was insufficient to quantify the mosaic at an appropriate scale for territorial waders, this not being among the original intentions of the survey in 1976 (Shaw *et al.* 1983). However, with some of the reported changes in land use (Section 3.5), it is possible to speculate on some potential changes.

A reduction in the number of people cultivating the machair might imply both a reduction in cultivated area and a spatial simplification of cropping patterns, but this assumption requires examination on a case-by-case basis. In most areas, the extent of machair under cultivation is reported to have remained the same (since the 1970s) but is worked by fewer people. However, the nature of the habitat mosaic created by cultivation may well have changed when worked by fewer people. In Liniclate (Benbecula) for example, where the number of people cultivating the machair is reported to have reduced from about 34 in the 1970s to 10 in 2009, the machair is still cultivated in relatively narrow strips. This might initially suggest the maintenance of a more heterogeneous habitat mosaic. However, in 2009, the majority of shares were being used to grow the same crop, grass silage, making for a relatively homogeneous habitat block. It is important therefore, to consider both the spatial organisation of cropping in combination with the types of crops being grown and also the intensity of production when considering potential effects on breeding wader assemblages. Changes in the use of fertilisers on the machair (greater use of inorganic compound fertilisers as a result of poorer deposition of seaweed and/or a lack of time to harvest and spread seaweed compared to the ease of spreading inorganic fertilisers; Section 3.5) could lead to a reduction in floristic diversity (Kent *et al.* 2003) and also faster vegetation growth thereby potentially reducing habitat heterogeneity. It proved difficult to obtain systematic information on changes in fallow management, however the introduction of under-sowing with grass seeds is likely to lead to a reduction in open fallow swards with bare patches (Crawford 1990). Although this was not generally supported by the recorded broad-scale changes in vegetation structure (actually an apparent trend towards reduced cover), such local changes could indeed occur at the finer scale. The reported deeper ploughing that is now practiced (compared to the 1970s) through influences on soil stability, crop establishment and subsequent fallow management could also change the mosaic of habitats. The timing of ploughing could also lead to losses of some nests (Wilson 1978), however no suggestion was given that this had changed since the 1970s. The reported increased depth of ploughing could potentially exacerbate soil fragility and expose deeper, potentially more saline soils. Other determinants of soil salinity and dune and machair stability will certainly include extrinsic factors such as storm frequency and episodic inundation with salt water (Richards and Phipps 2007). However the influences of some of the reported land use changes and their interaction with environmental changes should perhaps also be considered. The reported reduced frequency of clearing drains could potentially reduce the efficiency with which salt water can drain off the machair.

4.3 Predation

Predation by hedgehogs has influenced breeding wader densities on the machair of South Uist (Jackson and Green 2000, Jackson 2001, 2007, Jackson *et al.* 2004). Although hedgehogs are largely absent from North Uist and present in reduced numbers (through active control) on Benbecula, other predators are present. Predation risk, principally from common gulls has influenced the methodology for surveying breeding waders (Section 2.1). Common and other gull species (Laridae), hooded crow *Corvus corone cornix*, raven *Corvus corax*, raptors, otter *Lutra lutra,* American mink *Neovison vison* and domestic and feral cats *Felis catus* are predators that could influence the breeding wader assemblage in our study areas. The influences of predation, other than by hedgehogs, on machair waders deserves further attention, both to any changes in the levels of predation and how the wader assemblage responds to those predation risks. Predation can also interact with disturbance. Changes in the number of people actively farming the machair could have reduced some of that pressure, but alternatively, increased mechanisation may lead to greater losses of nesting attempts (Wilson 1978) and disturbance effects from other human activities on the machair (e.g. informal recreation) should not be excluded (Whitfield *et al.* 2008).

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6. TABLES

Table 1: The statistical significance of Site and Year and their interaction term in models investigating the differences in the vegetation indices.

Index	Site	Year	Site*Year
DCA Axis 1	0.16	0.57	0.90
DCA Axis 2	**<0.0001**	**0.0005**	0.21
EIV Light	0.81	0.33	0.51
EIV Water	**0.05**	0.75	0.62
EIV Reaction	**0.001**	0.81	0.96
EIV Nitrogen	**<0.0001**	**0.02**	0.74
EIV Salt	**0.006**	**0.002**	0.10
Arable	**<0.0001**	0.41	0.95
Density	**0.03**	0.13	0.90
Height	0.08	0.96	**0.04**
Cover	**<0.0001**	**<0.0001**	**0.0003**

Note The sources of statistically significant differences (indicated in bold above)

For DCA Axis 2	Baleshare > Borve	1976 < 2009
	Baleshare > Sollas	
	Berneray > Borve	
	Berneray > Sollas	
For EIV Water	Baleshare > Sollas	
	Berneray > Sollas	
For EIV Reaction	Baleshare < Sollas	
	Berneray < Borve	
	Berneray < Sollas	
For EIV Nitrogen	Baleshare < Borve	1976 > 2009
	Baleshare < Sollas	
	Berneray < Borve	
	Berneray < Sollas	
For EIV Salt	Baleshare > Sollas	1976 < 2009
	Berneray > Sollas	
For Arable	Baleshare > Sollas	
	Berneray > Borve	
	Berneray > Sollas	
	Borve < Sollas	
For Density	Baleshare < Borve	
	Berneray < Borve	
	Borve > Sollas	
For Height	Berneray in 1976 > Berneray in 2009	
For Cover	Baleshare > Berneray	1976 > 2009
	Baleshare > Sollas	
	Berneray < Borve	
	Berneray < Sollas	

Borve > Sollas
Baleshare in 1976 > Baleshare in 2009
Berneray in 1976 > Berneray in 2009

Table 2: The mean, 5th and 95th percentile vales of Axes 1 and 2 derived from Detrended Correspondence Analyses of the vegetation data.

		DCA Axis 1		DCA Axis 2	
Site	Year	Mean	95% int	Mean	95% Int
Baleshare	1976	3.86	3.14 – 4.60	2.34	0.00 – 3.54
Baleshare	2009	3.83	2.25 – 5.46	2.52	0.00 – 4.03
Berneray	1976	3.91	2.15 – 5.92	2.37	0.00 – 3.27
Berneray	2009	4.02	2.11 – 5.84	2.82	1.60 – 4.16
Borve	1976	3.86	2.56 – 4.85	1.81	0.00 – 2.78
Borve	2009	3.99	2.98 – 5.43	2.01	0.90 – 2.83
Sollas	1976	4.10	3.50 – 5.24	1.57	0.00 – 2.66
Sollas	2009	4.10	2.60 – 5.85	2.19	0.00 – 2.94

Table 3: The mean, 5th and 95th percentile vales of EIV scores derived from the vegetation data.

		Light		Water		Reaction		Nitrogen		Salt	
Site	Year	Mean	95% int	Mean	95% int	Mean	95% int	Mean	95% int	Mean	95% int
Baleshare	1976	7.65	7.15 - 8.08	5.18	4.54 – 6.23	6.07	5.67 – 6.89	4.46	3.40 – 6.70	0.85	0.02 – 1.88
Baleshare	2009	7.76	7.15 – 8.52	5.31	4.33 – 7.24	6.03	5.06 – 6.89	4.31	2.40 – 6.70	1.18	0.02 – 2.59
Berneray	1976	7.75	7.24 – 8.90	5.26	4.05 – 7.09	5.98	5.23 – 6.89	4.28	3.08 – 6.70	1.07	0.02 – 2.99
Berneray	2009	7.73	7.21 – 8.91	5.16	4.11 – 7.26	5.99	5.26 – 6.89	3.97	2.50 – 6.70	1.10	0.20 – 2.90
Borve	1976	7.61	7.17 – 8.02	5.19	4.64 – 6.41	6.20	5.75 – 6.89	5.01	3.99 – 6.70	0.86	0.02 – 1.68
Borve	2009	7.73	7.08 – 8.66	5.10	4.33 – 6.16	6.16	5.96 – 6.78	4.86	3.67 – 5.68	1.02	0.04 – 2.56
Sollas	1976	7.71	7.14 – 8.11	5.00	4.56 – 6.20	6.20	5.12 – 6.89	5.10	3.71 – 6.70	0.56	0.02 – 1.75
Sollas	2009	7.69	7.15 – 8.81	4.97	4.20 – 6.22	6.22	5.89 – 6.89	4.66	3.28 – 6.70	0.98	0.02 – 2.74

Table 4 The mean, 5th and 95th percentile vales of structure scores derived from the vegetation data.

		Arable		Density		Height		Cover	
Site	Year	Mean	95% int	Mean	95% int	Mean	95% int	Mean	95% Int
Baleshare	1976	0.28	0 – 1	2.61	1 – 3	1.75	1 – 2	115	0.58 – 1.82
Baleshare	2009	0.30	0 – 1	2.72	2 – 3	1.83	1 – 3	80	0.31 – 1.24
			0 – 1						
Berneray	1976	0.14		2.62	2 – 3	2.05	2 – 3	82	0.46 – 1.07
Berneray	2009	0.14	0 – 1	2.64	1 – 3	1.78	1 – 3	73	0.02 – 1.18
			0 – 1						
Borve	1976	0.61		2.79	2 – 3	1.96	1 – 2	98	0.68 – 1.15
Borve	2009	0.71	0 – 1	2.92	2 – 3	2.08	1 – 3	97	0.30 – 1.41
			0 – 1						
Sollas	1976	0.40		2.52	2 – 3	1.87	1 – 3	89	0.70 – 1.15
Sollas	2009	0.46	0 – 1	2.63	2 – 3	1.92	1 - 3	83	0.37 – 1.21

Table 5: The direction and statistical significance of relationships of wader abundance with measures derived from the surveys of vegetation in the 2000s. The figures present are the estimated slopes associated with that variable in the GLMMs (see Section 2.4.1).

	Axes from Detrended Correspondence Analysis		Ellenberg Indicator Values						Structure		
Species	DCA 1	DCA 2	Light	Water	Reaction	Nitrogen	Salt	Arable	Density	Height	Cover
Oystercatcher	**- 0.25 ****	**- 0.17 ****	0.07	**0.12 ****	**0.35 ****	- 0.11	**-0.28 ****	**0.53 ****	0.16 *	**- 0.14 ****	- 0.19
Lapwing	**- 0.43 ****	**- 0.13 ****	- 0.16	**0.19 ****	**0.30 ****	- 0.04	**- 0.46 ****	0.01	**0.18 ****	- 0.01	- 0.25 *
Ringed Plover	**- 0.20 ****	**- 0.51 ****	**- 0.80 ****	0.11	**1.09 ****	- 0.21	0.02	**1.98 ****	**- 0.12 ****	-0.09	**- 0.89 ****
Dunlin	**- 0.63 ****	- 0.07	**- 0.77 ****	**0.56 ****	**0.78 ****	- 0.18	0.13	0.20	- 0.23 *	0.04	- 0.01
Redshank	**- 0.33 ****	**0.14 ****	**- 0.66 ****	**0.27 ****	**0.34 ****	- 0.16*	0.01	**-0.56 ****	0.14	**0.24 ****	- 0.13
Snipe	**- 0.49 ****	0.08 *	- 0.82	- 0.03	0.38	- 0.01	- 0.77	**- 2.10****	- 0.55	- 0.13	- 0.06

Notes:
1. DCA 1 – reflects the change in physical structure from young dunes (a high score) through to the machair plain with fixed vegetation (a low score);
2. DCA 2 – reflects a gradation of machair grassland from uncultivated (a high score) through to more cultivated and more fertile grassland (a low score);
3. ** Figures in bold indicate a statistically significant ($P < 0.05$) relationship of breeding wader abundance with the vegetation measure;
4. * Indicates a marginally non-significant ($0.05 > P < 0.10$) relationship of breeding wader abundance with the vegetation measure

Table 6: The direction and statistical significance of relationships of changes in wader abundance (1980s – 2000s) with changes in the measures derived from the surveys of vegetation (1976 – 2009). The figures present are the estimated slopes associated with that variable in the GLMMs (see Section 2.4.2).

	Axes from Detrended Correspondence Analysis		Ellenberg Indicator Values					Structure		
Species	DCA 1	DCA 2	Light	Water	Reaction	Nitrogen	Salt	Density	Height	Cover
Oystercatcher	0.03	**0.12** **	- 0.23	-0.07	0.06	- 0.10	- 0.07	0.01	0.12	- 0.01
Lapwing	0.15	**- 0.40** **	- 0.11	**0.35** **	0.36	- 0.20	- 0.09	0.02	0.23 *	- 0.42
Ringed Plover	-0.04	- 0.04	**0.71** **	- 0.11	**- 0.65** **	**0.36** **	**- 0.32** **	0.03	0.04	- 0.18 *
Dunlin	0.13	**- 0.13** **	0.23	- 0.06	- 0.16	0.08	- 0.15	0.08	0.05	- 0.30
Redshank	**- 0.22** **	0.04	- 0.02	0.06	0.25	- 0.14	- 0.16	- 0.05	**0.20** **	- 0.01
Snipe	0.01	-0.01	0.02	- 0.02	- 0.03	0.01	- 0.01	- 0.01	- 0.01	0.04

Notes:

1. DCA 1 – reflects the change in physical structure from young dunes (a high score) through to the machair plain with fixed vegetation (a low score);
2. DCA 2 – reflects a gradation of machair grassland from uncultivated (a high score) through to more cultivated and more fertile grassland (a low score);
3. ** Figures in bold indicate a statistically significant ($P < 0.05$) relationship of breeding wader abundance with the vegetation measure;
4. * Indicates a marginally non-significant ($0.05 > P < 0.10$) relationship of breeding wader abundance with the vegetation measure

7. FIGURES

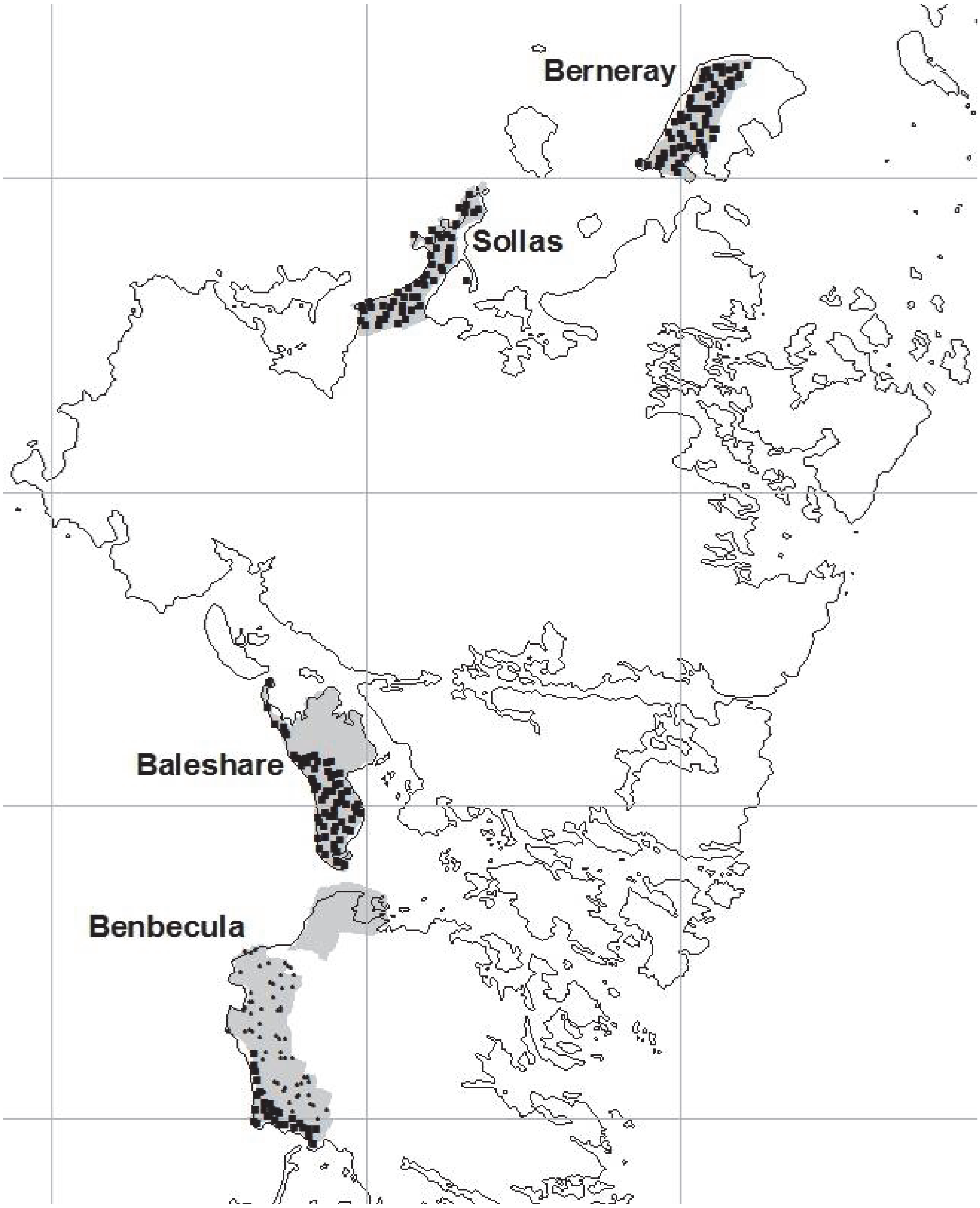
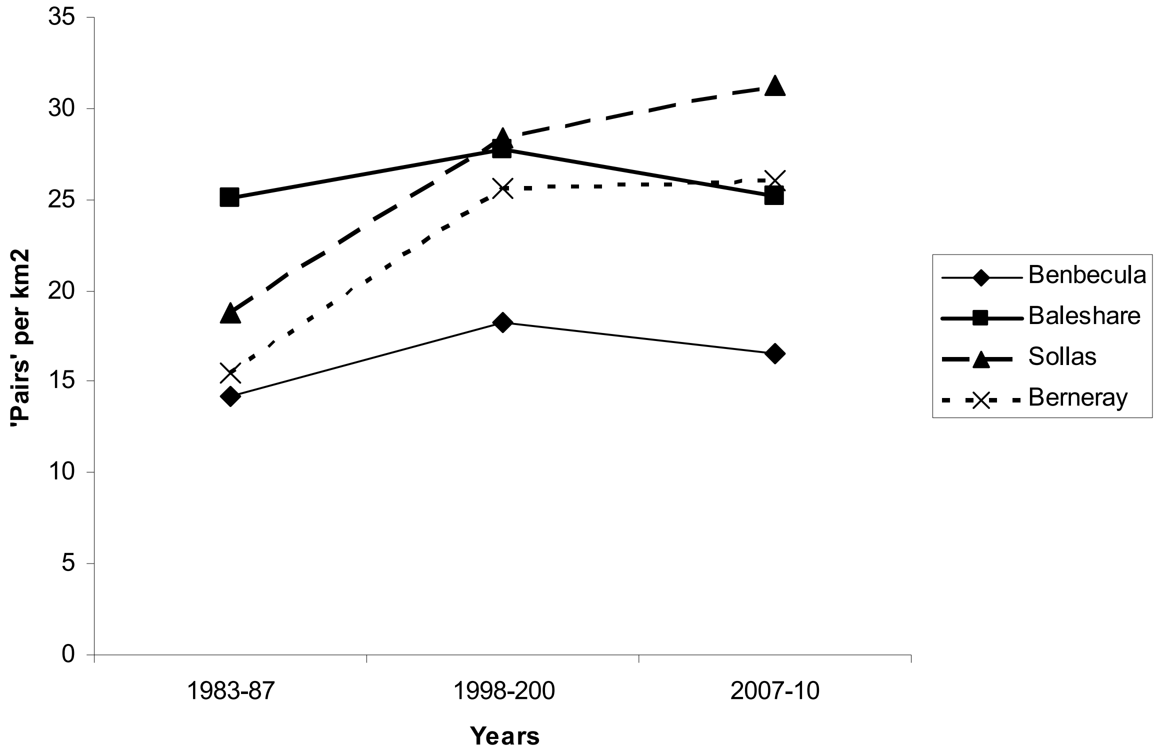
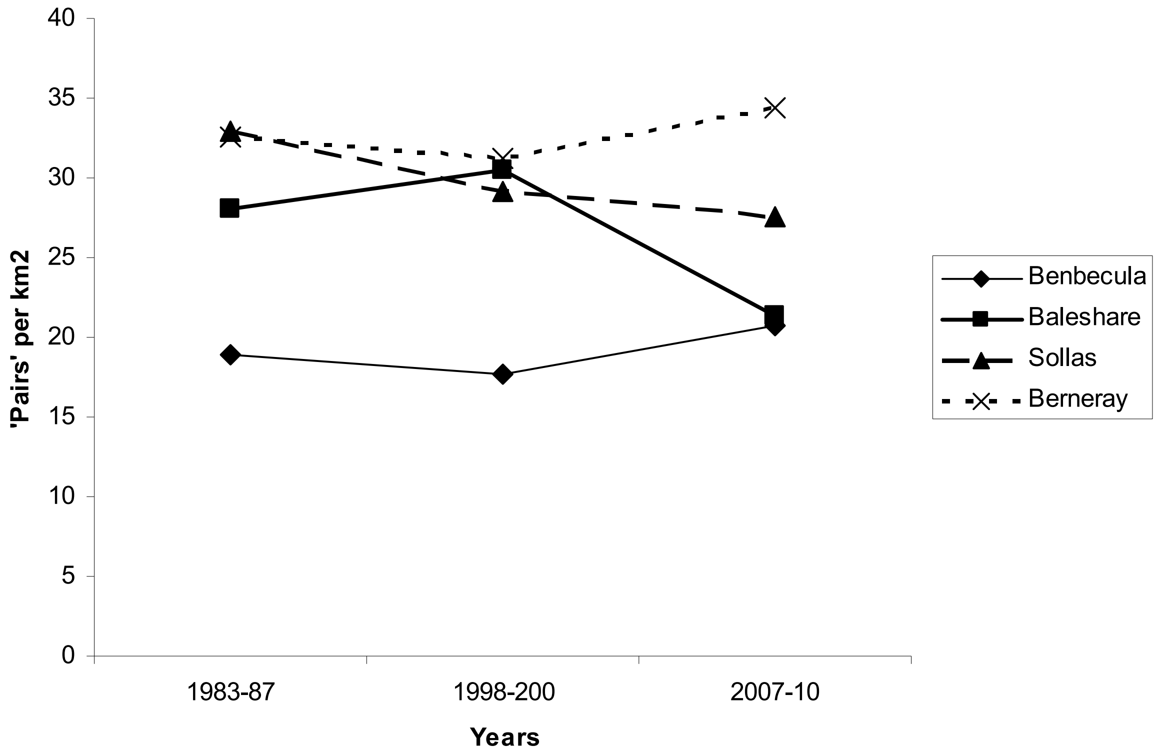


Figure 1: The study areas in North Uist and Benbecula. The shaded areas indicate the extent of the four areas where breeding waders have been surveyed between 1983 and 2010. The dots represent the vegetation sampling points, with squares showing sites sampled in both 1976 and 2009 and the smaller circles sites that were sampled in 2009 only. The grid represents the 10-km grid lines of the Ordnance Survey's national grid.



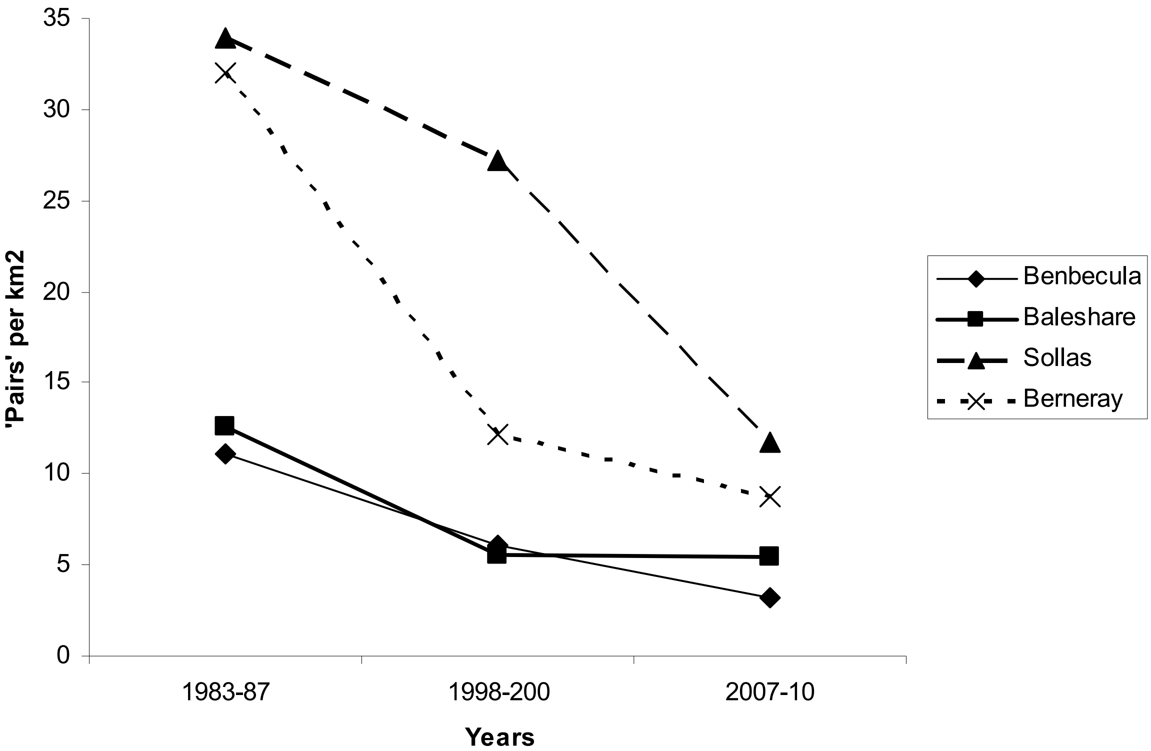
Benbecula	1980s < 1990s (>) 2000s
Baleshare	1980s = 1990s = 2000s
Sollas	1980s < 1990s = 2000s
Berneray	1980s < 1990s = 2000s

Figure 2: Changes in the breeding density of oystercatchers at four study sites on Benbecula and North Uist between 1983-87 and 2007-10. A statistically significant difference (Post hoc pair-wise comparisons) is indicated in the text below the figure by the symbol < or > as appropriate. Where that difference is marginally non-significant (i.e. 0.05 < P < 0.10) the symbol is included in parentheses.



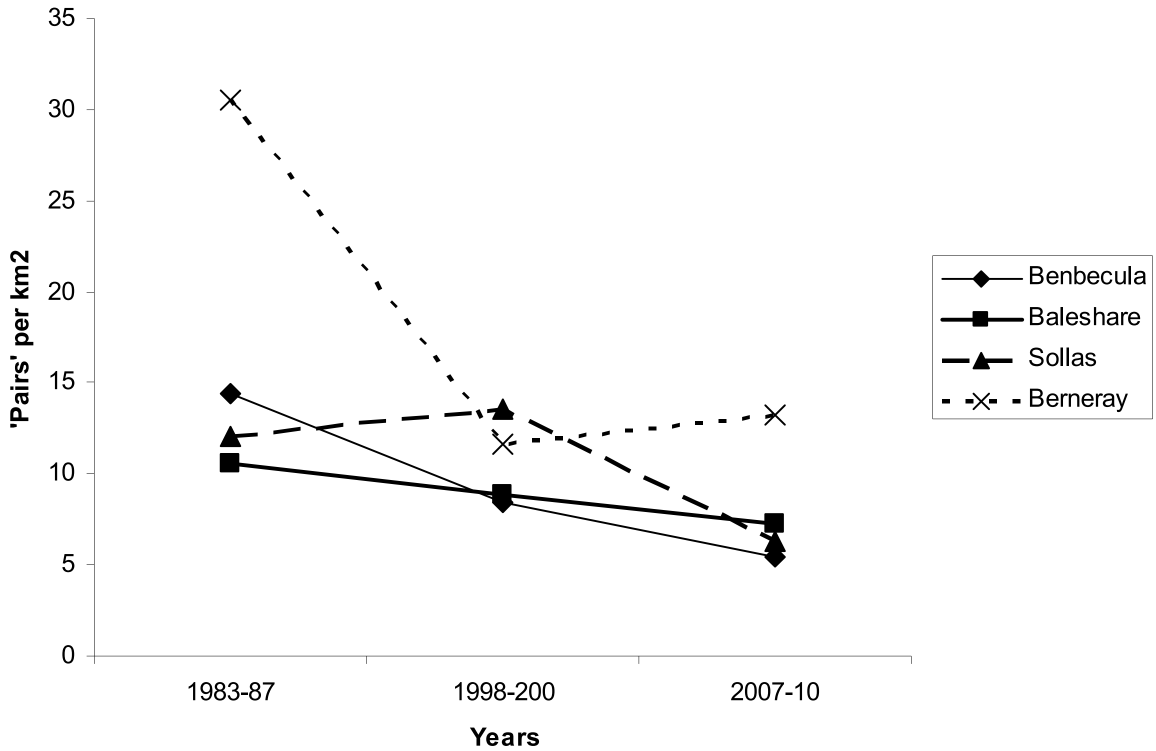
Benbecula	1980s = 1990s (<) 2000s
Baleshare	1980s = 1990s > 2000s
Sollas	1980s = 1990s = 2000s
Berneray	1980s = 1990s = 2000s

Figure 3: Changes in the breeding density of lapwings at four study sites on Benbecula and North Uist between 1983-87 and 2007-10. A statistically significant difference (Post hoc pair-wise comparisons) is indicated in the text below the figure by the symbol < or > as appropriate. Where that difference is marginally non-significant (i.e. 0.05 < P < 0.10) the symbol is included in parentheses.



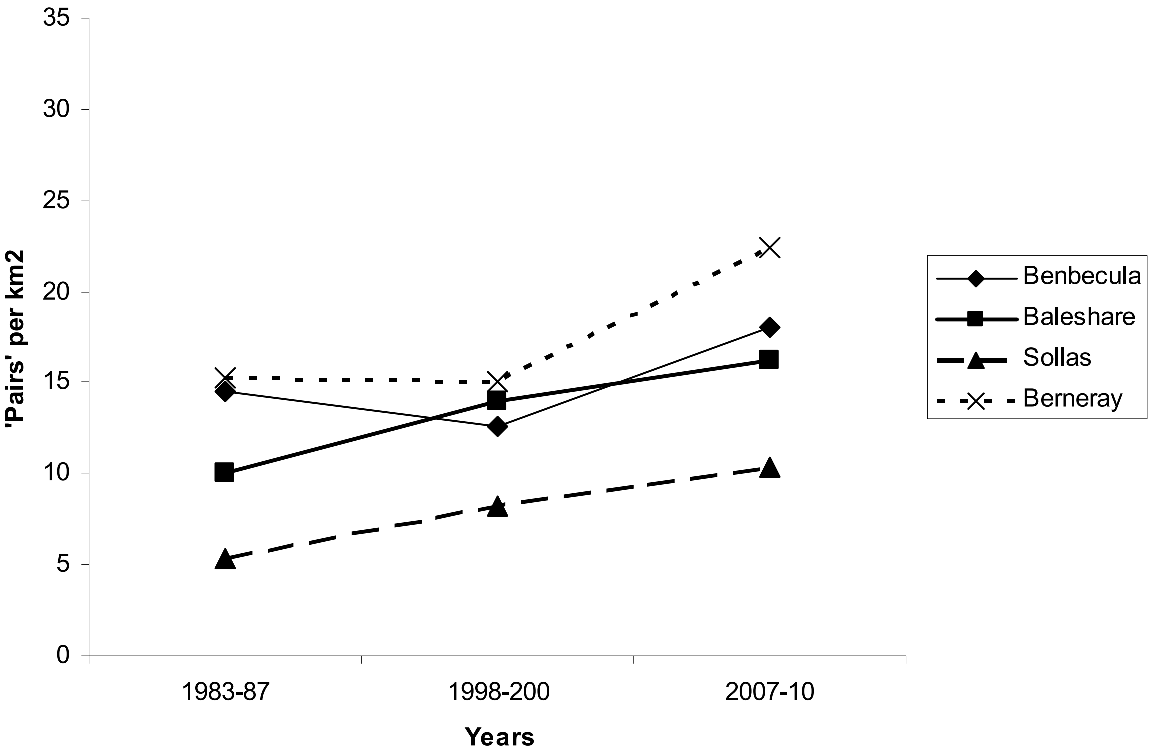
Benbecula	1980s > 1990s > 2000s
Baleshare	1980s > 1990s = 2000s
Sollas	1980s (>) 1990s > 2000s
Berneray	1980s > 1990s (>) 2000s

Figure 4: Changes in the breeding density of ringed plovers at four study sites on Benbecula and North Uist between 1983-87 and 2007-10. A statistically significant difference (Post hoc pair-wise comparisons) is indicated in the text below the figure by the symbol < or > as appropriate. Where that difference is marginally non-significant (i.e. 0.05 < P < 0.10) the symbol is included in parentheses.



Benbecula	1980s > 1990s > 2000s
Baleshare	1980s = 1990s = 2000s
Sollas	1980s = 1990s > 2000s
Berneray	1980s > 1990s = 2000s

Figure 5: Changes in the breeding density of dunlins at four study sites on Benbecula and North Uist between 1983-87 and 2007-10. A statistically significant difference (Post hoc pair-wise comparisons) is indicated in the text below the figure by the symbol < or > as appropriate. Where that difference is marginally non-significant (i.e. 0.05 < P < 0.10) the symbol is included in parentheses.



Benbecula	1980s = 1990s < 2000s
Baleshare	1980s < 1990s = 2000s
Sollas	1980s (<) 1990s < 2000s
Berneray	1980s = 1990s < 2000s

Figure 6: Changes in the breeding density of redshanks at four study sites on Benbecula and North Uist between 1983-87 and 2007-10. A statistically significant difference (Post hoc pair-wise comparisons) is indicated in the text below the figure by the symbol < or > as appropriate. Where that difference is marginally non-significant (i.e. 0.05 < P < 0.10) the symbol is included in parentheses.

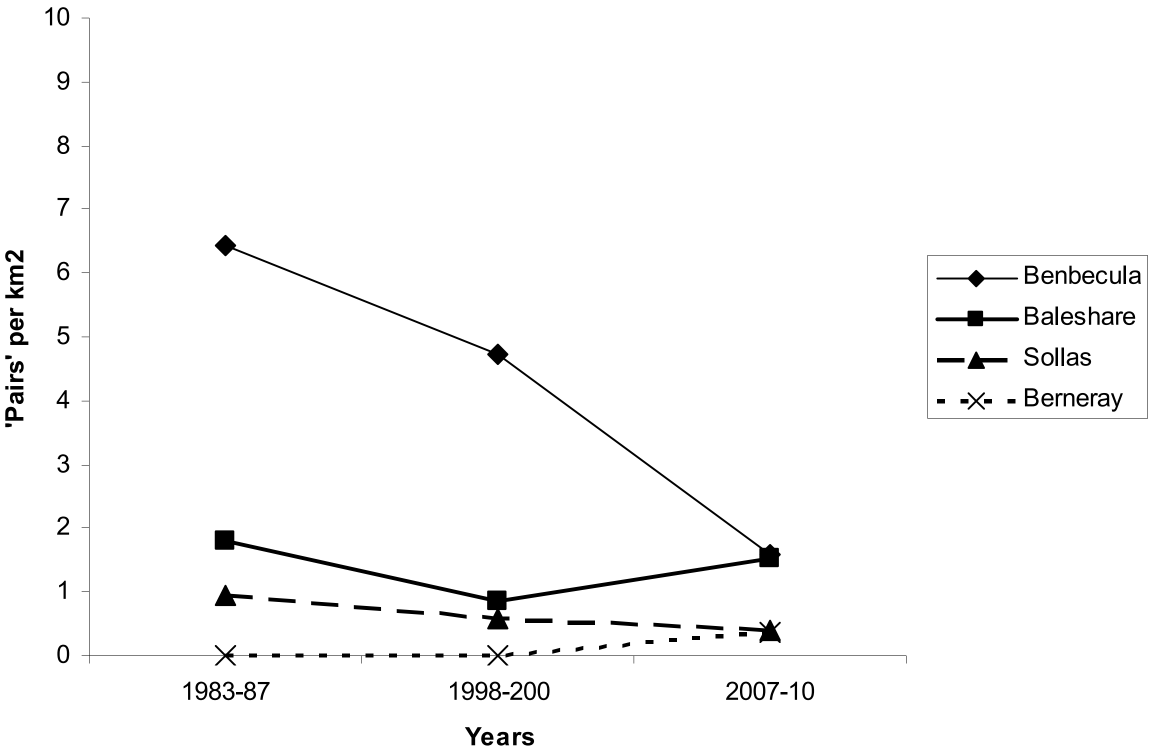


Figure 7: Changes in the breeding density of snipe at four study sites on Benbecula and North Uist between 1983-87 and 2007-10. Data were too sparse to permit model convergence hence no statistical assessment of the significance of changes was possible.

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