POPULATION ECOLOGY AND CONSERVATION OF RED-BILLED CHOUGHS IN SCOTLAND

Final report on Knowledge Transfer Project

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JANE M. REID[1], MARIA I. BOGDANOVA[2], ERIC M. BIGNAL[3], SUE BIGNAL[3], DAVY I. McCRACKEN[4] & PAT MONAGHAN[5]

[1]School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ.

[2]Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB.

[3]Scottish Chough Study Group, Kindrochaid, Bridgend, Isle of Islay, Argyll, PA44 7PT.

[4]Research Division, Scottish Agricultural College, Auchincruive, Ayr, KA6 5HW.

[5]Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ.

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1. Summary of scientific conclusions and recommendations

The evidence supporting each conclusion is presented in the sections of the report listed below each conclusion.

1) Conservation status

The islands of Islay and Colonsay hold virtually the entire Scottish population of red-billed choughs (*Pyrrhocorax pyrrhocorax*). This species is of high conservation concern across Europe and an important figurehead for the conservation of low intensity agricultural ecosystems and the mosaic of habitats such systems generally provide. The number of breeding pairs of choughs on Islay has varied over the last 25 years and was estimated at approximately 55 pairs in 2007. Adult breeding success and survival have remained relatively stable. However, first-year survival rates during 2007-2009 were lower than any observed during 1983-2007. Were the rates of survival and breeding success observed in recent years to continue, the number of choughs breeding on Islay would be expected to decrease over coming years. The status of the Scottish chough population as of high conservation concern should therefore be maintained.

Evidence: Sections 4 and 5

2) Sub-adult survival as a focus of management

Over the last 25 years, one main factor driving variation in the number of choughs on Islay has been variation in the probability that a chough will survive through its first two years of life (i.e., from fledging to age two). An effective way of maintaining or increasing the number of choughs on Islay would be to increase the probability that birds survive these sub-adult years, or at least reduce the frequency of years in which sub-adult survival is poor. There is therefore a need to consider whether it is feasible to identify and implement management practices designed to increase the survival of sub-adult choughs. Such management should not, however, have any detrimental consequences for the adult birds.

Evidence: Section 5

3) Monitoring adult survival and breeding success

The number of choughs on Islay is expected to be very sensitive to any change in adult survival (the probability that an adult chough will survive from one year to the next), and reasonably sensitive to any change in breeding success (the number of chicks fledged per breeding attempt). While adult survival and breeding success have recently been

relatively stable on Islay, it is important to continue to monitor adult survival and breeding success and to ensure that any decline can be rapidly recognised, investigated and effective mitigation measures put in place.

Evidence: Section 5

4) Among-year variation in sub-adult survival

During 1983-2005, variation in the survival of sub-adult choughs was correlated with variation in local weather (specifically, temperature and rainfall) and indices of the abundance of *tipulid* larvae (indices based on large scale surveys of inter-annual variation in *tipulid* larvae in Scotland). Although correlation cannot prove direct causation, these data indicate that among-year variation in sub-adult survival may be caused by large-scale variation in weather and food abundance. These factors are difficult to manage directly. However, there is some evidence that the effects of weather and *tipulid* abundance on chough survival depend on the density of breeding pairs of choughs, and on the habitat surrounding nest sites. Specifically, effects of variation in *tipulid* abundance on survival through the first year of life were less marked in choughs that had fledged from nest sites that were surrounded by more suitable foraging habitat and where neighbouring pairs of choughs were further away. Effects of poor weather and low food abundance on chough survival might therefore be minimised or ameliorated by appropriate management of the habitat surrounding nest sites and nest site density. Future nest site provision should be planned with these data in mind.

The possibility that variation in other factors, such as predation, disease and specific agricultural practices has caused the observed variation in chough survival during 1983-2005 could not be quantitatively tested and cannot be ruled out.

Evidence: Section 6 (specifically section 6c)

5) Predicting sub-adult survival

In theory, the statistical model that we developed using data from 1983-2005 (section 6) should allow us to predict the likely first-year survival rate for any particular cohort of choughs in advance. This could allow additional management to be implemented in years when sub-adult survival is expected to be low. Further years of data are required to validate how accurate and useful this approach might be. The model could be effectively validated in 2010 once five years of additional data have accumulated. However, preliminary analyses suggest that the model does not accurately predict the low first-year

survival observed during 2007-2009. Some additional and as yet unidentified factor may therefore have caused the extremely low first-year survival in these two years.

Evidence: Section 6

6) Spatial variation in sub-adult survival

Sub-adult survival varied with natal location such that choughs reared in specific nest sites, and in specific areas of Islay, were more likely to survive to breeding age than choughs reared in other nest sites or areas of Islay. Specific areas of Islay have therefore been particularly important in maintaining the island's chough population. These include the Ballygrant Valley, the area around Loch Gruinart and Sanaig, and the south-east Rhinns. The factors that cause this variation could not be fully identified in this study, but might include variation in habitat and properties of a nest site's physical location (such as its distance from exposed Atlantic coasts). In some of these areas (e.g. the Ballygrant Valley, breeding success has been poor in recent years, possibly associated with a decline in the condition of existing nest sites. It would therefore be prudent to provide and maintain suitable nest sites and foraging habitat in the areas of Islay that have consistently produced choughs that survive well.

Evidence: Sections 5, 6 and 12

7) Foraging sites: the importance of coastal dune systems

On Islay, *ca* 90% of observations of foraging flocks of choughs during April 2006 - March 2008 were in areas associated with coastal dune systems, particularly at Ardnave and Kilchoman. Sub-adult choughs used a variety of habitats within and around these areas, including grazed and largely ungrazed dune grasslands, kelp beds, bare sand, cliff and heath. Coastal dune systems are therefore of major importance for sub-adult choughs on Islay and should be maintained in a state that maximises the abundance and availability of the chough's invertebrate prey. Our data on the foraging behaviour of sub-adults suggest that this will be best achieved by maintaining a mosaic of suitable open habitats containing a diversity of vegetation heights and structures, thereby providing a variety of resources for choughs to exploit in different seasons and years.

Evidence: Sections 7 and 8

8) Foraging sites: the importance of silage fields

Most of the remaining *ca* 10% of observations of foraging flocks of choughs were in newly cut silage fields. This habitat was used by a substantial proportion of newly

fledged and sub-adult choughs during June-August, and is likely to provide an abundance of food for newly fledged young. The extensive use of this habitat when available suggests that cut silage fields are a highly profitable foraging resource for sub-adult choughs, particularly in summer (a time when sub-adult mortality can be high). Both the timing of the closing off of fields to grazing animals, which influences the pattern of change in grass length, and the timing of the silage cutting, therefore influences foraging opportunities for choughs. Some preliminary data suggest that silage fields that were cut in June may be used more, and used for longer, than fields cut in July or August. This possibility requires further investigation. More detailed study of the foraging sites used by young choughs in areas where silage fields are not available (e.g. on Colonsay) may be useful in evaluating its importance on Islay.

The introduction of support for grassland management schemes that influence the timing and synchrony of field closure and silage cutting across Islay should therefore be considered where appropriate. It might be beneficial to encourage some early (June) silage cutting in areas of importance for choughs, and this possibility urgently needs to be tested. Any encouragement of such early cutting should be accompanied by further detailed study of chough use of silage aftermath in relation to the timing and spatial pattern of cutting to further investigate and evaluate the importance of this resource.

Evidence: Sections 7, 8, 10 and 12.

9) Roost sites

During April 2006 - March 2008, sub-adult choughs used three main roosts, at Ardnave, Kilchoman and Dun nan Nighean. The Ardnave and Kilchoman roosts were located within the main sub-adult foraging sites. Choughs also roosted at the same or nearby sites during 1986-1988, suggesting that sub-adult choughs are relatively faithful to specific roosts. However, the relative use of the different roosts has changed over recent years, with a greater proportion of sub-adult choughs now using Ardnave rather than Kilchoman. It is not clear whether this change reflects the provision of a new roost site at Ardnave, changes in foraging habitat at one or both sites, or to some other factor.

Suitable roost sites need to be maintained at or near the key foraging sites for sub-adult choughs, particularly at Ardnave and Kilchoman. Suitable foraging habitat must also be maintained around the key roost sites. Provision of safe roost sites at other foraging sites could also be considered.

Evidence: Sections 7 and 8.

10) Specific foraging locations

Sub-adult choughs foraged at specific locations within Ardnave/Killinallan and Kilchoman/Kilchiaran. These locations tended to have relatively shorter and/or less variable swards, more old cow pats and sparser and more diverse vegetation than locations within these same sites at which sub-adult choughs were not observed to forage. However these effects varied among years (for example a difference in sward height was observed in one year of the study but not the other) and the magnitude of the difference was small (less than 1cm). Given the factors known to affect invertebrate populations, the best management approach may therefore be to aim to maintain a largely open habitat matrix that contains a variety of flora with differing vegetation heights and structures at a small spatial scale. Judicious use of grazing animals might be the best means of achieving this.

Evidence: Section 9

11) Sub-adult mortality and parental state

Years in which first-year survival was low were characterised by particularly low survival through the late summer. Most choughs that died before the end of their first year died after they had left their natal territories and joined sub-adult flocks in the coastal dunes and silage fields. The different survival rates of choughs reared in different areas of Islay therefore occurred after the young choughs had reached the flocks.

The extremely low first-year survival rate in 2007-2008 was associated with a marked reduction in the time that parents spent with newly fledged offspring compared to 2006-2007. First-year survival rates of fledglings also vary with characteristics of their parents, including age and lifespan.

These data suggest that the conditions that a chough experiences on its natal territory can have long-term effects on its subsequent survival. Sub-adult survival might therefore be linked with parental state and conditions at the nest site, as well as conditions experienced in the sub adult flocks. Maintaining appropriate habitat diversity and hence foraging conditions on breeding territories is also likely to be important in producing choughs that survive well.

To increase or maintain sub-adult survival rates, appropriate conditions should therefore be maintained on breeding territories as well as the foraging areas subsequently used by flocks of sub-adult choughs.

Evidence: Sections 5, 6 and 12

12) Comparison with other chough populations

Overall, chough breeding success and survival was broadly similar on Islay, Colonsay and the Isle of Man. However on average, choughs reared slightly fewer fledglings per breeding attempt on Islay than on Colonsay or the Isle of Man. Choughs on Islay were more likely to survive through their first year but less likely to survive through their second year and as adults than choughs on Colonsay or the Isle of Man. The relatively low population growth rate of choughs on Islay compared to Colonsay and the Isle of Man therefore reflected lower average breeding success, second-year survival and adult survival rather than lower average first-year survival. Breeding success was correlated across all three populations, suggesting that annual breeding success may be to some degree influenced by large-scale factors (such as climate).

This suggests that Islay's choughs may be slightly under-performing with respect to breeding success and adult survival, which again suggests a need for more appropriate management of the habitats around breeding territories.

Evidence: Section 13

13) Monitoring management efficacy

This study has demonstrated, through the combination of analysis of long-term data and targeted fieldwork, that there is considerable potential to build a conservation management strategy for choughs in Scotland based on a rigorous base of scientific evidence.

This approach should be maintained and improved through continued monitoring of breeding success and survival. In addition, there is a need to ensure that the effectiveness of any management actions applied at an individual farm level are also assessed, not solely by monitoring compliance with the management prescriptions but also monitoring the impact of the actions on habitat diversity and quality and whether the intended conservation benefits are indeed being achieved.

Evidence: Summarised in sections 2 and 3

2. Summary of agreed recommendations and actions

These recommendations were discussed and agreed at the project meeting on Islay, April 2009. In attendance were Rae McKenzie, Angus Laing and Stuart Shaw (Scottish Natural Heritage), Andy Schofield, Jeremy Wilson and Sarah Davies (Royal Society for the Protection of Birds), Eric, Sue and Caitlin Bignal (Scottish Chough Study Group), Davy McCracken (Scottish Agricultural College), Pat Monaghan (University of Glasgow), Maria Bogdanova (Centre for Ecology & Hydrology) and Jane Reid (University of Aberdeen). Jack Fleming and James How (RSPB) attended for the presentation and discussion of scientific results but not the discussion of recommendations.

1) Due to the low rates of sub-adult survival during 2007-2009, the number of choughs breeding on Islay is expected to decrease over the next 2-3 years. The status of choughs as being of high conservation concern should therefore be maintained and the policies of SNH and RSPB should reflect this status. Population size and demography of adults and sub-adults should continue to be monitored closely.

2) Successful conservation of choughs on Islay is likely to rely on appropriate management of the main flock foraging areas (i.e. the main dune systems and, where relevant, early-cut silage fields) and individual breeding territories. Data from the chough research project allows the key habitats and locations to be identified. The management aim should be to generate a diversity of habitats that support high plant and invertebrate diversity, thereby increasing the range of foraging options that will be available to choughs at any point in time. There should not be a focus on the provision of any single food resource by over-emphasis on any single management approach.

3) Over the coming years, the main mechanism available for funding appropriate conservation management for chough will be through developing appropriate farm-level applications to the Scottish Rural Development Programme (SRDP). There are currently no chough-specific options available within the SRDP. Introduction of any such new options to the SRDP will require approval from the European Commission. In the medium to long term, consideration needs to be given not only to what such chough-specific options would consist of but also what the potential impacts of any such chough-specific measures would be (since it would not be desirable to produce simple, uniform habitats for choughs rather than the complex diversity that seems to be required).

4) In the short-term, the conservation importance of choughs in Argyll should be emphasised by a combination of raising the profile of choughs more within the SRDP application interface and also directing prospective applicants from Islay and Colonsay to those existing options that are of direct relevance and potentially beneficial for choughs. These existing chough-relevant measures also need to be drawn to the attention of agricultural and conservation consultants who draw up SRDP applications for Islay and Colonsay.
Action: Scottish Natural Heritage to ensure that the profile of chough is raised within the accompanying SRDP documentation and that existing chough-relevant measures are adequately signposted on the SRDP website and related documentation.
Action: Eric Bignal to draft a brief for consultants that explains how available SRDP options can be used to benefit choughs in the context of chough areas.

5) A number of key farms on Islay have already had their SRDP plans approved, and the conditions of the contracts mean that further changes cannot be made for 5 years. Additional farms that cover key dune areas for which SRDP plans have not already been agreed should be encouraged to enter the scheme with a plan that is appropriate for choughs. In addition, any new plan should contain a clause which states that, if any management is found not to be having the intended effect, then that management can be changed during the course of the five years of the scheme.
Action: Scottish Natural Heritage and Eric Bignal to approach relevant farmers and encourage participation in SRDP.

6) Unlike the negotiation of an individual management agreement, to be successful any application to the SRDP needs to score sufficient points to be judged favourably against any other applications competing for the limited SRDP funds. It is unclear as yet what impact this will have the willingness of farmers to submit SRDP plans or on the content of those plans that are submitted (given that other options within the SRDP may be more financially rewarding when compared to options of relevance to chough). There is need within Argyll at least to ensure that the SRDP assessment process takes chough needs fully into consideration and does not (especially outwith designated sites but where choughs occur) approve plans that are more financially beneficial to the applicants but which contain SRDP options that may be less beneficial or detrimental for choughs.
Action: Scottish Natural Heritage to feedback to the SRDP review to encourage appropriate future development of options and associated payments.

7) There is presently no provision for biological (as opposed to basic compliance) monitoring within the SRDP scheme. To ensure that impacts can be measured and appropriate changes can be made to future SRDP plans, the biological outcomes of existing plans need to be monitored (using appropriate biological metrics) over and above the basic compliance monitoring that individual farms may or may not receive. In the immediate term, monitoring of outcomes should be prioritised on the major dune systems that are essential for sub-adult choughs.

Action: Scottish Chough Forum to write a letter to relevant ministers raising concerns over the provision for biological monitoring and assessment within the SRDP. This letter will raise specific issues resulting from research on choughs on Islay, but will discuss these issues in the context of more general aspects of the need for monitoring. Pat Monaghan to draft the letter and circulate to other Forum members for input.

8) Adequate nest and roost sites need to be maintained and/or provided in key areas of Islay, as informed by the long-term Scottish Chough Study Group data. The easiest means of resourcing nest and roost site maintenance and provision on those farms which fall within designated areas is to include this work within the SRDP plans (since the SRDP allows for funding capital works on designated sites). Hence relevant farms within designated areas that have yet to enter the scheme should be encouraged to include nest site repair/provision in their plans, while relevant farms who have already submitted plans should be encouraged to submit an additional proposal concerning nest site repair/provision. An additional mechanism needs to be put in place to either justify the funding through the SRDP of nest site repair/provision on farms outwith designated sites or identify appropriate funding sources that could be utilised in such instances. Although farms in the Ballygrant valley and other parts of Islay such as the south-east Rhinns lie outwith the designated area, the long-term importance of these sites (as emphasised in the findings from this study) for the maintenance of the chough population could potentially be used as a justification for the use of SRDP to fund nest site repair/provision on those farms

Action: Scottish Chough Study Group to provide SNH (in the form of a confidential annex to this report) with an updated list of existing nest sites that are in serious disrepair, and of historically productive or suitable habitat areas where no nest sites are currently available. These sites should then be prioritised for nest site maintenance or provision.

Action: Scottish Natural Heritage to encourage SRDP plans for the priority list of nest sites.

Action: Scottish Natural Heritage to liaise with Jane Reid and the Scottish Chough Study Group to ensure that long-term chough data are used to support SRDP applications where appropriate.

9) Further data regarding chough use of silage fields in relation to the timing of closing off of fields, fertilisation use and cutting need to be collected and/or analysed. This could include analysis of existing RSPB data on cutting dates in relation to chough survival patterns and use of dune systems. Meanwhile, SRDP plans for farms in key chough areas should include a diversity of grassland management options.
Action: Jane Reid and James How to liaise over access to and analysis of existing data. RSPB and Eric Bignal to consider options for early cutting specific fields at Ardnave and Smaull and monitoring chough usage.

10) The RSPB's plans to restore habitat for choughs on the Oa should be encouraged and supported.
Action: Scottish Chough Forum to write a letter to relevant RSPB managers to emphasise the potential importance of habitat restoration on the Oa for choughs, particularly given the context of the decrease in Islay's population that is predicted for coming years. Pat Monaghan to draft the letter and circulate to other Forum members for input, and to liaise with the RSPB members of the Scottish Chough Forum to decide the most appropriate recipients.

11) On Islay, survival rates of sub-adult choughs have recently been low. Consequently, the number of breeding pairs is likely to decrease in coming years. Choughs have retracted from areas of Islay that have recently been highly productive and/or held several breeding pairs. To attempt to address this situation, land management regimes that differ in emphasis from recent practices should be adopted under the SRDP. Given this situation, it is imperative that baseline monitoring of chough demography (breeding success and sub-adult and adult survival) should continue on Islay. These data will help provide a sound scientific basis on which the efficacy of SRDP plans can be evaluated. The most efficient and effective way to achieve this monitoring will be to support the Scottish Chough Study Group in the continuation of the long-term demographic study on Islay. Support may come through direct financial assistance, in-kind support through provision of accommodation and vehicles, and through assistance with data collection (for example through continued RSPB monitoring of choughs on the Oa).

Actions: Scottish Chough Study Group, Pat Monaghan and Jane Reid to draft and cost a proposal for ongoing monitoring and scientific work and to look for potential funders. Some support package urgently needs to be put in place to support monitoring through 2009-2010. Scottish Natural Heritage and Glasgow Natural History Society will be approached for this in the first instance.
Depending on the funding stream, future applications may require support from bodies such as RSPB and SNH and should be put together in a co-ordinated way that draws on expertise, opportunities and priorities afforded by the Scottish Chough Forum.

12) Opportunities to compare the demography and ecology of Islay's choughs with that of other chough populations should be exploited to the full. This may include demographic comparisons of the sort already run with the Manx Chough Project and Colonsay, but also closer comparison of foraging diversity and machair management.
Action: Jane Reid to continue to talk to Welsh chough researchers about the possibilities for demographic comparisons. Jeremy Wilson to look into unpublished RSPB data from Wales.

13) The final report should be made available electronically, together with supporting documentation and photographs. The executive summary and recommendations should also be available separately, and should be disseminated to farmers and land-owners in chough areas of Islay.

14) Consideration should be given to holding a meeting providing feedback from the project and emphasising (to farmers within and outwith designated sites and their associated consultants) the chough-relevant aspects of the SRDP and how best to develop appropriate plans

15) The Scottish Chough Forum should continue to meet bi-annually to ensure continuing and efficient exchange of information between scientists, conservationists and policy makers.

3. Introduction & Overview

3a) Overall aims

This report summarises the results of a Knowledge Transfer Research Project that was undertaken by Dr Jane Reid (University of Aberdeen), Professor Pat Monaghan, (University of Glasgow), Dr Eric and Mrs Sue Bignal (Scottish Chough Study Group) and Dr Davy McCracken (Scottish Agricultural College). Dr Maria Bogdanova was employed as the post-doctoral research assistant on the project. The work was carried out in partnership with Scottish Natural Heritage (SNH) and the Royal Society for the Protection of Birds (RSPB). Funding was provided by a Knowledge Transfer Grant from the Natural Environment Research Council (NERC, PIs P. Monaghan & J. Reid), with matching partnership funding and in-kind support from SNH and RSPB.

The overall aims of the project were to develop the scientific understanding of the population ecology of choughs on Islay, and to use this understanding to inform the development of appropriate conservation strategies and policies. The project built on existing long-term research on Islay's choughs. It involved further analysis of long-term data, plus two years of intensive fieldwork designed to answer specific questions. The work aimed primarily to understand the ecology of choughs in their sub-adult years (ie, from fledging to breeding age). Survival from fledging to breeding is a key factor in causing population change. However, relatively little was previously known about the behaviour and ecology of choughs during this time.

This report provides an overview of the results of the scientific study and focuses on presenting the scientific evidence on which resulting recommendations for chough conservation management on Islay are based. The report is written with the intention of presenting the results of the data analyses, and the rationale underlying those analyses, in a way that is accessible to non-specialists. Further details of analyses and technicalities are provided in published, peer-reviewed papers and/or are available on request.

The report provides information that will be of use to policy makers and conservation practitioners, and also highlights topics where further research is required before informed management decisions can be taken.

3b) Project rationale

One major and critical challenge facing conservation managers is the need to devise effective conservation management policies that are based on sound scientific evidence, but also feasible and compatible with agriculture and other competing demands on land-use, and with management aimed at conserving other species or habitats. Such evidence-based policies must be based on a sound scientific understanding of the factors that cause changes in the numbers of the focal species, and of the links between these factors and management policy. A key step in the development of any management policy should therefore be to identify which demographic rates (survival and reproduction) are primarily responsible for causing population change, and which environmental factors are in turn responsible for causing variation in these demographic rates.

The long-term demographic and ecological data that are required to achieve this understanding are rarely available for natural populations, especially those of immediate conservation concern. Furthermore, to provide adequate context and highlight the full range of appropriate management approaches, analyses should ideally be replicated across multiple populations of the focal species inhabiting different environments. Such parallel demographic and ecological studies would make it possible to assess the general applicability of findings, and to develop conservation policies that can be coordinated across populations and are locally effective. However, due to the substantial data required, the need for rigorous and detailed analysis, and difficulties in effectively communicating and implementing scientific knowledge, such large-scale application of rigorous ecological science to biodiversity conservation is rarely achieved with respect to any species of conservation concern.

Scottish and European pastoral agricultural ecosystems are of high biodiversity value, and reflect particular socioeconomic structures that are themselves increasingly rare. These ecosystems support numerous rare and threatened animal and plant species of high national and international conservation priority. The red–billed chough *Pyrrhocorax pyrrhocorax* is one such species, which serves as a high-profile figurehead for the conservation of pastoral agricultural ecosystems.

The overall aims of this project were to use existing long-term data, and further targeted fieldwork, to quantify and understand demographic variation in choughs in Scotland in relation to habitat and land-use, and to use this understanding to make recommendations for the successful conservation of choughs in Scotland.

3c) Specific aims and achievements

The project had five main aims as follows:

Aim 1: To establish an ongoing dialogue between scientists studying environmental factors driving population change and those responsible for managing the environment to conserve protected species.

This has been achieved through the Scottish Chough Forum, and through discussion meetings and informal contact between scientists, conservation managers and practitioners, farmers and landowners throughout the project.

Aim 2: To identify apparent drivers of temporal and spatial variation in chough demography on Islay, focusing particularly on demographic rates that are known to constrain population growth rate, and their links with environmental factors that could feasibly be managed.

This has been achieved as mainly reported in section 6 below.

Aim 3: To investigate whether patterns and correlates of demographic variation observed on Islay also apply to chough populations on Colonsay and the Isle of Man.

This has been achieved to the degree reported in section 13.

Aim 4: To use the resulting understanding of chough population ecology to identify management approaches, times and locations that are likely to be most effective with respect to chough conservation, and to consider how chough demographic rates might respond to management action.

This has been achieved as reported in sections 5, 7, 8, 9, 10, 11 and 12.

Aim 5: To facilitate wider transfer of knowledge among conservationists, population ecologists and land managers across Europe by hosting an international chough conference, and to communicate our work to local people by giving presentations on Islay and elsewhere.

This has been achieved as reported in section 14.

4. Background to choughs and chough research

4a) Range and status

Red-billed choughs occupy a restricted global range. In Britain, they are almost entirely confined to the Welsh coast, the Isle of Man and the Scottish Inner Hebridean islands of Islay and Colonsay, plus a very small, recently established population in Cornwall. Islay and Colonsay therefore constitute the northernmost point of the species' range and hold virtually the entire Scottish population.

Choughs are amber-listed in the UK, and protected under British and European law (Schedule 1, Wildlife & Countryside Act 1981; Annex 1, EU Birds Directive). They are consequently the focus of conservation action across Britain and Europe. Under the Birds Directive, the UK government has a responsibility to conserve choughs and the habitat on which they depend. SNH, as the relevant government agency, is responsible for implementing this work with respect to choughs in Scotland. In addition to their official protected status, choughs are of considerable cultural importance in Scotland and elsewhere. Furthermore, ecotourism, for which choughs provide one focus, is a valuable component of Islay's and Colonsay's economies. Successful conservation of choughs is therefore a priority for SNH and RSPB. However, since choughs utilise large land areas, chough conservation is expensive in terms of time and resources. Furthermore, choughs utilise sensitive coastal and grassland habitats, where they coexist with other protected species characteristic of pastoral agricultural systems, including corncrakes and marsh fritillaries. There is therefore a clear need to focus efficient management action on strategic aspects of chough ecology, whilst minimising the risk of negative effects on other species.

4b) Basic chough ecology

Choughs feed primarily on soil invertebrates. A primary dependence on *tipulid* larvae and *Aphodius* beetles has been reported on Islay, but a range of other prey is taken here and elsewhere. These include mining bee (*Andreninae*) larvae and kelp fly (*Coelopa*). It is well established that choughs require relatively short grazed grassland, which allows access to soil invertebrates.

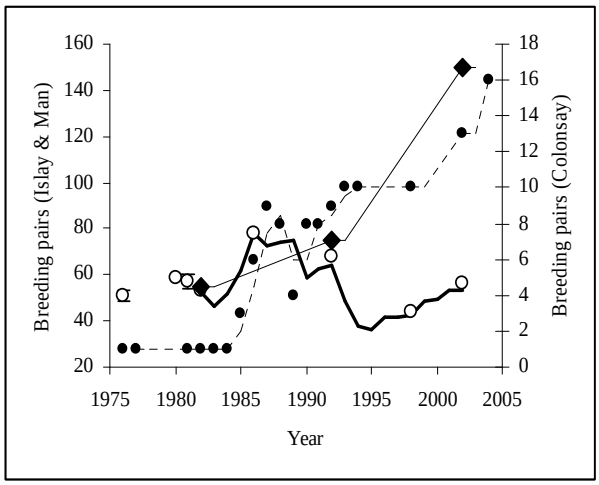
Choughs usually start to breed when they are two or three years old. They breed once each year between March and June, and nest in cavities in caves and buildings. Breeding pairs defend large (>>1km^2) feeding territories around their nest site. Fledged juveniles initially

remain on their natal territories, and are then usually escorted by their parents from their natal territory to flocking areas within a few weeks of fledging. There they form large communal foraging and roosting flocks where they remain until they disperse to breed (typically aged two or three).

4c) Chough research on Islay

The chough population on Islay has been the subject of an ongoing study, run primarily by the Scottish Chough Study Group (SCSG), since 1981. During the study, Islay's breeding chough population was censused fully in 1982, 1986, 1992, 1998 and 2002. The census data suggest that the population peaked at *ca* 78 breeding pairs in 1986 and declined to only *ca* 45 pairs by 1998 before increasing to *ca* 56 pairs by 2002 (figure 4.1). The Islay population therefore remains relatively small, and shows a very different trajectory from the number of breeding pairs on Colonsay and the Isle of Man, both of which increased substantially during the same period (figure 4.1).

Figure 4.1. The number of confirmed breeding pairs of choughs on Islay (o), Colonsay (•) and the Isle of Man (♦) as estimated from full population censuses. Symbols indicate the census counts for each island. The thin solid and dashed lines show smoothed trends based on the census data for the Isle of Man and Colonsay respectively. The bold line shows the estimated number of breeding pairs of choughs on Islay calculated from data on survival and breeding success. The left y-axis refers to Islay and the Isle of Man and the right y-axis refers to Colonsay.



The census data also show that breeding choughs are fairly widely distributed on Islay, inhabiting the Rhinns, the east coast of Loch Gruinart and the north-east coast, the Ballygrant Valley, Laggan and the Oa Peninsula.

The Scottish Chough Study Group have recorded breeding success (the number of chicks fledged per breeding attempt) at a sample of Islay nest sites in each year since 1981, and have colour-ringed the fledglings with unique combinations of coloured plastic leg-rings. These colour-ringed individuals have then been resighted across Islay throughout subsequent years. In 2001, all available data on Islay's choughs was collated into a database (facilitated by funding from SNH and RSPB). The database has subsequently been maintained and updated, and now holds >17000 resightings of >1300 colour-ringed individuals, and >900 records of individual breeding events. These long-term data are immensely valuable, and have proved to be of sufficient quality to enable detailed demographic analysis of Islay's chough population. These are exactly the sorts of data and analyses that are required to provide a rigorous scientific basis to conservation strategy.

5. Demography of Islay's choughs

5a) Introduction

One key component of science-based conservation planning is to identify which demographic rates cause variation in the population growth rate of the particular species or population that is the focus of conservation concern. For example, if we can work out whether it is variation in the survival of adult choughs, or in the survival of sub-adult choughs or in breeding success that is primarily responsible for causing a population to change in size, then we can target management appropriately. This approach should help achieve desired changes or stability in population size in the most efficient way.

Identifying which demographic rates (e.g. survival of different age classes or breeding success) cause a population to increase or decrease in size requires two key pieces of information.

First, we need to calculate the 'sensitivity' of the population growth rate to variation in any demographic rate. The sensitivity measures the degree to which population growth rate would be expected to change in response to a small change in any particular demographic rate. For example, a high sensitivity would indicate that a small change in a particular demographic rate (such as survival) will cause a large change in population growth rate. Management policy might then aim to increase demographic rates to which population growth rate is highly sensitive, since a small increase in performance would be expected to translate into a relatively large increase in population growth rate. In practise, population ecologists usually measure a quantity called 'elasticity' rather than 'sensitivity'. The elasticity is a scaled version of the sensitivity that enables us to compare the relative influence of different demographic rates on population growth rate.

Second, we need to calculate the extent to which each demographic rate has actually varied during the time for which the population of interest has been studied. This information tells us the extent to which observed changes in population size can be attributed to variation in each demographic rate. Small changes in a demographic rate to which population growth rate is very sensitive will in principle cause a big change in population size. However, if that demographic rate has not actually varied it cannot have caused observed changes in population size.

While management policy might ideally aim to increase the demographic rates to which population growth rate is most sensitive, this may not be possible if those rates are already high and vary little, and/or if an increase is difficult to achieve for practical reasons. Conservation policy might therefore most effectively focus on demographic rates to which population growth rate is reasonably sensitive, but which also show natural variation and which can realistically be managed.

Rigorous calculation of the sensitivity and variability of each demographic rate requires detailed long-term data on breeding success and survival from the population of interest. Such data are rarely available for populations that are the focus of conservation concern. However, as a result of the long-term Scottish Chough Study Group project, there are sufficient data to carry out these analyses for the Islay chough population. The following sections provide an overview of these analyses and the major results. Further details are presented in Reid et al. 2003a, 2003b, 2004 & 2006 (Appendices 1-5).

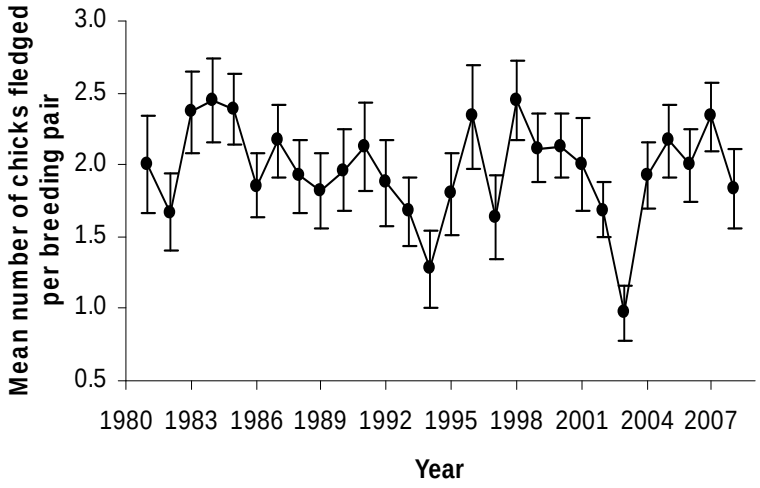
5b) Breeding success

The number of nests monitored per year averaged 31.1 ± 1.3 (standard error), and varied from 18 in 1982 to 48 in 2002. The monitored nest sites are broadly representative of the areas used by choughs on Islay, except that there are few data from the Oa (because most nest sites there are inaccessible). In general, nests in buildings were more likely to be monitored than nests in natural sites such as caves.

Breeding success of Islay's choughs, measured as the mean number of chicks fledged per monitored breeding pair, has varied among years (figure 5.1). Mean breeding success averaged 1.96 ± 0.05 fledglings/pair across all years, and varied from 2.45 fledglings/pair in 1984 and 1998 to 0.97 fledglings/pair in 2003. Mean breeding success has not decreased or increased significantly during the study, and has not differed between choughs nesting in buildings compared to those nesting in caves.

Choughs typically first bred aged two or three. Males first bred slightly younger than females on average, at mean ages of 2.5±0.1 and 2.9±0.1 respectively (based on data up to the year 2000, Reid et al. 2003a).

Figure 5.1. Mean breeding success (the number of chicks fledged per breeding pair of choughs monitored) on Islay from 1981 to 2008. Means for each year are presented ± 1 standard error.



5c) Survival

The resighting data from colour-ringed choughs allow annual survival probabilities to be calculated for three age classes: first-year (the probability that a chough survives from fledging to age one), second year (the probability that a chough survives from age one to age two) and adult (the probability that a chough survives through any subsequent year). Survival probabilities were estimated using 'capture-mark-recapture' models, which allow survival probabilities to be estimated while taking into account variation in the probability that a colour-ringed chough that is still alive will actually be observed in any year (this will vary due to variation in the amount of observer effort). This resighting probability can be estimated from the number of individuals that were not seen in one particular year but were then seen alive in a subsequent year. Survival probabilities were measured from the spring of one year to spring of the next. Currently we can estimate survival for the years 1983-84 through to 2007-08 (resighting probability in 2008 was assumed to be the same as in 2007, since observer effort was similar in these two years of intensive fieldwork). On average that 77% (± 3%) of colour-ringed choughs that are alive are seen in any one year. This resighting rate has varied from 43% in 1996 to 95% in 2007 (during the current project fieldwork). Since choughs that were colour-ringed on Islay are very rarely observed elsewhere is it reasonable to assume that individuals that disappear from Islay have died.

The estimated annual survival probabilities for the three age classes of choughs varied among years (figure 5.2).

On average, 40% (± 2%) of fledgling choughs survived to reach age one, ranging from 64% in 1984 to only 9% in 2007 and 2008. First-year survival did not increase or decrease significantly during 1983-2006 (Reid et al. 2008). However, with the addition of data from 2007-2009, there is some evidence of a long-term downward trend (figure 5.2).

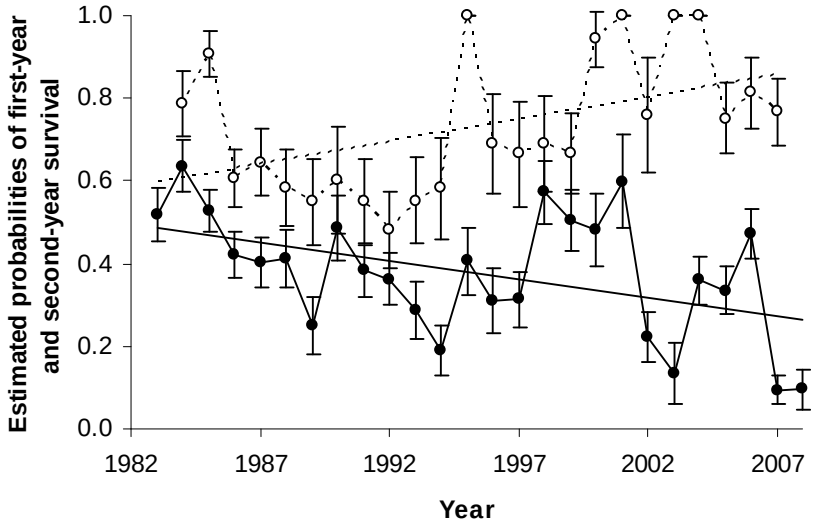
On average, 69% (± 3%) of one year-old choughs survived to reach age two. Very high second-year survival rates (100%) were estimated for 1995, 2001, 2003 and 2004 (figure 5.2). These high estimates reflect small sample sizes for cohorts where few fledglings were colour-ringed and/or first-year survival was low, and probably do not accurately represent true second year survival across the population. Excluding these four years, estimated second-year survival rates ranged from 94% in 2000 to 48% in 1992. There is some evidence that second-year survival rates may have increased during 1984-2008 (figure 5.2).

On average, 80% (± 1%) of adult choughs (choughs aged two or older) that were alive in one year were still alive the next year. The adult survival rate varied from 90% in 1985 to 72% in 2004, and has not increased or decreased across years (figure 5.2).

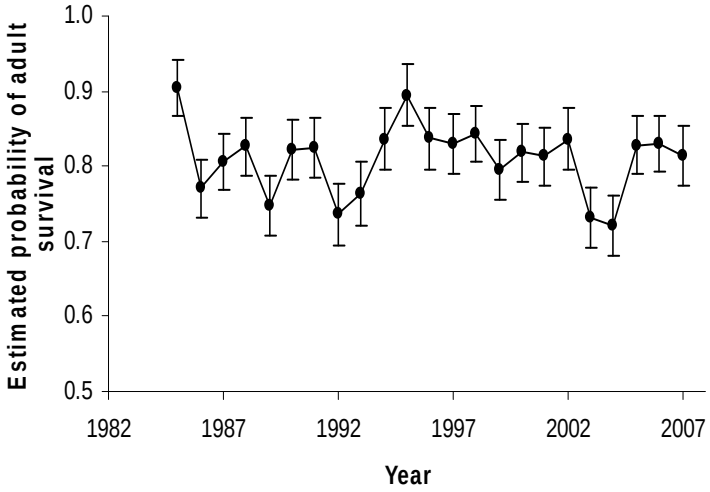
Figure 5.2. Estimated survival probabilities for choughs on Islay.

Figures show estimated (a) first-year survival (fledging to age one, filled symbols and solid line) and second-year survival (age one to age two, open symbols dotted line) and (b) adult survival (all choughs aged two or older). Year markers denote the start of each survival period: hence '1984' refers to survival from spring 1984 to spring 1985. Estimates are shown ± 1 standard error.

(a)



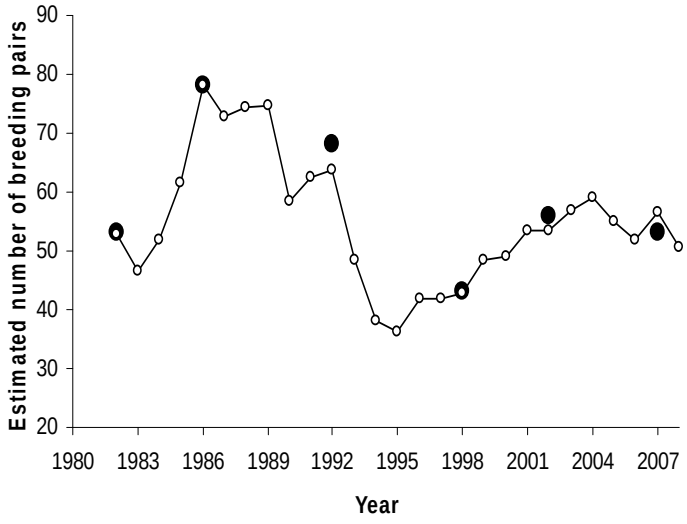
(b)



5d) Population growth rate

To check the accuracy of our estimates of breeding success and survival for each year, we used these estimates to calculate the number of breeding pairs of choughs we would expect to see on Islay in each year and compared this expected number with the actual number of pairs counted during population censuses. The changes in the number of breeding pairs of choughs that we estimated from the breeding success and survival data matched up with available census data extremely well (figure 5.3). This suggests that the Scottish Chough Study Group data provide reliable information on key demographic rates (ie breeding success and survival).

Figure 5.3. The number of breeding pairs of choughs found to be breeding on Islay in complete censuses (1982, 1986, 1992, 1998 and 2002) and the virtually complete census undertaken in 2007 as part of this project (filled symbols). The open symbols and line show the number of breeding pairs as estimated from demographic models (updated from Reid et al. 2004).



The average population growth rate of choughs on Islay estimated across all data from 1982-2008 is approximately $\lambda = 0.99$. A value of $\lambda = 1.0$ would indicate a stable population (no change in numbers from one year to the next) and a value of $\lambda < 1.0$ would indicate that a population will get smaller from one year to the next. The demographic data therefore match up with the observation that, on average across 1982-2008, the Islay chough population has remained stable or declined very slightly.

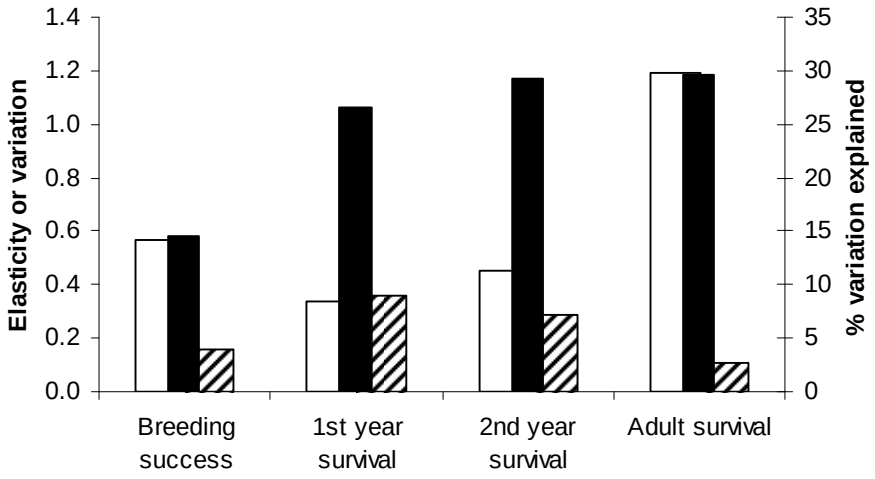
However, using data on breeding success and survival collected during the last five years (2003-2008), the average estimated population growth rate has dropped slightly, to approximately $\lambda = 0.97$. Therefore, were the recent breeding success and survival rates to continue, the number of breeding pairs of choughs on Islay would be expected to decrease by approximately 3% per year over coming years, representing a relatively rapid population decline.

5e) Sensitivity and population growth rate

The population growth rate for choughs on Islay was most sensitive to variation in adult survival, followed by breeding success, second-year survival and first-year survival (figure 5.4). All else being equal, a small change in adult survival would cause a bigger change in population size than a small change in any of the other three demographic rates. However, first-year and second-year survival varied more among years than adult survival or breeding success (figures 5.2 and 5.4). Overall, therefore, variation in first-year, second-year and adult survival all contributed approximately equally to observed variation in chough population growth rate, while variation in breeding success contributed less (figure 5.4). We can therefore conclude that among-year variation in survival caused most of variation in the number of choughs on Islay during 1983-2008. Furthermore, variation in survival through the first two years of life (ie, from fledging to age two) accounted for over half the total observed variation in population size.

The adult survival rate of choughs on Islay is already fairly high and varies relatively little among years (figures 5.2 and 5.4). It may therefore be difficult to achieve an increase in adult survival rate through management policy. Our data therefore suggest that sub-adult survival (ie, survival from fledging to age two) is one demographic rate on which management could effectively focus in order to increase the number of choughs on Islay. Full details of these analyses are presented in Reid et al. 2004 (provided as Appendix 3).

Figure 5.4. Three measures of the extent to which variation in breeding success, first-year survival, second-year survival and adult survival could cause variation in the number of choughs on Islay. The estimated elasticity, a measure of the sensitivity of population growth rate to each demographic rate, is shown by the white bars and the left axis. The degree to which each demographic rate was observed to vary among years is shown by the shaded bars and the left axis. The percentage contribution of each demographic rate to observed variation in population growth rate is shown by the black bars on the right axis.



5f) Variation in sub-adult survival in different areas of Islay

Survival rates have also varied markedly among choughs fledged from nest sites in different parts of Islay. While the average rate of first-year survival was approximately 40% (see section 5c), this varied from 0% to 73% across choughs fledged from different individual nest sites (figure 5.5).

Nest sites that produced fledglings that were more or less likely to survive were not randomly distributed across Islay. In particular, from 1983 to 2004, choughs fledged from nest sites in the Ballygrant Valley and surrounding Loch Gruinart and parts of the East Rhinns were more likely to survive to age one than choughs fledged in the North, West, South and Central Rhinns (figure 5.6). These same choughs also tended to be more likely to survive as second-years and as adults (table 5.1). Specific areas of Islay therefore consistently produced choughs that survived relatively well or relatively poorly. Full details of these analyses are presented in Reid et al. 2006 & 2008 (Appendices 4-5).

Figure 5.5. Variation in first-year survival probabilities estimated for choughs fledged from different nest sites. Each datapoint refers to a different nest site where a total of at least six fledglings have been colour-ringed across at least three different years during the course of the SCSG study. The estimated first-year survival probability of choughs fledged from each of 53 different nest sites is shown ± 1 standard error.

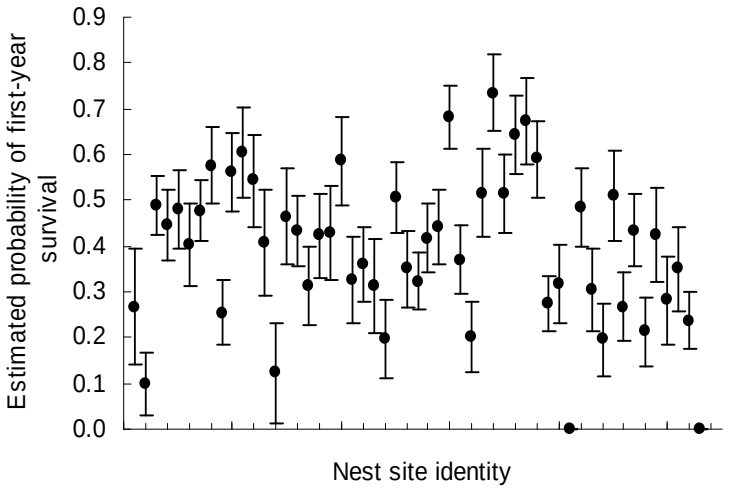
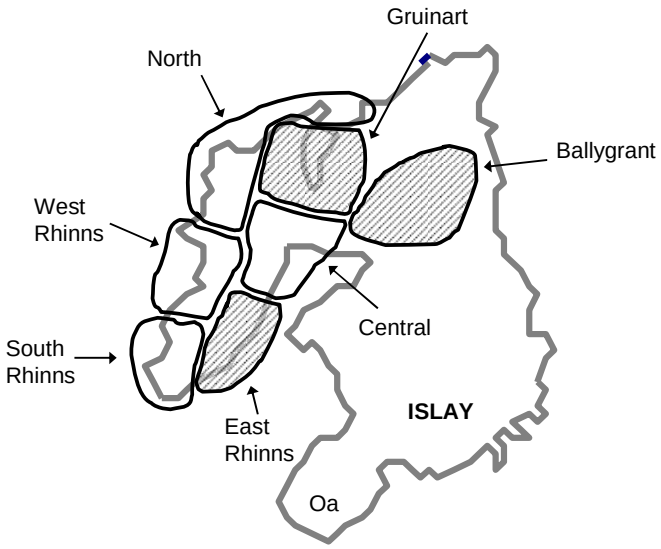


Table 5.1. Summary of estimated survival probabilities for choughs fledged in Ballygrant, Gruinart and East Rhinns (region BGE) as opposed to Central, North, South Rhinns and West Rhinns (region CNSW, see figure 5.6 for areas).

	Choughs fledged in region BGE	Choughs fledged in region CNSW
First-year survival probability	**0.61±0.04**	**0.38±0.05**
Second-year survival probability	**0.69±0.04**	**0.65±0.05**
Adult survival probability	**0.84±0.02**	**0.77±0.02**

Figure 5.6. Summary of areas that produced choughs that were on average more and less likely to survive through their first and subsequent years of life. Choughs fledged in the shaded areas (named 'Ballygrant', 'Gruinart' and 'East Rhinns') had higher survival probabilities than choughs fledged in the unshaded areas (named 'North', 'West Rhinns', 'South Rhinns' and 'Central'). There were insufficient data to estimate survival probabilities of choughs fledged on the Oa.



5g) Summary of key conclusions and implications: demography of Islay's choughs

1. The number of choughs breeding on Islay choughs is expected be strongly influenced (highly sensitive) by variation in adult survival. However, over the period for which we have data (1985-2008), adult survival has generally been high and has varied relatively little among years. Variation in adult survival has therefore contributed only moderately to observed variation in the number of choughs on Islay.

It is critical to continue to monitor adult survival and ensure that it remains high. A reduction in adult survival (for example due to reduced food abundance or availability or increased predation or disease) would be likely to cause a major and rapid decline in the number of choughs on Islay.

2. The survival of choughs from fledging to age two ('sub-adult survival') varied markedly during 1983-2008, and accounted for over half the observed variation in the number of choughs on Islay.

It is therefore important to determine what causes sub-adult survival to vary among years, and consider whether management practices could be used to stabilise and if possible increase sub-adult survival rates and/or reduce the frequency of years in which sub-adult survival is low.

3. Breeding success varied relatively little among years during 1981-2008, and consequently contributed relatively little to variation in the number of choughs on Islay. However, since population growth rate was moderately sensitive to variation in breeding success, breeding success should continue to be monitored to check that success does not decline.

4. Sub-adult and adult survival varied consistently among choughs fledged from different individual nest sites and from different areas of Islay.

This implies that certain areas of Islay make disproportionately large contributions to the chough population. It is therefore important to determine what causes this variation among areas and consider how management could be used to maintain areas that produce choughs that survive well and/or improve areas that currently produce choughs that survive poorly.

5. In summary, analysis of long-term demographic data from Islay's choughs suggest that managing sub-adult survival deserves specific consideration as one effective means of increasing or maintaining the number of choughs on Islay.

6. Long-term variation in sub-adult survival

6a) Introduction

Section 5 shows that one key process that causes the number of choughs on Islay to vary among years is variation in sub-adult survival (ie, the probability that a chough will survive from fledging to age two). Section 5 also emphasises that, if sub-adult survival is to be managed, we need to understand what causes survival rates to vary among years and among choughs fledged from different nest sites and areas. We therefore used the long-term Scottish Chough Study Group data to try to identify key ecological variables that might cause this variation.

6b) Methods

We tested whether variation in first-year survival, among choughs fledged in different years and from different nest sites, was correlated with a specific set of plausible ecological variables that were selected by reference to existing knowledge of chough ecology (table 6.1). We could only test for correlations between survival and the ecological variables for which reliable, quantitative data were available. Some potentially important variables could therefore not be included in our analyses. These include variation in the abundance of predators and competitors of choughs (such as peregrines and ravens), precise agricultural management practices (such as avermectin and fertiliser use), and rates of disease and disturbance.

It is important to remember that observed correlations between survival and any ecological variable might be caused by a common effect of some third factor rather than necessarily reflecting a direct causal effect of the main ecological variable on survival. However, it is still useful to examine how survival has varied in relation to certain key variables since this allows us to identify variables with potentially important effects.

Full details of the analyses and the sources of ecological and environmental data are described in Reid *et al*. 2008 (Appendix 3).

Table 6.1. Tested hypotheses linking ecological and environmental variables to variation in first-year survival in choughs.

Category	Variable	Hypothesised relationship with survival	Rationale
Weather	Summer temperature (year before fledging)	Positive	Greater invertebrate productivity in warmer summers (thus increased larvae abundance the following spring).
Weather	Breeding season temperature (natal year)	Positive	Greater invertebrate activity in warm weather.
Weather	Winter temperature (post-fledging)	Positive	Greater invertebrate activity in warmer weather, and frozen ground impedes foraging.
Weather	Breeding season rainfall (natal year and previous year)	Negative	Reduced invertebrate activity and productivity in wet springs.
Weather	Autumn rainfall (post-fledging)	Positive	Dry ground impedes foraging and drought can kill soil invertebrates.
Weather	Winter rainfall (post-fledging)	Negative	Flooding kills soil invertebrates and may impede foraging.
Prey	Winter *tipulid* larvae abundance (pre- and post-fledging)	Positive	Greater prey availability for parents and fledglings in high *tipulid* years.
Land-use	Areas of grazed and mowed (silage) grassland	Positive	Choughs preferentially forage on short grazed grassland and silage aftermath.
Land-use	Total number of cattle, sheep & livestock units, and stocking density	Positive or quadratic	Grazing creates short grassland and dung supports invertebrate prey. Possible detrimental effects of overgrazing?
Local habitat	Area of improved grassland within specific radius of nest	Positive	Choughs preferentially forage on short grazed grassland and silage aftermath ('improved' grassland).
Local habitat	Area of plantation, peatland & heather within specific radius of nest	Negative	Foraging choughs avoid these habitats.
Chough density	Chough population size and local breeding density	Negative or quadratic	Competition, but possibility of local facilitation through flocking & kin clustering?
Physical	Distance from exposed coastline	Positive	Exposure and salinity may reduce invertebrate abundance.
Physical	Distance to sub-adult flock	Negative	Increased mortality during dispersal to sub-adult flock.
Physical	Territory aspect	Negative (from south-east)	*Tipulid* larvae more abundant in south and east facing pastures.

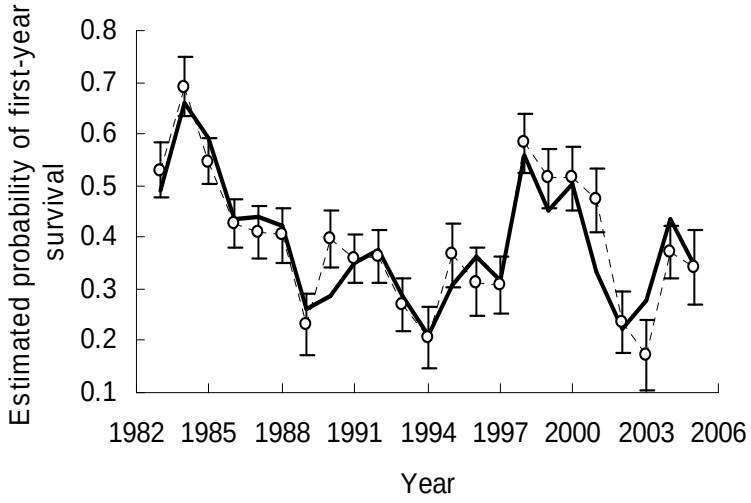
6c) Among-year variation in first-year survival

Among-year variation in first-year survival (the probability that a fledgling chough would survive to age one) was correlated with environmental conditions prevailing both in the season a chough fledged (rainfall during the breeding season) and previously (summer temperature and breeding season rainfall the previous year and the abundance of *tipulid*

larvae during the winter before fledging). Fledgling choughs were more likely to survive to age one when they were reared in years following relatively warm summers, dry breeding seasons, and winters when *tipulid* larvae were abundant. Together, these variables explained about 80% of the total among-year variation in chough survival (figure 6.1). In contrast, we found no correlation between chough survival and temporal variation in measures of agriculture on Islay, such as total number of cows or total stocking density.

These results suggest that among-year variation in first-year survival in Islay's choughs may primarily reflect variation in weather and prey abundance. It is also notable that the best statistical model explaining variation in first-year survival included effects of previous rather than current environmental conditions (ie, weather and *tipulid* abundance in the seasons before a chough fledged). This suggests that there are lagged effects of environmental conditions on how likely choughs are to survive. These lagged effects may reflect lasting effects of environmental variation on future prey populations, or on the state of adult choughs and hence their ability to raise fledglings that are able to survive.

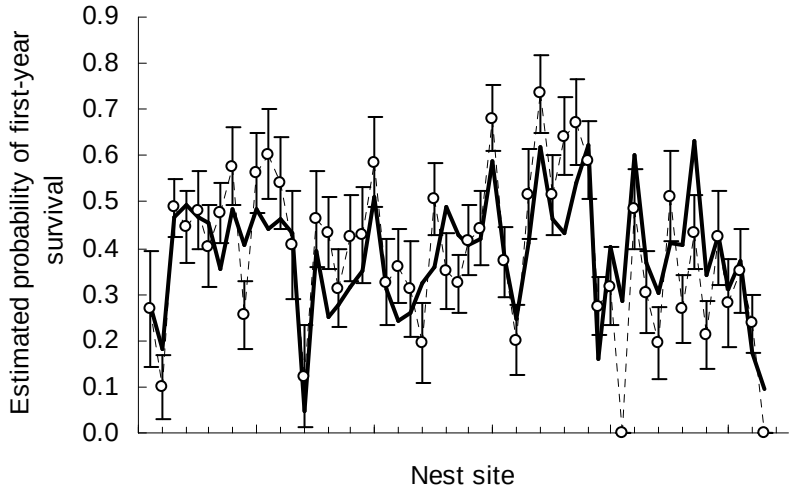
Figure 6.1. Among-year variation in first-year survival estimated from SCSG data (open symbols, dashed line) and the best statistical model explaining this variation (solid line). The best model included effects of breeding season rainfall in an individual chough's natal year and the previous year, summer temperature during the year before fledging and *tipulid* larvae abundance during the winter before fledging.



6d) Among-nest site variation in first-year survival

Variation in the first-year survival of choughs fledged from different nest sites was correlated with the area of unsuitable foraging habitat for choughs (specifically plantation, woodland, peat bog, gorse, heather moorland, wetland etc) surrounding the chough's natal nest site, local density of breeding choughs, and the distance from the nest site to the Atlantic coast and the nearest subadult flocking area (ie, Ardnave or Kilchoman). Fledgling choughs were more likely to survive to age one when they fledged from nest sites that had less unsuitable foraging habitat within 300m of the nest, that had other chough pairs closer by, that were relatively close to primary roost sites at Ardnave and Kilchoman, and that were further from exposed Atlantic coast. However, even taken together, these variables explained only about 50% of the total variation in first-year survival among the different nest sites (figure 6.2). Approximately 50% of among-nest site variation in survival therefore remained unexplained by these variables.

Figure 6.2. Estimated among-nest site variation in first-year survival for choughs fledged from 53 well-studied nest sites (open symbols, dashed line), and the best statistical model explaining this among-site variation (solid line). The model included effects of distance to exposed coast, area of unsuitable habitat surrounding a nest site, distance to the nearest subadult flock and local density of breeding choughs.



6e) Interactions between year and nest site

Finally, we tested for interactions between ecological variables that might explain among-year or among-nest site variation in survival. An 'interaction' means that the effect of one variable depends on the value of another variable. For example, an interaction between rainfall and habitat might mean that the effect of rainfall on chough survival depends on the habitat type; rainfall might have a negative effect in some habitats but no effect, or a positive effect in others. Such interactions are potentially crucial in a management context, since they may hold the key to maximising first-year survival given possible large effects of weather and *tipulid* abundance, which are difficult to manage directly. For example, if there were an interaction between weather and habitat, then it may be possible to minimise effects of bad weather by managing the habitat correctly.

We found statistical evidence of four interactive effects on first-year survival:

i) ***Tipulid* abundance and area of unsuitable foraging habitat within 300m of a chough's natal nest site.** The positive correlation between *tipulid* abundance and first-year survival was stronger for choughs fledged from nest sites that were surrounded by more unsuitable foraging habitat (ie, plantation, woodland, peat bog, gorse, heather moorland, wetland etc). This suggests that choughs fledged from nest sites surrounded by less suitable habitat may be more vulnerable in years when food is scarce.

ii) ***Tipulid* abundance and local density of breeding choughs around a chough's natal nest site.** The positive correlation between *tipulid* abundance and first-year survival was stronger for choughs fledged from nest sites with other pairs of choughs breeding closer by. This suggests that there may be increased competition for food in areas where there are more breeding pairs of choughs.

iii) **Rainfall and area of unsuitable foraging habitat within 300m of a chough's natal nest site.** The negative correlation between breeding season rainfall and first-year survival was stronger for choughs fledged from nest sites that were surrounded by more unsuitable foraging habitat. This suggests that effects of bad weather on fledgling survival may be less severe on choughs fledged on territories surrounded by better foraging habitat.

iv) ***Tipulid* abundance and breeding season rainfall the year before fledging.** The positive correlation between *tipulid* abundance and first-year survival was stronger in years following dry springs than in years following wet springs. The biological interpretation of this effect is not clear, but could suggest that the

importance of *tipulid* larvae to choughs depends on the abundance or availability of other food resources that are also influenced by weather conditions.

In summary, these interactions suggest that the relationships between weather, *tipulid* abundance and first-year survival of choughs are not fixed, but depend on other variables such as the habitat surrounding a particular nest site and the local density of choughs. This in turn suggests that detrimental effects of bad weather and/or low *tipulid* abundance on chough survival could perhaps be ameliorated or minimized through appropriate management of the density of nest sites and/or the habitat surrounding these nest sites.

6f) Predicting first-year survival in future years

In section 6c, we developed a statistical model that explains among-year variation in first-year survival as a function of weather and *tipulid* larvae abundance across the period 1983-2005 (figure 6.1). The best model included effects of summer temperature, breeding season rainfall and *tipulid* abundance during the seasons before a chough fledged, and rainfall during a chough's natal season. Since this model is based primarily on weather and *tipulid* abundance occurring before a chough fledges, it would in theory be possible to use the model to predict the first-year survival probability of any particular cohort of choughs. A prediction could be produced in June of the cohort's natal year (ie, at fledging). Furthermore, by dropping the 'natal breeding season rainfall' term from the statistical model, a prediction could be produced by March in a cohort's natal year (ie, before the eggs are laid). In this way, it would in theory be possible to provide an early warning of an impending poor year for first-year survival. This might help identify years in which specific management practices for choughs could be particularly beneficial.

To test how accurate such predictions might be, we used our statistical model (originally built using data from 1983-2005) to predict first-year survival probabilities for the 2006, 2007 and 2008 cohorts. We then compared these predictions with the survival probabilities that were actually observed for those cohorts. These predictions were based on a slightly different weather dataset from that used in the original model, because the original dataset has not yet been updated to cover 2006-2008. The first-year survival probabilities that the model predicted for the 2006 and 2008 cohorts are reasonably close to those that were actually observed (table 6.2). However, the prediction for the 2007 cohort is inaccurate – a high survival probability is predicted whereas the observed survival probability was in fact

the lowest on record (table 6.2). Unfortunately, at this point, it is difficult to judge whether the current statistical model will generally be a poor predicative tool, or whether survival of the 2007 cohort was dramatically reduced by some unusual circumstance that will rarely be repeated.

Table 6.2. First-year survival probabilities for the 2006, 2007 and 2008 cohorts of choughs that were (a) estimated from colour-ring resighting data and (b) predicted from the statistical model presented in section 6c.

Year	(a) Observed first-year survival probability	(b) Predicted first-year survival probability
2006	0.45	0.32
2007	0.09	0.54
2008	0.10	0.27

6g) Summary of key conclusions and implications: variation in first-year survival

1. On Islay, sub-adult survival has varied among choughs fledged in different years and among choughs reared in different nest sites (see section 5). This variation in sub-adult survival is a major cause of variation population growth rate, and hence in the number of choughs on Islay (see section 5). The next important stage of analysis is therefore to investigate what factors cause this variation in first-year survival and consider whether these factors could be managed so as to increase survival.

2. Among-year variation in first-year survival was correlated with weather and *tipulid* abundance; fledgling choughs were more likely to survive to age one in years following warm summers, dry breeding seasons and winters with high *tipulid* abundance.

Although correlation cannot prove causation, among-year variation in first-year survival may therefore be caused primarily by variation in weather and invertebrate abundance. These factors are difficult to manage directly.

3. Among-nest site variation in survival was correlated with local habitat, local chough density and distance from coast and subadult flocking areas. However these variables explained only 50% of observed variation in the survival of choughs reared in different nest sites.

More detailed investigation of the possible causes of variation in survival of choughs fledged from different nest sites was therefore required over and above that possible from existing long-term data. This detailed investigation was undertaken as part of the current project (see following sections).

4. There was evidence of interactions between temporal and spatial effects, for example between weather, the density of breeding choughs and the habitat surrounding nest sites. This suggests that any overarching effects of weather and *tipulid* abundance could potentially be ameliorated through appropriate management of nest site density and the habitat surrounding these nest sites.

5. There is a possibility that our statistical model would let us predict in advance the years in which sub-adult survival will be low. This would raise the possibility that additional management measures could be implemented in a targeted way to mitigate effects of particularly poor environmental conditions. However, further years of data are required to test this possibility.

7. Foraging and roosting sites used by sub-adult choughs on Islay

7a) Introduction

Section 5 shows that variation in sub-adult survival is one key factor that causes the number of choughs on Islay to vary among years. However, relatively little is known about the ecological requirements of sub-adult choughs, in terms of foraging and roosting sites, and hence how the availability of different habitats and management types might influence sub-adult survival. Previous work on choughs on Islay and elsewhere has focused primarily on adult breeders. The requirements of sub-adults may not be the same as those shown to be important for adults. Therefore, to provide information on which sites and habitats support sub-adult choughs, and may therefore be key to their survival, we first aimed to identify the precise foraging and roosting sites used by sub-adult choughs on Islay during two full years (April 2006 – March 2008).

7b) Methods

To identify which sites on Islay are used by sub-adult choughs, foraging and roosting flocks were located every month from April 2006 to March 2008. Intensive observations were carried out for approximately one week in the middle of each month. Additional observations were made throughout April-August 2006 and April-July 2007. Whenever a flock was located the time and place, the identities of any colour-ringed choughs and the number of unringed choughs was recorded.

Within each intensive monthly observation period, we aimed to locate all colour-ringed choughs aged two years or less. Our success rate was very high; on average 93% of individuals that were alive were recorded in each month from April 2006 – April 2008 (range 75% – 100%, see figure 12.1). Less than 10% of colour-ringed sub-adult choughs therefore went unobserved in a typical month. These individuals may have been present at a site that was visited but have been missed due to difficult viewing conditions (particularly in some winter months). Some individuals may have been missed because they were foraging or roosting at additional, unknown sites. However, given the high overall resighting rate of over 90%, any use of additional sites must have been limited.

In interpreting the data, we assume that the foraging and roosting sites used by colour-ringed sub-adult choughs are representative of those used by unringed sub-adult choughs. Indeed, despite substantial observation effort across all areas of Islay that are suitable for choughs,

flocks of unringed choughs were not encountered away from the areas where colour-ringed individuals were present. Furthermore, farmers and landowners, who were aware of the study and very helpful in alerting us to the presence of choughs on their land, very rarely noted flocks of which we were not already aware. The only exception is that we have few data on the presence or location of sub-adult choughs that remained on the Oa. The following analyses describe the foraging and roosting sites used by flocks of sub-adult choughs, and do not include observations of newly fledged choughs that were still on their natal territories.

Due to the presence of a high proportion of colour-ringed individuals within most flocks, we were certain that these flocks primarily comprised sub-adult choughs rather than breeding adults. However, colour-rings also revealed that some breeding adults did join the flocks, particularly in mid-summer and mid-winter. Since unringed breeders could not be distinguished from unringed sub-adults, we did not attempt to exclude breeders from flock counts. Strictly, the data therefore describe the foraging and roosting locations of sub-adult and adult choughs away from their breeding territories.

Data were primarily collected by Maria Bogdanova, Jane Reid and Eric and Sue Bignal. Data for the Oa were collected by RSPB, and are less complete in terms of monthly coverage. Some additional observations from other areas were also provided by RSPB staff.

7c) Foraging sites

Most flocks of choughs were located foraging in coastal dune systems, primarily on the Rhinns of Islay. The key sites were Ardnave, Kilchoman, Kilchiaran, Lossit, Killinallan, Sanaig, Smaull, Laggan and the Oa. These sites, and the relative use of each, are illustrated in figure 7.1. The estimated use of the Oa is approximate because data are not available for every month.

Most choughs were found foraging at Ardnave and Kilchoman (on average 48% and 28% of the total number of choughs observed each month, figure 7.1). Other dune systems, namely Lossit, Killinallan, Sanaigmore, Smaull and Laggan were used to a lesser extent (figure 7.1). Overall, during April 2006 – March 2008, flocks of choughs were therefore estimated to spend *ca*. 90% of their foraging time in or around dune systems, and there are no major dune systems on Islay where choughs were never observed. The remaining 10% of foraging time was almost entirely spent on newly cut silage fields, particularly at Kilchiaran and Lossit,

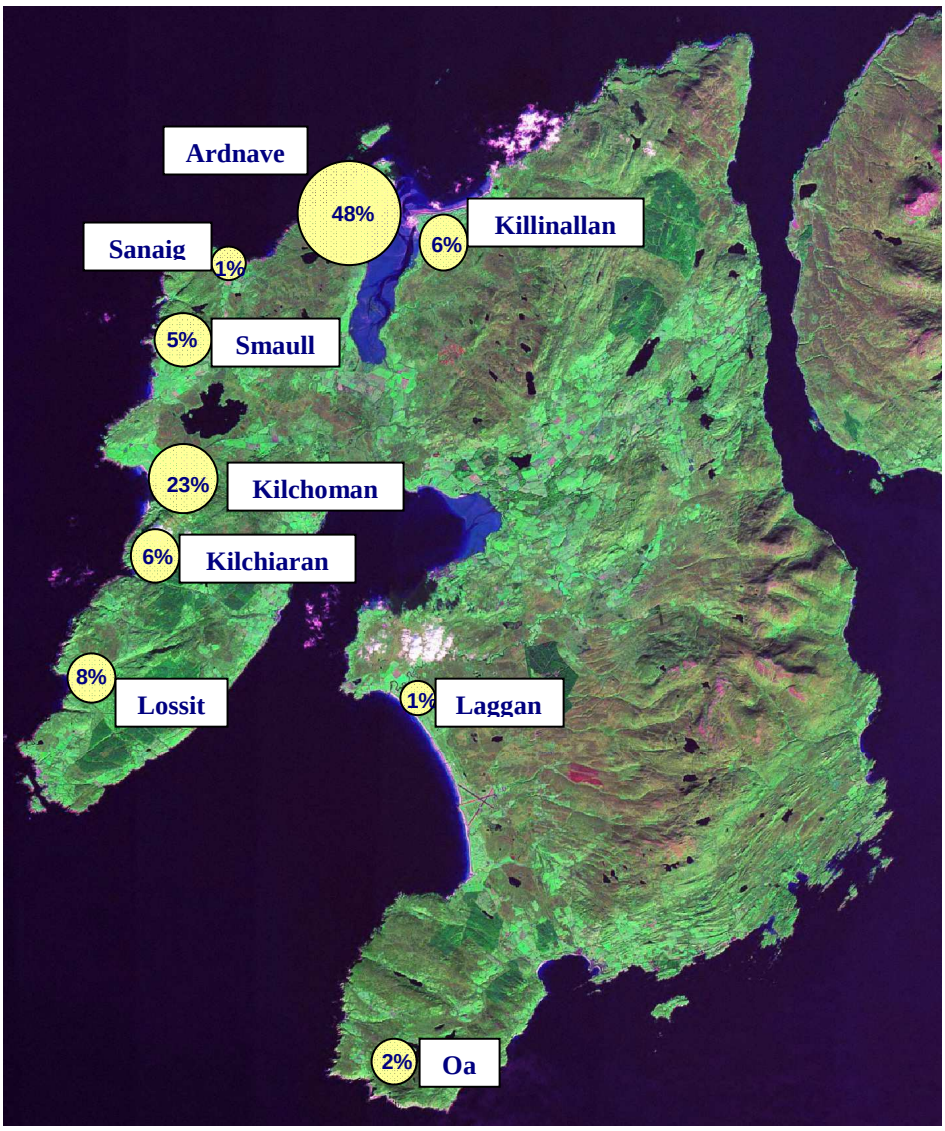
during the summer (figure 7.1). The total observation effort at each site is summarised in table 7.1. More visits were made to Ardnave and Kilchoman because extra visits were often required to ensure that all colour-ringed individuals present there were accurately identified.

The main foraging sites were used to a similar degree during both study years (ie 2006-2007 and 2007-2008). Slightly greater proportions of foraging choughs were observed at Ardnave during 2007-2008 than during 2006-2007, and at Kilchoman and Killinallan during 2006-2007 than during 2007-2008 (table 7.1).

Table 7.1. The number of visits made to each site used by flocks of choughs during April 2006 – March 2007 and April 2007 – March 2008, and the average percentage of sub-adult choughs that were observed in each month that were at each site in each year. Comprehensive monthly count data are not available from the Oa.

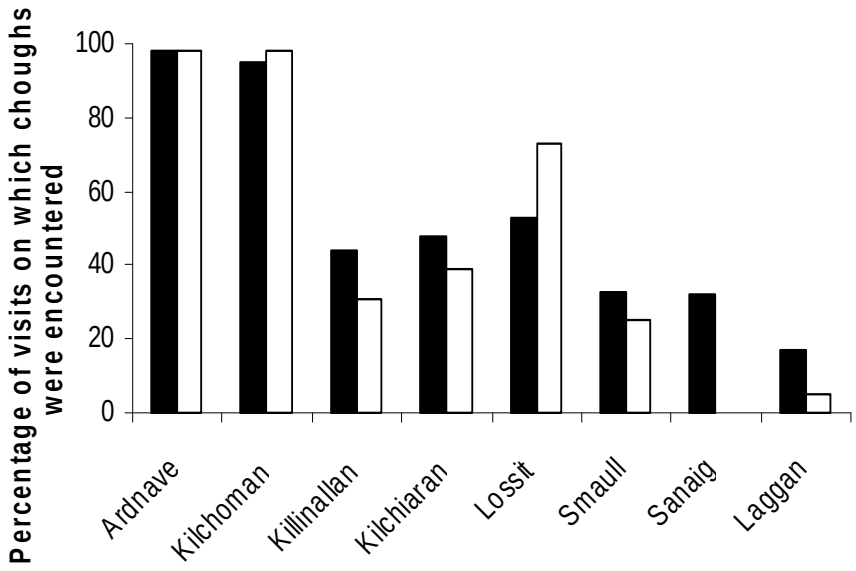
Site	Total number of visits		Average % of sub-adult choughs observed	
	2006-2007	2007-2008	2006-2007	2007-2008
Ardnave	57	59	41	57
Kilchoman	57	42	26	22
Kilchiaran	25	18	7	4
Lossit	19	15	7	8
Killinallan	16	13	10	2
Sanaig	19	17	1	0
Smaull	28	20	5	6
Laggan	12	20	1	1
The Oa	NA	NA	~2	NA

Figure 7.1. Location of sites at which flocks of choughs were observed foraging during April 2006 – March 2008, and the average percentage of all choughs observed in each month that were at each site.



Although the percentage of choughs that was observed to forage at some sites was low (ie, <10%), it is important to note that some of these sites were frequently used by small numbers of choughs. At least some of these individuals could be identified by their colour-rings and were known to be sub-adults rather than local breeding pairs. Figure 7.2 shows the percentage of visits to each site on which any choughs were observed. Choughs were encountered on almost all visits to Ardnave and Kilchoman. Although Killinallan, Kilchiaran and Lossit held a relatively small proportion of foraging choughs on average (figure 7.1, table 7.1), some choughs were encountered on 40-75% of visits to these sites (figure 7.2). These sites are likely to be of considerable value to these individuals.

Figure 7.2. The percentage of visits to sites used by foraging chough flocks on which some choughs were encountered. Data are not available for the Oa. Filled and open bars denote data from April 2006 – March 2007 and April 2007 – March 2008 respectively.

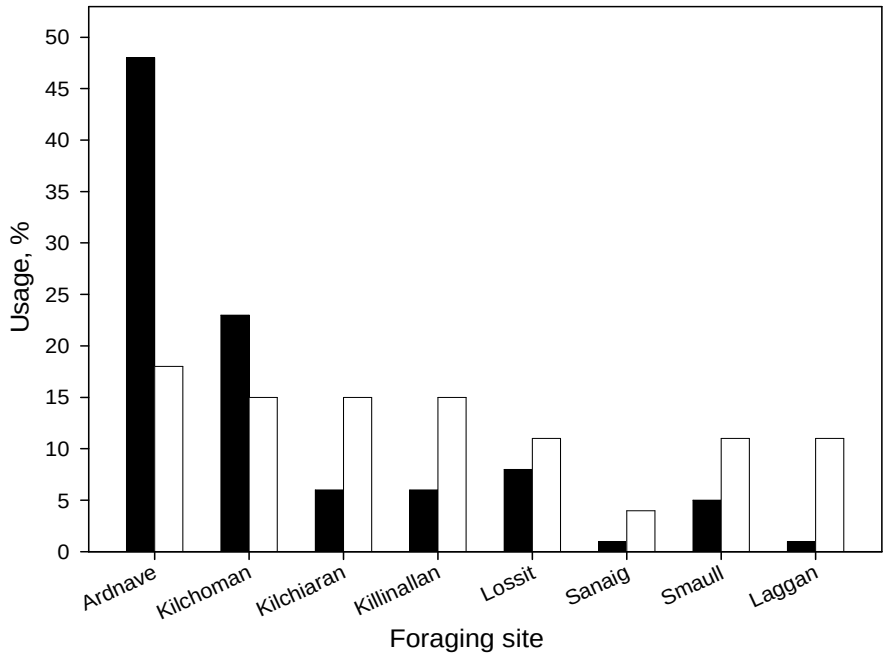


A greater percentage of the choughs that were foraging in flocks may have been at Ardnave and Kilchoman simply because Ardnave and Kilchoman are larger than other foraging sites, or because foraging choughs selected Ardnave and Kilchoman for reasons over and above simply their area. To distinguish these possibilities, we tested whether the average percentage of choughs observed at each site varied in proportion to their respective areas. The area of each site was estimated by summing the areas of relevant compartments and fields, which were provided by farmers or estimated from digitised 1: 10,000 maps of Islay.

This analysis suggested that Ardnave and Kilchoman on average held a greater percentage of flocking choughs than expected simply given their areas (figure 7.3). The other sites that were used to some extent by flocks of choughs held a smaller percentage of these choughs than expected from their area (figure 7.3). Sub-adult choughs therefore used Ardnave and Kilchoman more than expected simply given the area covered by these sites. However, across the eight main sites where flocks of sub-adult choughs were

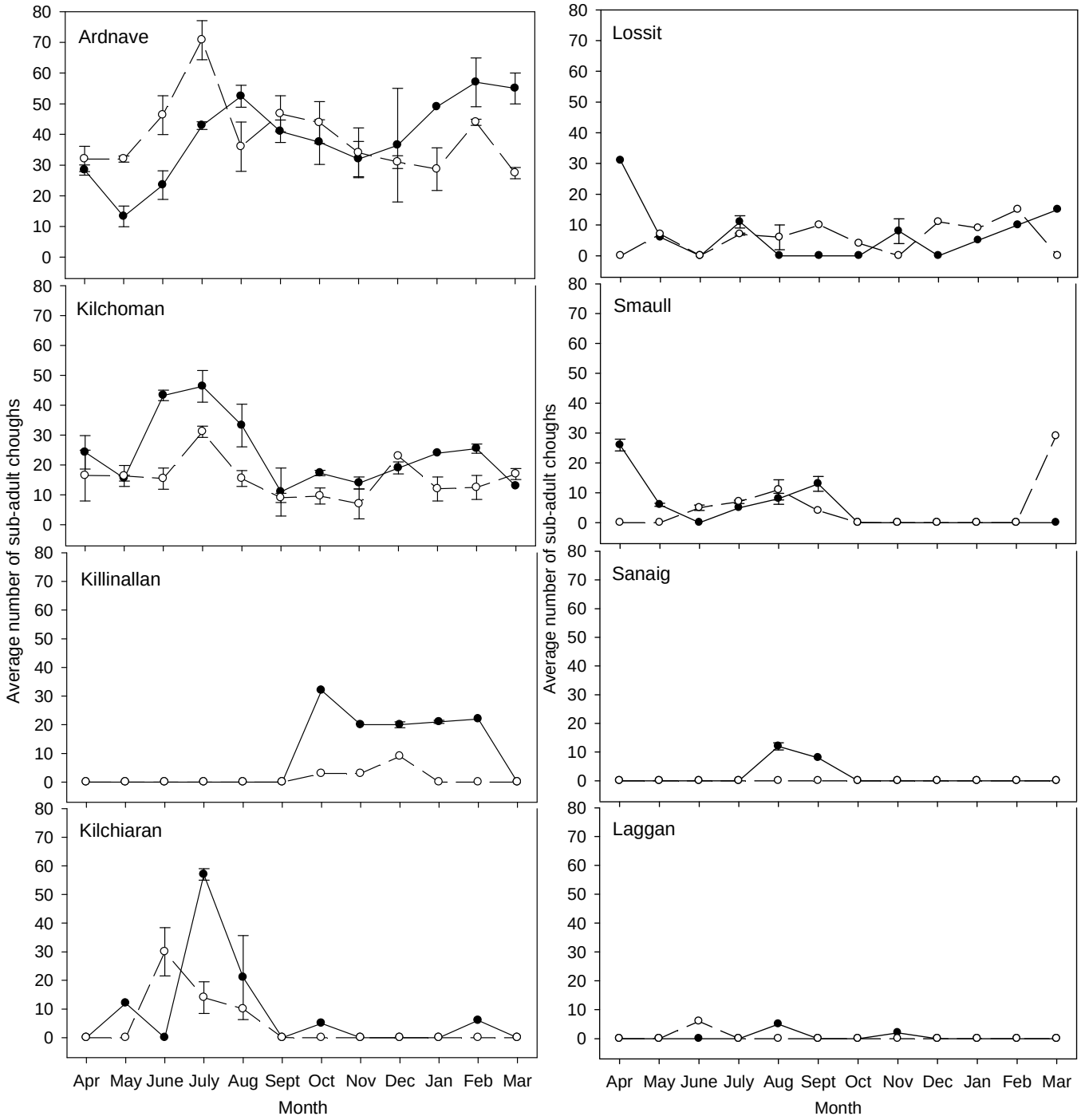
observed to forage, the average percentage individuals that was observed at each site was positively correlated with the sites area (r_s =0.78, P=0.02). Larger sites therefore tended to hold more foraging choughs.

Figure 7.3. Use of the main foraging sites used by flocking choughs relative to the area of the site. The filled bars show the average percentage of all flocking choughs recorded at each site during April 2006-April 2008. The open bars show the relative areas of each site, and hence the percentage of flocking choughs that might have been expected to be present based solely on area.



Flocks of sub-adult choughs used the different foraging sites to different degrees in different seasons. Ardnave and Kilchoman were used year-round (figure 7.4). Other sites were used only in some seasons and/or by fewer individuals in some seasons (figure 7.4). For example, the Kilchiaran silage fields were used primarily in summer while the Killinallan dunes were used only in winter. It is important to note that the summer peaks in use of Kilchoman and Kilchiaran are linked. At this time, large flocks of choughs used the silage aftermath at Kilchiaran during the day and then spent some time foraging at Kilchoman prior to roosting. The choughs that foraged at Killinallan during winter 2006-2007 roosted at Ardnave together with choughs that foraged at Ardnave. These seasonal patterns were broadly similar across both study years. The number of choughs recorded per month was generally higher during 2006-2007 than during 2007-08 due to higher survival rates during 2006-2007.

Figure 7.4. The mean number of flocking choughs observed at each foraging site in each month during April 2006 – March 2007 (filled symbols and solid line) and April 2007 – March 2008 (open symbols and dashed line). Means are presented ± 1 standard error for sites that were visited more than once during a particular month.



7d) Roost sites

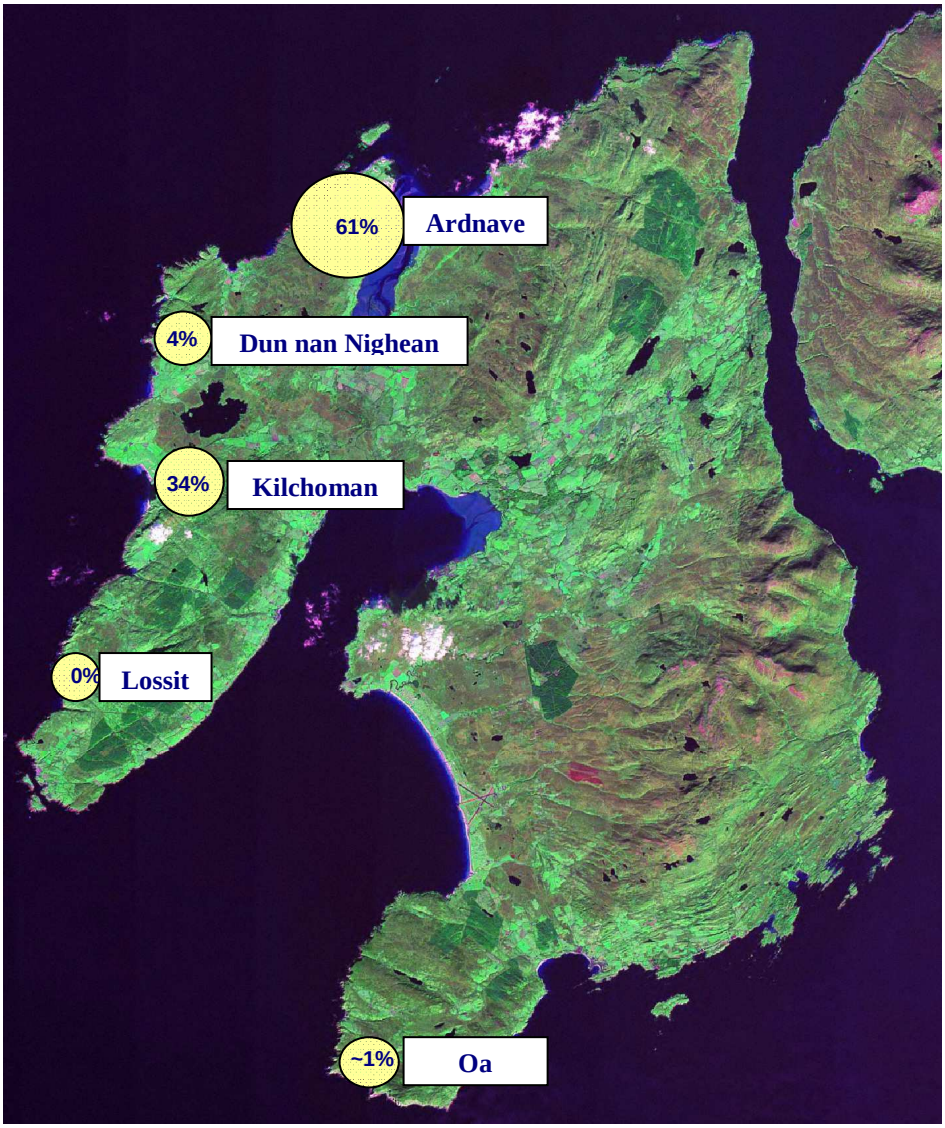
We located four roosts that were used by sub-adult choughs during April 2006 – April 2008 (figure 7.5). Most sub-adults roosted at Ardnave or Kilchoman throughout both years of the study, although a greater percentage of individuals roosted at Ardnave during 2007-2008 (table 7.2). Dun nan Nighean, the third roost on the Rhinns, was used for a relatively short period during 2006-2007, and by relatively few individuals. No flocks of sub-adult choughs (other than recent fledglings that were still on their natal territories) were observed to roost at Lossit or in the Ballygrant valley despite evening watches in both places. Quantitative data describing precise numbers or locations of sub-adult chough roosts on the Oa are not available. It is notable that the two main roosts are situated within the two main foraging sites used by sub-adult choughs.

The Ardnave roost was in a large barn that was constructed in 2002. The Kilchoman, Dun nan Nighean and Oa roosts were in natural cliff sites. Barns that could potentially be used for sub-adult roosts are available at Lossit and in the Ballygrant Valley.

Table 7.2. Comparison of the estimated percentage of sub-adult choughs that roosted at four main sites on Islay during April 2006 - March 2007 and April 2007 – March 2008. No data are available from the Oa in 2007-2008.

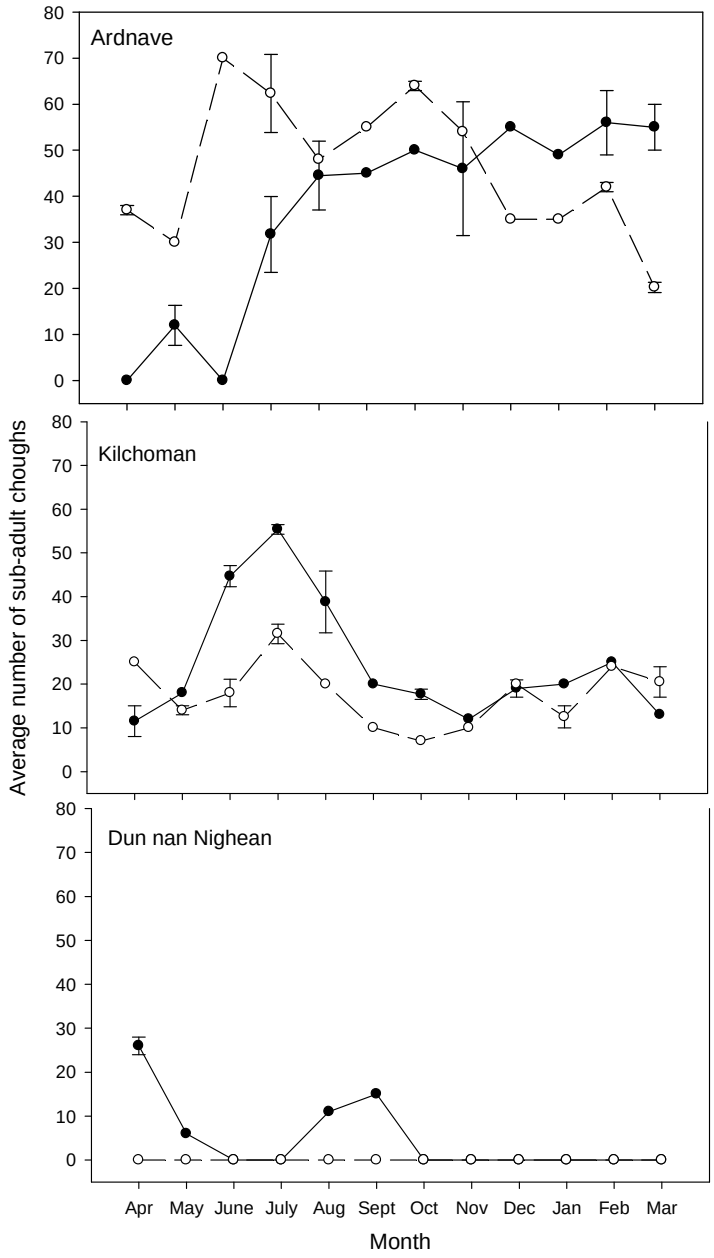
	Year	
Roost	April 2006 – March 2007	April 2007 – March 2008
Ardnave	51	71
Kilchoman	39	29
Dun nan Nighean	9	0
Dun Athad (the Oa)	1	NA
Lossit	0	0
Ballygrant Valley	0	0

Figure 7.5. Sites at which sub-adult choughs were observed to roost during April 2006 – April 2008 and the average percentage of individuals that were observed in each month that roosted at each site.



Choughs used the different roost sites to different degrees in different seasons. Use of Kilchoman peaked in summer, broadly coinciding with the movement of recent fledglings (and their parents) from their natal territories to the sub-adult flock, and with the extensive use of silage aftermath at Kilchiaran at this time of year (figure 7.6).

Figure 7.6. The mean number of flocking choughs observed to use each roost site in each month during April 2006 – March 2007 (filled symbols and solid line) and April 2007 – March 2008 (open symbols and dashed line). Means are presented ± 1 standard error for roosts that were visited more than once during a particular month.



7e) Historical context

Our current data refer solely to the period April 2006 – April 2008. It is therefore important to consider whether the areas the sub-adult choughs used for foraging and roosting during these two years are representative of the areas that have been used in the recent past, or could be used in the future. Detailed data similar to those collected during the current project do not exist for most previous years. However, some data are available for 1986-1988 (Elizabeth Still, unpublished PhD thesis, University of Glasgow) and for 2001 (observations made by Eric Bignal and Jane Reid). These data indicate that Ardnave and Kilchoman have been consistently important foraging and roosting areas for sub-adult choughs, and that the Dun nan Nighean roost has also been used in the past. Sub-adult choughs have therefore been broadly consistent in their use of different areas of Islay.

However, the relative use of Ardnave and Kilchoman has changed over time. During 1986-1988, most sub-adult choughs roosted at Kilchoman (range 40 – 120 individuals) with smaller roosts at Killinallan (near Ardnave) and Dun nan Nighean (4 – 40 individuals at both sites). Comparison with data from 1986 suggests that the degree to which choughs use the west Rhinns and the Oa has decreased since 1986, while the degree to which choughs use Ardnave has increased (figure 7.7).

Similarly, in January and February 2001, most colour-ringed sub-adult choughs were foraging and roosting at Kilchoman, with relatively few at Ardnave (table 7.3). In July 2001, most colour-ringed sub-adult choughs were foraging at Kilchoman and on newly cut silage fields at Lossit (table 7.3). The 2001 data were collected over a few days of fieldwork that was not designed to systematically identify sub-adult foraging sites. The large number of choughs observed foraging at Lossit in July 2001 was associated with silage cutting. These data show that the relative use of key foraging and roosting sites by choughs can vary over time, and that sites that were used relatively little by choughs during the current study may be of major importance in the slightly longer term.

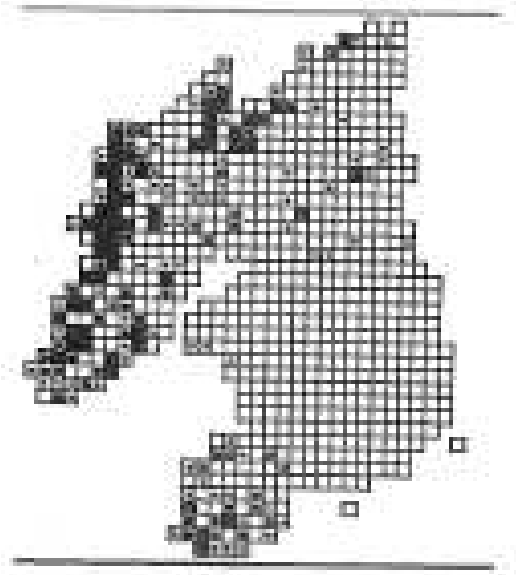
It is not clear why the apparent shift in relative distribution from Kilchoman to Ardnave has taken place. The increased of use of Ardnave approximately coincided with the construction of a new barn (in 2002) in which choughs now roost. Alternatively, the change in relative distribution may have been driven by a deterioration in foraging or roosting conditions at Kilchoman, or an improvement in foraging conditions at Ardnave. It is also notable that the move away from Kilchoman has broadly coincided with an average decrease in first-year

survival probability (see figure 5.2). However it is not clear whether there is a causal link between these changes.

Table 7.3. Approximate percentages of sub-adult choughs that were observed at the main foraging sites on Islay during January-February and July-August 2001. The Oa and Laggan were not visited during these periods. Compare with table 7.1.

Site	Jan & Feb 2001	July 2001
Ardnave	6	2
Kilchoman	83	65
Kilchiaran	1	4
Lossit	10	28
Killinallan	0	0
Sanaig	0	0
Smaull	0	1
Laggan	NA	NA
The Oa	NA	NA

Figure 7.7. Summary of locations where choughs were observed foraging during 1986 (reproduced from Curtis et al. 1989 – in Bignal & Curtis 1989). Open squares, small dots, medium dots and filled squares respectively indicate 1x1km squares where choughs were encountered on zero, 1-3, 4-10 and >10 occasions during 1986. Data comprise all observations of choughs rather than being restricted to sub-adults.



7f) Summary of key conclusions and implications: foraging and roosting sites of sub-adult choughs

1. During April 2006 – April 2008, most chough flocks were repeatedly located foraging at coastal dune sites. Ardnave and Kilchoman dunes held the majority of individuals during most of the year, and held a greater proportion of individuals than expected given the area these sites cover.

The maintenance of coastal dune ecosystems in a suitable state is therefore likely to be very important in maintaining or increasing the survival of sub-adult choughs on Islay.

2. The relative degree of use of the different foraging sites was broadly similar during both years of the study. However, some choughs were frequently encountered even at sites that held a small proportion of all individuals.

Conservation management should therefore consider the landscape scale, and ensure that a variety of suitable habitats and sites are available for foraging choughs.

3. The use of different foraging sites varied among seasons. Newly cut silage fields in Kilchiaran were particularly heavily used during June-August, while winter foraging was almost entirely restricted to dune systems.

These data suggest an importance of newly cut silage fields during the immediate post-fledging period (June-August).

4. Most sub-adult choughs roosted at Ardnave (barn) and Kilchoman (cliff) during the study period. Kilchoman has been an important feeding and roosting area for many years. Ardnave has been more heavily used more recently, possible due to the construction of a suitable barn for roosting.

Suitable natural or artificial roost sites need to be maintained at Ardnave and Kilchoman. Provision of roost sites at other foraging sites should be considered.

5. The relative use of the different foraging and roosting sites appears to have changed over recent years. In particular, the use of Ardnave has increased while the use of Kilchoman has decreased. It is not clear whether these changes reflect deterioration of foraging or roosting conditions at Kilchoman and/or improved foraging or roosting conditions at Ardnave, or some other factor.

These patterns reiterate the need for conservation management to consider the landscape scale, and ensure that a variety of suitable habitats and sites are available for foraging choughs.

8. Precise foraging locations used by sub-adult choughs

8a) Introduction

Section 7 identifies the major foraging sites (ie, geographical areas) used by sub-adult choughs on Islay, and identifies Ardnave/Killinallan and Kilchoman/Kilchiaran as being of major importance during April 2006 – March 2008. We next focused on these sites in more detail, and quantified exactly which locations within these sites sub-adult choughs used for foraging. Specifically, we quantified whether choughs repeatedly foraged at specific locations within Ardnave/Killinallan or Kilchoman/Kilchiaran, or whether they used the whole of each site relatively uniformly. We quantified whether locations that were used for foraging differed between seasons or between years. If choughs did repeatedly use specific locations, this might allow us to determine exactly what foraging choughs favour in terms of small-scale variation in habitat, and how management might be used to maintain or create the favoured conditions.

8b) Methods

During each visit to each foraging site used by sub-adult choughs (e.g. Ardnave or Kilchoman, see section 7), at least 60 minutes were spent searching for chough flocks. Different routes were followed on different visits to minimise any bias in the exact location where flocks would be encountered. In practice, flocks that were present at any site were generally located within 30 minutes, and were then followed for minimum of 120 minutes. During this time the flock's movements were monitored, and the locations where choughs settled to forage were recorded using a GPS receiver. GPS position accuracy was always less than 10m, and generally around 6m. However, since larger flocks often foraged over a reasonably dispersed area and moved gradually over the ground, GPS-marked foraging locations should be considered to be accurate at a scale of approximately 10-50m.

We used these data to visualise exactly where choughs foraged within Ardnave/Killinallan and Kilchoman/Kilchiaran. The intensity with which choughs used each foraging location within these sites was estimated as 'bird-occasions'. This was calculated as the average number of individuals in a flock observed foraging at a specific location, multiplied by the number of times a flock was observed foraging there across all visits to that site. Intensity was divided into high, medium and low categories for the purposes of visualisation, equating to the upper, middle and lower thirds of observed variation. Similar analyses were not done

for the other foraging sites (namely Smaull, Sanaig, Lossit, Laggan and Oa) because chough flocks were rarely observed foraging in these places (see section 7).

We also distinguished locations where chough flocks were observed to forage in the spring and summer (March – August) and in the autumn and winter (September – February). These seasons were defined by reference to the chough's biological year, given that choughs on Islay start to breed in March.

8c) Results

Figures 8.1 and 8.2 show the foraging locations used by flocks of sub-adult choughs at Ardnave/Killinallan and Kilchoman/Kilchiaran during April 2006 – February 2007 and March 2007 – February 2008. These figures highlight several important points.

1. Foraging choughs clearly favoured specific locations within both Ardnave/Killinallan and Kilchoman/Kilchiaran. Statistical analysis showed that the locations where choughs were observed to forage were clustered together much more than expected by chance. This implies that choughs foraging at both Ardnave/Killinallan and Kilchoman/Kilchiaran repeatedly visited certain locations within those sites, and did not simply range randomly over the land within a reasonable radius of the Ardnave and Kilchoman roosts, or even range randomly over the main dune areas.

2. Despite this clustering, foraging choughs use a variety of different locations and habitats within both Ardnave/Killinallan and Kilchoman/Kilchiaran. These include grazed dune grasslands (at Ardnave and Kilchoman), largely ungrazed dune grasslands (at Killinallan), mowed grasslands (silage fields at Kilchiaran), beaches with kelp (west coast of Ardnave) and heaths (cliff areas at Kilchoman).

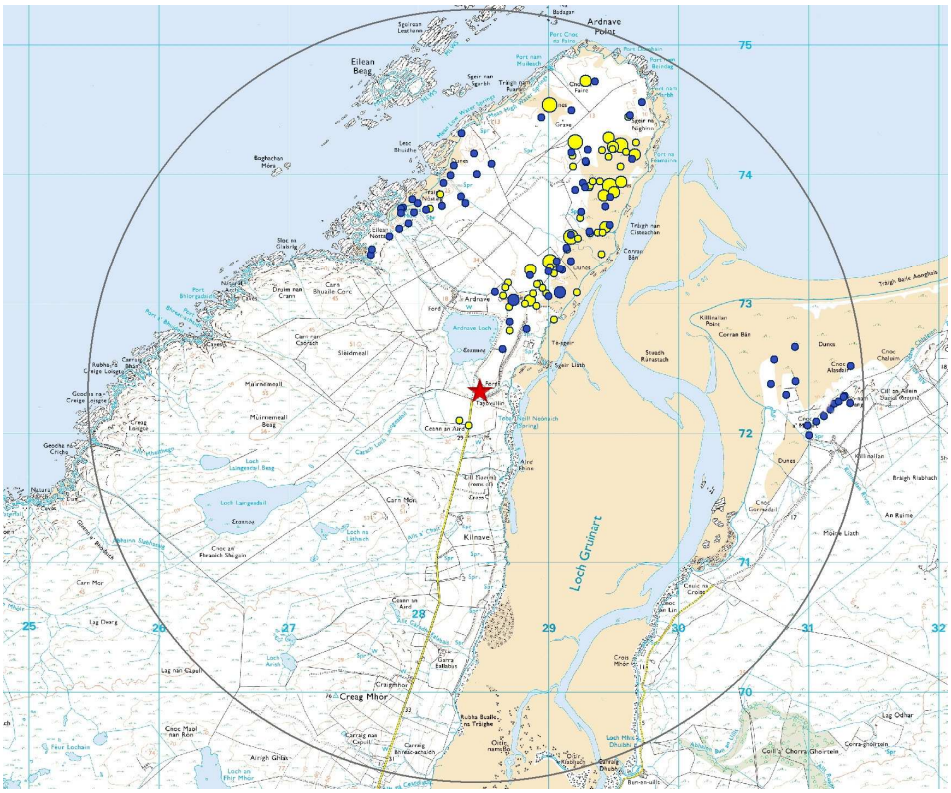
3. Some foraging locations were used throughout the year, such as the east coast of Ardnave and the main dune system at Kilchoman. However the use of other foraging locations differed between summer and winter. For example, choughs foraged more along the west coast of Ardnave and at Killinallan in winter than in summer, and in the silage fields at Kilchiaran in summer but not winter. The use of the Kilchiaran silage fields was closely associated with silage cutting in June-August (see section 7).

4. Although the distribution of foraging locations was broadly similar during both years of the study, some differences are evident. For example, sub-adult choughs often foraged at Killinallan during winter 2006-2007 but rarely did so during winter 2007-2008. They used the heath/cliff areas south of the Kilchoman roost during summer 2006 but rarely during summer 2007. This may reflect variation in the food resources that were available at different locations in different years. For example, foraging sub-adult choughs at Killinallan during winter 2006-2007 were primarily exploiting mining bee larvae, which may have been less abundant during winter 2007-2008.

5. Many locations that are clearly within range of the Ardnave and Kilchoman roosts were never seen to be used by foraging sub-adult choughs. These include the central area of Ardnave, the moorland areas south-west of Ardnave and south-east of Kilchoman and, perhaps surprisingly, the grazed fields at Rockside and along the west shore of Loch Gruinart. Since chough flocks were not observed continuously throughout the year, we cannot exclude the possibility that these locations were occasionally used by foraging sub-adult choughs. However, given the relatively large number of occasions on which chough flocks were searched for and located (see section 7), use of these locations must have been rare. It is important to note, however, that some areas that were apparently not used by foraging sub-adult choughs, such as the Rockside and Loch Gruinart fields, were used for foraging by breeding pairs of adult choughs that nested in these areas.

Figure 8.1. Foraging locations used by sub-adult choughs at Ardnave/Killinallan during (a) April 2006 – February 2007 and (b) March 2007 – February 2008. Locations used during the spring and summer (March – August) are shown in yellow. Locations used during the autumn and winter (September – February) are shown in blue. Locations where choughs foraged with high, medium and low intensity are indicated with large, medium and small symbols respectively. The red star indicates the Ardnave roost site. The circle defines a foraging area centred on the roost site with radius equalling the longest distance foraging chough flocks were observed away from the roost (*ca* 2km).

8.1a) Ardnave & Killinallan, April 2006 – February 2007



8.1b) Ardnave & Killinallan, March 2007 – February 2008

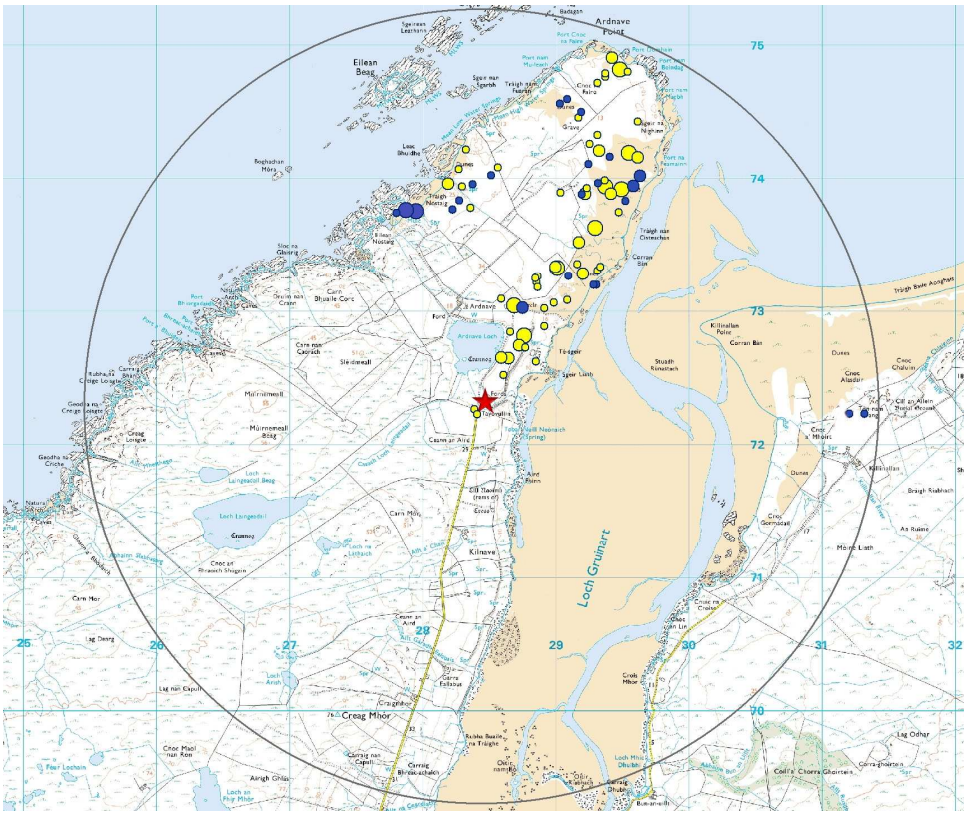


Figure 8.2. Foraging locations used by sub-adult choughs at Kilchoman/Kilchiaran during (a) April 2006 – February 2007 and (b) March 2007 – February 2008. Locations used during the spring and summer (March – August) are shown in yellow. Locations used during the autumn and winter (September – February) are shown in blue. Locations where choughs foraged with high, medium and low intensity are indicated with large, medium and small symbols respectively. The red star indicates the Kilchoman roost site. The circle defines a foraging area centred on the roost site with radius equalling the longest distance foraging chough flocks were observed away from the roost.

8.2a) Kilchoman & Kilchiaran, April 2006 – February 2007

8.2b) Kilchoman & Kilchiaran, March 2007 – February 2008

8d) Summary of key conclusions and implications: precise foraging locations used by sub-adult choughs

1. During April 2006 – February 2008, sub-adult choughs foraged repeatedly at specific locations within Ardnave/Killinallan and Kilchoman/Kilchiaran, and were never observed to forage at other locations within these same sites. The locations where chough flocks foraged covered a variety of habitats, and differed to some extent between seasons and years.

This suggests a need to maintain a mosaic of habitat types within the key foraging sites of Ardnave/Killinallan and Kilchoman/Kilchiaran in order to ensure that some food resource for choughs is always available.

2. A selection of photographs of chough foraging locations is provided as an electronic appendix.

9. Habitat characteristics of foraging locations

9a) Introduction

Our study showed that flocks of sub-adult choughs forage primarily in short grazed and mowed grassland (section 7), as also shown by previous studies on the foraging behaviour of adult choughs. Flocks of sub-adult choughs also tended to forage at specific locations within the main grazed dune grasslands at Ardnave and Kilchoman (section 8). This pattern of utilisation could reflect several different factors. Variation in prey abundance or availability, which will itself depend partly on habitat type, may be a particularly important determinant of where sub-adult choughs forage. Other factors such as predation risk, disturbance and travel time from roosts could also play a role.

However, it is not clear what precise habitats sub-adult choughs use for foraging within grazed grasslands. Understanding the finer detail of foraging habitat selection might allow management of grazed grasslands to be optimised for choughs. We therefore investigated whether habitat characteristics differed between locations where flocks of sub-adult choughs were and were not observed to forage within the Ardnave and Kilchoman grassland sites.

9b) Methods

During April 2006 – February 2008, comprehensive habitat descriptions were recorded at a large sample of foraging locations that were used by sub-adult choughs (see section 8). At each foraging location, a suite of ten habitat characteristics were measured within a 2x2m quadrat. These characteristics are listed and defined in table 9.1, and were chosen because they might be expected to influence the abundance or availability of the soil and dung-associated invertebrates that comprise the main prey of choughs. For comparison, the same ten habitat characteristics were also measured at a sample of locations where sub-adult choughs were never observed to forage ('non-foraging locations'). These non-foraging locations were situated within the same broad habitat type (eg dune grassland) and within the same radius of major roost sites as the foraging locations. Habitat measurements made at foraging and non-foraging locations were approximately balanced in time. We then tested whether habitat characteristics differed between locations where chough flocks were and were not observed to forage within Ardnave and/or Kilchoman, and whether patterns were consistent across the two years of the study (April 2006-March 2007 and April 2007-

February 2008). For these analyses, seasons were defined as follows: spring = March-May; summer = June-August; autumn = September-November; winter = December-February.

Table 9.1. List of habitat characteristics that were measured at foraging and non-foraging locations within each site used by foraging flocks of sub-adult choughs.

Characteristic	Description
Aspect	Major aspect of the location, attributed as N, NE, E, SE, S, SW, W, NW or flat.
Slope	Major slope of the ground, estimated to the nearest 5°.
Elevation	Recorded using a GPS receiver, to the nearest 5m.
Vegetation type	Proportion of the vegetation within the quadrat that comprised grass, moss or broad-leaved plants, estimated to the nearest 5%.
Vegetation density	Average density of vegetation within the quadrat, categorised as dense, medium, sparse or none (ie bare ground).
Sward height (mean and variance)	Sward height measured at ten evenly scattered points across the vegetated part of the quadrat. The mean and variance of each set of ten measurements was calculated.
Soil hardness	Soil hardness measured at three points within each quadrat using a pocket penetrometer (kg/cm^2).
Cow pats	Number of old, medium and fresh cowpats present within each quadrat.
Sheep droppings	Number of old and medium/fresh sheep droppings present within each quadrat.
Carcass presence	Presence or absence of an animal carcass (usually sheep).
Soil type	Soil type underlying each site, extracted from a soil map provided by the Macaulay Institute.

9c) Results

Table 9.2 summarises the habitat characteristics of foraging and non-foraging locations at Ardnave and Kilchoman during April 2006-March 2007 and April 2007-February 2008 (see section 8 for maps showing these sites).

Table 9.2 is at the end of the document because it's on a landscape page format.

Table 9.3 summarises the statistical comparison of habitat characteristics between foraging and non-foraging locations at Ardnave and Kilchoman during April 2006-March 2007 and April 2007-February 2008. Grass cover, vegetation density, number of cowpats and soil hardness all differed significantly between foraging and non-foraging locations at Ardnave and/or Kilchoman in one year or the other.

Table 9.3. Summary of statistics comparing habitat characteristics at foraging and non-foraging locations at Ardnave and Kilchoman during April 2006-March 2007 and April 2007-February 2008. The sample size is the total number of locations at which habitat characteristics were measured at each site in each year. For each habitat characteristic, the estimate of the difference between foraging and non-foraging locations is presented ± 1 standard error. Characteristics that differed significantly between foraging and non-foraging locations are highlighted in bold.

Habitat characteristic	Ardnave April 2006-March 2007	Ardnave April 2007-February 2008	Kilchoman April 2006-March 2007	Kilchoman April 2007-February 2008
Sample size	93	68	44	28
Season	-0.27±0.22	-0.19±0.27	-0.29±0.34	-0.20±0.44
Elevation	-0.04±0.03	-0.06±0.04	0.01±0.02	-0.01±0.02
Slope	-0.03±0.03	0.001±0.03	0.02±0.04	-0.03±0.03
Aspect	-0.04±0.25	-0.60±0.31	-0.33±0.34	-0.38±0.41
Grass cover	**-0.03±0.01**	**-0.03±0.01**	**-0.16±0.06**	-0.06±0.04
Moss cover	-0.13±0.10	-0.11±0.11	0.07±0.18	0.03±0.14
Other (broad-leaved) plants cover	-0.01±0.01	-0.002±0.01	0.07±0.04	0.02±0.04
Sward height (average)	-0.02±0.01	**-0.09±0.03**	0.01±0.02	-0.04±0.04
Sward height (coefficient of variation)	-0.04±0.02	-0.04±0.02	-0.05±0.03	0.05±0.05
Vegetation density	**-1.57±0.38**	**-1.42±0.43**	-0.83±0.53	-1.05±0.73
Number of old cow pats	**2.17±1.03**	0.43±0.44	0.74±0.86	0.48±0.51
Number of medium cow pats	**1.53±0.69**	0.55±0.55	1.59±1.04	0.58±1.03
Number of fresh cow pats	-0.77±0.85			
Number of old sheep droppings	0.02±0.15	0.01±0.12	-0.19±0.17	0.09±0.09
Number of medium sheep droppings	0.12±0.09	0.01±0.05	0.10±0.10	-0.13±0.11
Soil hardness	**-0.47±0.21**	**-0.99±0.37**	0.44±0.39	0.10±0.61

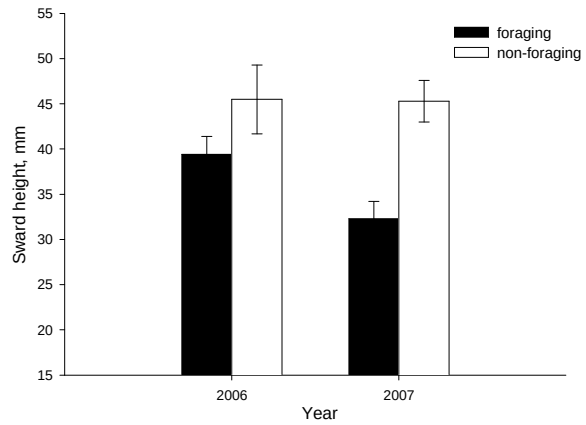
We then combined these analyses of the two sites in the two years into a single analysis, and tested for overall differences in habitat characteristics between foraging and non-foraging locations. Table 9.4 lists the habitat characteristics that differed significantly between foraging and non-foraging locations across Ardnave and Kilchoman during April 2006 – February 2008. There was no evidence that differences in habitat between foraging and non-foraging locations differed between Ardnave and Kilchoman.

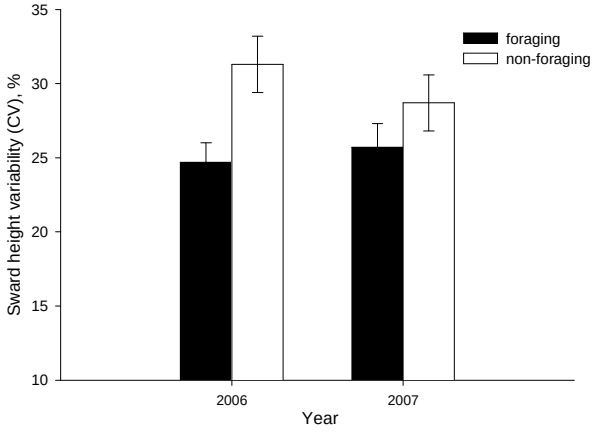
In 2006-2007, sward height was similar at foraging and non-foraging locations but was less variable at foraging locations. In contrast in 2007-2008, sward height was shorter at foraging locations than non-foraging locations while sward height variability did not differ between foraging and non-foraging locations. In both 2006-2007 and 2007-2008, there was sparser vegetation and less grass cover at foraging locations than at non-foraging locations. In 2006-2007, foraging locations contained old and medium cow dung more often than non-foraging locations, but there was no such difference in 2007-2008. In 2006-2007, foraging locations contained medium sheep droppings more often than non-foraging spots. However in 2007-2008, foraging locations tended to contain sheep droppings less often than non-foraging locations. These patterns are illustrated in figure 9.2.

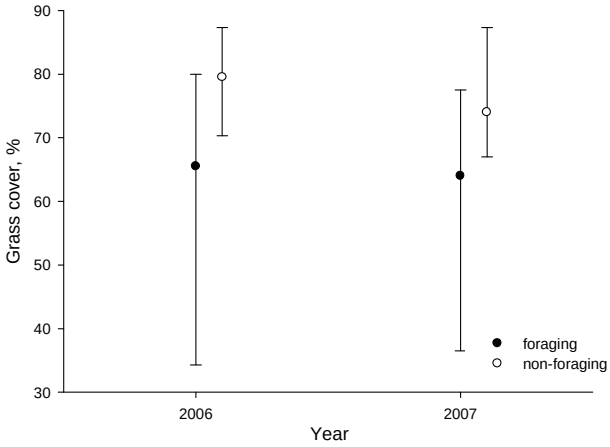
Table 9.4. Summary of habitat characteristics that differed between foraging and non-foraging locations across Ardnave and Kilchoman during April 2006-February 2008. The sample size is the total number of locations at which habitat characteristics were measured. For each habitat characteristic, the estimate of the difference between foraging and non-foraging locations is presented ± 1 standard error. Habitat characteristics that are not listed did not differ significantly between foraging and non-foraging locations.

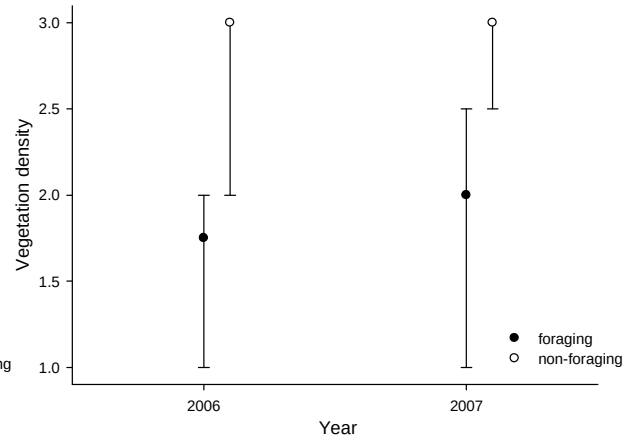
Habitat characteristic	Difference between foraging and non-foraging locations
Sample size	233
Year	-1.02±1.77
Grass cover	-0.04±0.01
Sward height (average)	0.11±0.05
Sward height (coefficient of variation)	-0.24±0.08
Vegetation density	-1.24±0.35
Number of old cow pats	5.11±1.88
Number of medium cow pats	2.40±0.50
Number of medium sheep droppings	0.11±0.04
Year * sward height (average)	-0.10±0.03
Year * sward height (coef. variation)	0.17±0.05
Year * number of old cow pats	-1.75±1.01

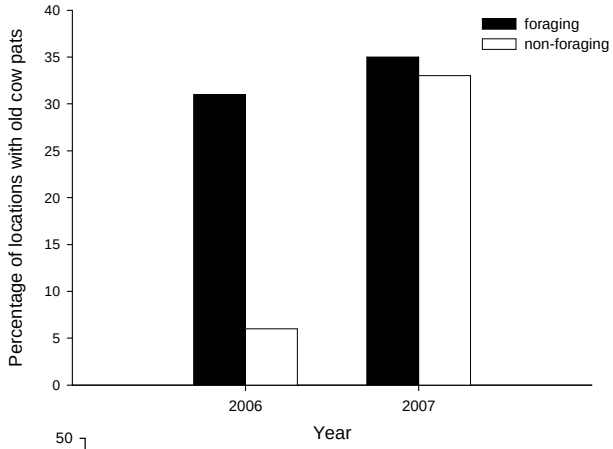
Figure 9.2. Habitat characteristics measured at foraging and non-foraging locations across Ardnave and Kilchoman during April 2006 – February 2008. (a) mean sward height (mean ± 1SE), (b) sward height variability (mean ± 1SE), (c) grass cover (median and upper and lower quartiles), (d) vegetation density (median and upper and lower quartiles), (e) percentage of locations with old cow dung, (f) percentage of locations with medium cow dung, (g) percentage of locations containing medium sheep droppings and (h) soil hardness (mean ± 1SE). Histograms show means (used for variables that were normally distributed) and dotplots show medians (used for variables that were not normally distributed). Sample sizes for foraging and non-foraging locations were 104 and 33 for 2006-2007 and 65 and 31 for 2007-2008.

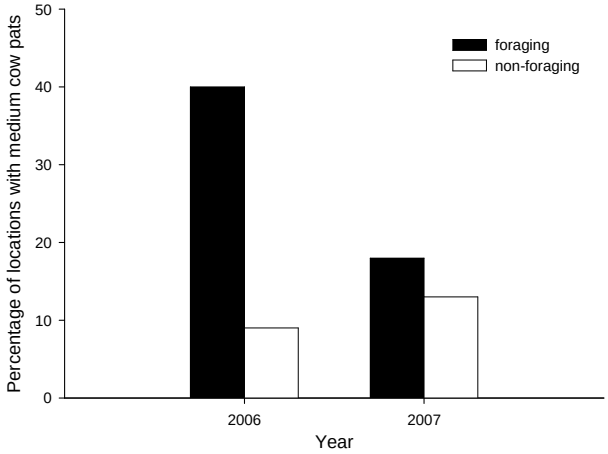

Sward height, mm
55
50
45
40
35
30
25
20
15
2006
2007
Year
foraging
non-foraging

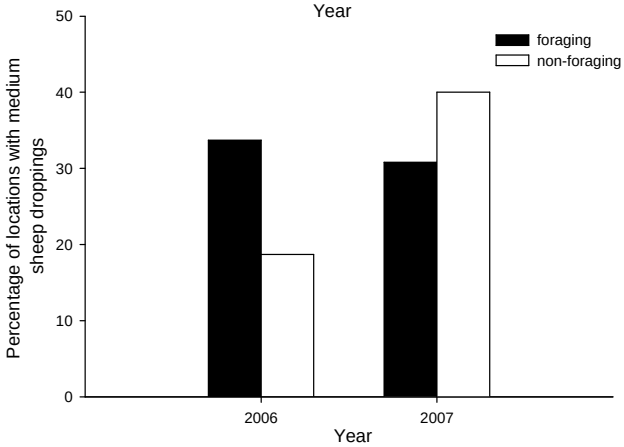

Sward height variability (CV), %
35
30
25
20
15
10
2006
2007
Year
foraging
non-foraging

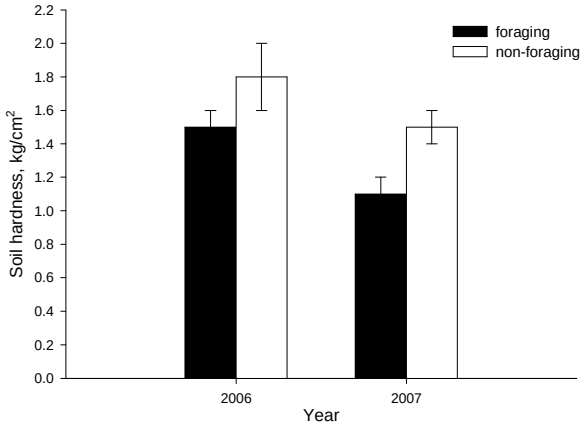

Grass cover, %
90
80
70
60
50
40
30
2006
2007
Year
foraging
non-foraging


Vegetation density
3.0
2.5
2.0
1.5
1.0
2006
2007
Year
foraging
non-foraging


Percentage of locations with old cow pats
40
35
30
25
20
15
10
5
0
2006
2007
Year
foraging
non-foraging


Percentage of locations with medium cow pats
50
40
30
20
10
0
2006
2007
Year
foraging
non-foraging


Percentage of locations with medium sheep droppings
50
40
30
20
10
0
2006
2007
Year
foraging
non-foraging


Soil hardness, kg/cm2
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
2006
2007
Year
foraging
non-foraging

It is important to note, however, that our ability to detect any associations between chough foraging and habitat characteristics is constrained by the degree of variability in habitat characteristics that we were able to observe. For example, since Ardnave and Kilchoman are both heavily grazed (under existing management agreements for choughs) the mean sward height observed at these sites was only *ca* 4cm, and varied relatively little. Experimental variation in habitat within or across Ardnave and Kilchoman would ideally be required to definitively measure associations between chough foraging and habitat characteristics.

Choughs have previously been observed to forage extensively on or around animal carcasses at Ardnave, Kilchoman and other sites. However, during our field study, carcasses were present too infrequently to allow us to collect quantitative data on their use.

9d) Summary of key conclusions and implications: habitat characteristics in relation to foraging locations

1. During April 2006 – April 2008, habitat characteristics were measured at locations where flocks of sub-adult choughs were and were not observed to forage within the main dune sites at Ardnave and Kilchoman.

2. Overall, locations where chough flocks foraged tended to have shorter and more variable swards, less dense vegetation cover and more medium and old cowpats than locations where flocks were not observed to forage.

These results suggest that sub-adult choughs utilise locations within Ardnave and Kilchoman differentially with respect to fine-scale habitat variation.

3. Relationships between chough foraging and habitat characteristics varied among years. Specifically, chough foraging was associated with more dung in one year of the study but not the other, and more strongly associated with shorter and more variable swards in one year than the other.

These results suggest that the precise resources that sub-adult choughs use for foraging vary among years. Without detailed knowledge of which resource will be most important in any particular year, an effective management strategy may be to ensure that a range of habitat variation is always available.

4. Flocks of sub-adult choughs foraged at locations with less dense vegetation and less grass cover across both years of the study.

Vegetation density may therefore be a consistent cue for preferred foraging, perhaps reflecting increased access to soil and therefore soil invertebrates.

5. There was no evidence that foraging locations of sub-adult choughs were associated with other habitat characteristics, including the number of fresh cowpats that were present or physical features such as slope, aspect and elevation.

6. However, it is important to note that habitat characteristics were measured at foraging and non-foraging locations within heavily grazed dune grasslands, that moreover have been heavily grazed for several years. The magnitude of the difference in habitat difference between foraging and non-foraging locations was very small (eg, a 5mm difference in sward height).

An experimental study, in which a greater range of variation in habitat characteristics was experimentally created, would ideally be required to determine relationships between fine-scale habitat variation and the preferred foraging locations of sub-adult choughs.

10. Use of silage aftermath

10a) Introduction

Section 7c shows that although flocks of sub-adult chough foraged primarily in coastal dune systems, cut silage fields (silage aftermath) were also used by a substantial proportion of flocking individuals during the summer. We therefore quantified the pattern of availability and use of silage aftermath in more detail.

10b) Methods

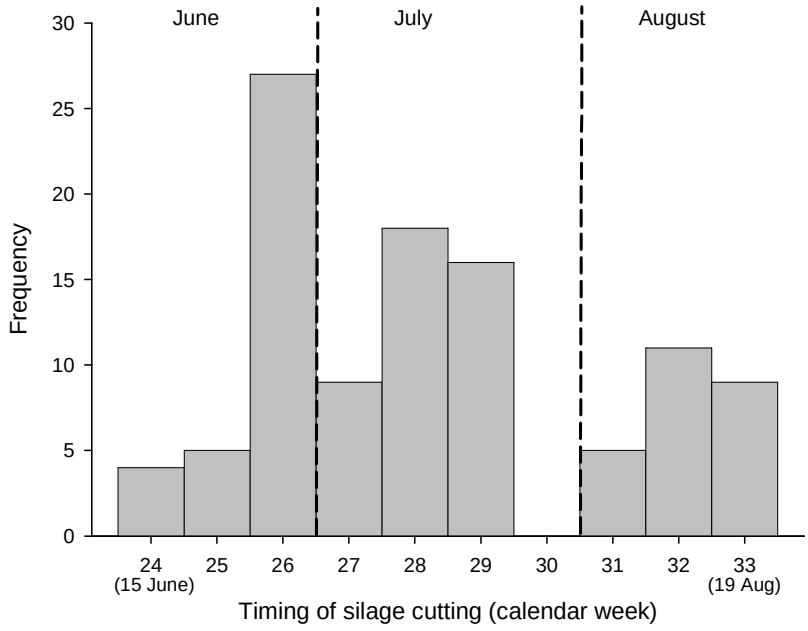
During visits to chough nest sites and flocking areas during June – August 2006 and June – July 2007, we recorded the dates on which silage fields were cut and whether choughs were observed foraging in cut or uncut silage fields. A high proportion of silage fields within the main areas used by flocking and/or breeding choughs (Rhinns, Loch Gruinart and Ballygrant valley) were monitored in this way. However, since continuous summer fieldwork ended in July 2007, exact cutting dates for silage fields that were cut in August 2007 were not recorded. During August 2007 and September 2006 and 2007, observations were made during a single week in the middle of the month (approx 15^{th} – 20^{th}).

10c) Results

Silage fields in the areas used by foraging fledgling and sub-adult choughs were cut on a range of dates from mid-June to late August (figure 10.1). Of 103 fields surveyed in 2006, 36 were cut in June, 42 in July and 25 in August. In 2007, 45 fields were cut in June and 40 in July.

Recently fledged choughs were observed to forage in silage aftermath both while still with their parents in their natal areas (particularly in the Ballygrant valley and at Lossit), and after joining sub-adult flocks (particularly at Kilchiaran). During June-August 2006, a substantial proportion of observations of foraging fledglings and sub-adult flocks were in silage aftermath (table 10.1). Use of silage aftermath was not observed in mid-September (table 10.1). Sub-adult choughs were not observed to forage in uncut silage fields (at least during the weeks and days immediately prior to cutting). Cut silage fields were used by a substantial proportion of sub-adult choughs during June, July and early August.

Figure 10.1. Distribution of dates on which silage fields in areas of Islay utilised by sub-adult choughs were cut in (a) 2006 and (b) 2007.



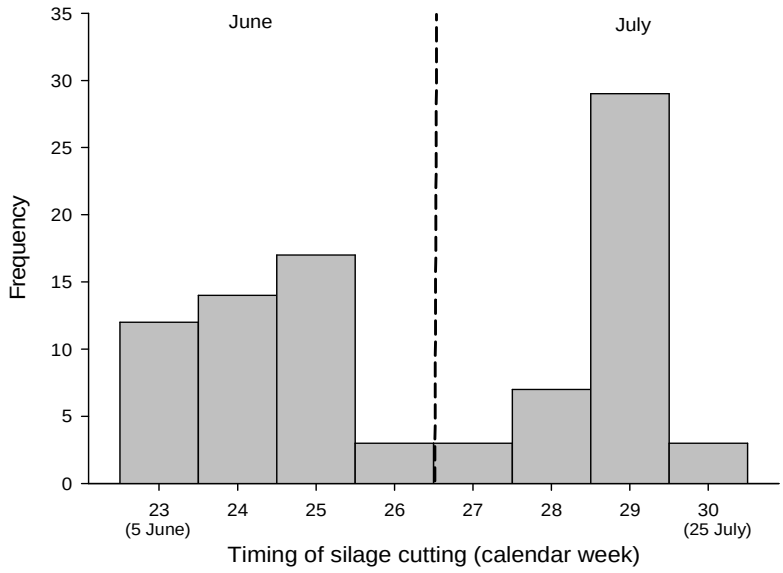


Table 10.1. Use of silage aftermath by sub-adult choughs in 2006 and 2007. *Data are from the middle week of the month only.

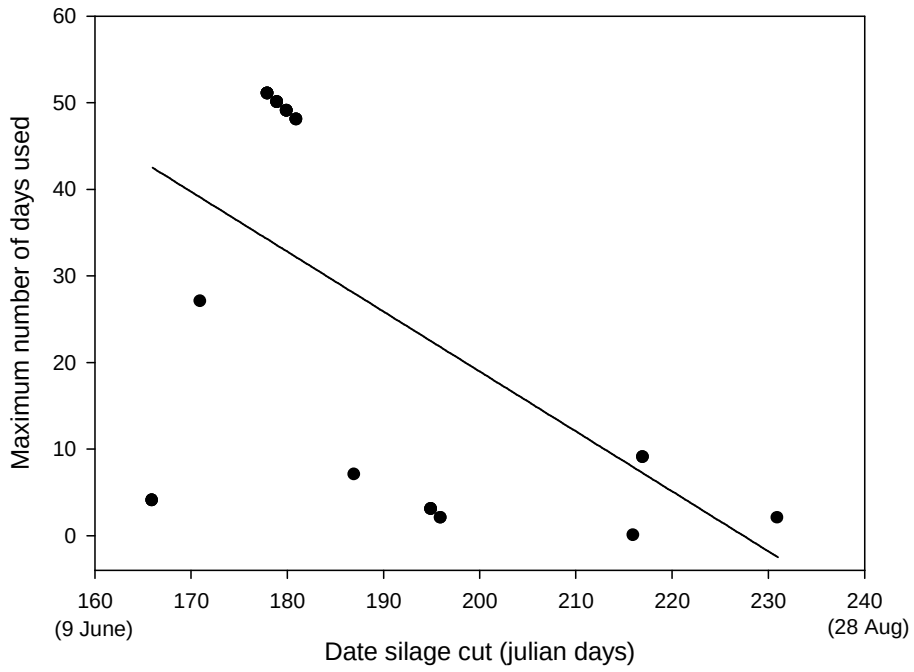
	% of all observations of foraging sub-adult choughs that were in silage aftermath	% of the average number of foraging sub-adult choughs observed in each month that were in silage aftermath
2006		
June	13	17
July	44	51
August	15	47
September*	0	0
2007		
June	10	63
July	30	24
August*	0	0
September*	0	0

Fields where silage was cut in June were used to a greater extent by foraging chough fledglings or sub-adult flocks than fields where silage was cut in July and August. In 2006, 62% of all observations of choughs foraging in silage aftermath were in fields cut in June, 24% were in fields cut in July and 14% were in fields cut in August. Furthermore, 71%, 14% and 15% of the average number of newly fledged or flocking choughs observed foraging in silage aftermath habitat were observed in fields cut in June, July and August respectively. These apparent differences in use were not simply because a larger number of silage field were cut in June than in July and August (figure 10.1).

There is some evidence that sub-adult choughs used silage fields that were cut in June for longer than silage fields that were cut in July and August (figure 10.2). For example, fields cut in June at Kilchiaran were used for *ca* 6 weeks, while fields cut in July and August in Ballygrant, Lossit and Smaull were used for *ca* 10 days. There is a risk that the duration of use of late-cut silage fields could have been underestimated due to the end of intensive fieldwork in late August. However, in 2006, choughs using fields cut in July could have been observed up to 30-40 days later, and choughs using fields cut in July and August could also have been observed during the mid-September observation period (ie, up to *ca* 60 or 30 days later respectively). In 2006, most silage fields that were cut in June were cut at the end of June (figure 10.1). Their use by foraging choughs therefore occurred primarily in July and into August (table 10.1).

Shorter use of silage fields that were cut later in the summer could reflect a reduced abundance of invertebrate prey in these fields. It is likely that sub-adult choughs use silage aftermath because the cutting procedure disturbs surface-dwelling invertebrates making them easy to locate, and provides increased access to soil-dwelling invertebrates and larvae in newly uncovered and relatively moist soil. These benefits may be reduced when silage is cut late in the summer, by which time many invertebrates have completed their lifecycles and larvae and adults are no longer present in large numbers.

Figure 10.2. Relationship between the date on which a silage field was cut and the number of days for which it was observed to be used by foraging sub-adult choughs in 2006. Multiple datapoints coincide because adjacent fields were often cut on the same day and then used by choughs for the same period.



10d) Summary of key conclusions and implications: use of silage aftermath

1. During 2006 and 2007, silage fields in the areas of Islay used by newly fledged and sub-adult choughs were cut on a range of dates during June – August.

2. Fledgling and sub-adult choughs foraged in cut silage fields extensively during June – August. Silage aftermath may therefore be an important resource for foraging sub-adult choughs in summer (a time when sub-adult mortality can be high).

3. There is some evidence that silage fields cut during June were used more and for longer than fields cut during July and August, although further data are required to rigorously evaluate this possibility.

Managers may therefore need to consider whether it is feasible to maintain a range of silage cutting dates, including some fields that are cut in June and July, in areas of Islay that are used by choughs.

4. Any management of silage cutting for newly fledged and sub-adult choughs needs to be balanced against current management for Corncrakes (where farmers are subsidised to cut silage after August 1st). This management would tend to cause relatively synchronised late cutting in key Corncrake areas, which sometimes overlap with key Chough areas.

Given this potential overlap between species management programmes, further detailed study of chough use of silage aftermath in relation to the timing and spatial pattern of cutting may be advisable in order to inform the most effective management policy.

11. Relationships between chough foraging and farm management

11a) Introduction

One focus of conservation management for choughs on Islay may be to encourage appropriate management of agricultural land. To inform this approach, we collected data on existing land management from farmers, and investigated whether sub-adult choughs were more or less likely to forage in fields that had been managed under specific regimes.

11b) Methods

During July and August 2007, 9 farmers whose farms cover the main areas used by foraging flocks of sub-adult choughs (section 7) were interviewed using a questionnaire. These farms covered Ardnave, Kilchoman, Kilchiaran, Lossit, Killinallan, Smaull, Sanaig and Laggan.

The questionnaire had two parts, aiming to collect land management data at the farm level and the field level respectively. The questionnaire is provided as Appendix 7.

Data collected in the first part (farm level) described the total areas of different grassland management types (grazed grassland, mowed grassland and rough grazing), livestock numbers and general usage of fertilisers and avermectins on the farm.

Data collected in the second part (field level) described the physical and vegetation characteristics, intensity and timing of grazing by different herbivores, and fertiliser and herbicide application in fields within each farm. Data on soil type for the same fields were obtained from a 1:50 000 soil map of Islay produced by the Macaulay Institute.

Data were collected for 226 fields or compartments within the 9 farms. In dune areas that are not divided into fields, we used SNH's Goose Scheme compartments. As farmers had limited time for answering questions, we focused on gathering data for samples of fields/compartments belonging to each of the main grassland management types (grazed, mowed and rough grassland).

During April 2006 – April 2008, the precise foraging locations of sub-adult choughs were recorded (sections 7 and 8). We categorised each field or compartment for which land management data were available as used or unused by foraging choughs, respectively comprising fields where sub-adult choughs had been observed foraging at least once or had never been observed to forage. We then related the location of chough foraging to land management.

11c) Results

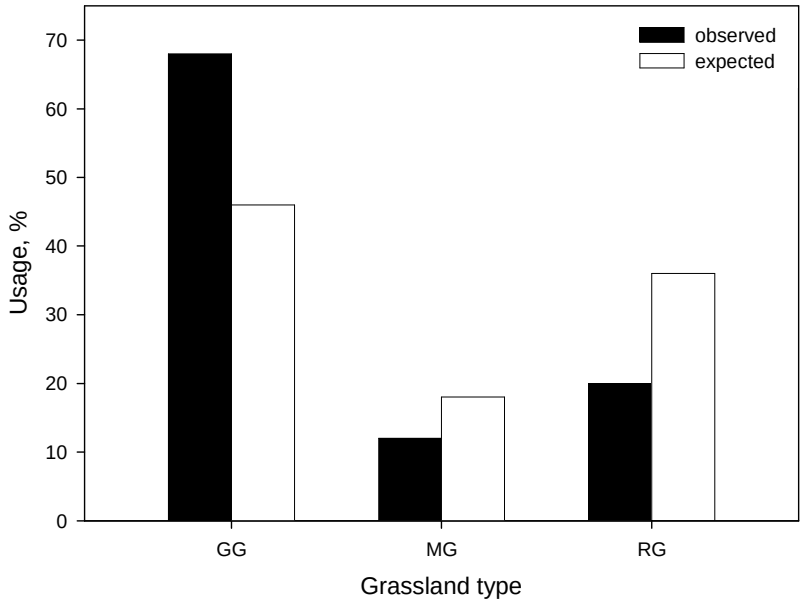
Statistical analyses confirmed that the three main grassland types (grazed grassland (GG), mowed grassland (MG) and rough grazing (RG)) could be clearly distinguished based on their management and physical characteristics. These characteristics are summarised in table 11.1.

Table 11.1. Management and physical characteristics of grazed grassland, mowed grassland and rough grazing fields. Values are medians (for continuous variables) and modes (for categorical/binomial variables). For binomial variables, the percentage of fields where the value equals the mode is shown in brackets.

Variable	Grazed grassland (n=89)	Mowed grassland (n=81)	Rough grazing (n=59)
Number of months grazed by sheep	12	7	12
Number of months grazed by cattle	10	3	12
Number of months grazed by geese	7	7	0
Timing of grazing by sheep	All seasons	Spring + autumn + winter	All seasons
Timing of grazing by cattle	All seasons	Summer + autumn	All seasons
Grazed by rabbits	Yes (75%)	No (72%)	No (88%)
Years since last ploughing/reseeding	30	3	50 or never
Grass cut for silage	No (97%)	Yes (100%)	No (100%)
Over 5% cover by plants other than grass	Yes (53%)	No (93%)	Yes (96%)
Type of fertiliser used	None	Combined (chemical and organic)	None
Timing of fertiliser application	-	Spring	-
Herbicide used	No (98%)	No (100%)	No (100%)
Aspect	Any (undulating)	Flat	Any (undulating)
Soil type	Podzols	Podzols	Peaty soils
Tendency to waterlog	No (74%)	No (75%)	Yes (61%)

Sub-adult choughs were observed to forage in all three grassland types, but the extent of use varied among types. Grazed grassland was used most relative to the area available and rough grazing was used least relative to the area available (figure 11.1). These data suggest that sub-adult choughs selectively forage in grazed grassland and avoid rough grazing. Mowed grassland was used slightly less than expected given the overall area available (figure 11.1). However, it is important to note that a substantial proportion of sub-adult choughs foraged in newly cut silage fields in the summer, suggesting that mowed grassland provides a key resource at this time of year (see sections 7 and 10). Sub-adult choughs also foraged on beaches, bare sand and kelp, particularly during the winter (section 7)

Figure 11.1. Percentage of fields of grazed grassland (GG), mowed grassland (MG) and rough grazing (RG) that were used by foraging sub-adult choughs (filled bars) relative to the total areas of these habitat types that were available (open bars).



We then related the management and physical characteristics of each field to the use of that field by foraging sub-adult choughs. These analyses suggested that fields where sub-adult choughs were observed to forage differed from fields where choughs were never observed to forage in several characteristics: timing and intensity of grazing by sheep, cattle and rabbits, years since last ploughing or reseeding, use for silage production, fertiliser application and aspect, number of months grazed by geese and cover by plants other than grass. On average, sub-adult choughs tended to forage in fields with variable aspect and relatively well drained soils, that were grazed year round by sheep and rabbits and most of the year by cattle, where grass was not cut for silage, fertilisers were not used and vegetation composition was relatively diverse (table 11.2, figures 11.2, 11.3 and 11.4). Sub-adult choughs therefore predominantly foraged in old grazed grasslands (see also section 7). However, the potential importance of silage aftermath in summer should again be emphasised (section 10).

Table 11.2. Management and physical characteristics of fields where sub-adult choughs were and were not observed to forage. Values are medians (for continuous variables) and modes (for categorical and binomial variables). For binomial variables, the percentage of fields where the value equals the mode is shown in brackets. For categorical variables, percentage of fields in each category is shown in figures 11.2, 11.3 and 11.4.

Variable	Fields used for foraging (n=89)	Fields not used for foraging (n=99)
Number of months grazed by sheep	12	9
Number of months grazed by cattle	9	7
Number of months grazed by geese	7	7
Timing of grazing by sheep	All seasons	All seasons
Timing of grazing by cattle	All seasons	All seasons
Grazed by rabbits	Yes (63%)	No (72%)
Years since last ploughing/reseeding	25	20
Grass cut for silage	No (74%)	No (56%)
Over 5% cover by plants other than grass	Yes (55%)	No (59%)
Type of fertiliser used	None	None
Timing of fertiliser application	-	-
Aspect	Any (undulating)	Flat
Soil type	Podzols	Peaty soils
Tendency to waterlog	No (74%)	No (66%)

Figure 11.2. Percentage of fields in which sub-adult choughs were and were not observed to forage with different grazing regimes for a) sheep and b) cattle. sp = spring, s = summer, a = autumn, w = winter.

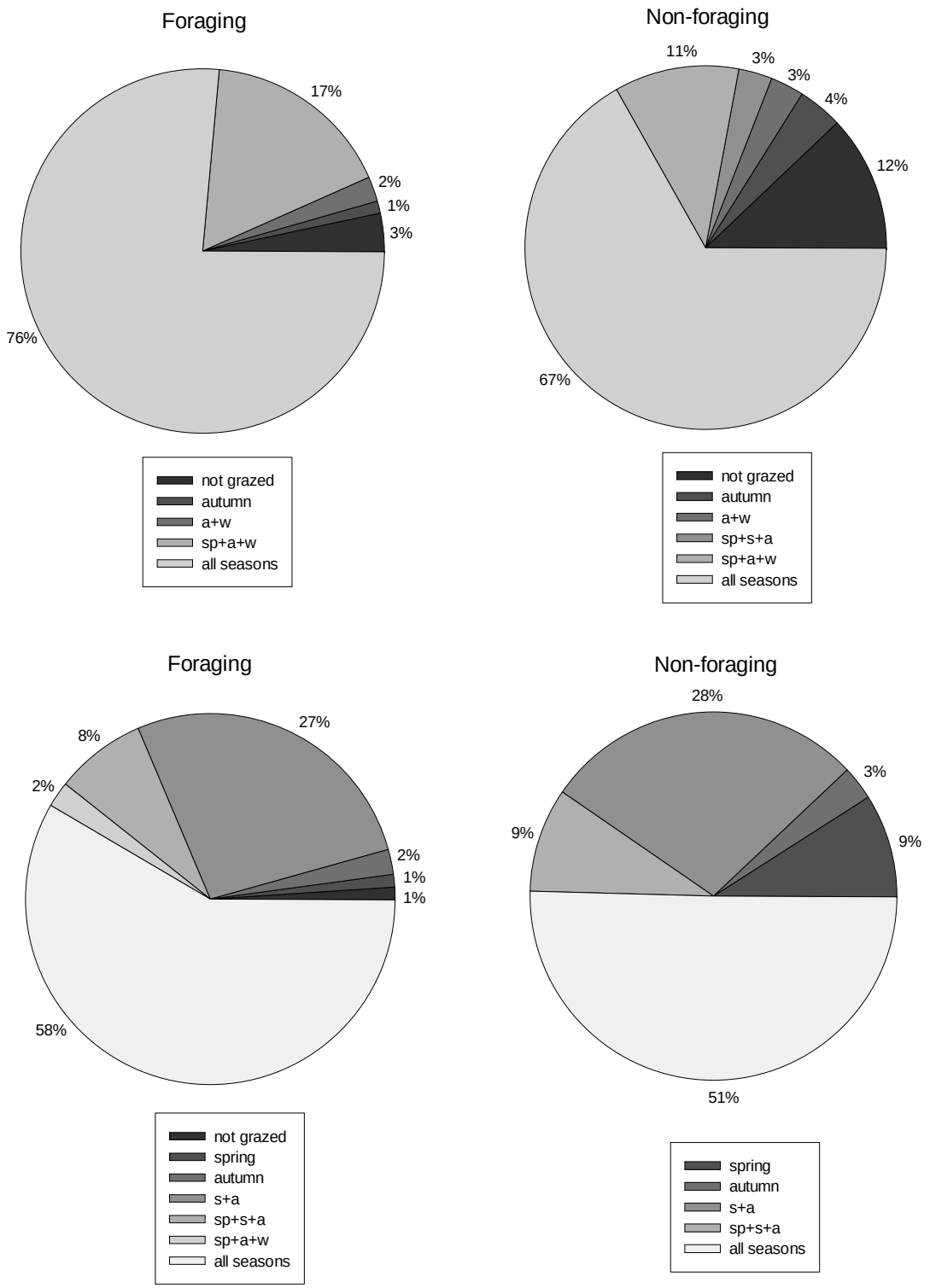


Figure 11.3. Percentage of fields in which sub-adult choughs were and were not observed to forage in relation to a) type of fertiliser used and b) timing of fertiliser use.

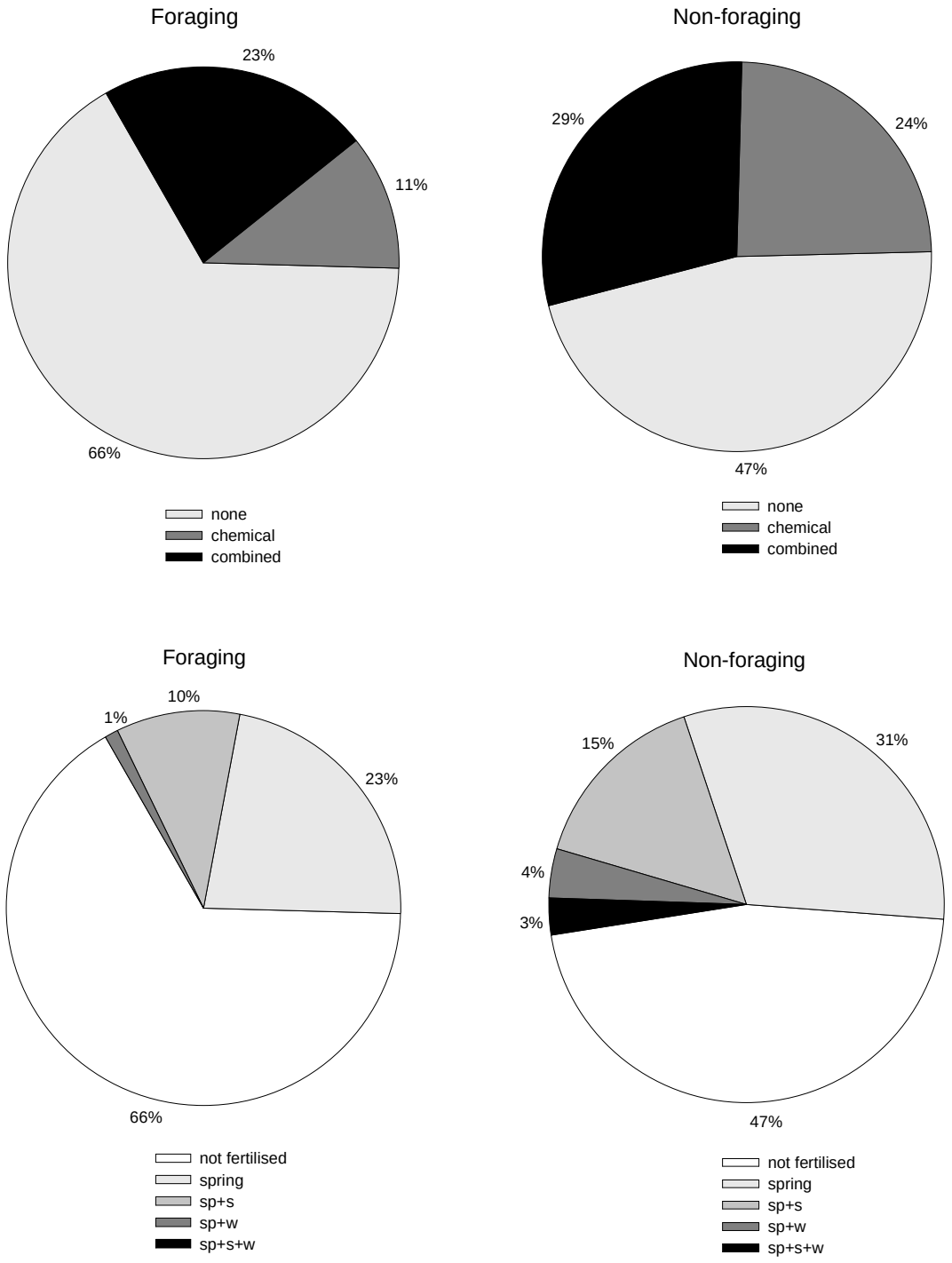
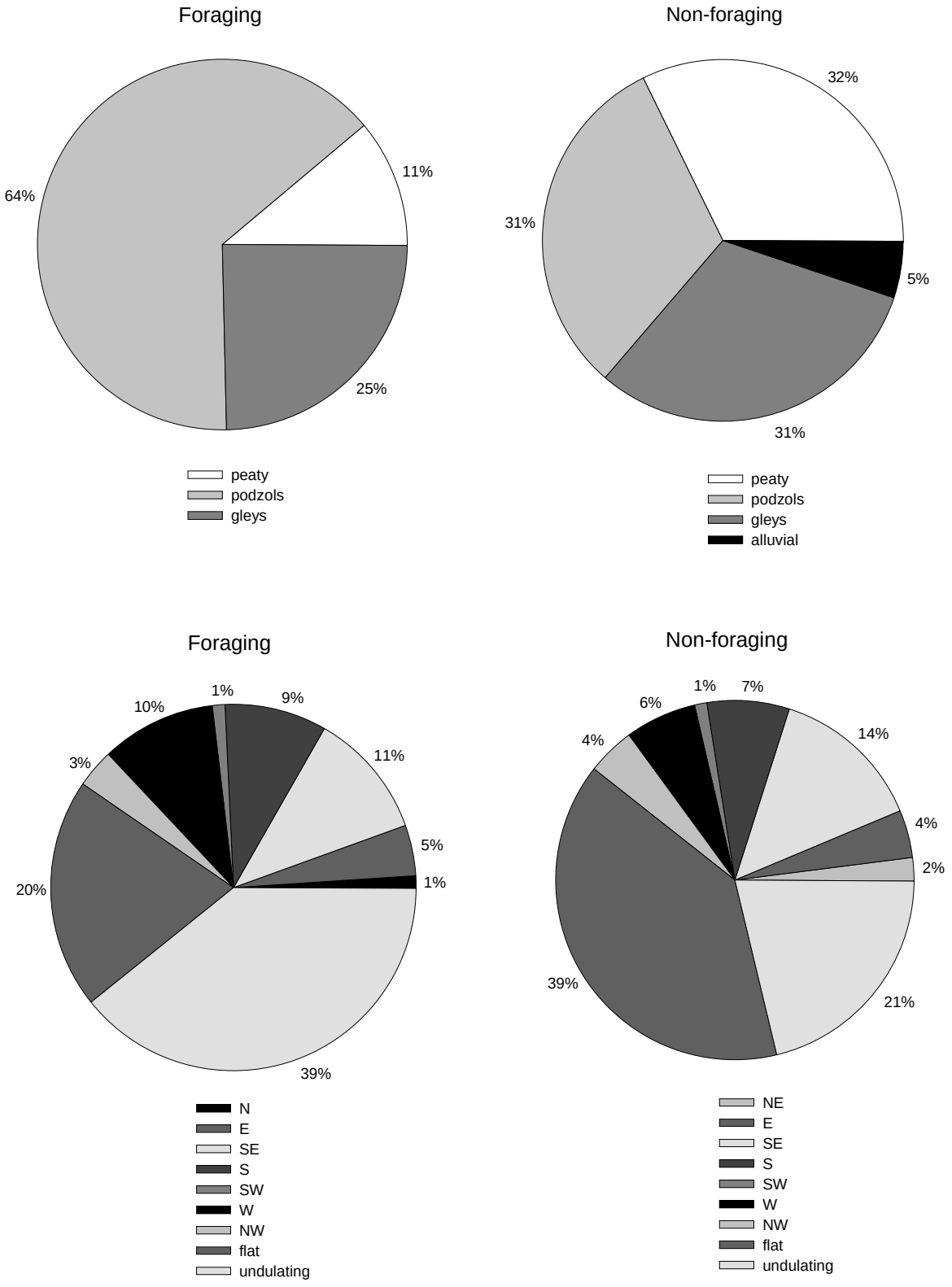


Figure 11.4. Percentage of fields in which sub-adult choughs were and were not observed to forage in relation to a) soil type and b) aspect.



11d) Summary of key conclusions and implications: chough foraging and farm management

These data provide further evidence that choughs forage primarily on grazed grassland created by low intensity agriculture (as characterised by sheep and cattle grazing and low fertiliser use). Choughs also tended to forage in compartments with well-drained soil and variable aspect.

12. Fine-scale variation in sub-adult survival

12a) Introduction

Section 5 shows that sub-adult survival varies among choughs fledged in different years and from different nest sites, and explains a substantial proportion of variation in the number of choughs on Islay. In section 6, we identified ecological variables that are correlated with the among-year and among-nest site variation in first-year survival. However, a substantial proportion of variation remained unexplained, particularly of variation in survival among choughs fledged from different nest sites. Furthermore, long-term data describing rates of survival from one year to the next do not tell us exactly when or where most sub-adult mortality occurred within each year. Understanding the precise timing and location of mortality could allow key periods and locations for the survival of sub-adult choughs to be pinpointed, potentially allowing targeted management to be designed to help maintain or increase survival at key times or locations. We therefore examined patterns of variation in sub-adult survival at finer temporal and spatial scales, and identified the times and locations when most mortality occurred.

We tracked the survival of colour-ringed sub-adult choughs every month through the main project period (April 2006 to April 2008). Less intensive resighting effort was maintained through the subsequent year (May 2008 to April 2009), and through the year preceding the main project period (May 2005 – March 2006) by the Scottish Chough Study Group. Similar data also exist from a previous period of relatively intensive fieldwork on Islay, during May 1984 to June 1987. Monthly sub-adult survival rates have previously been calculated for part of this period. However, in 1984-1987, first-year survival rates were relatively high (figure 5.2). We are therefore able to compare the pattern and magnitude of monthly mortality occurring in years when overall first-year survival was high, average and low (figure 5.2).

Our principal aims were to determine:

1. whether mortality of sub-adult choughs tends to occur in specific months of the year or occurs at a constant rate across all months.
2. whether variation in sub-adult survival among cohorts can be attributed to variation in the magnitude of the same periods of peak mortality, or to additional periods of high mortality.

3. whether sub-adult mortality primarily occurs before or after fledglings leave their natal territories and join sub-adult flocks.

12b) Methods

Identifying the timing and location of sub-adult mortality requires more intensive observations of colour-ringed fledglings than has typically been possible during the long-term SCSG study. We therefore carried out intensive periods of resighting effort during approximately the 15th – 20th of every month from April 2006 – April 2008. During each period, all areas of Islay that appear to provide suitable foraging habitat for sub-adult choughs were visited and searched for colour-ringed individuals (see section 7). Territories on which fledglings had been colour-ringed were also visited during the months immediately post-fledging (typically June-July) to search for fledglings that had not yet moved to sub-adult flocks. Similar but less intensive resighting effort was continued by the Scottish Chough Study Group during May 2008 – April 2009, after the main project fieldwork finished. A less intensive regime of monthly resightings was also carried out during June 2005 – March 2006 in the build-up to the current project. In addition, monthly resighting data are also available for May 1984 – June 1987.

Capture-mark-recapture models were used to estimate monthly survival and resighting probabilities for each cohort. Data collected during 2005-2009 allowed monthly survival rates to be estimated for the 2005, 2006 and 2007 cohorts for their first 23-24 months of life and the 2008 cohort for its first eleven months of life. Data collected during 1984-1987 allowed monthly survival rates to be estimated for the 1984 and 1985 cohorts for their first 24 months of life and the 1986 cohort for their first 12 months of life. Fortuitously, the set of years for which monthly survival data are available cover the complete spectrum of observed among-cohort variation in overall first-year survival: the 1984, 1985 and 2006 cohorts survived well, the 1986 and 2005 cohorts survived moderately and the 2007 and 2008 cohorts survived poorly (figure 5.2).

Totals of 54, 95, 70, 53, 57, 65 and 61 fledgling choughs were colour-ringed in 1984, 1985, 1986, 2005, 2006, 2007 and 2008 respectively. The estimated monthly resighting probability (the probability that any particular chough would be observed in a particular month given that it was alive) varied during 2005-2009 (figure 12.1). Monthly resighting probabilities did not differ between first-year and second-year choughs during this time, so a single value is shown for each month. Resighting probability varied among months during

the pre-project period (average $p = 0.56$) and post-project period (average $p = 0.71$), but was consistently high during the main project fieldwork period (average $p = 0.93$). The project therefore achieved very high monthly resighting probabilities for sub-adult choughs.

The probability of resighting a colour-ringed individual that was alive also varied during 1984-1987 (figure 12.2). Monthly resighting probabilities differed between first-year and second-year choughs, so two values are shown for each month when two cohorts were under study. In particular, resighting probabilities were higher for second-year choughs than for first-year choughs during 1985-1986. In general, resighting probabilities were lower during 1984-1987 and 2005 than during 2006-2008, meaning that monthly survival estimates may be less reliable for the earlier years.

Figure 12.1. Estimated resighting probabilities of sub-adult choughs on Islay for each month from June 2005 – August 2008. The pre-project period (June 2005 – March 2006), the main project period (April 2006 – April 2008), and the subsequent SCSG resightings (May – March 2009) are indicated by open circles, filled circles and open squares respectively. Estimated resighting probabilities for each month are shown ± 1 standard error.

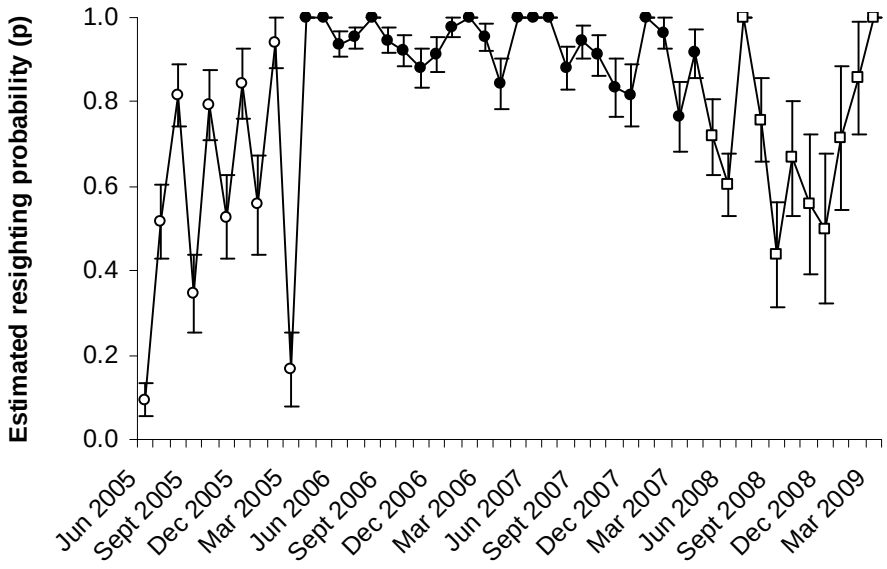
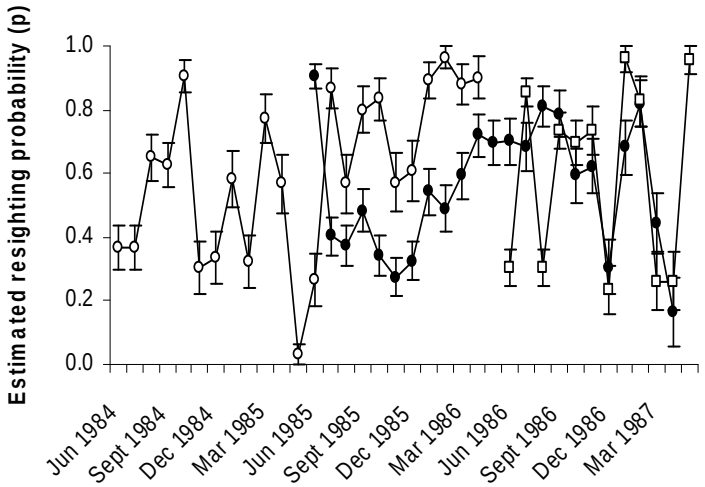


Figure 12.2. Estimated resighting probabilities of sub-adult choughs on Islay for each month from June 1984 – May 1987. Monthly resighting probabilities for the 1984, 1985 and 1986 cohorts are indicated by open circles, filled circles and open squares respectively. Estimated resighting probabilities for each month are shown ± 1 standard error.



12c) Monthly survival rates

Monthly survival probabilities for the 2005-2008 cohorts and 1984-1986 cohorts are shown in figures 12.3 and 12.4. These probabilities were consistently higher through the second year after fledging than through the first, and are frequently estimated as 1.0. This indicates that all colour-ringed fledglings that were still alive in one month were also still alive the next month. The slight apparent declines in survival at the end of the second year probably reflect some dispersal of recruiting two-year old choughs away from sub-adult flocks rather than true increases in mortality.

Monthly survival probabilities during the first year of life varied significantly among months for the 1985, 1986, 2007 and 2008 cohorts but not the 1984, 2005 or 2006 cohorts. Some general patterns of variation are evident.

1. Survival through the first month after ringing (May – June) is generally relatively low, reflecting mortality occurring immediately before or soon after fledging.
2. Most cohorts experienced relatively low survival during mid-winter (November – January).

3. Cohorts with low overall first-year survival showed low monthly survival probabilities during the late summer and autumn (July – October) compared to cohorts that showed higher overall first-year survival. Specifically, the unusually low first-year survival of the 2007 and 2008 cohorts primarily reflects unusually low survival during the late summer.

Figure 12.3. Estimated monthly survival probabilities for sub-adult choughs on Islay. Survival probabilities for the 2005, 2006, 2007 and 2008 cohorts are shown in filled and open circles and filled and open squares respectively, for every month from fledging until age two (2005 and 2006 cohorts) or up to April 2009 (2007 and 2008 cohorts). Standard errors are not shown for clarity. Labels denote the final month of each survival period (for example, 'S' indicates survival from August to September).

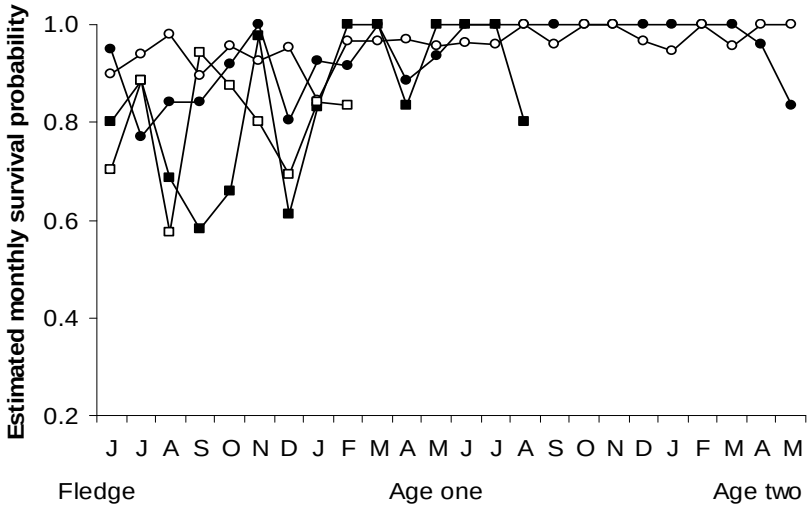
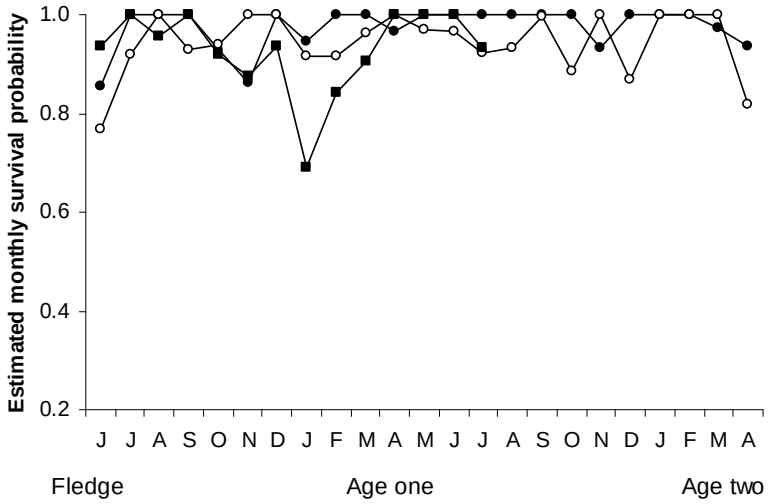


Figure 12.4. Estimated monthly survival probabilities for sub-adult choughs on Islay. Survival probabilities for the 1984, 1985 and 1986 cohorts are shown as filled and open circles and filled squares respectively, for every month from fledging until age two (1984 and 1985 cohorts) or age one (1986 cohort). Standard errors are not shown for clarity. Labels denote the final month of each survival period (for example, 'S' indicates survival from August to September).



12d) Summary of key conclusions and implications: monthly survival rates

1. Monthly survival rates were estimated for seven cohorts of choughs on Islay (1984, 1985, 1986, 2005, 2006, 2007 and 2008). The overall first-year survival rates of these cohorts covered the full range of variation observed on Islay during 1983-2008.

2. Most cohorts showed relatively low survival during May – June in their first year (the pre- and immediate post-fledging period). Most cohorts also showed relatively low survival during mid-winter (approximately November – February). The cohorts with the lowest overall first-year survival (2007 and 2008) also showed particularly low survival during the late summer and early autumn (July – October).

3. These data indicate that survival may typically be relatively low during the immediate fledging period and mid-winter, but that cohorts that show particularly low first-year survival experience additional periods of low survival during late summer.

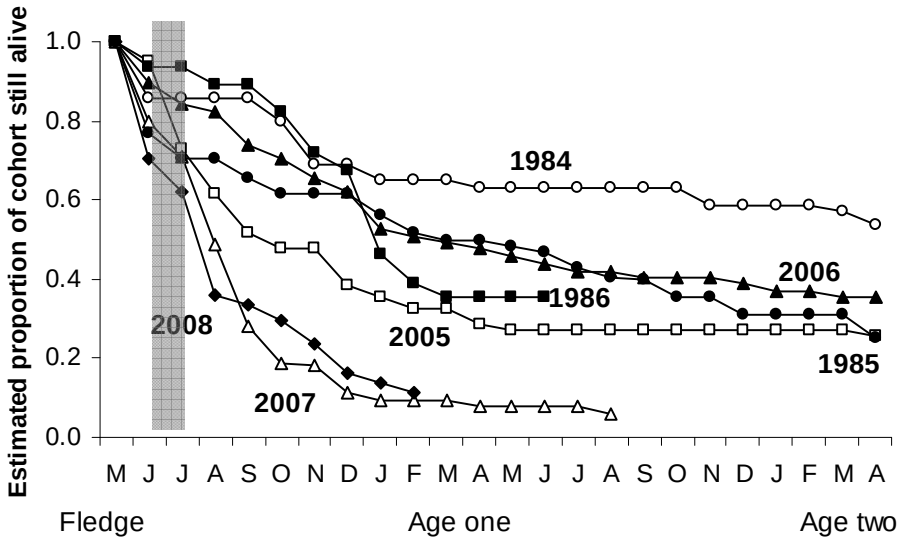
4. Sub-adult survival through the late-summer period appears to have been worse in recent years than in the 1980s. It is not clear why this is, but possible links to changes in weather and in the timing of silage cutting and other components of land management could potentially be responsible.

12e) Location of first-year mortality

By multiplying consecutive monthly survival probabilities for each cohort, 'survival curves' can be created, showing the proportion of each cohort estimated to be still alive in each month through the first two years after fledging. Survival curves for the 1984-86 and 2005-2008 cohorts are shown in figure 12.5. Fledglings typically move from their natal territories to flocking areas during late June or early July (shown by the grey bar on figure 12.5). These summary data suggest that although some mortality occurs before fledglings leave their natal territories, substantial mortality also occurs after fledglings reach the flocking areas.

To verify this conclusion, detailed data on the timing of movements of fledglings from natal territories to sub-adult flocks was recorded for the 2006 and 2007 cohorts during the project fieldwork. 43 of 57 (75%) and 42 of 65 (65%) colour-ringed fledglings from the 2006 and 2007 cohorts respectively were observed to reach the sub-adult flocks. Given that the overall first-year survival rates for these cohorts were 0.48 and 0.08 respectively, these data confirm that substantial mortality occurred in the flocking areas rather than on natal territories. Furthermore, it is possible that a small number of fledglings may have reached the flocks but died before being observed there. Our estimate of the proportion of mortality that occurred at the flocking areas is therefore a minimum.

Figure 12.5. Estimated survival curves (the proportion of cohort members estimated to be alive in each month) for the cohorts of choughs fledged in 2005 (open squares), 2006 (filled triangles), 2007 (open triangles), 2008 (filled diamonds), 1984 (filled circles), 1985 (open circles) and 1986 (filled squares). The grey bar indicates the typical timing of movement from natal territories to sub-adult flocks.



Although substantial sub-adult mortality occurred at the flocking areas rather than on breeding territories, we cannot necessarily conclude that the key areas to manage in order to maximise sub-adult survival are the flocking areas. Analyses of long-term SCSG data (up to 2004) showed that choughs fledged from particular nest sites and particular areas of Islay are more likely to survive through their first and subsequent years (regions BGE versus CNSW, figures 5.6 and 6.2, table 5.1, Reid et al. 2006). This suggests that even though most mortality occurs in the flocking areas, an individual's probability of survival is influenced by its natal location. We therefore investigated what might cause this dependence of subsequent survival on natal location. We first examined whether broad patterns of spatial variation in survival observed across the long-term data continued across more recent years. Specifically, we tested whether choughs fledged in the regions BGE during 2005-2007 were more likely to survive to ages one or two than choughs fledged in CNSW.

On average, choughs fledged in region BGE during 2005 to 2007 were again more likely to survive to age one than choughs fledged in CNSW. This difference in annual survival was particularly marked in 2006, but was non-existent in 2007 (the year in which overall first-

year survival was unusually low across the whole population). On average, choughs fledged in BGE also tended to be more likely to survive from age one to age two than choughs fledged in CNSW. However, this difference was not statistically significant, primarily due to the small sample size of individuals remaining. These analyses continue to support the suggestion that choughs fledged in specific areas of Islay (BGE) have higher post-fledging survival rates than choughs fledged in other areas (CNSW, figure 5.6).

Table 12.1. Estimated first-year and second-year survival probabilities for choughs fledged in the regions BGE and CNSW during 2005-2007. The regions BGE and CNSW are depicted in figure 5.6.

	Estimated probability of first-year survival		Estimated probability of second-year survival		Mean estimated probability of survival from fledging to age two	
Fledged in: Cohort	BGE	CNSW	BGE	CNSW	BGE	CNSW
2005	0.38±0.09	0.26±0.09	0.82±0.12	0.83±0.15	0.31	0.22
2006	0.76±0.09	0.25±0.08	0.79±0.09	0.63±0.17	0.60	0.16
2007	0.04±0.04	0.10±0.05	_____	_____	_____	_____

12f) First-year survival by foraging and roost site

The difference in first-year survival between choughs fledged in different regions of Islay could arise because conditions experienced during growth directly increase a chough's subsequent survival, or because choughs fledged in different regions subsequently use different foraging or roosting areas. In 2006 (and 2007), choughs fledged in BGE primarily moved to Ardnave and choughs fledged in CNSW primarily moved to Kilchoman (figure 12.6). Choughs that moved to Ardnave and Kilchoman survived at different rates through the late summer and autumn (figure 12.7). Based on data from 2006 and 2007, it is therefore difficult to determine whether variation in first-year survival observed across choughs fledged in BGE and CNSW is due to direct effects of natal location, or to links between natal location and movements to particular foraging and roosting flocks.

Figure 12.6. The percentage of colour-ringed fledglings that were observed to reach the main sub-adult foraging and roosting sites at Ardnave (filled bars) and Kilchoman (open bars) in 2006. Data are divided into families from the region of Islay where first-year survival has historically been high (BGE) and low (CNSW, see figure 5.6). Similar movements were observed in 2007.

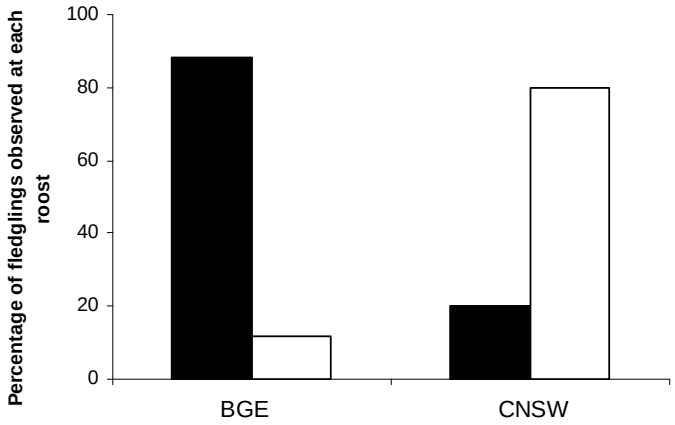
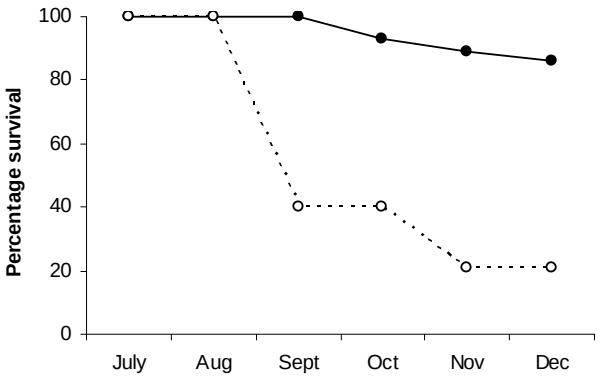
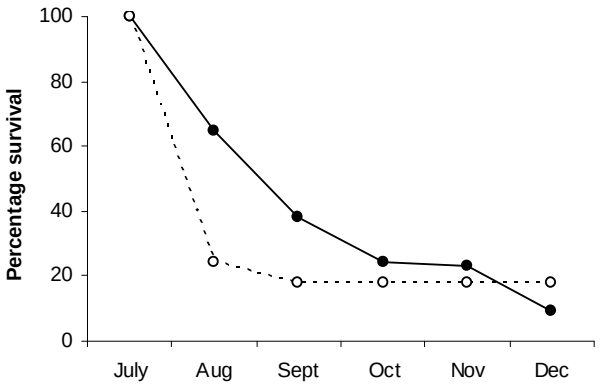


Figure 12.7. The percentage of sub-adult choughs that joined foraging and roosting flocks at Ardnave (filled symbols and solid line) and Kilchoman (open symbols and dashed line) that were still alive in each subsequent month in (a) 2006 and (b) 2007.





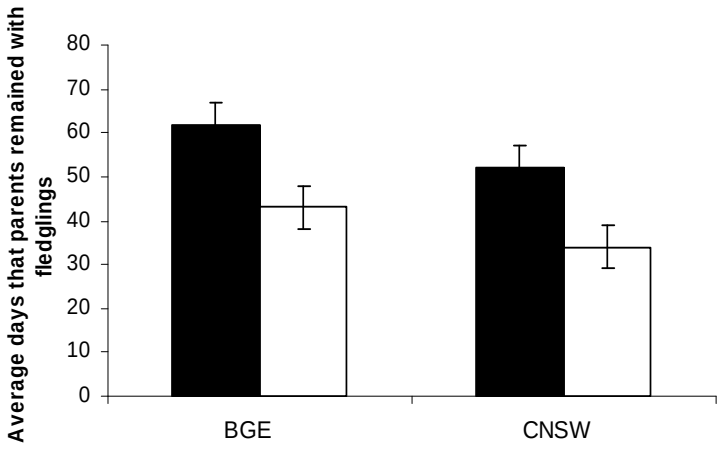
Some direct effect of natal location is likely given that, over the long-term data, choughs fledged in BGE survived better than those fledged in CNSW even in years when all subsequently foraged and roosted at Kilchoman. Such a direct effect of natal location may, however, be exacerbated by differences in the conditions experienced at different foraging and roosting sites.

12g) First-year survival and parental state

Our study also suggested that survival of sub-adult choughs covaries with varies aspects of the state of their parents. Two points are summarised below rather than being reported in detail.

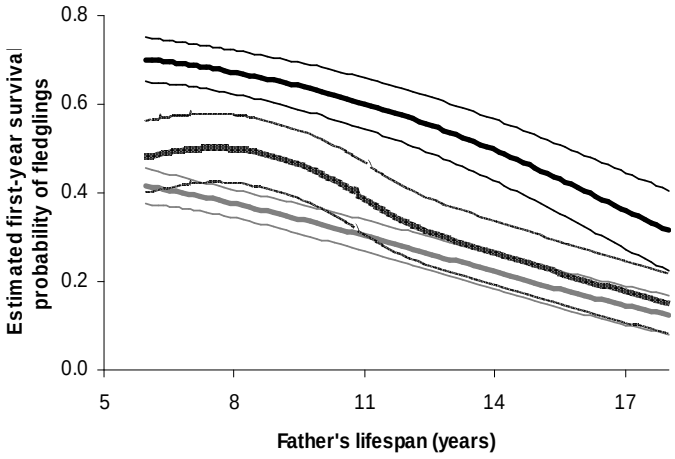
First, parents stayed with their offspring for substantially longer after fledging in 2006 (the year when first-year survival was high) than in 2007 (the year when first-year survival was very low, figure 12.8). Figure 12.8 also shows that, in both 2006 and 2007, parents that had bred in regions of Islay where first-year survival has historically been high (BGE) spent longer with their fledglings than parents from regions of Islay where first-year survival has historically been low (CNSW). Fledgling survival was therefore correlated with the duration of parental care. This may reflect a causal effect of parental care on fledgling survival, or indicate that both parental care and fledgling survival depend on some other variable (such as food availability).

Figure 12.8. The average number of days that parents remained with fledged offspring in 2006 (filled bars) and 2007 (open bars). Data are divided into families from the region of Islay where first-year survival has historically been high (BGE) and low (CNSW, see figure 5.6).



Second, analyses of long-term data showed that first-year survival of choughs was correlated with the longevity of parents. Specifically, parents that lived for more years tended to produce fledglings that were less likely to survive through their first year of life (figure 12.9). The mechanisms underlying these relationships are not clear, but further highlight that survival of sub-adult choughs may be tightly linked to the state of their parents.

Figure 12.9. Relationships between the estimated first-year survival probability of fledgling choughs and the lifespan of their father. Black, stippled and grey lines indicate years when first-year survival was high, medium or low. First-year survival was similarly correlated with maternal lifespan.



Our original plan was to relate variables such as parental provisioning rate, distances travelled and fledging date to fledgling survival. However, since almost all fledglings that were colour-ringed in 2007 died before the end of their first year there is little statistical power to detect effects.

12h) Summary of key conclusions and implications: location and parental effects on sub-adult survival

1. Most mortality of sub-adult choughs occurred after fledglings had left their natal territories and moved to sub-adult foraging and roosting sites (see section 7). However, sub-adult survival rates varied with natal location (see also sections 5 and 6).

2. In 2006 and 2007, choughs fledged in different regions of Islay tended to move to different foraging and flocking areas. It was therefore not possible to clearly distinguish whether variation in sub-adult survival among choughs fledged in different regions reflected direct effects of natal location or correlated variation in environmental conditions experienced in subsequent months.

3. Further analyses suggested that fledgling survival was correlated with the duration of parental care and with parent longevity, suggesting that the survival of sub-adult choughs may be to some degree linked with the state of their parents.

Sub-adult survival may be maximised by maximising parental state, for example through appropriate management of breeding territories.

13. Comparative demography of chough populations

13a) Introduction

All analyses presented so far have focused entirely on data from choughs on Islay. It would be extremely valuable to consider the wider context, and to compare the ecology of Islay's choughs with the ecology of choughs elsewhere. This is because, when looking at any one population such as Islay, only a small part of the natural range of variation in chough ecology (specifically, variation in breeding success and survival and links with habitat and environment) may be observed. By looking at other populations, some additional management options may become evident, and it may be possible to understand more about the possible consequences of management actions that take the focal population beyond the range of variation it has recently experienced.

To place our understanding of the ecology of Islay's chough population in wider context, a final aim of the current research project was to the compare breeding success and survival observed on Islay with that observed in other chough populations.

13b) Data and methods

Some degree of monitoring has been undertaken in other European chough populations in recent years. Monitored Atlantic coast populations include Colonsay, Isle of Man, Wales (North Wales and Pembrokeshire), Ouessant, Cornwall and Ireland. Of these, data on breeding success and survival were kindly provided for Colonsay by David Jardine and Mike Peacock, the Isle of Man by Allen Moore, and for Ouessant by Christian Kerbiriou.

Islay breeding success and survival data cover 1981-2008 and 1983-2008 respectively. Colonsay breeding success and survival data cover 1986-2008 and 1999-2008 respectively. Isle of Man breeding success and survival data cover 1986-2008 and 1989-2008 respectively. Ouessant breeding success data cover 1996-2007, and no survival data are available.

13c) Results

Table 13.1 shows the mean breeding success and survival rates estimated for each population. Mean breeding success has on average been slightly higher on Colonsay and the Isle of Man than on Islay. However, mean breeding success in all three populations has been higher than on Ouessant.

First-year survival (the probability that a fledgling chough would survive to age one) has on average been similar on Islay and Colonsay, and slightly lower on the Isle of Man (table 13.1). Second-year survival averaged slightly higher on Colonsay and the Isle of Man than on Islay (table 13.1), although these estimates are based on small sample sizes and so cannot be calculated for exactly the same periods. Adult survival was similar on all three islands, but tended to be slightly higher on the Isle of Man and lower on Islay (table 13.1).

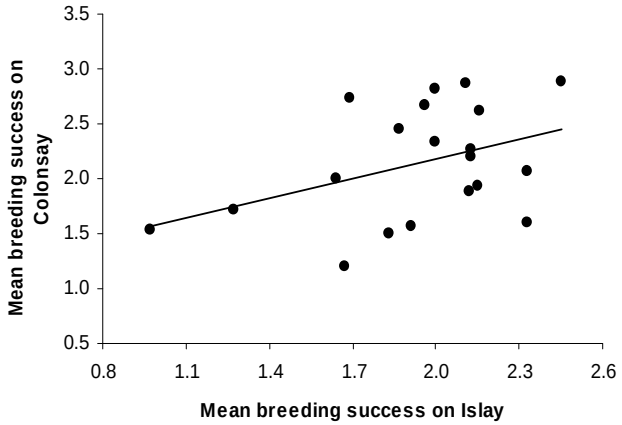
Table 13.1. Mean estimated breeding success and survival rates in different chough populations. Breeding success (the number of chicks fledged per monitored breeding attempt) and survival rates were estimated across all data for each population and, to allow direction comparison, across equivalent periods for each population. These periods are denoted by B1 (1981-2008), B2 (1986-2008) and B3 (1996-2007) for breeding success and S1 (1983-2008), S2 (1989-2008) and S3 (1999-2008) for survival. Islands can be compared directly by reading along individual lines. The figures in brackets give the number of breeding attempts across which mean breeding success were estimated. Survival rates are estimated from up to 1214, 127 and 643 colour-ringed fledglings on Islay, Colonsay and Isle of Man respectively. Means are presented ± 1 standard error.

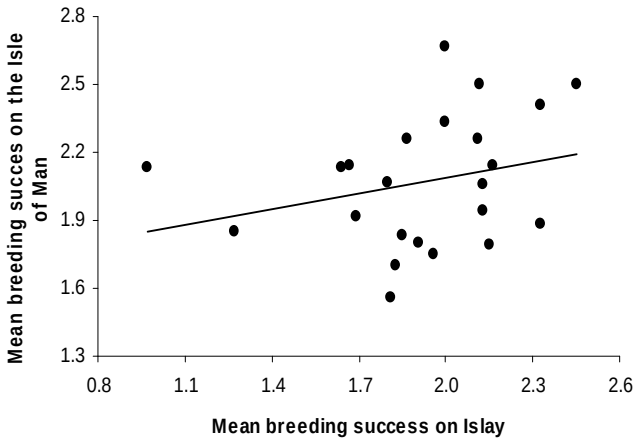
	Islay	Colonsay	Isle of Man	Ouessant
Breeding success	1.96±0.05 (881)^{B1} 1.91±0.05 (746)^{B2} 1.96±0.06 (378)^{B3}	 2.13±0.11 (194)^{B2} 2.25±0.13 (128)^{B3}	 2.07±0.06 (626)^{B2} 2.17±0.08 (401)^{B3}	 1.60±0.12 (151)^{B3}
First-year survival	0.40 ± 0.02^{S1} 0.36 ± 0.03^{S2} 0.36 ± 0.04^{S3}	 0.36 ± 0.05^{S3}	 0.30 ± 0.02^{S2} 0.28 ± 0.04^{S3}	 _____
Second-year survival	0.69 ± 0.05^{S1} 0.68 ± 0.06^{S2} 0.79 ± 0.08^{S3}	 0.85 ± 0.07^{S3}	 0.82 ± 0.05^{S2} 	 _____
Adult survival	0.80 ± 0.02^{S1} 0.81 ± 0.02^{S2} 0.80 ± 0.04^{S3}	 0.83 ± 0.06^{S3}	 0.85 ± 0.02^{S2} 0.83 ± 0.04^{S3}	 _____
Resighting rate	0.77 ± 0.03^{S1}	0.83 ± 0.04^{S3}	0.60 ± 0.02^{S2}	

Mean breeding success was positively correlated across years on Islay and Colonsay, showing that a successful breeding year on Islay also tended to be a successful year on Colonsay (figure 13.1). This is perhaps not surprising, since Islay and Colonsay are close together and might therefore be expected to experience similar environmental variation from one year to the next.

However, mean breeding success was also correlated across Islay and the Isle of Man (figure 13.1). This relationship suggests that some large-scale component of environmental variation, such as weather, simultaneously influences chough breeding success in both Scotland and the Isle of Man. There was no correlation between mean breeding success on Islay and Ouessant, which is perhaps not surprising since these populations are so far apart.

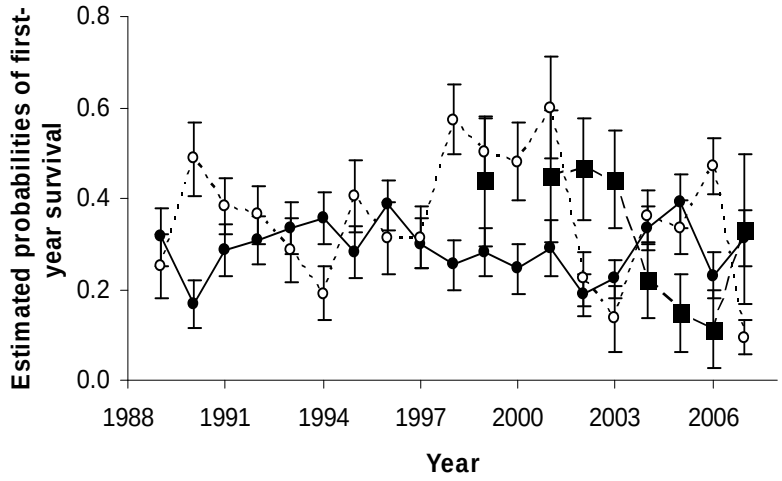
Figure 13.1. Correlations between mean annual breeding success (the number of chicks fledged per breeding attempt) on (a) Islay and Colonsay and (b) Islay and the Isle of Man. Each data point represents a single year.





First-year survival rates have varied among years on all three islands (figure 13.2, see also figure 5.2 for the full Islay dataset). First-year survival probability could not be estimated for Colonsay in 2000 because only four chicks were colour-ringed in that year. Variation in first-year survival probability is not correlated across the three islands. However, annual estimates for Colonsay are based on very small sample sizes, meaning that patterns of among-year variation should be interpreted with caution. Despite this, first-year survival estimates for Colonsay are much lower for 2004-2006 than for 1999-2003 (figure 13.2).

Figure 13.2. Estimated first-year survival probabilities for colour-ringed choughs fledged on Islay (open circles, dotted line), Isle of Man (filled circles, solid line) and Colonsay (filled squares, dashed line).



13d) Summary of key conclusions and implications: comparative demography of chough populations

1. Overall, estimates rates of chough breeding success and survival were broadly similar across Islay, Colonsay and the Isle of Man. This broad similarity of independent estimates from different populations suggests that our estimates for Islay,

and our estimates of the sensitivity of population growth rate to breeding success and survival, are likely to be robust.

2. However, mean breeding success (the number of chicks fledged per breeding attempt) on Islay was slightly lower than on Colonsay or the Isle of Man (but higher than on Ouessant).

Islay's choughs may therefore be slightly under-performing in terms of breeding success compared to neighbouring populations.

3. First-year survival averaged slightly higher on Islay and Colonsay than on the Isle of Man. However, first-year survival has varied markedly among years on both Islay and Colonsay, and choughs on both these islands have experienced very low first-year survival rates since 2003.

3. Second-year survival has been higher on Colonsay and the Isle of Man than on Islay, although all estimates are based on small sample sizes.

4. Although adult survival has been broadly similar across all three islands, adult survival has been lowest on Islay. Since chough population growth rate is sensitive to variation in adult survival, bringing the adult survival rate on Islay up to that observed on Colonsay and the Isle of Man would be expected to appreciably increase population growth rate.

5. The lower population growth rate observed on Islay than on Colonsay and the Isle of Man over recent years can be attributed to lower breeding success, second-year survival and adult survival, and not to lower first-year survival.

6. Continued monitoring should be supported on Colonsay and the Isle of Man as well as Islay. These datasets will ultimately allow ecological correlates of variation in breeding success and survival to be compared across populations.

14. Summary of knowledge transfer events and presentations

Formal knowledge transfer events and presentations carried out under this project are as follows. In addition, throughout the project, there were frequent interactions among researchers, farmers, conservation practitioners, policy makers and the wider public.

a) International Chough Conference, Ayr, September 2007.

This two-day meeting was attended by conservation managers and chough researchers from across Europe.

Proceedings are attached (Appendix 6).

b) Farmer's meeting, Islay, January 2008.

This evening meeting was attended by *ca* 35 farmers and landowners from across Islay.

Presentations were made by Jane Reid and Maria Bogdanova.

A DVD was subsequently produced for Lord Margadale.

c) Direct feedback to farmers and landowners.

Letters were written to farmers and landowners providing feedback on their own choughs.

d) Machair Ecology Conference, Glasgow, December 2009.

Presentation by Maria Bogdanova.

e) Scottish Ringers' Conference, Braemar, November 2006

Presentation by Jane Reid.

f) Scottish Chough Forum Meeting, Islay, April 2009.

Final project meeting at which conclusions and recommendations were presented, discussed and agreed.

15. Acknowledgements

We particularly thank all the farmers and landowners that generously allowed access to their land, SNH and RSPB staff for their support and encouragement throughout the project, and for the provision of accommodation, vehicles and other resources.

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17. Glossary

Breeding success – number of chicks fledged from any particular breeding attempt.

Demographic rate – a component of demographic variation that is expected to contribute to variation in population growth rate and hence the number of choughs in any population. The main demographic rates considered in this report are breeding success, first-year survival, second-year survival and adult survival.

Elasticity – a scaled sensitivity, that allows sensitivity to be directly compared across different demographic rates.

Foraging site – a broad area used by foraging choughs (e.g. Ardnave, Kilchoman, Killinallan, Kilchiaran, Smaull, Sanaig, Lossit, Laggan and Oa).

Foraging location – a specific location used by foraging choughs within a foraging site.

Mortality rate – the estimated probability that a chough will die between one month or year and the next.

NERC – Natural Environment Research Council

Population growth rate – the relative change in population size from one year to the next. A population growth rate of 1 means that population size is the same as last year. A population growth rate of great than 1 means that the population is larger than last year, and a population growth rate of less than 1 means that the population is smaller than last year.

Resighting probability – the estimated probability that a particular colour-ringed chough would be seen in any given month or year given that it was still alive.

RSPB – Royal Society for the Protection of Birds

SCSG – Scottish Chough Study Group

Sensitivity – a quantity that describes the extent to which population growth rate would be expected to change in response to a small change in any particular demographic rate.

SNH – Scottish Natural Heritage

Survival probability – the estimated probability that a chough will survive from one month or year to the next.

Table 9.4. Description of habitat characteristics observed at foraging locations and non-foraging locations at Ardnave and Kilchoman during April 2006-March 2007 and April 2007-March 2008. Legends are defined below the tables.

Ardnave
April 2006 – March 2007: Sample sizes for foraging and non-foraging locations were 70 and 23

type	elevation	slope	aspect	SHm	SHcv	SCg	SCm	SCo	VD	CDo	CDm	CDf	SHDo	SHDm	SoilH	ST
foraging	18 ± 1	5	1 (S/E/flat)	36.7 ± 2.6	23.8 ± 1.6	64	0	9	1 (sparse)	0	0	0	0	0	0.9 ± 0.1	2 (podzols)
non-foraging	20 ± 1	5	1 (S/E/flat)	46.9 ± 4.8	30.0 ± 1.8	75	0	16	3 (dense)	0	0	0	0	0	2.1 ± 0.3	2 (podzols)

Ardnave
April 2007 – March 2008: Sample sizes for foraging and non-foraging locations were 47 and 21

type	elevation	slope	aspect	SHm	SHcv	SCg	SCm	SCo	VD	CDo	CDm	CDf	SHDo	SHDm	SoilH	ST
foraging	17 ± 1	5	1 (S/E/flat)	30.2 ± 2.5	23.9 ± 2.0	60	0	16	2 (medium)	0	0	0	0	0	0.9 ± 0.1	2 (podzols)
non-foraging	19 ± 2	5	1 (S/E/flat)	46.5 ±2.8	29.7 ±2.2	73	0	20	3 (dense)	0	0	0	0	0	1.5 ± 0.2	2 (podzols)

Kilchoman
April 2006 – March 2007: Sample sizes for foraging and non-foraging locations were 10 and 34

type	elevation	slope	aspect	SHm	SHcv	SCg	SCm	SCo	VD	CDo	CDm	CDf	SHDo	SHDm	SoilH	ST
foraging	35 ± 4	10	1 (S/E/flat)	45.0 ± 2.9	26.6 ± 1.9	67	0	19	2 (medium)	0	0	0	0	0	1.7 ± 0.2	2 (podzols)
non-foraging	32 ± 5	15	3 (N/W)	42.1 ± 6.0	34.6 ± 4.7	81	0	10	2 (medium)	0	0	0	0	0	1.2 ± 0.2	2 (podzols)

Kilchoman
April 2007 – March 2008: Sample sizes for foraging and non-foraging locations were 10 and 18

type	elevation	slope	aspect	SHm	SHcv	SCg	SCm	SCo	VD	CDo	CDm	CDf	SHDo	SHDm	SoilH	ST
foraging	25 ± 4	10	1 (S/E/flat)	37.8 ± 2.4	30.6 ± 2.0	67	0	22	2 (medium)	0	0	0	0	0	1.4 ± 0.2	2 (podzols)
non-foraging	27 ± 5	10	1 (S/E/flat)	42.4 ± 4.3	26.5 ± 3.8	76	0	17	3 (dense)	0	0	0	0	0	1.4 ± 0.2	2 (podzols)

Ardnave & Kilchoman, April 2006 – March 2008: Sample sizes for foraging and non-foraging locations were 169 and 64

type	elevation	slope	aspect	SHm	SHcv	SCg	SCm	SCo	VD	CDo	CDm	CDf	SHDo	SHDm	SoilH	ST
foraging	22 ± 1	5	1 (S/E/flat)	36.7 ± 1.5	25.1 ± 1.0	64	0	15	2 (medium)	0	0	0	0	0	1.3 ± 0.1	2 (podzols)
non-foraging	22 ± 1	5	1 (S/E/flat)	45.4 ± 2.2	30.1 ± 1.3	76	0	17	3 (dense)	0	0	0	0	0	1.7 ± 0.1	2 (podzols)

Legend:

Elevation	elevation at quadrat (m)
Slope	slope at quadrat (degrees)
Aspect	aspect at quadrat, recorded in 9 categories (flat, N, NE, E, SE, S, SW, W, NW), then given a score between 0 and 4 (as a difference of SE, so SE=0; S, E, flat=1; NE, SW=2; N, W=3; NW=4).
SHm	mean sward height (mm)
SHcv	variability in sward height: coefficient of variation (%)
SCg	grass cover (%)
SCm	moss cover (%)
SCo	other (broad-leaved) plants cover (%)
VD	vegetation density, recorded in 4 categories (0=none, e.g. on beach, 1=sparse, 2=medium and 3=dense)
CDo	number of old cow pats per quadrat/location
CDm	number of medium cow pats
CDf	number of fresh cow pats
SHDo	number of old sheep droppings per quadrat/location
SHDm	number of medium sheep droppings
SoilH	soil hardness (kg/cm^2)
ST	soil type, 4 main types found at these sites (1=peaty, 2=podzols, 3=gleys, 5=alluvial)