ISSN 1758-3276

Journal
of the
Lundy Field Society

LUNDY
FIELD
SOCIETY

Volume 6, 2018

Journal of the Lundy Field Society

Volume 6

2018

Editor: Jennifer George

Production Editor: André Coutanche

LUNDY
FIELD
SOCIETY

Journal of the Lundy Field Society

Volume 6, 2018

First published 2018

www.lundy.org.uk

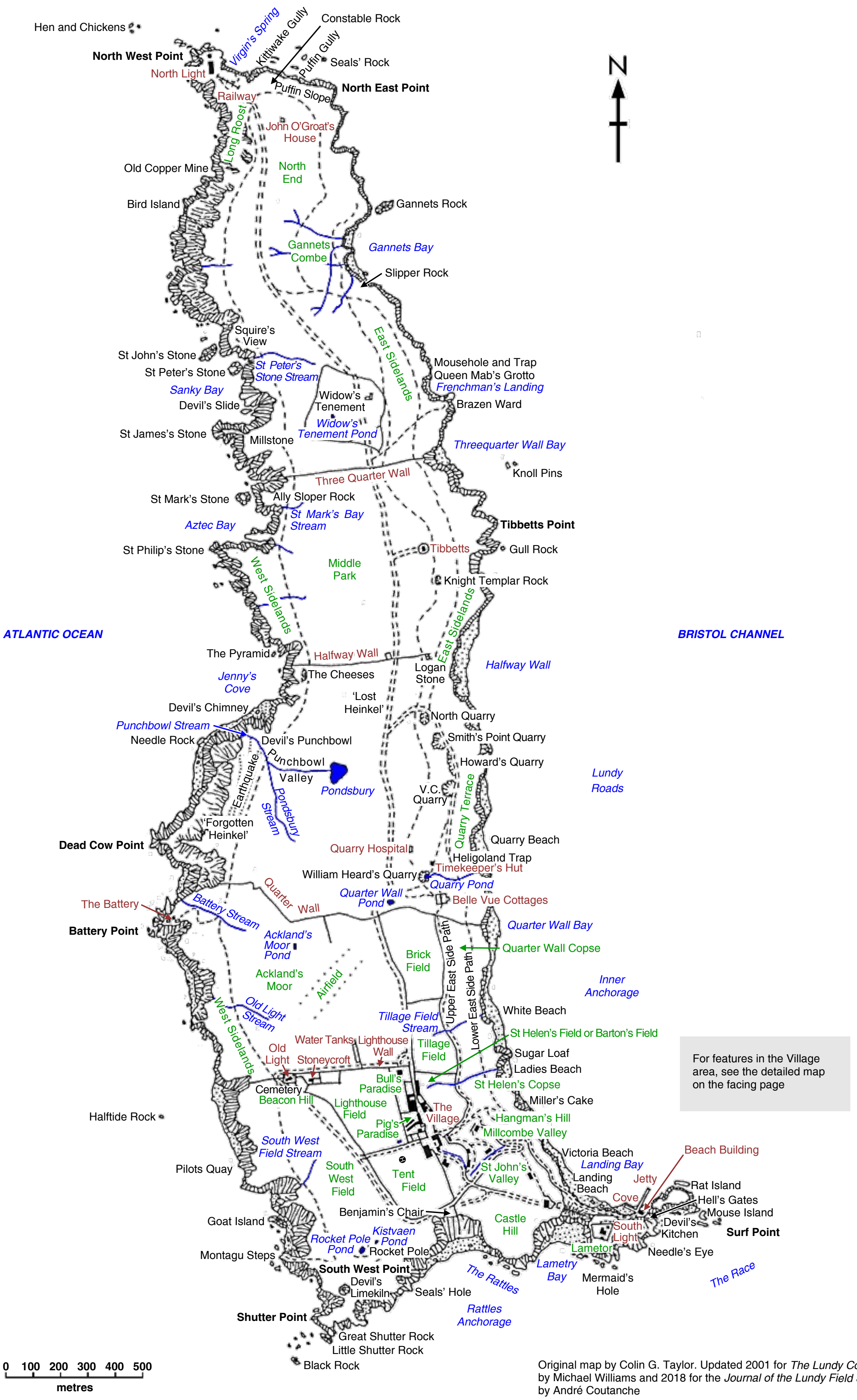
Printed by Short Run Press, Exeter

ISSN 1758-3276

CONTENTS

SHORT COMMUNICATION

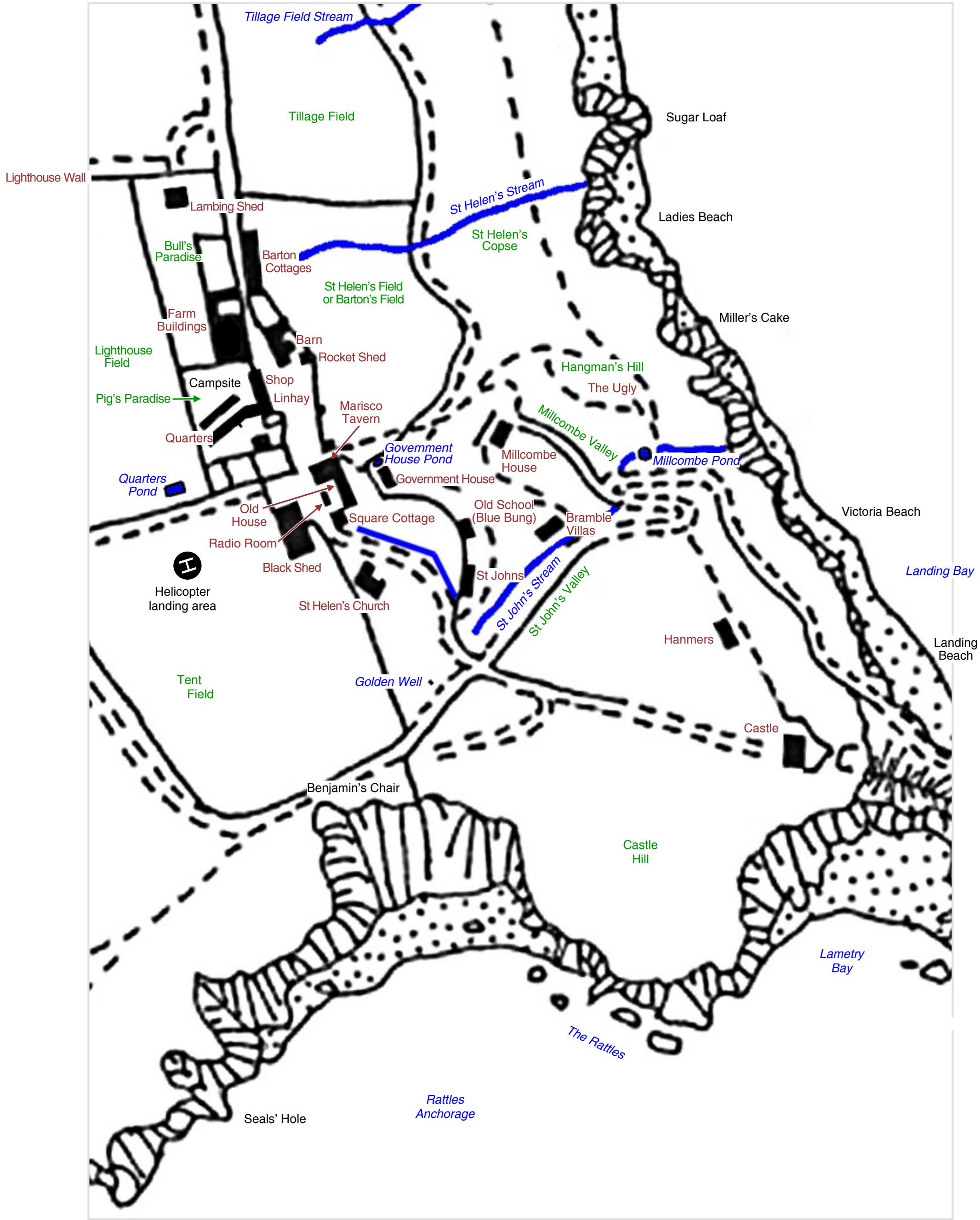
MAP OF THE ISLAND OF LUNDY



For features in the Village area, see the detailed map on the facing page

Original map by Colin G. Taylor. Updated 2001 for *The Lundy Companion* by Michael Williams and 2018 for the *Journal of the Lundy Field Society* by André Coutanche

MAP OF THE LUNDY VILLAGE AREA



Colour key:
Brown: built features
Green: named areas of land
Blue: water features
Black: everything else

EDITORIAL

Welcome to the sixth volume of the LFS Journal. Lundy birds have flown strongly into this issue with 50% of the papers dealing with their population numbers and behaviour.

In 2014 a seventeenth century document, the Clayton manuscript, describing the buildings, agriculture, birds and fish of Lundy came on to the market and was bought by four members of the LFS Committee on behalf of the LFS. *Alan Rowland* with support from *Michael Williams, André Coutanche* and *Roger Chapple* has written a fascinating account of the manuscript discussing its authenticity and provenance, then proceeding to an interpretation of the text of the document.

The first birds to fly into the volume are the Kittiwakes whose numbers have been in decline for decades particularly in northern areas of the UK. *Thomas Dickins, Kirsty Neller* and *Robert Spencer* have been studying clutch size of one colony on Lundy for two seasons. This study is part of a larger programme of measuring productivity and the ecological factors affecting this declining species.

There has been very little research carried out on the carnivorous Sundew plant on Lundy and *Barbora Lekosyte, Stephen Kett* and *Martijn Timmermans* have studied the invertebrate prey that the plant catches to supplement its diet. The use of DNA barcodes to identify the prey is probably the first such study carried out on this plant.

Population numbers of the cliff-nesting Lundy seabirds have been monitored since 1981. *Helen Booker, Peter Slader, David Price, A.J. Bellamy* and *Tim Frayling* give an account of the recent 2017 monitoring which shows further increases in numbers of several species since the rat eradication.

The Lundy Cabbage (*Coincya wrightii*) usually harbours pollen beetles, but in 2007 they were present in very large numbers on the plant. Their effect on the reproductive success of the Cabbage that year is discussed by *Rosy Key, Roger Key, Mohine Alam* and *Stephen Compton.*

Puffins are one of Lundy's most popular and photogenic birds and their behaviour on the open sea has been studied by *Peggy Liebig, Henrietta Pentony* and *Eleanor Tarrant Taylor*. Their research provides insight into specific behaviours observed on the water.

Lundy House Sparrows have been studied for 26 years on Lundy and the paper by *Julia Schroeder*, *Isabel Winney*, *Sophie Bennett, Alfredo Sánchez-Tójar* and *Antje Girndt* examines the advantages and disadvantages of infidelity between pairs in relation to breeding success.

Are the Lundy Black Rabbits descended from Tudor ancestors? By using DNA techniques on tissue from animal carcases, *Martijn Timmermans, Hanna Elmi* and *Stephen Kett* attempt to answer this question.

The eight papers are followed by a short communication from *Charles Ellis* who has been researching the monumental standing stones in the burial ground on Lundy and the people who may have erected them.

Jennifer George
Editor
January 2018

A PARTICULER OF LUNDY ISLAND: THE CLAYTON MANUSCRIPT

by
ALAN ROWLAND[1], MICHAEL WILLIAMS, ANDRÉ COUTANCHE AND ROGER CHAPPLE
[1]Mole Cottage, Chapel Close, Woodford, Morwenstow, Cornwall, EX23 9JR
[1]*Corresponding author, e-mail: morwenstow@btinternet.com*

ABSTRACT

The acquisition of a unique seventeenth century document describing the buildings, state of agriculture, stock levels, industries, birds and fish of Lundy provides the earliest documentary record for these subjects and a view of the island 450 years ago. The authenticity, author, and this new information are all explored and described and a full annotated transcript is provided of the manuscript.

Keywords: *Lundy, Civil War, Grenville, manuscript, seventeenth century*

DISCOVERY AND HISTORY

This manuscript first came to attention when offered for sale in May 2014 when a notice from Julian Browning Autographs Ltd (Browning, 2014; Williams, 2015) referred to the sale of a document relating to Lundy of 'An early and original manuscript survey of Lundy …'.

In dialogue with Julian Browning further information was elicited. He stated that, regarding provenance and date, the Lundy manuscript emerged from a collection sold at Bonhams, London, in 2012. These were mostly manuscripts and letters of West Country interest accumulated by a clergyman called Kempthorne, who bought from dealers and auctions (Hodgson's Rooms, later to be Sothebys) in the 1930s. The collection (or the part he purchased) appears to have lain undisturbed since then. At that time the Clayton manuscripts were being dispersed. These well-known manuscripts (sometimes designated in the trade Clayton MSS) were from the estate of Sir Robert Clayton (1629-1707), Lord Mayor of London (1679-1680) and his family. The Lundy manuscript bears the distinctive annotation in black ink (upper left of the first page, Figure 2) which indicates that it formed part of that historic manuscript collection. This information, and the 'grapes' watermark and writing style, ties the manuscript to the seventeenth century. This convinced four LFS committee members to form a consortium to purchase the document with the objective of making its contents more widely known, preserving it for posterity and, after publication of this paper, depositing it in a West Country archive. The purchase was effected on 20 May 2015 – the names of the members of the consortium appear at the beginning of this paper.

The purpose of this paper is to explore and support the assertions above, establish the provenance, determine the date and writer of the document and throw more light on the information contained within the 'Particuler'.

Initial work undertaken in 2014 was to transcribe the text written in Secretary Hand, decipher some of the less legible words and translate some of the idioms. The original document is reproduced in Figure 1 (page 10). The resulting translation is explored and explained later in this paper.

Provenance

Enquiries of Julian Browning suggest that before the document arrived at Auction at Bonhams in 2014 it had been in the collection of Reverend John Ley Kempthorne. Browning (pers. comm.) further stated that this owner collected manuscripts and letters of West Country interest from dealers and auction rooms. Apparently 'the Particuler' had lain undisturbed from the 1930s. Bonham's catalogue (Bonham's, 2014) details the relevant lot 93 offered for sale on 12 November 2014 thus:

> 'Collection of deeds and correspondence formed by the Rev. J.L. Kempthorne of St Enoder Rectory, Summercourt, Cornwall, in the years prior to the Second World War ... with especial emphasis on the South West of England and the life of Charles Kingsley … a group of 17th century Devon and Cornwall obligations, letters, etc, plus documents from the Clayton MSS ...'

The lot realised £2,375 (Bonhams, 2014).

This in turn had been bought two years previously (lot 16 on 13 November 2012), when it was put up for sale, presumably by the Kempthorne family:

> 'BANKING – CLAYTON & MORRIS PAPERS
> Collection of letters from the papers of the bankers Clayton & Morris, comprising an autograph letter by Frances Teresa Stuart, Duchess of Richmond, "La Belle Stuart", ... address panels, 8 pages, "Clayton MSS" stamp and the usual typed identifying dockets, minor browning, dust-staining, repairs etc., folio and small 4to, 1667-1688'

The lot realised £2,125 (Bonhams, 2012).

John Ley Kempthorne

John Ley Kempthorne was born in 1892 in Clerkenwell, London, the only child of James Keigwin Kempthorne and Florence Cecilia. Despite his London birth, his ancestry stretches back into Cornwall where his father, one of seven children of a farmer, variously recorded as a Medical Practioner, a Physician and Surgeon, was born in Mullion. All the family were from the Mullion/Manaccan area of the county. John Ley was an Associate of King's College London in 1915 shortly after which he married Marie Gertrude le Blond Landert Marks on 21 August in St Bartholomew's Church, London. He was ordained Deacon in 1916 and Priest in 1917 at the Church of St Philip Tottenham where he stayed until 1918. He then moved back to Cornwall where he became Rector of St Enoder (Crockford, 1929). Their only child, Loveday Ley, was born in 1921 in Falmouth. John remained there until his death on 22 May 1962 aged 70. Probate was granted to his widow Marie of Boscear St Just-in-Penwith when he left £5257 6s 10d (Probate). She subsequently died on 14 August 1968. Probate Bodmin 7 January £1110.

In this will, after various local parish bequests, he left his estate to the benefit of his wife, and 'at her death to daughter Loveday Ley Kempthorne and her heirs, on whom the trust shall devolve absolutely if they assume name and aims of Kempthorne. Cousin Renatus Kempthorne to have family documents and papers and any article of furniture descended to me from the Kempthorne family'.

Contact has been made with the son and subsequent heir of Renatus, another Renatus now living in New Zealand. He confirmed (pers. comm.) that he has the family papers referred to above, but no knowledge of the manuscript relating to Lundy. It has not been possible to ascertain whether the estate left to Marie and subsequently to Loveday contained this document. Given that Loveday was born in 1921 and that the papers appeared in auction in 2012, it is highly likely that they were sold on her decease.

Continuing with provenance, the next link backwards is to where and when J.L. Kempthorne acquired it. Hodgson's Rooms auction catalogue of Thursday 16 May 1929, catalogue page 39:

> 'A Collection of 14th - 18th century Deeds (from the Clayton MSS.) comprising Rentals, Surveys, "Particulars" and other documents and papers relating to London and various counties of England, mostly on parchment, many with seals, arranged in alphabetical order, with carefully compiled list to each one, details of which may be had on application.' (Hodgson, 1929).

There follows a list of 20 lots – 585 to 604 – of most counties of England together with the number of documents included totalling 5601. Devon is not included, but Lot 592 includes 166 documents: 91 from Gloucestershire, 60 from Somersetshire and 15 from Cornwall with a hand annotation of price realised of £1 4s. It seems the Particular of Lundy Island was included in this lot attributed to Cornwall rather than Devon.

Robert Clayton

Robert Clayton was born on 29 September 1629, son of John, a carpenter, and Alice in Bulwick Northamptonshire. His maternal uncle, Robert Abbott, was a scrivener who took him on as apprentice. Robert rose to become chief clerk and, on the death of his uncle, inherited his house and shop together with an annual income of £100. He went into partnership with his brother Peter, who became their chief clerk, and a fellow clerk, John Morris, to found a brokering, banking, conveyance and land agency.

They effectively founded the modern banking company, lending money on the security of deeds or promissory notes. The business was lucrative and as a by product they accumulated masses of documents. Robert incidentally was knighted in 1671 and elected to Parliament in 1679 (Melton, 2004).

All the paperwork generated from this business stayed with the family until just before the First World War when the Claytons' family seat, Marden Hall, was sold to the Greenwells. The bulk of these papers were passed on to the new owners. A sale of some papers took place in 1929 when Sir Peter Greenwell divided them into estate muniments, which he retained, and seventeenth century business and family records, which were sold. Many of these papers went directly to the Surrey Record Office and the Surrey Archaeological Society.

The largest group of papers was owned by George Sherwood, a private dealer in manuscripts who had obtained them from the Greenwells. They were sold at Sotheby's on 26 March 1929 to three principal purchasers. Seven hundred items went to the Public Record Office of Ireland; 5389 estate documents and title deeds were acquired by Hodgson's; and G. Michelmore acquired a collection of manuscripts and 3500 seventeenth century letters. Sherwood had other Clayton papers that he had acquired from sources other than the Greenwells which were sold later (Melton, 1979).

The document

The document consists of two sheets 14¾×11¾ inches (37.5×29.7mm) each folded in half to produce eight leaves; four contain the text and a fifth leaf forms a cover bearing various notations.

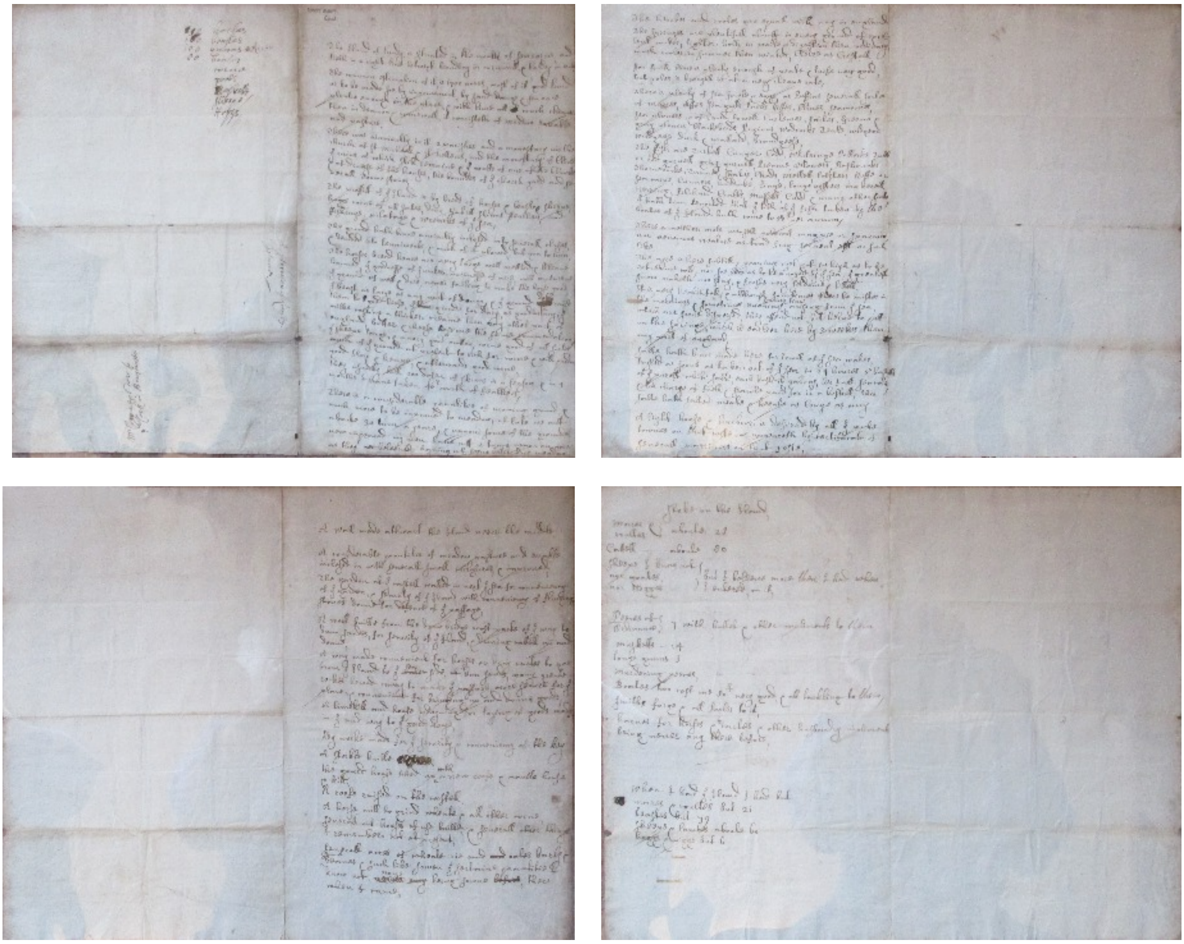


Figure 1: The two sheets – four sides, eight leaves – of the Particuler of Lundy Island, showing the arrangement of the the four leaves which contain the text and the fifth which, when the sheets are folded, forms a cover and summary

Each sheet of paper has two watermarks and shows clear lines from the paper making process (Figure 2). The larger watermark with grapes and figures enclosed the letters ‘PDC’; the smaller is a shield-shaped motif enclosing the letter ‘GA’. The wires are a consistent ⅞ inches (23mm) apart.

Research has been made into the documents that the Bodleian Library holds of the Clayton brothers archives (M.A. Williams, pers. comm.). Clayton documents were folded vertically so that they could be filed with a thin upper edge and long vertical axis. Along the top of this fold was written a brief description of the document. Figure 5 shows that this document conforms to this usage with the title ‘A particuler of Lundy Island’ written along it. The handwriting is also comparable to that seen on Bodleian documents.

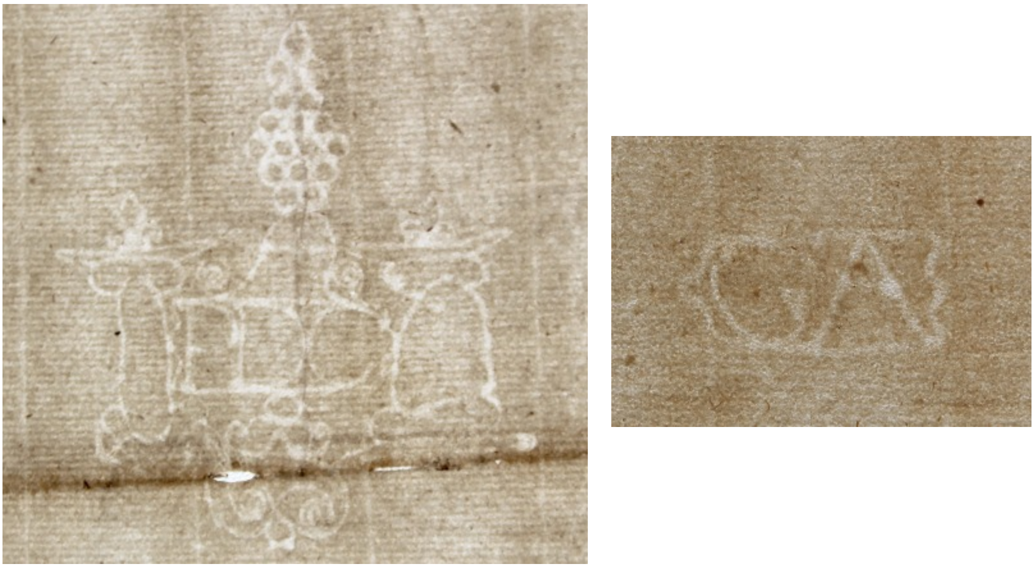


Figure 2: The regular lines and the two watermarks on both sheets of the document. Left: the ‘grapes and PDC’ watermark. Right: the ‘GA’ watermark

Paper

If light is allowed to pass through the paper, the watermarks and lines are clearly visible (Figure 2).

The regular lines are produced by the wires used in the handmade papermaking frame. The paper is darker near to the wires but in antique laid paper it is without shadow and dates the paper to post 1500 in a ‘new style improved design’. The paper certainly dates from before 1757, when woven paper was introduced and the wire and chain lines, intrinsic to earlier paper making, disappeared. Wires and chains were used in the paper mould to support the paper during production leaving their distinctive outline (Bertrand, 2017).

The paper has been subjected to hyperspectral imaging courtesy of the Bodleian Library to determine whether the paper had been used previously. It was proven not to be a palimpsest. That is, it is not reused papers; the only writing it has ever borne is that of the Particuler of Lundy Island.

TRANSCRIPTION

No attempt has been made to modernise or make consistent the spellings or to rationalise the use of upper or lower case letters. An attempt at explaining archaic words has however been made with some success. There are words which defy transcription which are signified by either a '?' or by an ellipsis where they are illegible.

In order to make it easier to relate the original to this transcription, pages and lines have been numbered – these do not appear on the original. The Old English 'thorn', often written as 'ye', has been transcribed as 'the'. The unusual symbol for 'and' has of necessity been transcribed as '+'. Occurrences of 'ff' have been transcribed to indicate the capital letter 'F'.

Cover (Figure 3)

1. A p[ar]ticuler of Lundy Island

2.	ii0 horses	[110]
3.	i60 beastes	[160]
4.	i00 gunns ...k...tt	[100 guns and possibly muskets]
5.	80 boates	
6.	Corne	
7.	Goods	
8.	Musketts	
9.	Sheepe	
10.	Hoggs	

11. Mr Couper next door to the Cock in Bowstreete

The first line gives the title to the document using an abbreviation based on the looped letter 'P' which is short for 'Par'.

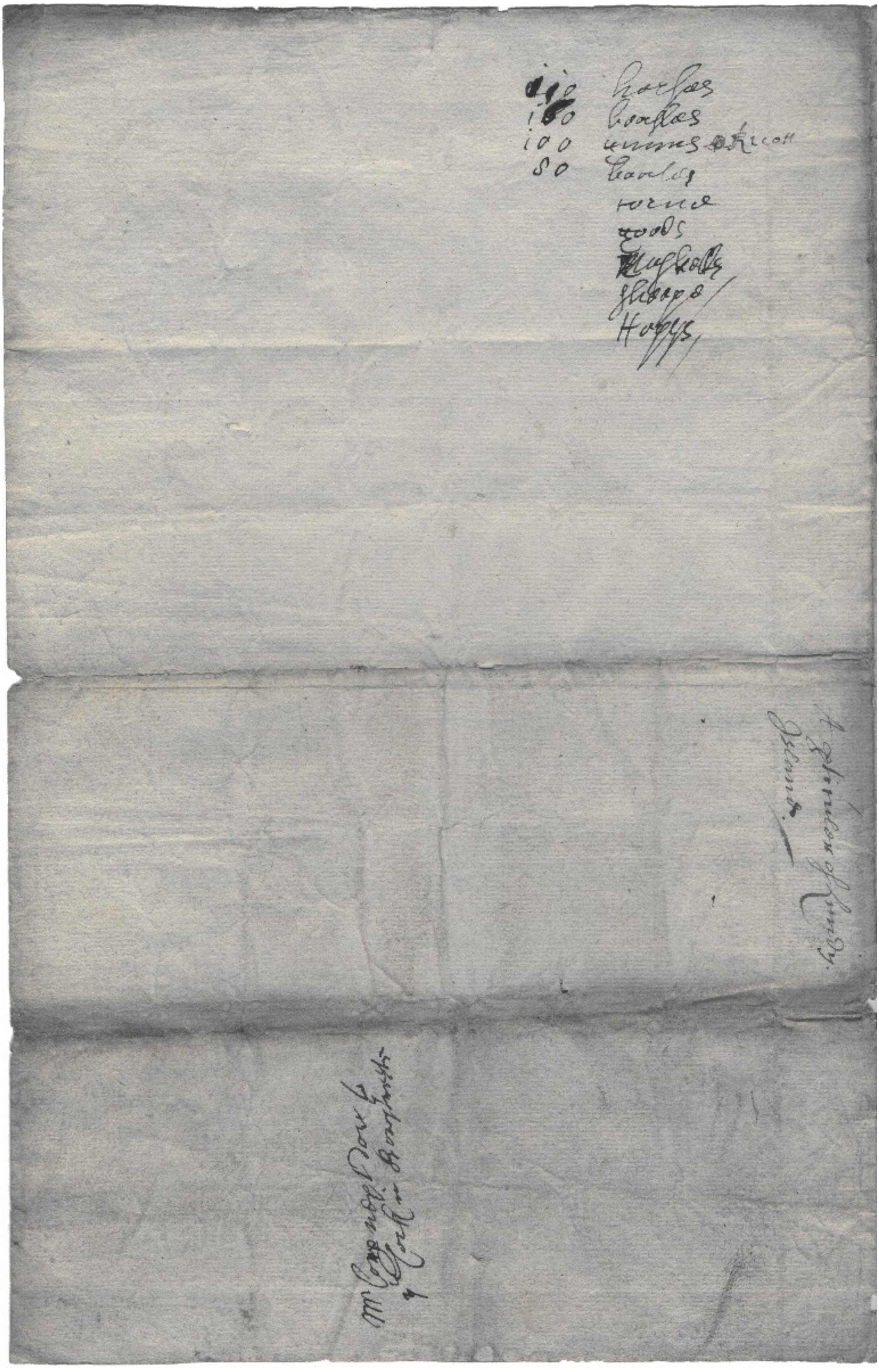
The list from lines 2 through 10, which is in a different hand from that of the main document, appears to show rough working out of the extent and perhaps value of stock, stores and other goods on the island. 'Beasts' at this period means specifically cattle as opposed to horses, sheep, pigs etc. '80 boats' is implausible, but it is likely that the writer of this summary has confused the number of the boats with their cost – see the transcription of page 4, line 13 of the document on page 29.

The final line indicates that the document was at some time addressed to Mr Couper at an address in Bow Street probably located in London.

Page 1 (Figure 4**)**

LUNDY ISLAND,
Cornw.

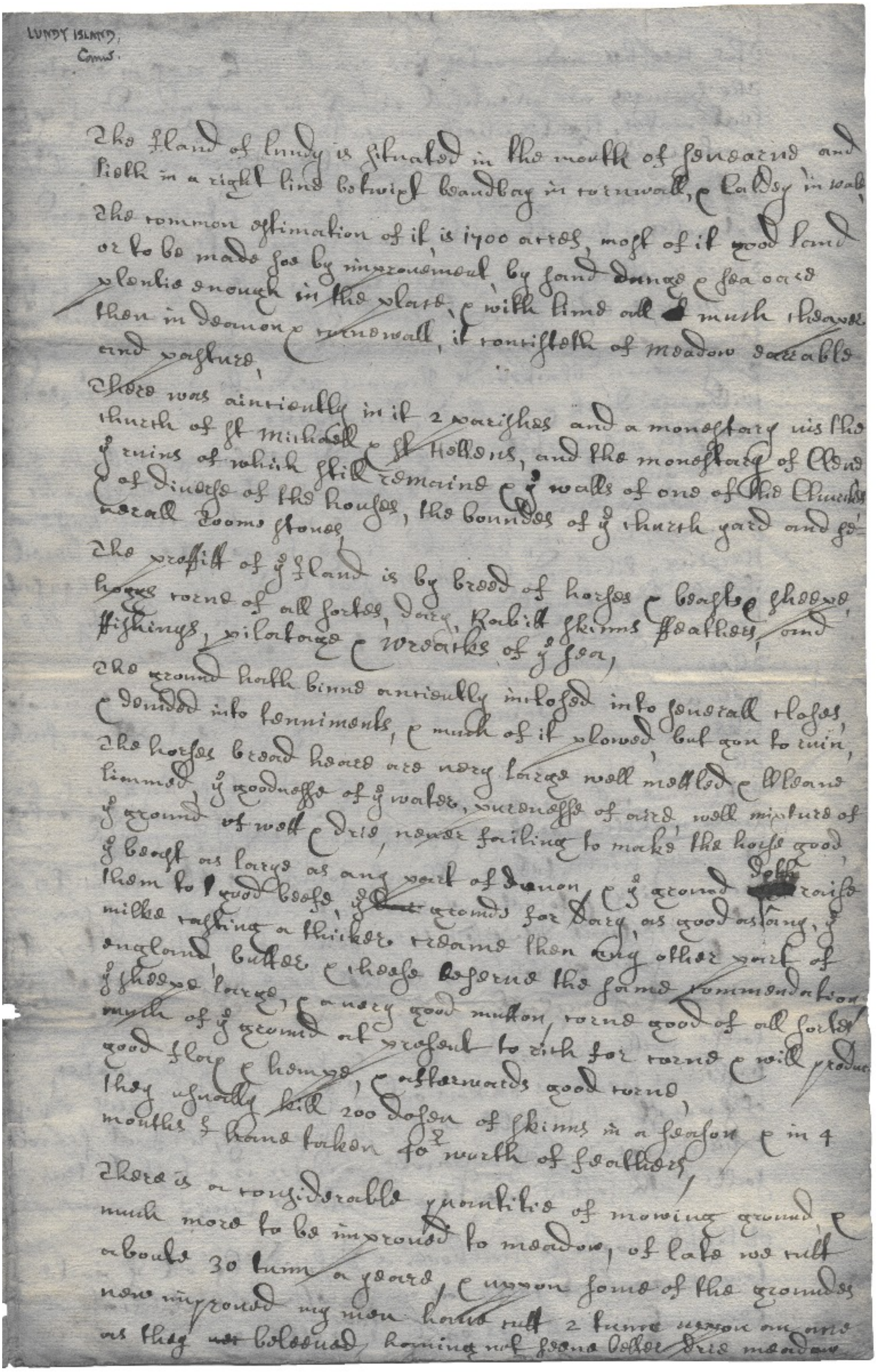
1. The Iland of lundy is situated in the mouth of sevearne and
2. lieth in a right line betwixt beaudbay in cornwall, + Caldey in Wales,
3. The common estimation of it, is 1700 acres, most of it good land
4. or to be made soe by improvement, by sand dunge + sea oar



[illegible] horses
[illegible] beastes
100 [illegible]
80 barley
corne
[illegible]
[illegible]
sheepe
Hoggs

A Relation of Lundy Island.

Figure 3: The Cover



LUNDY ISLAND,
Cornw.

The Island of Lundy is situated in the mouth of Severne and
lieth in a right line betwixt Handbay in Cornwall, & Caldey in Wales,
The common estimation of it is 1700 acres, most of it good land
or to be made soe by improvement, by sand dunge & sea oare
plentie enough in the place, & with lime all [illegible] much cheaper
then in Devon & Cornwall, it consisteth of meadow arable
and pasture,

There was anciently in it 2 parishes and a monestary viz the
church of St Michaell & St Hellens, and the monestary of Clone
ye ruins of which still remaine & ye walls of one of the Churches
& of divers of the houses, the bounds of ye church yard and se-
verall Toome stones

The proffitt of ye Island is by breed of horses & beasts & sheepe,
hoggs corne of all sortes, Dary, Rabitt skinns ffeathers, and
ffishings, pilotage & wreackes of ye sea,

The ground hath binne anciently inclosed into severall closes
& devided into tennements, & much of it plowed but gon to ruin,
The horses breed heare are very large well metled & cleane
limmed ye goodnesse of ye water, purenesse of aire well mixture of
ye ground of wett & drie, never failing to make the horse good,
ye beast as large as any part of Devon, & ye ground doth raise
them to good beefe, ye grounds for Dary, as good as any, ye
milke casting a thicker creame then any other part of
england butter & cheese deserve the same commendation
ye sheepe large, & a very good mutton, corne good of all sortes
much of ye ground at present to tith for corne & will produce
good flax & hempe, & afterwards good corne
They usually kill 200 dozen of skinns in a season & in 4
months I have taken 40l worth of feathers,

There is a considerable quantitie of mowing ground &
much more to be improved to meadow, of late we cutt
aboute 30 tunn a yeare, & upon some of the groundes
now improved my men have cutt 2 tunne upon an acre
as they ~~are~~ beleeved, having not seene better drie meadow

Figure 4: Page 1 (reverse of Page 2)

5. plentie enough in the place, + with lime all [erasure] much cheaper
6. then in deavon + cornewall, it consisteth of meadow areeable
7. and pasture,

The dark ink note in the top left-hand corner was applied to documents originating from the Clayton manuscript collection (Julian Browning pers. comm.) and offers further confirmation of originating from the Clayton Papers. Cornwall places it in the Sale at Hodgson's Rooms Thursday 16 May 1929 catalogue page 39 (Hodgson, 1929).

The document begins with a general geographical description of Lundy where it is placed in relation to Bude Bay in Cornwall rather than Bideford Bay in Devon. The black ink note also ascribes Lundy to Cornwall as do popular writings of the time: 'Over against the Coast of Cornwall is the Isle of Lundy in the Severn Sea' (Morden, 1701).

The area of the island has been variously given ranging from 3000 acres (1214 hectares) in 1775 (Martyn, 1837) to 1047 acres (424 hectares) at the last sale (1969). Around 1050 acres (425 hectares) is the currently accepted area of Lundy (Loyd, 1925; Sale, 1925; Compton & Key, 2000) but 1700 acres (688 hectares) was a fair estimation for this period when the shape and size of the island was similarly inaccurate.

'Sand dunge + sea oare' are exactly what they appear, using the archaic words 'sea oare' for Oar weed (*Laminaria digitata*) which was traditionally used as a fertiliser.

8. There was ainciently in it 2 parishes and a monestary vis the
9. church of St Michaell + St Hellens, and the monestary of Cleve
10. the ruins of which still remaine + the walls of one of the Churches
11. + of diverse of the houses, the boundes of the church yard and se=
12. verall toome stones,

The two 'parishes' of St Michael and St Helens have been referred to by Ternstrom (2008) and Orme (2012). This double dedication dates to between 1641 and 1671 (NAO, 1641, 1657 and 1670/1) and indeed Ternstrom and Orme agree this dedication was only in use in the sixteenth and seventeenth centuries.

Rather than there being two buildings, there would most probably have been one dedicated to St Helen (Ellen) with the other, St Michael, perhaps referring to an aisle or chapel within the original structure. The lower courses of the chapel or cell do still remain and a later account (Anon, 1787) gives dimensions which can still be verified.

The 'ruins of a monastery' is consistent with usage that describes such property owned by, in this instance, Cleeve Abbey which possessed Lundy for the purpose of collecting tithes. The reference to several tombstones begs the question of who they commemorated. The oldest extant grave stones in the United Kingdom are generally seventeenth century. Typically, early gravestones were erected inside the church by those wealthy and literate enough to do so. There was little need to commemorate those of lesser stature. Being illiterate nothing other than a cross or device to show their trade would have been recognised by most of their mourners (White, 1978).

There could have been inscribed stones on Lundy. Or did this reference to these several stones mean the more recently discovered four inscribed early Christian memorial stones on Beacon Hill in their original positions, or does it refer to another burial place in Bulls Paradise? Given that the whole paragraph groups the church, graveyard and its boundary and tombstones all together, were 'diverse of the houses' within this enclosure? It may be that the subsequently excavated archaeology was more visible at this time.

13. The proffitt of the Iland is by breed of horses + beasts + sheepe
14. hoggs corne of all sortes, dary, Rabitt skins Feathers, and
15. Fishings, pilotage + wreacks of the sea,

This is a fairly straightforward statement of income from farming, fishing and salvage. The sale of Rabbit skins and seabird feathers features frequently in subsequent accounts of Lundy (e.g. Sale, 1822).

16. The ground hath binne anciently inclosed into severall closes,
17. + devided into tenniments, + much of it plowed, but gon to ruin,

The reference to closes – a piece of land enclosed within hedges, fences or walls – and tenements – any holding of land and buildings (FitzHugh, 1985) – are land and agricultural terms and are amply depicted in Wyld's map of 1822 (Sale, 1822, Figure 7). This is the earliest map which gives any detail of what Lundy looked like and may show the relics of the features which existed from the seventeenth to the nineteenth centuries. It lists six closes as well as other fields and of course Widow's Tenement and two other holdings, Morisco and Newtown, which may at one time have been individual tenements.

18. The horses bread heare are very large well mettled + Cleane
19. limmed, the goodnesse of the water, purenesse of aire, well mixture of
20. the ground of wett + drie, never failing to make the horse good,
21. the beast as large as any part of Devon, + the ground [erased] doth raise
22. them to good beefe, the [erased] grounds for Dary, as good as any, the
23. milke casting a thickere creame then any other part of
24. england, butter + cheese deserve the same commendation
25. the sheepe large, + a very good mutton, corne good of all sortes
26. much of the ground at present to rich for corne + will produce
27. good flax + hempe, + afterwards good corne,

Expanding further on the benefit of Lundy to breeding of horses, it is little wonder that in a time when the only motive power available was horse driven they should feature so importantly. As well as describing the land as being used for arable agriculture, dairy farming is highlighted as too is raising stock for beef, mutton and pork together with crops of corn, flax and hemp. There is some indication of good farming practice too in reference to enriching the land by growing flax and hemp before planting with corn.

28. they usually kill 200 dozen of skinns in a season + in 4
29. months I have taken 40£ worth of feathers,
30. There is a considerable quantitie of mowing ground, +

31. much more to be improved to meadow, of late we cutt
32. aboute 30 tunn a yeare, + uppon some of the groundes
33. now improved my men have cutt 2 tunne upon on acre
34. as they ner beleeved having not seene better drie meadow

The 200 dozen of skins (2400 pelts) undoubtedly refers to the killing and skinning of rabbits (*op. cit.* page 1 line 4) as well as the harvesting of sea birds for their feathers. A further sales pitch is the yield of up to 2 tons per acre for silage.

Page 2 (Figure 5)

1. The hearbes and rootes are equall with any in England
2. The springes are plentifull almost in every ground of excel=
3. lent water, lighter both in waite + digestion then ordinary,
4. much cooler in summer then winter, Cleere as Cristall,

There has not been much change in the 450 years since the document was written. These statements are repeated in each subsequent publication about the island, for example Risdon, 1605; Fiennes, 1647; Morden, 1701; Martyn, 1775 (in Steinman, 1836); Sale, 1822.

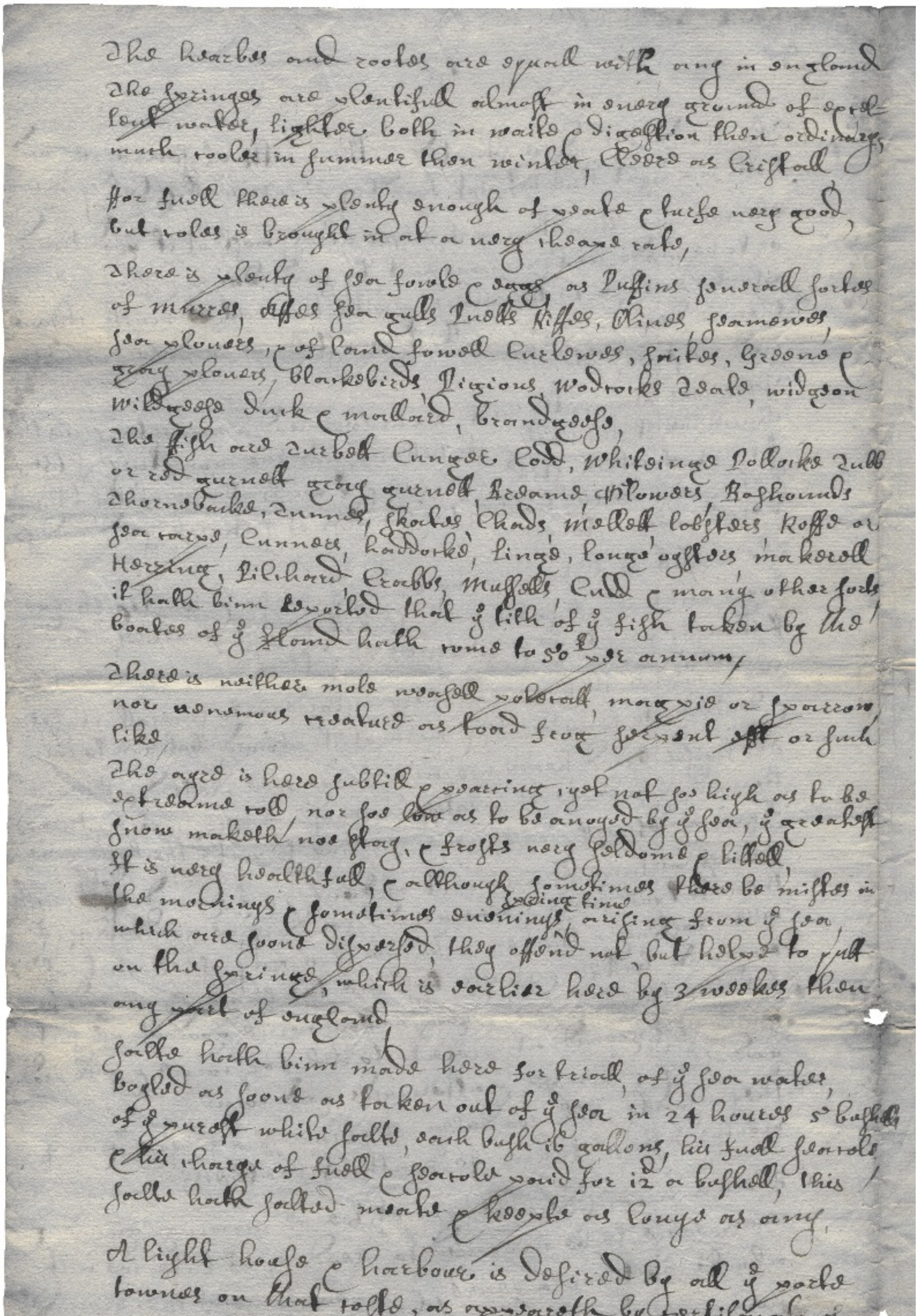
5. For fuell there is plenty enough of peate + furze very good,
6. but coles is brought in at a very cheape rate,

Although peat and furze (furze=gorse, *Ulex* sp.) are still present on the island, there is no evidence of any peat digging although the Sale (1822) document does mention peat for firing. The mention of ‘coles’ is relevant to the production of salt mentioned later on this page.

7. There is plenty of sea fowle + eggs, as Puffins severall sortes
8. of murres, affes sea gulls Puetts Kiffes, Olives seamewes,
9. sea plovers, + of land fowell Curlewes, srikes Greene +
10. gray plovers, blackebirds, Pigions, Wodcocks, Teale, widgeon
11. Wildgeese duck + mallard, brandgeese,

Tables 1 and 2 (page 19) show the names of marine birds and terrestrial birds listed in lines 7-11 together with their modern and scientific names. Table 3 (page 20) shows the names of the fish listed in lines 12-16 together with their modern and scientific names.

12. The Fish are Turbott Cunger Codd, Whiteinge Pollocke Tubb
13. or red gurnett gray gurnett, Breame, Plowers [?], Bashounds
14. Thornebacke, Tunnes, skates, Chads, Mellet, lobsters, Roffe or
15. sea carpe, Cunners, haddocke, Linge, longe oysters makerell
16. Herring, Pilchard, Crabbs, Mussells, Cudd + many other sorts
17. it hath binn reported that the tith of the fish taken by the
18. boates of the Iland hath come to 50£ per annum,



The hearbes and rootes are equall with any in england

The ſpringes are plentifull almoſt in euery ground of excellent water, lighter both in waite & digeſtion then ordinary, much cooler in ſummer then winter, cleere as criſtall

ffor fuell there is plenty enough of peate & turfe very good, but coles is brought in at a very cheape rate,

There is plenty of ſea fowle & eggs as Puffins ſeuerall ſortes of murres, eſſes ſea gulls Noddes Kittes, Olines ſeamewes, ſea plouers, & of land fowell curlewes, ſnites, greene & gray plouers, blackebirds Pigions, Wodcocks Teale, widgeon wildgeeſe ducke & mallard, brandgeeſe,

The fiſh are Turbott Cunger, Codd, whitinge Pollocke Tubb or red gurnett gray gurnett Breame, fflowers Roghounds Thornebacke, Tunnes, ſkates, Chads, mellett lobſters Koffe or ſea carpe, Cunners, haddocke, linge, longe oyſters makerell Herring, Pilchard, crabbs, Muſſells, Cull & many other ſorts it hath bin reported that ye tith of ye fiſh taken by the boates of ye Iland hath come to 50li per annum,

There is neither mole weaſell polcatt, magpie or ſparrow nor venemous creature as toad frog, ſerpent ~~eft~~ or ſuch like

The ayre is here ſubtill & peircing, yet not ſoe high as to be extreame cold, nor ſoe low as to be anoyed by ye ſea, ye greateſt ſnow maketh noe ſtay, & froſts very ſeldome & little

It is very healthfull, & although ſometimes there be miſtes in the mornings & ſometimes euenings ſpring time ariſing from ye ſea which are ſoone diſperſed, they offend not, but helpe to putt on the ſpringe, which is earlier here by 3 weekes then any part of england

ſalte hath bin made here for triall, of ye ſea water, boyled as ſoone as taken out of ye ſea in 24 houres 5 buſhells of ye pureſt white ſalte, each buſh 16 gallons, his fuell ſeacole & his charge of fuell & ſeacole paid for 12d a buſhell, this ſalte hath ſalted meate & keepte as longe as any,

A light houſe & harbour is deſired by all ye porte townes on that coaſte, as appeareth by certificate of ſeuerall marriners on that coaſte,

Figure 5: Page 2 (obverse of Page 1)

Table 1: Sea Fowle (Marine Birds)

Manuscript	**Modern Name**	**Scientific Name**	**Refs/notes**
Puffin	Puffin	*Fratercula arctica*	
murres	Auks Razorbill or Guillemot	Alcidae *Alca torda* or *Uria aalge*	Greenoak, 1979
affes/asses	Assilag=Storm Petrel	*Hydrobates pelagicus*	Hett, 1902
sea gulls	Sea Gull	Laridae	
Puetts Puit Gull	Peewit Gull Black-headed Gull	*Vanellus vanellus* *Croicocephalus ridibundus*	Greenoak, 1979; Hett, 1902
Kittes/Kiffes	Kites or Kittewakes Kitiwake (Hett)	Accipitrae sp. *Buteo buteo* *Rissa tridactyla*	'Kite' in the south west is a generic term for both Kite and Buzzard
Olives	Oyster Catcher	*Haematopus ostralegus*	Greenoak, 1979; Hett, 1902 Essex dialect
seamewes	Common Gull Herring Gull	*Larus canus* *Larus argentatus*	Greenoak, 1979 Hett, 1902
sea plovers	Golden Plover	*Pluvialis apricaria*	Jones, pers. Comm.

Table 2: Land Fowell (Terrestrial Birds)

Manuscript	**Modern Name**	**Scientific Name**	**Refs/notes**
Curlewes	Curlew	*Numenius arquata*	
srikes	Shrikes	*Lanius* sp.	Hett, 1902
Green plovers	Green Plover/Lapwing	*Vanellus vanellus*	Hett, 1902
gray Plovers	Golden Plover	*Pluvialis apricaria*	Jones, pers. comm.
blackebirds	Blackbird	*Turdus merula*	
Wodcocks	Woodcock	*Scolopax rusticola*	
Teale	Teal	*Anas crecca*	
Widgeon	Widgeon	*Anas penelope*	
Wildgeese	Wild Geese	Anserinae	
ducks	Ducks	Anatidae	
mallards	Mallard	*Anas platyrhynchos*	
brandgeese	Brent Goose	*Branta bernicla*	Hett, 1902

Table 3: Fish

Manuscript	**Modern Name**	**Scientific Name**	**Refs/notes**
Turbott	Turbot	*Scophthalmus maximus*	
Cunger	Conger	*Conger conger*	
Codd	Cod	*Gadus morhua*	
Whiteinge	Whiting	*Merlangius merlangus*	
Pollocke	Pollock	*Pollachius pollachius*	
Tubb	Tub Gurnard	*Chelidonichthys lucerna*	
Red Gurnett	Red Gurnard	*Chelidonichthys cuculus*	
Gray Gurnett	Grey Gurnard	*Eutrigla gurnardus*	
Breame	Bream	*Abramis* sp.	12 species from British waters
Plowers			No modern synonym found
Bashounds	Bass	*Dicentrarchus labrax*	
Thorneback	Thornback Ray	*Raja clavata*	
Tunnes	Tunny	*Thunnus* sp.	Probably Bluefin Tuna *Thunnus thynnus*
Skates	Skate	Family Rajidae	
Chads	Shadd	*Alosa* sp.	
Mellet	Mullet	Family Mugilidae	3 species most likely Grey Mullet *Chelon labrosus*
Lobster	Lobster	*Homarus gammarus*	
Roffe/Sea Carpe	Ruffe	*Gymnocephalus cernuus*	Freshwater or brackish water
Cunners	Bergall	*Tautogolabrus adspersus*	Wikipedia
Haddocke	Haddock	*Melanogrammus aeglefinus*	
Linge	Ling	*Molva molva*	
Longe Oysters	Spiny Lobster	*Palinurus elephas*	Sea Crayfish (OED Online)
Makerell	Mackerel	*Scomber scombrus*	
Herring	Herring	*Clupea harengus*	
Pilchard	Pilchard	*Sardina pilchardus*	
Crabbs	Crab	Decapoda - Brachyura	
Mussells	Mussels	*Mytilus edulis*	
Cudd	Cod	*Gadus morhua*	

19. There is neither mole weasell polecatt, magpie or sparrow
20. nor venomous creature as toad frog serpent eft or such
21. like

This is a reference to the Tudor vermin acts. An eft is a newt. In order to protect grain stocks following periods of plagues such as the Black Death and subsequent dearth of labourers in farming, Henry VIII and later Elizabeth I enacted ‘An Acte made and ordeyned to dystroye Choughs, Crowes and Rokes 1533’ (24 Henry VIII cap 10) and ‘An Acte for the preservation of Grayne 1566’ (8 Eliz cap 15) respectively. These acts specifically mention, amongst other species, Moles, Weasel, Magpies and Sparrows on which a bounty per head was paid through the parish.

The absence of amphibians and reptiles would equate this island to places such as Ireland where they are also absent. It is echoed by Grose (1776) when he quotes from ‘Walter Baker, a Canon of Osney (Lundy)’.

22. The ayre is here subtill + pearcing, yet not so high as to be
23. extreame cold, nor soe low as to be anoyed by the sea, the greatest
24. snow maketh noe stay, + frosts very seldom + littell,
25. It is very healthfull, + although sometimes there be mistes
26. in the mornings + sometimes evening springtime [inserted] arising from the sea,
27. which are soone dispersed, they offend not, but helpe to putt
28. on the springe, which is earlier here by 3 weekes then
29. any part of england,

All recent visitors to Lundy will no doubt concur as to these statements. The rarity of snow and ice, the occurrence of layers of sea mist and the comparatively mild weather are all still to be relished – another sentiment that has been repeated each time there is a publication about Lundy (Anon, 1787).

30. Salte hath binn made here for triall of the sea water,
31. boyled as soone as taken out of the sea in 24 houres 5 bushells
32. of the purest white salte, each bush 16 gallons, his fuell seacole,
33. + his charge of fuell + seacole paid for 12d a bushell, this
34. salte hath salted meate + keepte as longe as any,

The Grenville family owned Lundy for most of the seventeenth century. One of them, Sir Bevil Grenville (owner 1619-43), was an experimenter who pioneered the smelting of tin with coal instead of charcoal (Granville, 1895). He could be credited with similar experiments with the production of salt. Charles Thomas (1994) excavated briquetage from the Iron Age site in the graveyard. This is the term used to describe broken ceramic material used to make salt evaporation vessels or the pillars that supported them. There is no suggestion that this is where the seventeenth century salt making took place. Adjacent to the east wall of the castle is what is described as a furnace (NT HRO 109054) which is presumed to have been a smithy. Andrew Fielding (pers. comm.)

suggests that this could have been where sea water was heated to evaporate salt. It would seem more efficient to evaporate salt at sea level where saltwater and coal would both be present without carriage. However the extreme tidal range – up to 11m – and lack of any permanent area which could be used militates against this location. The connection with the Grenvilles and Bushell suggests that the technology and will was there which, together with the description in the manuscript, suggests salt was locally produced for domestic purposes at least.

35. A light house + harbour is desired by all the porte
36. townes on that coste, as appeareth by certifacate of
37. severall marriners on that coste,

Although generally thought to be desirable, nothing officially is recorded regarding a request for such a light-house until the seventeenth century. No light-house was built until undertaken by Trinity House in 1819 (see also Discussion).

Page 3 (Figure 6)

1. A wall made athwart the Iland neere the middle,

This is the wall known today as Quarter Wall. The map which accompanies the Sale of 1822 shows ‘Halfway Wall’ – now known as Quarter Wall – and the newly erected ‘North Wall’ (Figure 7), subsequently ‘Halfway Wall’. The southernmost wall, now known as Quarter Wall is undoubtedly medieval in origin (NT HRO MNA 102667) but may have been rebuilt or repaired by John Warren Borlase post 1752. Benson employed convict labour to erect what is now Halfway Wall around 1750 and the third and most northerly wall, Threequarter Wall, was built in 1878 during the Heaven ownership by the tenant farmer Thomas Wright (Langham, 1970, NT HRO 108122).

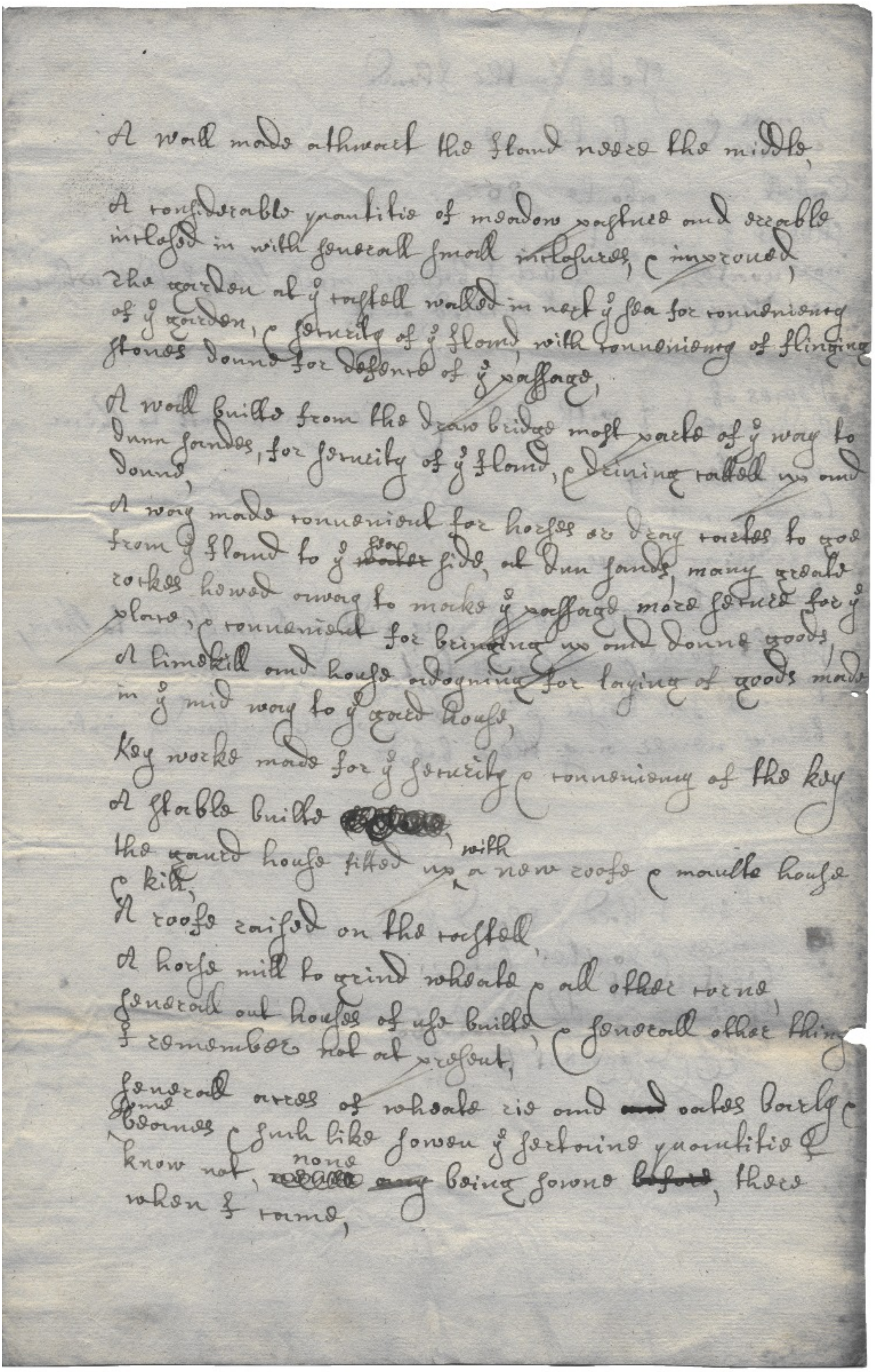
2. A considerable quantitie of meadow pasture and arrable
3. inclosed in with severall small inclosures, + improved,

This is a repetition of the statements made on the first page lines 16-17 (Figure 7).

4. The garden at the castell walled in next the sea for conveniency
5. of the garden, + security of the Iland, with conveniency of flinging
6. stones dovne for defence of the passage,

Grose (1776) shows this enclosed garden in his map of the castle. The National Trust Heritage record dates it to the late seventeenth century (NT HRO 108756) (Figure 8).

7. A wall builte from the draw bridge most parte of the way to
8. dunn sandes, for security of the Iland, + driving cattell up and
9. dovne,
10. A way made convenient for horses or dray cartes to goe
11. from the Iland to the water sea side, at dun sands, many greate
12. rockes hewed away to make the passage more secure for the
13. place, + convenient for bringing up and dovne goods,



A wall made athwart the Iland neere the middle,

A considerable quantitie of meadow pasture and errable inclosed in with severall small inclosures, & improved

The garden at ye castell walled in next ye sea for conveniency of ye garden, & securitie of ye Iland, with conveniency of flinging stones downe for defence of ye passage,

A wall builte from the draw bridge most parte of ye way to Dunn sandes, for securitie of ye Iland, & being called up and downe,

A way made convenient for horses or dray cartes to goe from ye Iland to ye ~~water~~ sea side, at Dun sands, many greate rockes hewed away to make ye passage more secure for ye place, & convenient for bringing up and downe goods,

A limekill and house adjoyning for laying of goods made in ye mid way to ye guard house,

Key worke made for ye securitie & conveniency of the key

A stable builte ~~[illegible]~~,

the guard house fitted ~~up~~ with a new roofe & maulte house & kill,

A roofe raised on the castell,

A horse mill to grind wheate & all other corne,

Severall out houses of use builte, & severall other things I remember not at present,

Severall acres of wheate rie and ~~and~~ oates barly & some beanes & such like sowen ye certaine quantitie I know not, none ~~[illegible]~~ ~~any~~ being sowne ~~before~~, there when I came,

Figure 6: Page 3 (reverse of Page 4)

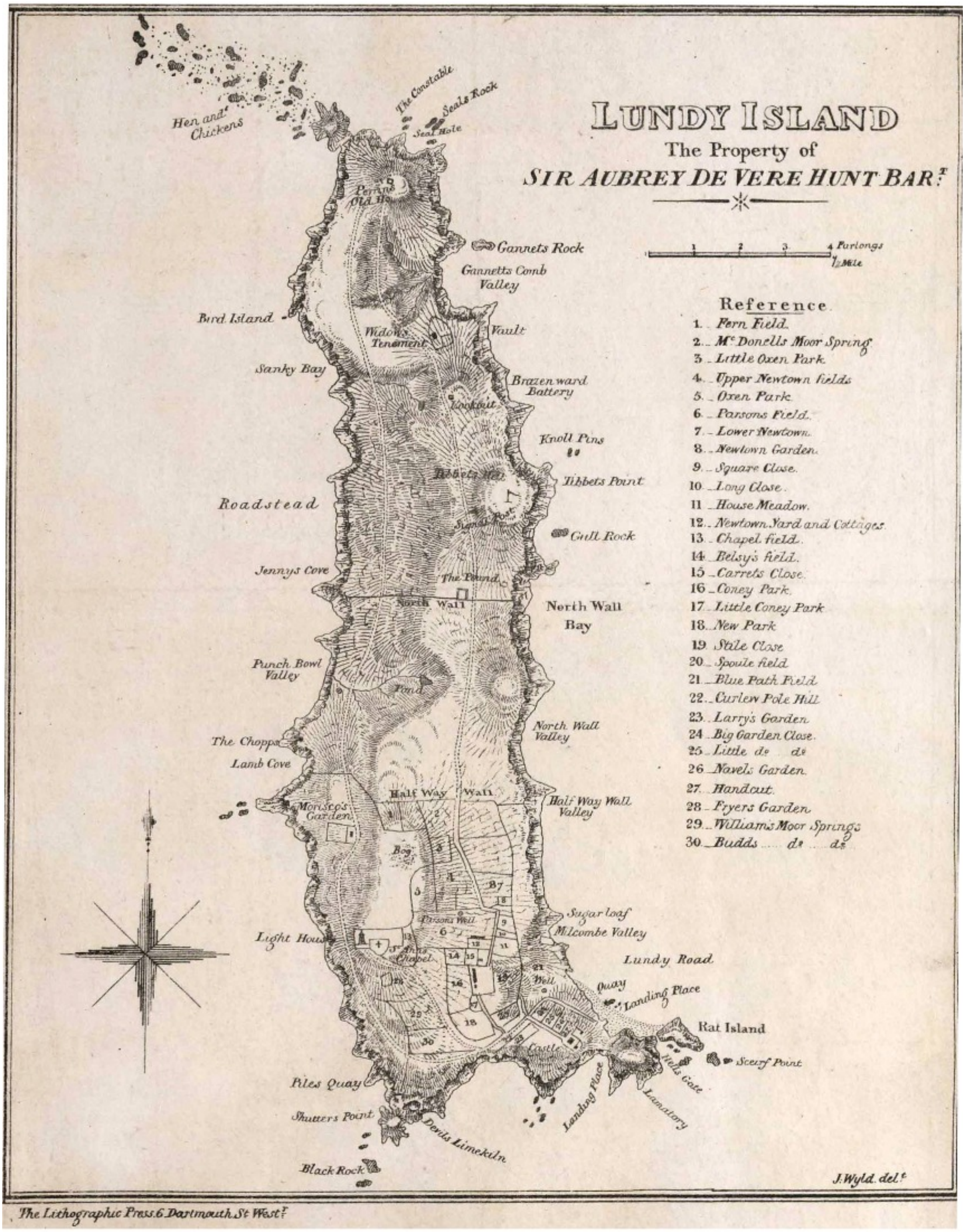


Figure 7: Wyld's map for De Vere Hunt 1822 showing existing closes and tenements, the dividing walls 'athwart the island', castle environs and roads most of which may not have changed between the mid-seventeenth and early nineteenth centuries.
© British Library Board add ms 4034s

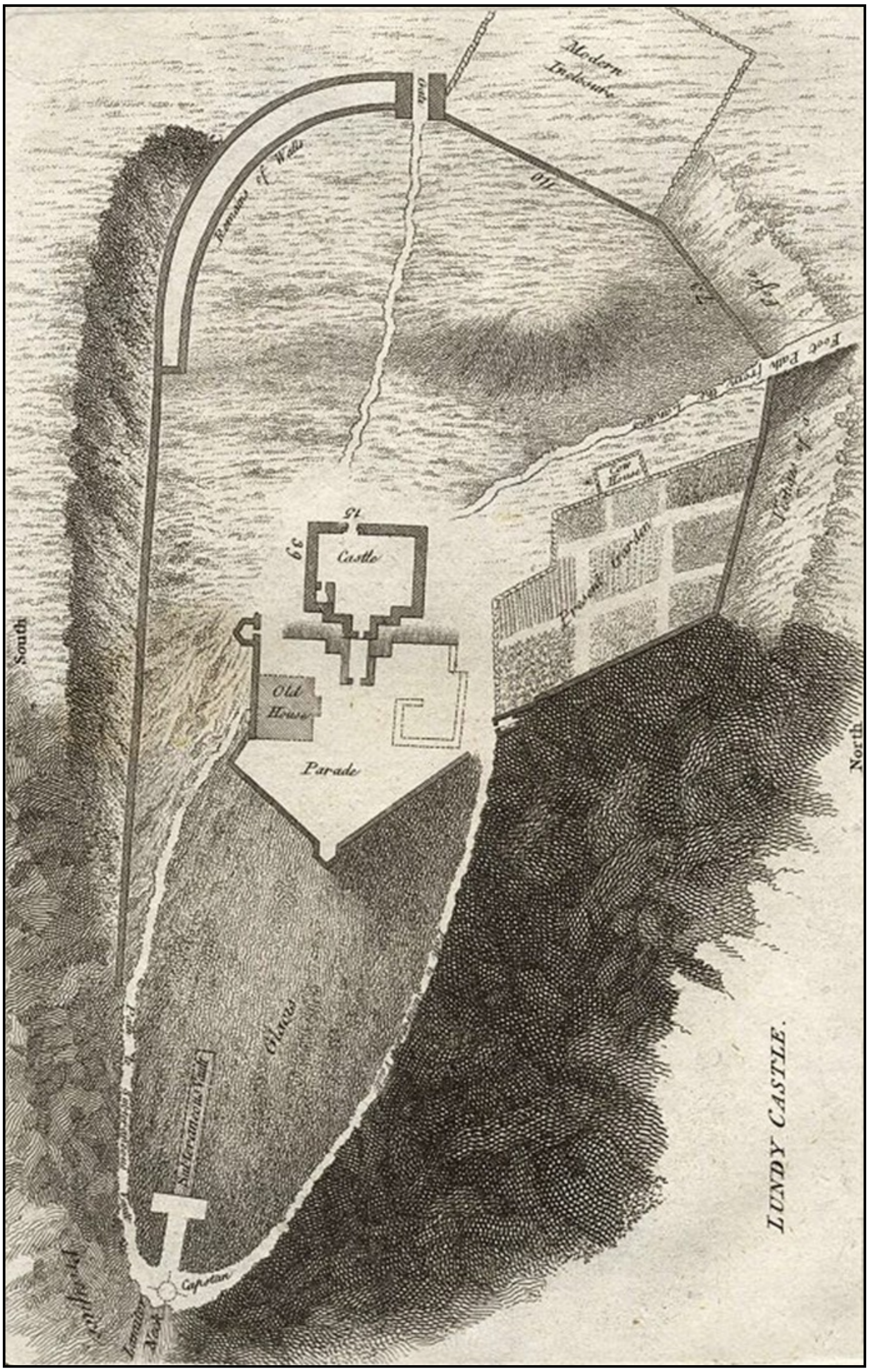


Figure 8: Illustration from Grose (1776) showing the castle, gatehouse and gardens

The draw bridge features in Grose (1776) (Figure 8). The existence of the wall is later confirmed in the description of the island given by the anonymous writer of 1787 (Anon, 1787). So too is the description of the road down to the landing beach. Cattle were obviously taken down this road to be embarked or disembarked and it was of sufficient gradient that carts could be used for transportation of goods. The description of how this was achieved is new information revealed in this manuscript.

14. A limekill and house adoyning for laying of goods made
15. in the mid way to the gard house,

A limekiln existed until its destruction in 1954 (NT HRO 108954) (Figure 9). Grose (1776) quotes the account of a visitor who describes 'a watch tower near the landing place …'. The NT Heritage database refers to a possible guardhouse built into the corner of the castle curtain wall which may have been subsequently used as a 'privy' (NT HRO 109051).

Figure 9: The limekiln in 1951 (author's collection)

16. Key worke made for the security + conveniency of the key

The Parkyas map (1804) (Figure 10) shows a quay in existence. When the foundations for the current shore building were being excavated, a cobbled wall and floor were uncovered looking very like this original quay (Roger Fursdon pers. comm.). Although it was backfilled during the construction phase, there are sea-worn granite blocks recovered from the Landing Beach which could well have been part of the quay that collapsed at some time. These were recovered from the lower Landing Beach during construction of the road in 2008 (Derek Green pers. comm.) (Figure 11).

17. A stable builte [erased],
18. the gaurd house fitted up with [inserted] a new roofe + maulte house
19. + kiln,

The lime kiln stood on the slipway adjacent to the landing beach (Figure 9), but the existence and locations of stable and malt house were previously unknown. See line 15 regarding the guard house.

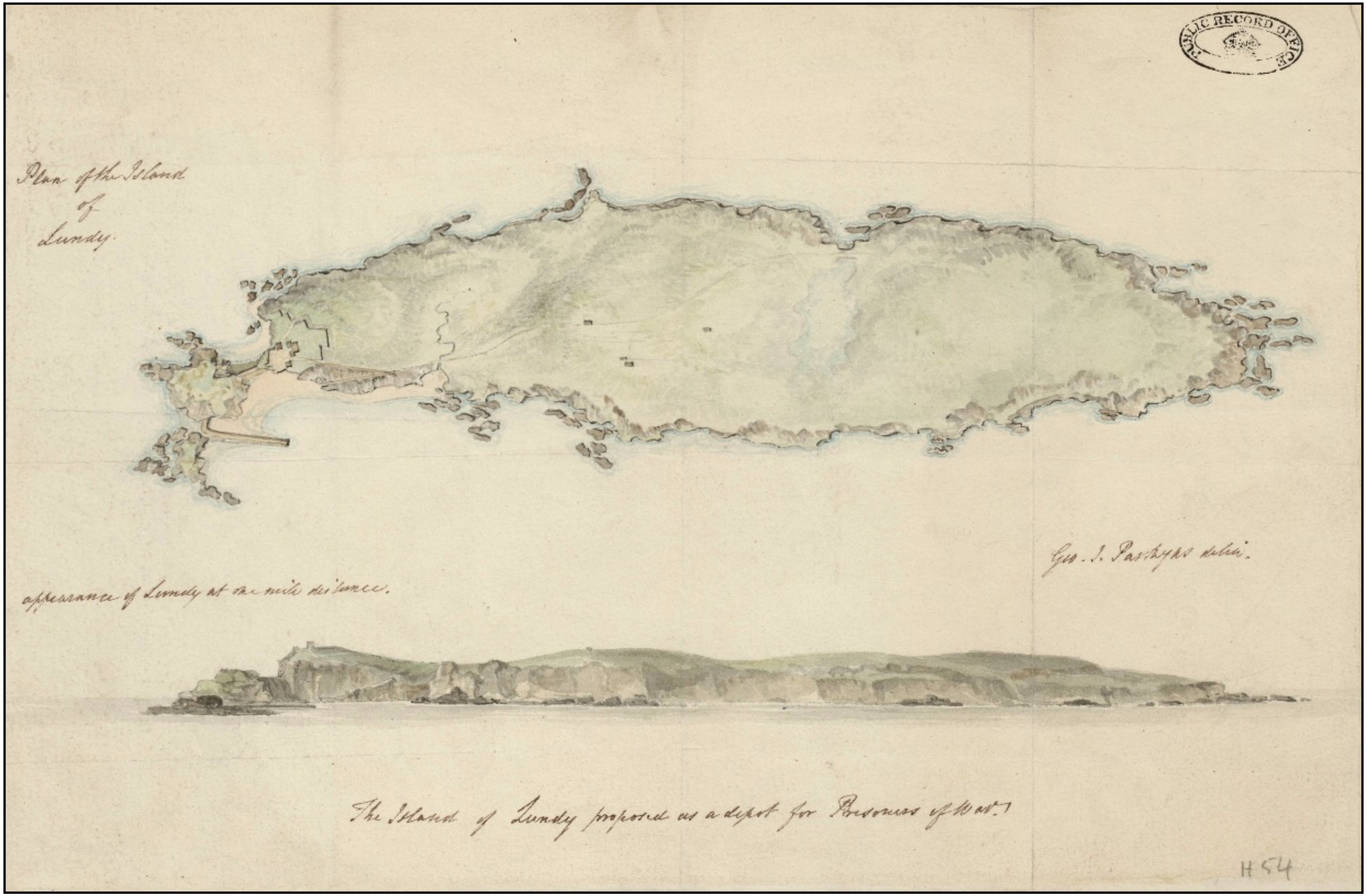


Figure 10: The Parkyas map of 1804 clearly showing the quay, access road, the castle and its walls. © British Library Board MPH 1 54

Figure 11: Contemporary photograph of sea-worn granite from an old quay.
© Alan Rowland

20. A roofe raised on the castell,
21. A horse mill to grind wheate + all other corne,

There was a horse mill in what is now known as the barn, housed in the round house. It is not known how old this building is or if it could be the building referred to.

22. severall out houses of use builte, + severall other thing[s]
23. I remember not at present,

These are developments in and around the present village or castle although exactly what and where is unclear. Grose (1776) quotes a visitor describing the buildings on the island to include the Castle, the Chapel, the remains of a house near St Helen's Well (present day Barton's field area) and an adjacent brewhouse, and watch towers at both north and south of the island.

24. Severall acres of wheate rie and ~~and~~ oates barly +
25. some [inserted] beanes + such like sowen the sertaine quantitie I
26. know not, [illegible crossing out] none ~~any~~ being sowne ~~before~~, there
27. when I came,

This list of crops shows that new crops were being experimented with.

Page 4 (Figure 12)

1. Stoke on the Iland,
2. Mares + } aboute 28
3. coultes }
4. Cattell aboute 80
5. Sheep I know not }
6. nor goates, } but I beleeve more then I had when
7. nor Hogges } I entered, on it,

8. Peeces of } 7 with bullet + other impliments to them
9. Ordinance }
10. musketts 14
11. longe gunns 3
12. Murdering peeces,
13. Boates two cost me 80£ very good, + all tackling to them,
14. smiths forge + all tooles to it,
15. harnes for horses + 2 cartes + other husbandry impliments
16. being never any there before,

17. When I had the Iland I had but
18. mares + coultes but 21
19. beastes but 79
20. sheepe + lambes about 60
21. hoggs + piggs but 6

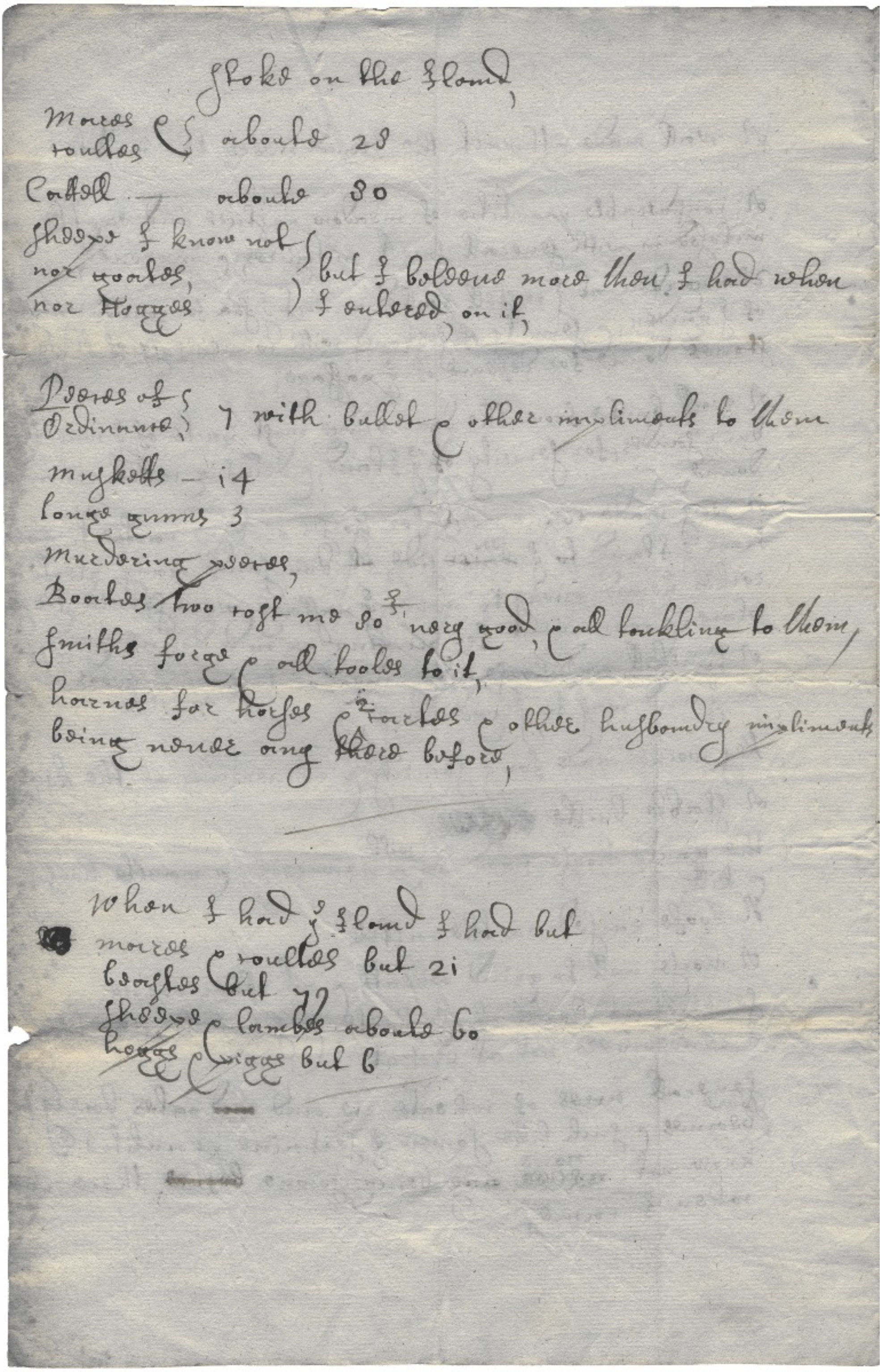
This is the inventory page, summing up much of what has gone before.

A musket is a firearm designed to be fired with the stock braced against the shoulder.

A long gun listed between musket and murdering piece and numbering only three probably refers to a type of cannon with a long barrel as opposed to a short howitzer or carronade. A ‘murdering peece’ in contrast was a small piece of artillery designed to be fired from loopholes or embrasures in towers, fortifications or portholes in a ship (Hamlet iv 5. 92) – essentially anti-personnel cannon loaded with case-shot which was filled with small bullets, nails, old iron, etc. ‘Murdering peece’ became obsolete later in the seventeenth century when carronades replaced them (OED, 2015).

It is relevant to consider the reported number of horses – 28 compared with 21 when the writer was on the island. Similarly 80 cattle compared with 79 and his lack of knowledge of sheep, goats and pigs when he formerly husbanded 60 sheep and 6 pigs. It suggests that he had left the island some time previously. Compare these figures with the current stock levels of: Lundy ponies 20; Domestic Sheep 300; Soay Sheep 250; Feral Goats 20; Domestic Pigs 6 sows, 1 boar and 33 weaners; plus Sika Deer 100 (Kevin Welsh pers. comm.)

The possession of a boat for access, harness for the working horses and a smithy to maintain their hooves and the necessary farming implements show the self-sufficiency of the island community.



Stocke on the Iland

Mares & coultes aboute 28
Cattell aboute 80
Sheepe I know not
nor goates, } but I beleeve more then I had when
nor Hogges } I entered on it,

Peeces of Ordinance 7 with bullet & other implements to them
muskettes – 14
longe gunns 3
murdering peeces,
Boates two cost me 80 li very good, & all tackling to them,
smiths forge & all tooles to it,
harnes for horses & cartes & other husbandry implements
being none any there before,

When I had ye Iland I had but
mares & coultes but 21
beastes but 77
sheepe & lambes aboute 60
hogges & pigges but 6

Figure 12: Page 4 (obverse of Page 3)

DISCUSSION

The manuscript reads like an estate agent's persuasive description to buy an attractive and lucrative island and business. This contrasts with Grenville's desire to retain ownership at all costs and, where it passed to state-appointed occupiers, demands for recompense for the drain the island had on the occupiers' income. In the first instance, in 1630, Sir Bevil Grenville, who had recently spent considerable amounts on improving Lundy, refused to sell it to Sir William Godolphin for 'less than £5000'. In 1631, in a letter from Sir Bevil Grenville to Sir John Eliot, he mentions he had recently made a quay and harbour. In Sir Bevil's letters to his father, Sir Bernard Grenville, he mentions sending gulls' eggs and salt birds from the island and his failure to catch some Knots and inability to send butter (Granville, 1895).

Around 1631-2 Sir Bevil was approached by Sir Henry Bouchier to purchase Lundy. His father, Sir Bernard, who always felt the island to be a financial and burdensome drain on him, encouraged the sale. Sir Bevil wrote to his father to explain why he would not sell. His enthusiasm and expectations for the island shine through. The phrases used, and affection apparent, in this letter are mirrored in the text the Particuler (Stucley, 1983).

However, in 1638 the island was apparently offered up for sale when an 'offer to purchase' was recorded (Hervey 1921). Later, in 1646, Lord Saye and Sele appears to have bought the island. This is supported by an indenture of 1669 between John Cooper and John Earl of Bath being a release for £2600 (PRO, 1663). This has been interpreted as the redemption of a loan secured on Lundy, or Lundy may have been sold by Say and Sele to a third party who then sold it back to the Grenville family.

Certainly during the Civil War period it passed through Royalist hands from the Grenvilles to others such as Bushell.

Sir Bernard Grenville wrote to the Secretary of State on 30 June 1633, officially putting into words what had been spoken about freely in the early years of the seventeenth century. From 1608, when a commission took dispositions from three persons to the effect that pirates had taken Lundy and were robbing passing ships, until the mid-seventeenth century pirates were present and widely complained about. In 1625 Turkish pirates had taken the island and threatened to set fire to Ilfracombe. From 1628 to 1634 the pirates occupying Lundy were perpetually causing problems along the adjacent coasts. There is no evidence for petitions for the erection of a lighthouse until Thomas Benson was on the island in 1751 (Ternstrom, 2007) (see also the manuscript page 2 lines 35-37).

With regard to all the building work referred to in the manuscript (e.g. page 3 line 16) Sir Bevil may not be responsible for all of this work. Up until 1639 he had devoted himself to improving and adding to his home at Stowe in Kilkhampton. It would appear that once this project was completed he turned his attention to his island of Lundy (Stucley, 1983). His letter to his father around 1630-31 refers to his impending visit to Lundy: 'I am going thither this week to see my great works finished, which I hope will be within this month.' (Figure 8).

There still exists a letter written on 17 September 1631 (Granville, 1895) from Sir John Eliot to Sir Bevil Grenville from the Tower of London in which he was imprisoned. In this, Sir John advises his friend that 'Keyes ar usuall and unquestioned … but no color of fortifications is allowable …'.

Sir Bevil's reply also exists written on 9 October *(ibid)*: '… you have dealt so ingeniously with me concerning my late undertaking at Lundey.'

It is clear that Sir Bevil had begun work on his quay before September 1631 and continued its construction with the cautious consent of Sir John.

And again (manuscript page 3 line 20) Stucley (1983) asserts that not only did Grenville build the harbour and quay but also either built or, as suggested in this document, made repairs to the castle and guard house as protection from the marauding pirates in the Bristol Channel.

There can be little doubt that this is an original document. In fact it does beg the question as to what advantage would there be to create such a document with so many verifiable as well as new facts (Chris Webster, pers. comm.). The paper is original and contemporary with the seventeenth century; it has not been used for any other purpose; and the Secretary Hand was in use at the time of its origin. The phraseology used and reference to the 'parishes' of St Michael and St Ellen are all of the seventeenth century. It is unfortunate that the document is neither signed nor dated.

As to when it was written, it was later than 1631 as the Grenville Quay completed around that time is in existence. The period when the Clayton brothers were collecting their documents and establishing their banking system was between 1660 and 1682 (Melton, 1979) which further narrows down the date of the document to a 50-year period.

Who wrote it and why is another difficult question to determine. The phraseology echoed that used by Sir Bevil Grenville in the surviving letters that he wrote to his father and to Sir John Eliot. The originals of Grenville's letters stored in the Devon Record Office (Chris Webster pers. comm.) show a completely different hand, so he can be ruled out as the writer, and this is in any case consistent with his refusal to sell the island in his lifetime (Granville, 1895).

The last page discloses that the writer, who is no longer on the island, did occupy it and remembers various items of stock and husbandry that were there when he resided there. He may have been the owner or the owner's bailiff, but contrary to most accounts of this time he describes the island as fruitful and with affection. This is in contrast to the expenditure subsequent owners report incurred on erecting or maintaining buildings and the means by which to journey to and from the island.

A most intriguing document is an indenture of 1669. There is much of it which is illegible, but it appears to be the redemption of a loan secured on Lundy between John Cooper and John Earl of Bath for release of an indenture of £2600. This indenture could have been a supporting document to prove the value of the island (PRO, 1663).

It is unique in listing birds and fish for this early period. The mention of salt-making was previously unknown as were the stock levels. Details of the island's arms and of the buildings also throw new light on seventeenth century Lundy.

ACKNOWLEDGEMENTS

Richard Samways is a retired archivist and a registered member of the Archives and Records Association. Andrew Fielding is an archaeologist with a particular interest and expertise in the production of salt. Tim Jones, co-author of the Birds of Lundy and co-recorder of birds for Lundy, is an ornithologist with wide knowledge with particular depth on Lundy. Dr Keith Hiscock is an Associate Fellow of the Marine Biological

Association who has been closely involved with the LFS as Chairman and with Lundy as promoter and surveyor of the Lundy Marine Conservation Zone. Chris Webster who obtained a copy of Sir Bevil Grenville's handwriting to prove he was not the writer of the manuscript nevertheless reassured us that the document is genuine.

REFERENCES

Anon. 1787. *A Journal of the time I spent on the island of Lundy in the year 1787.* North Devon Record Office 3704/SS/LUI

Bertrand, A., Institut d'histoire du livre, *The Shape of Paper.* http://ihl.enssib.fr/en/paper-and-watermarks-as-bibliographical-evidence/the-shape-of-paper (accessed 30 May 2017)

Bonham, *Auction catalogue Lot 93 2014.* https://www.bonhams.com/auctions/21764/lot/93/ (accessed 30 May 2017)

Bonham, *Auction catalogue Lot 16, 2012.* http://www.bonhams.com/auctions/20139/lot/16/ (accessed 30 May 2017)

Browning, J. Historical Autographs Ltd. http://www.historicalautographs.co.uk/ (accessed May 2014)

Compton, S.G. & Key, R.S. 2000. *Coincya wrightii* (O.E. Schulz) Stace. *Journal of Ecology*, 88, 535-547

Crockford's clerical directory. 1929. London: Oxford University Press

Fiennes, R., *A brief declaration of the serverall passages in the Treaty concerning the Surrender of the garrison of Lundy, now under the command of Tho. Bushell Esq. Governour thereof for his Majestie. Printed in the year 1647.*, Parliament London 1648

FitzHugh, V.H. 1985. *The Dictionary of Genealogy*, Alphabooks: Dorset

Granville, R. 1895. *The History of the Granville Family.* W. Pollard & Co.: Exeter

Greenoak, F. 1979. *All the Birds of the Air.* Deutsch

Grose, F. 1776. The Castle in the Isle of Lundy. *The Antiquities of England and Wales*. Vol. 4, London: Hooper

Hervey, M.F.S. 1921. *Life, Correspondence and Collections of Thomas Howard Earl of Arundel.* Cambridge University Press

Hett, C.L. 1902. *A Glossary of Popular, Local and Old-Fashioned Names of British Birds*. Henry Sotheran & Co.

Hodgson & Co. 1929. A *Catalogue of Books with other properties for sale by auction* No 21 of 1928-9. London

Klein, M.E. *et al.*, *Quantitative Hyperspectral Reflectance Imaging*. Sensors 2008 www.mdpi.com/1424-8220/8/9/5576/pdf (accessed 6 June 2017)

Langham, A. and M. 1970. *Lundy (The Island Series)* David & Charles: New York

Loyd, Lewis R.W. 1925. *Lundy its History and Natural History*. Longmans: London

Melton, F. 2004. 'Clayton, Sir Robert (1629-1707)', *Oxford Dictionary of National Biography*, Oxford University Press; online edition, Oct. 2007. http://www.oxforddnb.com/index/5/101005579/ (accessed 13 June 2015)

Melton, F.T. 1979. The Clayton Papers. *Journal of Historical Research,* Vol. 52, issue 125. Blackwell

Morden, R. 1701. *The New Description and State of England*. London

National Archives CP 25/410/17, (1641) CP 25/2/547/ (1658), CP/645/22 (1670-1)

NTHRO - National Trust Heritage Records Online https://heritagerecords.nationaltrust.org.uk/ (accessed 20 August 2017)

OED Online. March 2015. Oxford University Press. http://www.oed.com.libezproxy.open.ac.uk/view/Entry/123869?result=1043&rskey=JHoBuD& (accessed May 24, 2015).

Orme, N. 2012. *The Ecclesiastical History of Lundy.* Journal of the Lundy Field Society, 3, 125-6

Parkyas, Geo. 1804. *Plan of the Island of Lundy* British Library MPH_1_54

PRO C 12 822/3. BL1663. Bushell

Risdon, T. *The chorographical description, or, survey of the county of Devon*, London, c.1605

Sale notice de Vere Hunt, British Library add_ms_4034s 1822

Sale notice Messrs Knight, Frank & Rutley. London 1925

Steinman, G.S. 1836. *Some Account of the Island of Lundy*. Collectanea Topographica et Genealogica. Volume 4

Stucley, J. 1983. *Sir Bevill Grenville and his times.* Chichester: Phillimore

Ternstrom, M. 2007. *Light over Lundy.* Whittle: Caithness

Ternstrom, M. 2008. *Questions concerning the Ecclesiastical History of Lundy*. Journal of the Lundy Field Society, 1, 65-86

Thomas, C. 1994. *And Shall These Mute Stones Speak?* University of Wales: Cardiff

White J. 1978. *Monuments and their Inscriptions*. Society of Genealogists

Williams, M.A. 2015. The Clayton sampler. *Discovering Lundy: The Bulletin of the Lundy Field Society*, No. 45 December

CLUTCH SIZE IN KITTIWAKES *(RISSA TRIDACTYLA)* ON LUNDY

by
Thomas E. Dickins[1], Kirsty Neller and Robert Spencer
Faculty of Science and Technology, Middlesex University, London, NW4 4BT
[1]Corresponding author, e-mail: t.dickins@mdx.ac.uk

ABSTRACT

Kittiwake *(Rissa tridactyla)* numbers on Lundy have been in decline for many decades. This decline is monitored using occupied nest counts and productivity data. More recently we have begun collecting data on clutch size at one colony on Lundy. Clutch size is a direct response by a bird to prevailing conditions. Therefore, clutch size data is potentially revealing in terms of what it tells us about Kittiwake response to factors such as food availability and predation risk, in a way that occupied nest counts and productivity data is not. Calculating clutch size is not straightforward for a colonial cliff nesting bird. In this paper we present a pilot study that has calculated clutch size, and then use that data to assess differences in clutch size across the colony with reference to possible differences in predation risk as a function of colony structure. We discuss the limitations of this pilot and also key aspects of the broader ecology, which we believe should also be monitored in order to better understand the plight of this seabird.

Keywords: *Lundy, kittiwakes, clutch size, productivity*

INTRODUCTION

There is much research investigating Kittiwake (*Rissa tridactyla*) decline in the north of the United Kingdom (U.K.) and in particular the North Sea. Far less work has been conducted on southern populations (McMurdo Hamilton *et al.* 2016).

We have begun monitoring a colony on Lundy in order to address this issue, but also to pilot the collection of reliable clutch size data. In this paper we present pilot data, discuss the methods involved, and test to see if differences in clutch size are related to key aspects of colony structure that may increase or reduce threats to breeding success. We also make comment on predation and food webs in the context of a broader discussion about key ecological factors.

CLUTCH SIZE

As a direct investment in fitness, the causes and consequences of clutch size variation have been much studied (Ricklefs 2000; Stearns 1992; Winkler & Walters 1983). Clutch size varies within and between species; but females in a given species can be said to produce a modal number of eggs.

Lack assumed that the key factor influencing clutch size is food availability; natural selection acted to set clutch size at a value that can be supported by background food resource

(Lack 1947). This hypothesis was modified to include foraging effort and maintenance (Cody 1966) and the costs of reproduction associated with larger broods (Ricklefs 1970), but at root it was food availability that was seen as the principal factor. As Ricklefs (1970) pointed out, the food web dynamics, incorporating predator-prey interactions, may help to account for variation in clutch size. For example, clutch size is lower nearer to the equator, possibly as a consequence of higher rates of inter-specific competition for prey items. This would impact upon functional prey abundance. This view sees clutch size as responsive to local ecological parameters, within limits set by natural selection.

Lack's hypothesis was applied to all birds without consideration of life-history differences (Winkler & Walters 1983) and his sole concern was with the optimum number of offspring that resource would allow. Life-history theory has since been incorporated, using individual fitness maximization as the modelling assumption, and allowing consideration of trade-offs between current and future reproductive effort, and quality and quantity of offspring (Stearns 1992). The longevity, and developmental trajectory of birds will introduce different solutions to these trade-offs; and longevity and development are themselves subject to natural selection and niche specialization (Winkler & Walters 1983). Some of these solutions will be plastic, in response to local ecological variation, and will be optimal solutions (Stearns 2000)

Nest predation has also been hypothesized as a factor in reducing laid clutch size. Larger clutches may take longer to process, and thus increase exposure to predators; predators may more readily detect larger broods; and, smaller clutches make the production of a replacement clutch easier, due to 'saved resource', or increase parent survival chances across more than one breeding season (Julliard *et al.* 1997).

It is clear that clutch size is sensitive to ecological variables. Variation in clutch size is a direct response to conditions in the recent past and present breeding season; a response based on the information processing capacities of the birds themselves. Various mathematical models allow clutch size data to predict the number of fledglings produced, assuming no predation (Stearns 1992) which would allow estimates of fledging success to be more accurate following productivity surveying. In essence, a shortfall could be accurately calculated that was sensitive to the adult birds' reproductive decision each season. Given this, clutch size data should be of great use in the monitoring of species of conservation concern, alongside the more usual data on apparently occupied nests and productivity (Bibby *et al.* 2000).

THE KITTIWAKE

The Kittiwake is the most common gull worldwide, found in both the North Atlantic and North Pacific oceans. Kittiwakes are a long-lived species, with some birds living 28 years or more. They are a seasonal breeder, returning to the coast in the late winter and beginning their breeding effort in April (Coulson 2011). They have low levels of philopatry, recruitment relying upon immigration, and high levels of nest site loyalty (Coulson & Coulson 2008). Kittiwakes are highly monogamous, with a 25% divorce rate and an 11% partner mortality rate per annum. Divorce is associated with poor breeding success the previous year (Coulson 1966).

Kittiwakes are a nidicolous species, with chicks in need of adult care for food up until fledging and thermoregulation during the early days post hatching. Most models of clutch size discussed above rely upon altricial, or nidicolous, species whose young put demands upon their parents. These demands yield specific life-history trade-offs. In a long-lived species, those trade-offs can span across future generations leading to sabbatical years in breeding and calibration of breeding effort in part through control of clutch size (Erikstad *et al.* 1998; Stearns 1992).

Clutch size varies from one to three eggs, with the mean clutch size slightly below two-eggs, and more one-egg clutches than three (Coulson, 2011). Average clutch size can vary annually in some regions, whilst remaining stable in others. Clutch size is possibly related to individual quality and also breeding experience, with inexperienced breeders producing more eggs (Coulson & Porter 1985). It is also possible that clutches of more than one egg are a bet-hedging response, such that the beta chick in this asynchronously hatching species is an insurance policy against the loss of an alpha chick. Such a strategy should be sensitive to local conditions and may lead to the emergence of obligate siblicide (Anderson & Ricklefs 1992; Dickins & Clark 1987). Experimental evidence suggests that Kittiwakes produce optimal clutch sizes that match the number of young they can successfully fledge (Jacobsen *et al.* 1995).

The status of the Kittiwake

In the U.K., Kittiwakes are red-listed due to a 40% decline in breeding populations between 1969 and 2008 (Eaton *et al.* 2015; JNCC 2009). Food availability has been linked to colony success, especially in northern populations (Coulson *et al.* 1985; McMurdo Hamilton *et al.* 2016). During the breeding season, year-zero sand-eels *(Ammodytidae)* are the principal source of food for adults and their chicks. Sand-eels prefer cold winters to spawn (Frederiksen *et al.* 2004) and climate change has affected sand-eel recruitment, in turn affecting Kittiwakes (Frederiksen *et al.* 2005). It is possible that food availability impacts upon adult survival rather than breeding effort (Oro & Furness 2002). There is also evidence that commercial fisheries, marine contaminants, introduced species and visual disturbance to the marine environment are all contributing to a widespread decline in seabird populations (JNCC 2009). Few data are available on clutch size effects but, in one study, Hamer and colleagues found that it was not affected by food availability. Instead, food availability appeared to impact upon fledging success (Hamer *et al.* 1993).

Populations on Lundy have declined over many years, with many colonies collapsing (Davis & Jones 2007; Price *et al.* 2013). Records began in 1939 when there were 3,000 occupied nests. 1950 saw the next complete survey, when there were 1,387 occupied nests. From 1950 to 1973 11 surveys were undertaken and the numbers peaked at 2,026 and dropped to 718. From 1981 (933 occupied nests; Figure 1) there has been a steady decline, to a population of 127 occupied nests (Price *et al.* 2013).

Wardens have undertaken productivity surveys on the island since 2007, going beyond nest occupancy data. The data have been published for the current field site (Figure 2a,b) (Saunders 2008; Wheatley 2011; Wheatley & Saunders 2010; Brown *et al.* 2011; MacDonald 2014).

Whilst food resource may be an issue, so is predation risk. Avian predators will take eggs and chicks at the nest, and adults in flight. Key predators, such as Great Black-backed Gulls (*Larus marinus*) and Peregrines (*Falco peregrinus*) have thrived in recent years (Davis & Jones 2007).

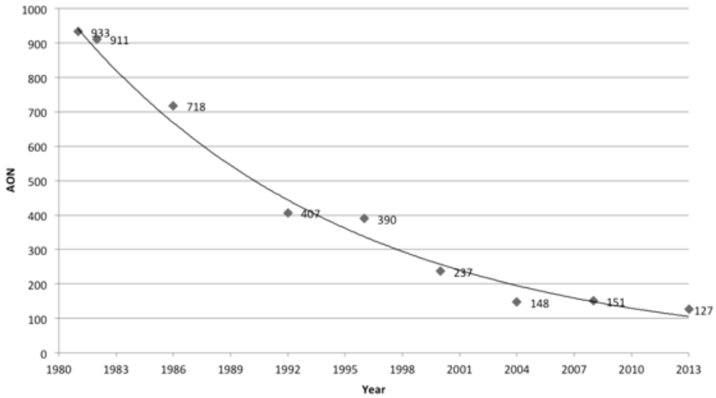


Figure 1: Declining Kittiwake numbers (unit: apparently occupied nests, AON) on Lundy over nine surveys from 1981 to 2013, with exponential fitted ($y=6E+61e^{-0.068x}$)

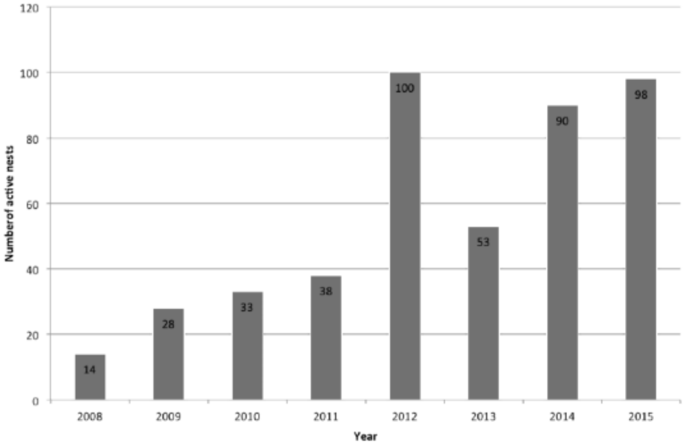


Figure 2a: Number of active nests for the Aztec Zawn colony across eight years. Data for 2012, 2014 and 2015 provided directly by Beccy MacDonald (Warden); all else sourced from JNCC: http://jncc.defra.gov.uk/smp/ and publications cited

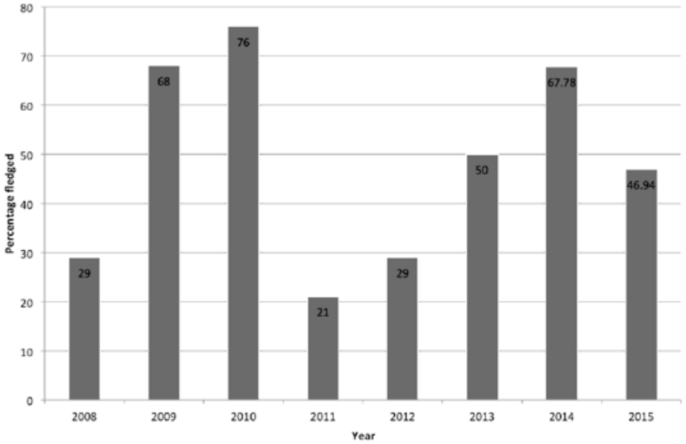


Figure 2b: Kittiwake breeding success data for the Aztec Zawn colony across eight years. Success is the number of birds fledged per active nest site, expressed as a percentage. Data for 2012, 2014 and 2015 provided directly by Beccy MacDonald (Warden); all else sourced from JNCC: http://jncc.defra.gov.uk/smp/ and publications cited

COLONIAL NESTING

Colonial nesting provides group defence, which can deter predators. Colony-level hatching synchrony reduces the chances that an individual egg or chick is predated (Birkhead 1977). Benefits may also accrue in foraging: mass feeding on fish schools will disrupt fish defences, but also information about foraging sites is possibly shared (Clode 1993).

Kittiwakes nest on narrow ledges on sea-cliffs (Coulson 2011; Cullen 1957; Danchin & Nelson 1991), and occasionally on buildings (Coulson *et al.* 1985). Naturally occurring sites can be on broad, exposed cliff faces, or within narrow gullies and inlets. Kittiwakes often share ledges with Guillemots *(Uria aalge)* in the U.K. and other auk species elsewhere. Nesting density, ledge accessibility and wind conditions have all been shown to correlate with predation rates of auks by *Laridae* (Birkhead 1977; Gaston & Nettleship 1981; Gilchrist *et al.* 1998).

Kittiwake eggs and chicks are commonly predated by large gulls, including Herring gulls *(Larus argentatus)* and Great Black-backed gulls, and corvid species (Coulson 2011; Dixon 1979). Peregrine falcons also take chicks at night (Collins *et al.* 2014) and will take adults in flight (Hipfner *et al.* 2011). Hipfner and colleagues demonstrate that the presence of Peregrines deters other predators, thereby reducing the overall predation rate on Kittiwakes. A similar hypothesis has been mooted for the relationship between Guillemots and *Laridae* on Lundy (Davis & Jones 2007), such that territorial gulls nesting nearby would chase off other gulls and corvids, thereby reducing the overall predation rate. It is possible this may extend to Kittiwakes given the close proximity of their nesting to territorial Great Black-backed gulls.

Kittiwakes rarely raise an alarm call and they allow predators to approach much closer than a ground nesting bird would (Cullen 1957) prior to taking flight. Kittiwakes rarely attack predators, although intense predation may lead to greater defence (Massaro *et al.* 2001). According to Cullen, it is the inaccessibility of the nest sites that is the main defence.

Nest sites will vary individually with respect to ledge structure, position in the colony, and therefore accessibility to predators, such that variation in predation rates within colonies should be expected (Aebischer & Coulson 1990; Massaro *et al.* 2001; Regehr *et al.* 1998). Aebischer and Coulson (1990) demonstrated that there was no difference in mortality risk for adults nesting in the centre of the colony, compared with the periphery. However, peripheral nesters had a higher rate of mortality at sea in the winter months, possibly indicating some fitness differential across the colony. There was no evidence of increased egg and chick loss at the periphery of colonies, relative to the centre. The colonies used in this work were under very low predation risk (Regehr *et al.* 1998).

Regehr and colleagues (1998) studied populations under very high predation rates. The predators were Great Black-backed gulls, Herring gulls and Ravens *(Corvus corax)*, all under food stress, and they took 90% of Kittiwake eggs in each year of a two-year study. This is exceptionally high, the authors citing a 5% loss, mostly to Ravens, when other prey items were abundant in previous years. Regehr *et al.* found that productivity was ‘highest on sheer cliffs, and lowest on irregular and less steep cliffs’ (p.913), indicating that access was important to predators. Great Black-backed gulls found landing on more regular, steep cliff structures more difficult; overhangs above nests reduced predator access and led to higher productivity. In the second year of the study a central position in the colony predicted productivity.

The central portion of a colony is that which is settled first during annual recruitment (Coulson 2011) and is not related to the topography of the site. However, if Aebischer and Coulson (1990) are correct, and centrally nesting birds are of higher quality in some way, it is possible that these are more dominant birds that are actively choosing a safer set of nest sites. Regehr *et al.* (1998) have partially supported the idea of a central benefit to productivity, and this may simply be a consequence of reduced ease of access and increased group defence. However, this effect was only found during one year. It is also of note that birds settling the centre of a colony tend to be older and have arrived at the coast earlier (Coulson, 2011). It is possible that this population is larger, and aggregates more densely enabling reduced predation risk and higher productivity at times.

Nests in areas of high and medium nesting density were twice as likely to be attacked as nests in low density areas (Massaro *et al.* 2001). However, high-density nests had greater breeding success, in part due to observed greater recruitment to group mobbing in these zones. The upper sections of the cliffs were more likely to be attacked than lower sections, but there were no breeding success differences between upper and lower. Nests on narrow ledges had higher breeding success than those on wider. When there were high winds Herring gulls seemed able to land on a greater variety of positions, increasing their opportunities (Gilchrist *et al.* 1998).

RESEARCH OBJECTIVES

In June 2015 clutch size data was collected at the current study colony. During that period, informal observations indicated that gull predation was a regular occurrence (Dickins 2016). However, the colony did not appear under intense predation at this time; Figure 2b displays a 47% fledgling success rate. Given these observations, a systematic method was planned for piloting in 2016, the aims of which were:

1. To describe the colony in terms of physical nest site characteristics following Massaro *et al.* (2001);
2. To calculate the daily rate of predation attempts and map the sites of those attempts with reference to 1;
3. To collect data on clutch size and determine if there is an association between clutch size and physical nest site characteristics.

The underlying assumption is that certain nests are more vulnerable to predation and this could be reflected in different clutch size decisions, following Julliard *et al.* (1997).

METHODS

Field site

The colony is on a south-facing cliff (Figure 3) of a narrow gully, north of St Mark's Stone. An established observation site was adopted (51.18719° N, 4.6747° W) on a promontory 116m south of the colony, and 54m above sea level (asl). This elevation enabled observers to look down on the colony, which extends to approximately 45m asl (Bibby *et al.* 2000). Three observers (TD, KN and RS) took turns (independently) to collect data at this site from 6-17 June 2016. This is the late incubation period for Kittiwakes, which is the recommended time window for survey work (Bibby *et al.* 2000).

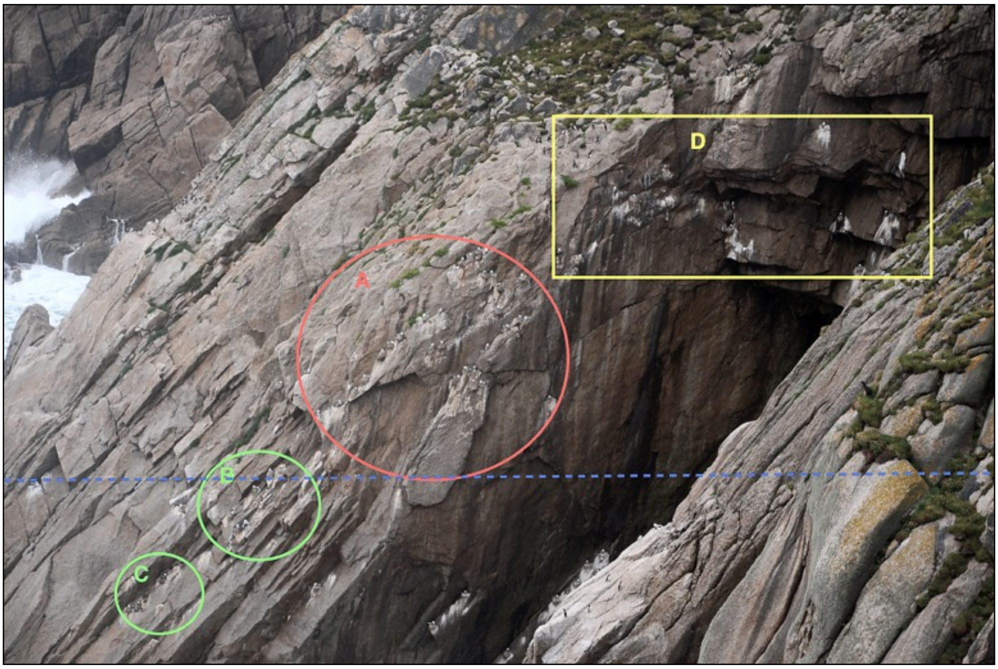


Figure 3: Photographic map of the Aztec Zawn colony with regions marked out, and a dotted line dividing the upper and lower portion of the colony (see main text for details). © Tom Dickins, 2016

Procedure

Hand drawn maps of the colony were produced, and a nest number system agreed. The map relied upon a few distinctive geological features and the clustering patterns of the sites. This minimal approach reduces confusion when the colony is viewed from differing angles. The maps were found to accord with photographic images taken in 2015 and 2016 (Bibby *et al*. 2000).

Table 1: RSPB bird monitoring codes for a Kittiwake survey

Code	Description
I	Apparently incubating adult
c/n	Clutch of n eggs
c/0	Empty, well built nest with adult in attendance
c/x	Well built nest with adult standing, contents unknown

A daily census sweep was made to assess the status of the colony using standard codes (see Table 1; (Gilbert *et al*. 2011)) to count the number of incubating adults and to gain some knowledge of nest contents. Apparently occupied nests (AON) are the main census unit for seabird monitoring (JNCC 2009) but this method is prone to overestimate breeding success as Kittiwakes will occupy nests and not lay (Bibby *et al*. 2000; Walsh *et al*. 1995). Whilst the standard codes record contents a typical census will not have time to systematically collect contents data and so AON data is most commonly reported. None the less, this information usefully describes the activity of the colony and enables an upper estimate of possible productivity to be calculated. Final counts should be the mean of at least three AON counts (Bibby *et al.* 2000).

Once the census was completed, a direct count opportunity sampling method was undertaken each day, to collect more detailed data on clutch size. Opportunity sampling involved visually scanning the colony for movement of adults at the nest and then using binoculars, or more powerful optical equipment, in order to yield an egg or chick count for each nest. For example, when an adult stood up from an apparently incubating position this would provide an opportunity to inspect the nest contents. The colony was regularly scanned with binoculars to assess movement. On occasion data were gathered during the initial census sweep if adults were moving on the nest.

Whilst the direct count methods yields more detail it is not the case that perfect information is collated about colony clutch size. All surveys are time-limited and during observation periods some adults do not move from their nest. This leads to missing data (see below).

This survey work commenced at different times of day and under varied weather conditions (Table 2) and used standardized sheets.

Colony and nest characteristics

Figure 3 displays a zoning system applied to the colony, after all the data were collected. Zones A-D represent distinct clusters of AON. All other AON that are not clustered were allocated to zone E. This clustering is subjective but that subjective perception could introduce biases into data collection and so warranted analysis.

Figure 3 shows a line demarcating the colony into the upper and lower regions (Massaro *et al.* 2001). All previous predation attempts witnessed by the first author occurred above this line.

Each nest was photographed using a telephoto lens and these images were used to characterise nesting ledges once back from the field (following (Gaston & Nettleship 1981)). Ledges were categorized as narrow if nest material hung over the seaward side, wide if there was clear space between the nest and the edge of the ledge, and medium if the nest fitted snugly, with no overlap, onto the ledge. The number of vertical walls, more than twice the height of a sitting adult at the nest, was counted. A nest might be on a ledge directly abutting the cliff face, thereby having one vertical wall only; but nests may also be in a corner (two vertical walls) or in a more complex niche with three or more vertical walls. A nest was considered to have a roof if rock protruded over the nest, covering the whole cup, within twice the height of an adult Kittiwake.

The number of neighbouring nests for each nest was calculated. A neighbouring nest had to be within pecking distance of the focal nest. Pecking distance only included pecking that occurred/might occur between adults seated on their nests. This was estimated, based on observations from 2015 and 2016. All neighbour disputes were recorded.

Predation risk

Counting the number of key predator species that flew within 10m of the colony during observations assessed predation risk; at this distance predators could reasonably be described as surveying the colony. Any predation events were recorded, noting predator species, nest site targeted and the outcome (egg or chick loss). Any post predation courtship and copulation were also recorded to assess any attempts to lay again.

Permissions

The island Warden gave permission for the study to be undertaken (by email, available upon request) and in person on the island in 2015. All observers followed the code of conduct of the U.K. Association for the Study of Animal Behaviour.

Table 2: Duration of observations and weather conditions for all observers. Note that RS had access to an anemometer. This amounts to 4088 minutes (68.13 hours) of observation across 25 sessions

Observer	Date	Start time	Stop time	Weather			
				Rain	Wind speed	Wind direction	Cover (%)
TD	12/06/16	09:57	11:20	None	Light	W	100
	13/06/16	06:15	07:45	Light	Light	W	100
	14/06/16	06:20	07:42	None	Strong	W	100
	15/06/16	06:10	07:48	None	Light	W	100
KN	07/06/16	11:55	14:15	None	Still	-	20
	08/06/16	12:30	14:45	None	Slight	-	100
	09/06/16	10:55	13:35	None	Still	-	10
	10/06/16	11:15	13:30	Light	Slight	-	90
	11/06/16	14:55	15:55	None	Slight	S	0
	12/06/16	11:30	15:00	None	Slight	S	100
	13/06/16	08:00	11:10	Light/Mod.	Breezy	-	100
	14/06/16	11:35	14:00	None	Strong	N	100
	15/06/16	09:55	13:00	Light	Strong gusts	N	100
	16/06/16	08:30	09:40	None	Breezy	-	100
	17/06/16	10:45	13:50	None	Strong	-	100
RS	06/06/16	06:30	10:30	None	5 kph	SE	50
	07/06/16	06:30	11:00	None	2.8 kph	SW	100
	08/06/16	14:30	17:30	None	1.4 kph	SW	37.5
	09/06/16	06:30	10:30	None	8.6 kph	SE	12.5
	10/06/16	06:20	11:20	Light	5.4 kph	E	100
	12/06/16	06:15	10:00	Light	3 kph	SW	100
	13/06/16	11:00	13:15	Light	3.5 kph	SW	100
	14/06/16	13:55	16:45	None	17 kph	SW	87.5
	15/06/16	12:55	15:55	None	5 kph	NW	100
	16/06/16	13:00	16:00	None	1.5 kph	NW	50

RESULTS

Analysis strategy

No predations or attempted predations were witnessed during the entire study.

The raw data is presented and missing data biases analysed. The census data is described, to give a sense of colony activity, a dependent variable of clutch size for each nest is calculated. Clutch size is compared across nest characteristics and zones.

Means and standard deviations will be reported as mean (standard deviation) throughout. Inferential statistics were calculated using IBM SPSS v21 on an iMac OSX.

Raw count data

Tables 3a-c display the summarized counts of eggs and chicks for 58 nests for each observer on the project; missing data are reported. Late in the study a new nest (nest 60) was established. This was excluded from all subsequent analyses as the adults had not had time to lay. Nest 57 proved to be just a perch. Upon photographic analysis, 57 was close to an apparently abandoned nest wedged behind 15.

Table 3a: TD data: number of eggs and chicks in each category of count and total egg and chick counts for the day. Missing data also represented. N=58 nests

Date	Eggs						Chicks				
	Zero	One	Two	Three	Total eggs	Missing Data	Zero	One	Two	Total chicks	Missing Data
12/06/16	2	8	8	-	24	40	17	1	0	1	40
13/06/16	8	8	3	-	14	39	15	2	2	6	39
14/06/16	5	4	3	-	10	46	10	2	0	2	46
15/06/16	6	12	6	-	24	34	21	1	2	5	34

Table 3b: KN data: number of eggs and chicks in each category of count and total egg and chick counts for the day. Missing data also represented. N=58 nests

Date	Eggs						Chicks				
	Zero	One	Two	Three	Total eggs	Missing Data	Zero	One	Two	Total chicks	Missing Data
07/06/16	3	11	6	-	23	38	-	-	-	-	58
08/06/16	3	10	5	-	20	40	-	-	-	-	58
09/06/16	3	6	13	1	35	35	-	1	-	1	57
10/06/16	2	5	17	-	39	34	-	1	-	1	57
11/06/16	3	3	5	-	13	47	-	-	1	2	57
12/06/16	4	11	19	2	55	22	-	2	1	4	55
13/06/16	5	7	12	-	31	34	-	3	1	5	54
14/06/16	7	7	6	-	19	38	-	4	3	10	51
15/06/16	7	11	4	1	22	35	-	5	3	11	50
16/06/16	10	3	2	-	7	43	-	2	3	8	53
17/06/16	16	8	7	1	25	26	1	9	6	21	42

Table 3c: RS data: number of eggs and chicks in each category of count and total egg and chick counts for the day. Missing data also represented. N=58 nests

Date	Eggs						Chicks				
	Zero	One	Two	Three	Total eggs	Missing Data	Zero	One	Two	Total chicks	Missing Data
06/06/17	-	4	5	1	17	48	-	-	-	-	58
07/06/16	-	2	5	1	15	50	-	-	-	-	58
08/06/16	-	4	5	-	14	49	-	-	-	-	58
09/06/16	-	10	11	-	32	37	-	1	-	1	57
10/06/16	-	2	3	-	8	53	-	-	1	2	57
12/06/16	-	5	6	-	17	47	-	-	1	2	57
13/06/16	-	4	2	-	8	52	-	3	-	3	55
14/06/16	-	8	6	1	23	43	-	5	2	9	51
15/06/16	-	8	3	1	17	46	-	7	2	11	49
16/06/16	-	6	5	1	19	45	-	5	4	9	49

Missing data biases

Missing data refers to nests for which no data were collected during an observation; so a missing data value gives the number of nests for which there is no data. For each observer, the percentage of missing data was calculated for each nest over the complete study. The distribution of percentage missing data across the three observers and five zones of the colony was then analysed, in order to check for any biases in observation. The missing data were normally distributed, however a Levene's test revealed that the homogeneity of variance assumption was violated between the three observers ($F=22.27_{2,171}$; p=0.0001). To this end, a non-parametric two-tailed Kruskal-Wallis test was conducted to assess equality in the distribution of missing data across observers. The result was significant (H=10.12; df=2; p=0.006). The null hypothesis can be rejected, as the distribution of missing data was unequal across all observers. TD had the lowest mean missing data [68.10], RS the highest [85.80], with KN in the middle [77.12].

A Levene's test revealed that the homogeneity assumption was not violated for missing data across zones. Given this, a one-way ANOVA was conducted to assess the inequality in the distribution of data across zones. Data were unevenly distributed across the five zones ($F=4.91_{24,169}$; p=0.001). Post-hoc tests revealed that there were significantly more missing data from zone D.

A Fisher's Exact test was conducted to assess any association between observer and zones with regard to the recording of missing data. This was found to be non-significant, providing no evidence of observer bias in favour of particular parts of the colony.

Census data

Census data for 59 sites (including one perch) was collapsed across each complete census and across observers in order to assess AON (Bibby *et al.* 2000). The modal occupancy was 57 nests and the mean AON was 53.10 (11.77).

Clutch size variable (c_i)

Missing nest data is an issue, but so too is incomplete nest data. As contents were often only briefly and partially observable it is not possible to be certain of final counts. There was also a lot of variance in count data across observers ($F=46.73_{2,760}$; p=0.001). To this end all methods of calculating clutch size used measures of central tendency across the entire data set. Given the number of observations taken, and the use of more than one observer, the probability of gathering data from a significant number of nests in the colony is also increased.

Using last day data from each contributing observer a mean clutch size variable was computed for each nest (c_i), combining egg and chick counts. The last day is simply the last day an egg or chick count is recorded for a nest site. Where standard codes revealed count data, in the absence of other data, it was assumed that count referred to eggs and this was entered into the analysis, given the low number of chicks relative to eggs (Tables 3a-c).

The mean was calculated across the number of observers contributing to each nest: nests with complete data could have contributions from between 1 and 3 observers. In this way the number of nests with missing data were reduced to only three, giving data for 55 nests (94.83% of the overall observed colony).

Alternative calculation of c_i

Three mean clutch size variables for each nest were calculated, one for each observer, across all egg and chick counts, across all days. The mean of these means was then calculated, yielding one value for each nest. This reduced the missing data to only three nests. All the analyses reported below were conducted using this variable also, and the same results were found. For ease of exposition they are not reported here.

Nest characteristics

c_i was found to be normally distributed using P-P plots, and used as a dependent variable in four separate one-way ANOVAs (Table 4). Each of these analyses tested to see if clutch size varied across key nest variables: namely, zone; position (upper/lower portions of the colony); the number of neighbours within pecking distance from a sitting position; and, the number of vertical walls (Gaston & Nettleship 1981). All results were non-significant indicating an even distribution of clutch size across the colony, as defined by these variables.

Table 4: Results of four one-way ANOVAs with mean clutch size, c_i, as the dependent variable. As can be seen the zone, position, number of neighbours and number of vertical walls had no impact upon the mean clutch size. This suggests that potential productivity is potentially even across the colony, at the time of survey

	Degrees of freedom				
	Between	**Within**	**Total**	***F***	***p***
Zone	4	50	54	0.750	0.563
Position	1	53	54	0.054	0.816
Neighbours	2	52	54	0.608	0.548
Vertical	3	51	54	1.483	0.230

Pearson Chi-square tests revealed no association between the number of neighbours and position in the colony, nor between the number of neighbours and the number of vertical walls. Subsequent linear regression analyses revealed no significant interactions between these characteristics. Ledge width and the presence or absence of a roof were also recorded (Gaston & Nettleship 1981) but there was a great deal of uniformity across the colony with 54 nests on narrow ledges (4 medium) and only three with a roof. These independent variables were not analysed further.

Possible instances of egg/chick loss were calculated. Loss, for each nest, was defined as follows: where two or more counts of zero contents were recorded on the 16 and 17 June, in conjunction with three or more egg/chick counts across one or more observers at any time prior to 16 June. This set of criteria were quite stringent, but enabled consistent observations across more than one observer to be used, increasing their reliability. (There were 10 nests that had last day data of zero registered by one of the observers, so this method discounted 50% of the final zero counts.) The exact amount of loss could not be determined due to variation in the preceding data. In effect, all egg and chick registrations were simply seen as presence data, but missing data were not counted as evidence of loss; only definite zero counts.

This method yielded five potential losses: three in Zone C (nests 9, 12, 14) and two in Zone A (nests 22, 24). None of the nests had a roof, three had one vertical wall, one had two vertical walls and one had three. Three nests were on narrow ledges, and two on medium.

Comparison of 2015 and 2016 data

Data were collected for the same colony from 6-12 June 2015 (Dickins 2016). At that time there were 71 AON. (Note that AON=71 is c.28% lower than the AON=98 in Figure 2a, possibly due to overestimates introduced by only counting occupancy (Bibby *et al.* 2000).) The average clutch size was calculated as 0.933 (last day method) eggs per nest. For 2016 the average clutch size was 1.42 (last day method) with a mean AON of 53.10.

Using photographs and maps from both years, the 2015 nest codes (N=71) were translated to 2016 codes (N=58). There were 48 nests in common across both years. Perches from 2015 had become nests in 2016, and vice versa. More ledges were used for nest sites in 2015 than in 2016.

Both sets of data for the 48 common nests were normally distributed according to inspection of P-P plots. A two-tailed paired sample t-test revealed a significant difference between the two years (t=-3.62; df=32; p=0.001) with 2016 having a higher mean of 1.09 (0.91) compared with a 2015 mean of 0.45 (0.67).

The 48 common nests and their last day data were analysed for vertical wall and zone characteristics. These characteristics did not change across the two-year period, whereas the number of neighbours had. Due to the uniformity of ledge and roof structures, group sizes were too small for meaningful comparisons of difference across these categories. The 2016 data met all parametric assumptions and two one-way ANOVAs were non-significant (Table 5).

Table 5: Results of two one-way ANOVAs with 2016 mean clutch size from the common nests as the dependent variable

	Degrees of freedom				
	Between	**Within**	**Total**	***F***	***p***
Vertical	3	41	44	0.568	0.639
Zone	4	40	44	1.596	0.194

Levene's tests revealed that the 2015 data were non-parametric, therefore Kruskal-Wallis tests were performed across the vertical (H=3.21; df=3; p=0.36) and zone (H=6.94; df=35; p=0.139) categories and both were found to be non-significant. As with the 2016 data, the clutch size data were evenly distributed across all categories.

Table 6: Number of adult and juvenile loafing birds at the beginning and end of each observation period for all observers. The mean and standard deviation across all observers indicates considerable variance in the data. Discussion after the observations were conducted revealed some differences of opinion between observers about where to count loafers and this had caused some difficulty in the field. To this end there may be considerable measurement error. Nonetheless, all of these birds were loafing within sight of the colony and there are no other colonies in the immediate vicinity

		Loafing adults		**Loafing juveniles**	
Observer	**Date**	**Beginning**	**End**	**Beginning**	**End**
TD	12/06/16	7	20	0	0
	13/06/16	7	14	0	0
	14/06/16	19	20	0	0
	15/06/16	67	18	1	0
KN	07/06/16	4	3	0	0
	08/06/16	5	4	0	0
	09/06/16	13	7	0	0
	10/06/16	9	8	0	0
	11/06/16	5	5	0	0
	12/06/16	28	39	0	0
	13/06/16	30	16	0	0
	14/06/16	64	72	6	7
	15/06/16	30	48	3	4
	16/06/16	18	18	1	0
	17/06/16	4	26	0	4
RS	06/06/16	10	13	0	0
	07/06/16	17	16	0	0
	08/06/16	4	3	0	0
	09/06/16	4	8	0	0
	10/06/16	9	5	0	0
	12/06/16	7	9	0	0
	13/06/16	12	6	0	0
	14/06/16	20	16	0	0
	15/06/16	11	17	1	0
	16/06/16	5	5	0	0
Statistics	Mean	16.36	16.64	0.48	0.60
	Standard deviation	16.87	15.86	1.33	1.73

Other data

Data were collected on the number of loafing Kittiwakes near to and in the colony, and neighbour disputes between nesting birds (Tables 6 and 7). The number of fly-bys by predatory birds (within 10m of the colony) was recorded. There were 25 nest disputes across 25 observations; a low number. There was great variation in the number of loafers, but only a small number of juveniles in keeping with low philopatry as these birds tend to disperse. Across all observers a total of 67 Herring gulls, 11 Lesser Black-backed gulls *(Larus fuscus)*, 18 Great Black-backed gulls, two Carrion Crows *(Corvus corone)* and four Peregrine falcons flew within 10m of the colony. With 68.13 hours of observation this yields a rate of 1.497 fly-bys per hour.

Table 7: Nest disputes organized by observer, date and time of occurrence. Nests 15 and 57 had eight recorded disputes. Nest 57 was technically a perch, next to a nest wedged behind nest 15. There had been a nest more toward the perch position in 2015. The wedged nest in 2016 had an egg in it but the adult was not observed to incubate

			Causality determined		**Causality undetermined**	
Observer	**Date**	**Time**	**Actor**	**Recipient**	**Nest**	**Nest**
TD	13/06/16	06:50	15	57	-	-
	15/06/16	06:35	30	31	-	-
KN	07/06/16	12:35	27	31	-	-
	10/06/16	12:23	11	10	-	-
	10/06/16	12:31	23	24	-	-
	11/06/16	15:10	-	-	39	40
	11/06/16	15:40	-	-	28	29
	12/06/16	12:34	-	-	45	46
	13/06/16	08:45	23	24	-	-
	13/06/16	09:25	15	57	-	-
	14/06/16	13:25	15	57	-	-
	15/06/16	11:05	15	57	-	-
	15/06/16	11:17	-	-	39	40
	15/06/16	11:27	45	46	-	-
	15/06/16	11:40	-	-	44	47
	15/06/16	12:30	45	46	-	-
	17/06/16	13:40	57	15	-	-
RS	06/06/16	08:10	15	57	-	-
	06/06/16	09:00	57	15	-	-
	12/06/16	06:50	14	12	-	-
	12/06/16	08:00	23	24	-	-
	12/06/16	08:20	57	15	-	-
	14/06/16	14:20	44	47	-	-
	15/06/16	15:20	22	23	-	-
	16/06/16	14:45	35	36	-	-

DISCUSSION

No predation or predation attempts were observed during this study, but predators were present, indicating some predation risk. The mean clutch size for the colony was 1.42 eggs; larger than the preceding year by 0.487 eggs, suggesting better breeding conditions (Jacobsen *et al.* 1995). No significant effects of colony or nest characteristics were found in clutch size for 2016, nor for the common nests across 2015 and 2016. This suggests that risk may be evenly distributed across the colony, at least for these two years.

Limitations and future directions

The current study was time limited. Twenty-five observation periods took place over 11 days, with a mean observation period of 163.52 minutes (standard deviation=63.15) with 68.13 hours of data collected. All observations were conducted during the day. Predation attempts could easily have been missed, especially in the early evening, dusk and night when no sampling occurred. A more thorough sampling across the day is required, possibly introducing camera traps to capture nocturnal data (Collins *et al.* 2014).

Given previous observations (Dickins 2016), the predator fly-by rate and the healthier status of the colony in 2016 it is not unreasonable to assume a change in predation regime. Such a change may be attributable to shifts in abundance in other prey items (Charnov 1976) and also to changes in predator abundance. During the course of the study it was noted that rabbit abundance was very high, and that the number of rabbit carcasses around the island was also high. Upon later enquiry it was discovered that some of these carcasses had been left after deliberate control. Rabbit populations on the island have fluctuated from a high of around 15,000 individuals (Smith & Compton 2008) to a low of fewer than 200 individuals following an outbreak of myxamatosis in 2006 (Saunders 2008). The impact of rabbit activities upon the archaeology and conservation effort on the island has been seen as a problem, and it is a policy to control numbers to avoid the excesses of a 15,000 population (Saunders 2008).

Optimal foraging theory would predict that the increased rabbit abundance, and the decision to leave rabbit carcasses as available carrion, would lead to shifts in predation strategy for Great Black-backed gulls and other predators (Charnov 1976; Krebs *et al.* 1977). Effectively the ratio of search time costs to energy return from eggs is very likely less favourable than that for freely available carrion. To this end it would be of great use to collect data on rabbit and other prey abundance and relate it to Kittiwake and other seabird productivity. More generally, modelling the food web dynamics on the island would help to untangle predation risk for Kittiwakes (Abrams 2000; Abrams & Ginzburg 2000; Abrams 2010; Beckerman *et al.* 2006; Petchey *et al.* 2008).

Sand-eel availability at sea is also important. Sand-eel abundance data is not available for the Lundy Kittiwakes. It might be possible in the future to estimate annual variation from careful counts of sand-eels fed to young Kittiwakes and auk species.

The production of a last-day mean for individual nest clutch size (c_i) enabled missing data to be reduced significantly. This variable treated all observations as equal. However, we can be reasonably confident that the detectable biases in missing data between observers will be averaged out. For future study it would be wise to assess observers over a time limited survey of the same site and check to see how many eggs they detect and how many of those eggs are in common nests (Gaston & Nettleship 1981). It would also be good practice to have consistent time periods for observations across observers, in order to equalize survey effort and standardize.

Ideally the colony would be followed throughout the entire breeding season for at least one year to assess how useful June count data are. This would also assay any changes in risk profile across the year. Related to this, information about predator phenology would be useful, in the context of general prey abundance. It is assumed that predators time their own reproductive effort to match peak productivity in their prey (Lack 1950). At present the phenology of Great Black-backed gulls, and other predators on the island is not monitored. It is possible that Great Black-backed gull and Kittiwake breeding was asynchronous this season. The lack of specialism in Great Black-backed gulls will also introduce variance as they pursue different prey items according to abundance.

Conclusion

Two seasons of average clutch size data have been collected for this colony, whilst productivity has been surveyed for longer. Productivity has been measured in relation to AON counts, which is not as precise as direct count methods. With longer-term data it will be possible to work out more accurate percentage success and loss and to develop a richer picture of Kittiwake reproductive decisions in this southern population.

REFERENCES

Abrams, P.A., 2010. Implications of flexible foraging for interspecific interactions: Lessons from simple models. *Functional Ecology*, 24(1), pp.7-17

Abrams, P.A., 2000. The Evolution of Predator-Prey Interactions: Theory and Evidence. *Annual Review of Ecology and Systematics*, 31, pp.79-105

Abrams, P.A. & Ginzburg, L.R., 2000. The nature of predation: Prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution*, 15(8), pp.337-341

Aebischer, N.J. & Coulson, J.C., 1990. Survival of the Kittiwake in Relation to Sex, Year, Breeding Experience and Position in the Colony. *Journal of Animal Ecology*, 59(3), pp.1063-1071. Available at: http://links.jstor.org/sici?sici=0021-8790(199010)59:3%3C1063:SOTKIR%3E2.0.CO;2-V

Anderson, D.J. & Ricklefs, R.E., 1992. Brood Size and Food Provisioning in Masked and Blue-Footed Boobies (Sula Spp.). *Ecology*, 73(4), pp.1363-1374

Beckerman, A.P., Petchey, O.L. & Warren, P.H., 2006. Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences of the United States of America*, 103(37), pp.13745-13749

Bibby, C.J. *et al.*, 2000. *Bird Census Techniques* 2nd ed., London: Academic Press

Birkhead, T.R., 1977. The Effect of Habitat and Density on Breeding Success in the Common Guillemot (Uria aalge). *Journal of Animal Ecology*, 46(3), pp.751-764

Brown, A. *et al.*, 2011. Seabirds on Lundy: Their current status, recent history and prospects for the restoration of a once important bird area. *British Birds*, 104(3), pp.139-158

Charnov, E.L., 1976. Optimal Foraging: Attack Strategy of a Mantid. *The American Naturalist*, 110(971), pp.141-151

Clode, D., 1993. Colonially breeding seabirds: Predators or prey? *Trends in Ecology and Evolution*, 8(9), pp.336-338

Cody, M.L., 1966. A general theory of clutch size. *Evolution*, 20(2), pp.174-184

Collins, P.M. *et al.*, 2014. Predation of Black-legged Kittiwake Chicks Rissa tridactyla by a Peregrine Falcon Falco peregrinus: Insights from Time-lapse Cameras. *The Wilson Journal of Ornithology*, 126(1), pp.158-161

Coulson, A.J.C., Thomas, C.S. & Coulson, J.C., 1985. Changes in the biology of the kittiwake Rissa tridactyla: a 31-year study of a breeding colony. *Journal of Animal Ecology*, 54(1), pp.9-26

Coulson, J.C., 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull Rissa tridactyla. *Journal of Animal Ecology*, 35(2), pp.269-279

Coulson, J.C., 2011. *The Kittiwake*, London: T & A D Poyser

Coulson, J.C. & Coulson, B.A., 2008. Measuring immigration and philopatry in seabirds; Recruitment to Black-legged Kittiwake colonies. *Ibis*, 150(2), pp.288-299

Coulson, J.C. & Porter, J.M., 1985. Reproductive success of the Kittiwake. *Ibis*, 127, pp.450-466

Cullen, E., 1957. Adaptations in the Kittiwake to cliff-nesting. *Ibis*, 99(2), pp.275-302

Danchin, É. & Nelson, J.B., 1991. Behavioral Adaptations to Cliff Nesting in the Kittiwake (Rissa tridactyla): Convergences with the Gannet (Sula bassana) and the Black Noddy (Anous tenuirostris). *Colonial Waterbirds*, 14(2), pp.103-107

Davis, T. & Jones, T., 2007. *The Birds of Lundy*, Exeter: Devon Bird Watching & Preservation Society and Lundy Field Society

Dickins, D.W. & Clark, R.A., 1987. Games Theory and Siblicide in the Kittiwake Gull, Rissa tridactyla. *Journal of theoretical biology*, 125, pp.301-305

Dickins, T.E., 2016. Average clutch size for a Kittiwake Rissa tridactyla colony on Lundy. *Devon Birds*, 69(1), pp.7-13

Dixon, F., 1979. *A study of some factors influencing breeding of the kittiwake gull Rissa tridactyla (L.)*. Durham University. Available at: http://etheses.dur.ac.uk/8373/

Eaton, M.A. *et al.*, 2015. Birds of conservation concern 4: The population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, 102(6), pp.296-341

Erikstad, K.E. *et al.*, 1998. On the Cost of Reproduction in Long-Lived Birds: The Influence of Environmental Variability. *Ecology*, 79(5), pp.1781-1788

Frederiksen, M. *et al.*, 2005. Regional patterns of Kittiwake Rissa tridactyla breeding success are related to variability in sandeel recruitment. *Marine Ecology Progress Series*, 300(February 2016), pp.201-211

Frederiksen, M. *et al.*, 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology*, 41(6), pp.1129-1139

Gaston, A.J. & Nettleship, D.N., 1981. *The Thick-billed Murres of Prince Leopold Island*, Ottawa: Canadian Wildlife Service

Gilbert, G., Gibbons, D.W. & Evans, J., 2011. *Bird monitoring methods: A manual of techniques for key UK species*, Exeter: Pelagic Pub

Gilchrist, H.G., Gaston, A.J. & Smith, J.N.M., 1998. Wind and Prey Nest Sites as Foraging Constraints on an Avian Predator , the Glaucous Gull. *Ecology*, 79(7), pp.2403-2414

Hamer, K.C. *et al.*, 1993. The influence of food supply on the breeding ecology of Kittiwakes Rissa tridactyla in Shetland. *Ibis*, 135(1984), pp.255-263

Haywood, S., 2013. Origin of evolutionary change in avian clutch size. *Biological Reviews*, 88(4), pp.895-911

Hipfner, J.M., Morrison, K.W. & Darvill, R., 2011. Peregrine Falcons Enable Two Species of Colonial Seabirds to Breed Successfully by Excluding Other Aerial Predators. *Waterbirds*, 34(1), pp.82-88

Hurrell, J., 2016. *The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (station-based).*, Available at: https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based. [Accessed July 7, 2016]

Jacobsen, K.-O., Erikstad, K.E. & Saether, B.-E., 1995. An experimental study of the cost of reproduction in the Kittiwake Rissa tridactyla: a comment. *Ecology*, 76(5), pp.1636-1642

JNCC, 2009. *UK Seabirds in 2008: Seabird Monitoring Programme*, Available at: www.jncc.gov.uk/seabirds

Julliard, R. *et al.*, 1997. Phenotypic Adjustment of Clutch Size Due to Nest Predation in the Great Tit. *Ecology*, 78(2), pp.394-404

Krebs, J.R. *et al.*, 1977. Optimal prey selection in the great tit (Parus major). *Animal Behaviour*, 25(PART 1), pp.30-38

Lack, D., 1950. The breeding seasons of European birds. *Ibis*, 92(2), pp.288-316. Available at: http://onlinelibrary.wiley.com/doi/10.1111/j.1474-919X.1950.tb01753.x/abstract [Accessed July 5, 2014]

Lack, D., 1947. The Significance of Clutch-size. *Ibis - International Journal of Avian Science*, 89(2), pp.302-352

MacDonald, B., 2014. Lundy Warden's Report 2013

Massaro, M. *et al.*, 2000. Delayed capelin (*Mallotus villosus*) availability influences predatory behaviour of large gulls on black-legged kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success. *Canadian Journal of Zoology*, 78(June), pp.1588-1596

Massaro, M., Chardine, J.W. & Jones, I.L., 2001. Relationships Between Black-Legged Kittiwake Nest-Site Characteristics and Susceptibility to Predation by Large Gulls. *The Condor*, 103, pp.793-801

McMurdo Hamilton, T., Brown, A. & Lock, L., 2016. Kittiwake declines extend to southern England and beyond: an update on colonies at the southern edge of the species' Northeast Atlantic range. *British Birds*, 109, pp.199-210

Nettle, D. & Bateson, M., 2015. Adaptive developmental plasticity: what is it, how can we recognize it and when can it evolve? *Proc R Soc B*, 282(1812), p.2015.1005. Available at: http://rspb.royalsocietypublishing.org/content/282/1812/20151005

Oro, D. & Furness, R.W., 2002. Influences of Food Availability and Predation on Survival of Kittiwakes. *Ecology*, 83(9), pp.2516-2528

Petchey, O.L. *et al.*, 2008. Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, 105(11), pp.4191-4196

Price, D. & Slader, P., 2013. *Lundy Site Register*, Lundy

Price, D., Slader, P. & Booker, H., 2013. Breeding Cliff-Nesting Seabirds 2013. *Lundy Field Society Annual Report*, pp.85-92

Regehr, H.M., Rodway, M.S. & Montevecchi, W.A., 1998. Antipredator benefits of nest-site selection in Black-legged Kittiwakes. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 76(5), pp.910-915

Ricklefs, R.E., 1970. Clutch Size in Birds: Outcome of Opposing Predator and Prey Adaptations. *Science*, 168(3931), pp.599-600

Ricklefs, R.E., 2000. Lack, Skutch, and Moreau: the Early Development of Life-History Thinking. *The Condor*, 102(1), pp.3-8. Available at: http://dx.doi.org/10.1650/0010-5422(2000)102[0003:LSAMTE]2.0.CO;2

Saunders, N., 2008. Lundy Warden's Report 2007

Smith, C. & Compton, S., 2008. Exclosures may overestimate the impact of rabbit. *Journal of the Lundy Field Society*, 1, pp.21-32

Stearns, S.C., 2000. Life history evolution: successes, limitations, and prospects. *Die Naturwissenschaften*, 87(11), pp.476-86. Available at: http://www.ncbi.nlm.nih.gov/pubmed/11151666

Stearns, S.C., 1992. *The Evolution of Life Histories*, Oxford: Oxford University Press

Walsh, P.M. *et al.*, 1995. *Seabird monitoring handbook for Britain and Ireland*, Peterborough: JNCC/RSPB/ITE/Seabird Group

Wheatley, S., 2011. Lundy Warden's Report 2011

Wheatley, S. & Saunders, N., 2010. Cliff Nesting Seabird Productivity on Lundy 2008. *Journal of the Lundy Field Society*, 2, pp.85-90

Winkler, D.W. & Walters, J.R., 1983. The determination of clutch size in precocial birds. In *Current ornithology*. Springer, pp. 33-68

WHAT'S ON THE MENU: *DROSERA ROTUNDIFOLIA* DIET DETERMINATION USING DNA DATA

by

BARBORA LEKESYTE[1,2], STEPHEN KETT[2] AND MARTIJN J.T.N. TIMMERMANS[2,3]
[2]Department of Natural Sciences, Middlesex University, The Burroughs,
Hendon, London, NW4 4BT
[3]Department of Life Science, Natural History Museum, Cromwell Road,
London, SW7 5BD
[1]*Corresponding author, e-mail: barbora.lekesyte@gmail.com*

ABSTRACT

The round-leaved sundew, *Drosera rotundifolia*, is a carnivorous plant species. On Lundy it is found in the nutrient-poor bog environments of Pondsbury and the northernmost quarry, where it supplements its diet with invertebrate prey. To gain insight into the diet of these two sundew populations a metabarcoding approach was trialled. This is, to our knowledge, the first study to use DNA barcodes to identify *Drosera* prey. At each site, a 0.25m^2 quadrat was placed in a representative *Drosera* patch and two days' worth of prey were collected. To identify prey items, Cytochrome c oxidase subunit I (COX1) sequences were obtained and compared to the Barcode of Life database. This revealed that Lundy sundews have a mixed diet. In total at least 20 different prey taxa were detected in the two 0.25m^2 areas sampled. Sixteen taxa could be identified to species, indicating that metabarcoding permits accurate species level identification of sundew prey items. The majority of prey taxa were dipterans (two-winged flies), of which several have previously been reported on Lundy. Most prey taxa were detected in only one of the two quadrats examined (Jaccard's index of Similarity=0.01; 'dissimilar'). This might indicate that the two *Drosera* populations feed on distinct prey communities, but more research is needed to confirm this.

Keywords: *Lundy, carnivorous plants, sundew Drosera, DNA barcodes, prey taxa, Diptera*

INTRODUCTION

Carnivorous plants of the genus *Drosera* (sundews) are typically found in nutrient poor environments (Ellison and Gotelli, 2001). They thrive under these deprived conditions by supplementing their diet with arthropod prey (Millett *et al.*, 2003). Prey are caught and digested with modified leaves ('blades'). Blades possess large numbers of glandular 'hairs' that secrete drops of viscous adhesive solution. When arthropods contact with these drops they are trapped and die (Adlassnig *et al.*, 2010) (Figure 1). Digestive enzymes produced by the plants then dissolve prey items, releasing nutrients to be absorbed by the plant (Adamec, 2002).

Figure 1: *Drosera rotundifolia* with prey items. © S. Kett

The genus *Drosera* has attracted scientific attention since the eighteenth century, most of which focussed on benefits of prey capture on plant growth and survival (e.g. ‘Botany’, 1874; Darwin, 1875; Roth, 1782; Thum, 1988; Hooker, 1916). For example, Thum (1988) showed that artificially increased food supply *Drosera* increases dry weight, flower and leaf number and the overall trapping area of individual plants. Equally, plant traits (Foot *et al.*, 2014) and microhabitat (Thum, 1986) have also been shown to affect prey capture efficiency and diet composition.

Investigating natural *Drosera* diet, via morphological identification of prey, however, is often hampered by the rapid digestion of prey tissue. To overcome this difficulty a DNA barcoding approach to identify prey was trialled. DNA barcodes are standardised genetic markers used for taxonomic identification, ideally to species level (Hebert *et al.*, 2003). DNA sequences are obtained from specimens and then compared to sequences from accurately identified and vouchered specimens in a reference database. Matches between ‘unknown’ DNA sequences and sequences in the database result in a positive identification for specimens of interest.

This study focussed on the round-leaved sundew, *D. rotundifolia* L., Lundy’s only carnivorous plant species. Samples were taken from two populations (Figure 2). One population is found at the edge of Lundy’s largest pond, Pondsbury (51°10'38"N, 4°40'12"W). Much of the surface vegetation in this area is *Sphagnum* bog with frequent tussocks of *Juncus* sp. The other population is found in the northernmost quarry (51°10'45"N, 4°39'53"W). Here vegetation is characterised by *Sphagnum* and other plants adapted to acid, poorly drained soils.

This study aimed to test whether sundew prey items can be identified to species level using molecular barcoding and to compare obtained identifications to existing Lundy species records.

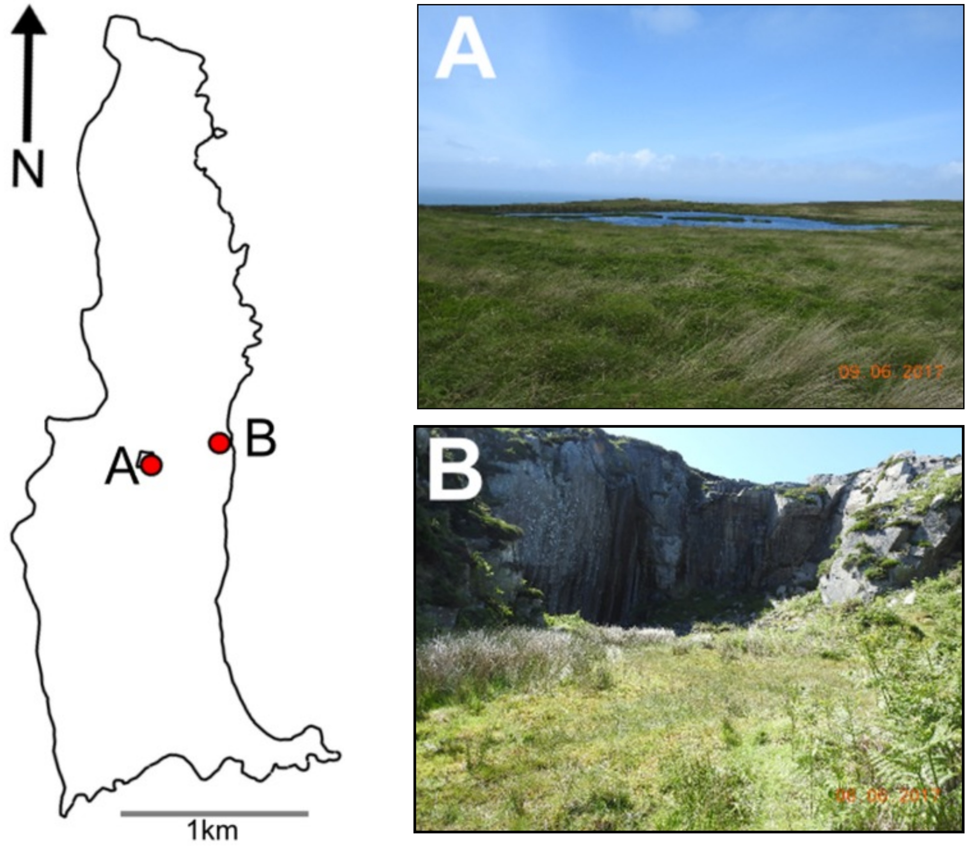


Figure 2: The two Lundy *Drosera rotundifolia* populations sampled.
A) Pondsbury, B) the northernmost quarry. © B. Lekesyte

MATERIAL AND METHODS

Field work methods

In June 2016, 0.5×0.5 m quadrats were established within the Pondsbury and Quarry *D. rotundifolia* populations. Quadrats were placed in locations judged ‘typical’ of a dense *Drosera* ‘patch’. Flags were used to indicate the four quadrat corners to permit relocation of each quadrat. On the first day of the experiment, plant blades were ‘cleaned’ using forceps to remove all prey items. To determine prey composition, prey were collected two days after cleaning occurred. Collected prey items were stored in tubes of absolute ethanol.

Laboratory methods

For each quadrat, prey samples were pooled in a single tube. DNA extractions were performed on these pooled samples. Ethanol was removed by pipetting. A heating block (56°C) was used to evaporate residual ethanol. DNA extractions used the Blood and Tissue Kit (Qiagen) and followed manufacturer’s recommendations, except that double volumes were used for buffer ATL, buffer AL and 100% ethanol. Extracted DNA was subsequently sent to NatureMetrics Ltd for metabarcoding. Metabarcoding followed NatureMetrics Ltd standard procedures. In brief, a short fragment of the cytochrome oxidase c subunit 1 (COI) barcode was amplified using primer Fol-degen-rev 5’-

TANACYTCNGGRTGNCCRAARAAYCA-3' (Yang *et al.* 2012) combined with Leray primer mlCOIintF: 5'-GGWACWGGWTGAACWGTWTAYCCYCC-3' (Leray *et al.* 2013) or combined with primer 'Short2' 5'-CCNGAYATRGCNTTYCCNCG-3' (NatureMetrics Ltd, pers. comm.) (Figure 3). All PCR reactions were performed in triplicate. PCR products were purified and quantified (Qubit high sensitivity kit). PCR products for the same site (quadrat) were pooled and Next Generation Sequencing (NGS) libraries were prepared as specified by Illumina for amplicon sequencing on the Illumina MiSeq System (Illumina Inc. 2013) and sequenced using an Illumina MiSeq 2×300 kit.

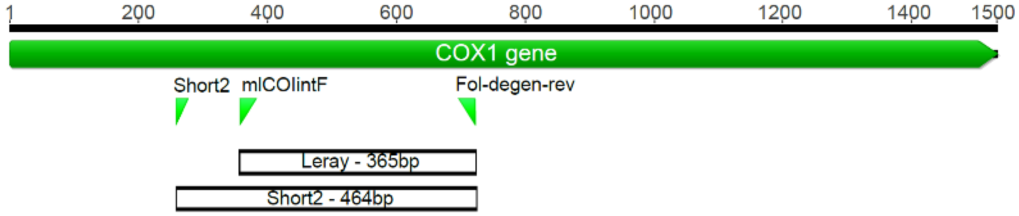


Figure 3: Two fragments of the COX1 gene were amplified using PCR. Primers Short2 and Fol-degen-rev amplify a 365bp fragment. Primers mlCOIintF and Fol-degen-rev a 464bp fragment. Positions of the three primers (green triangles) on the COX1 gene sequence (green bar) are given

Bioinformatic methods

Raw sequencing reads for each site were stitched using PEAR (Zhang *et al.*, 2014) and subsequently split by forward primer sequence using cutadapt (Martin, 2011). This step also trimmed uninformative PCR primer sequences. Low quality sequences were removed using the prinseq-lite Perl script (Schmieder and Edwards, 2011), removing all sequences that contained at least a single 'N', had a single position with a Phred quality below 20 and an average Phred quality below 30. Sequences were then converted to FASTA format using fq2fa (Peng *et al.*, 2012). Operational Taxonomic Units (OTUs) were constructed from these files using the UPARSE pipe-line (Edgar, 2013). Sequences were de-replicated (merging all exact duplicates) and singletons (sequences that were observed once only) were removed. Remaining sequences were clustered at 97% similarity in USEARCH (Edgar, 2010) to generate OTUs and all sequences were subsequently assigned to each of the different OTUs (again at 97% similarity). OTUs with less than 10 sequences for both quadrats combined were discarded. To identify OTUs in the final dataset, sequences were compared to the Barcode of Life (BOLD) database (http://www.boldsystems.org/). Identifications were compared to the Diptera checklist for Lundy (Lane, 1977) and various other sources (Figure 4). Prey taxon approximate sizes were obtained from a variety of generic sources.

Jaccard's Index of Similarity

Jaccard's Index of Similarity was used to determine overall similarity of composition between the two sets of identified prey taxa, from the Pondsbury and the quarry sites. It was applied only where prey taxon presence could be unequivocally determined, e.g. if a genus occurs in both prey sets, it was not possible to determine without species identification whether a species level difference occurred between the two taxa.

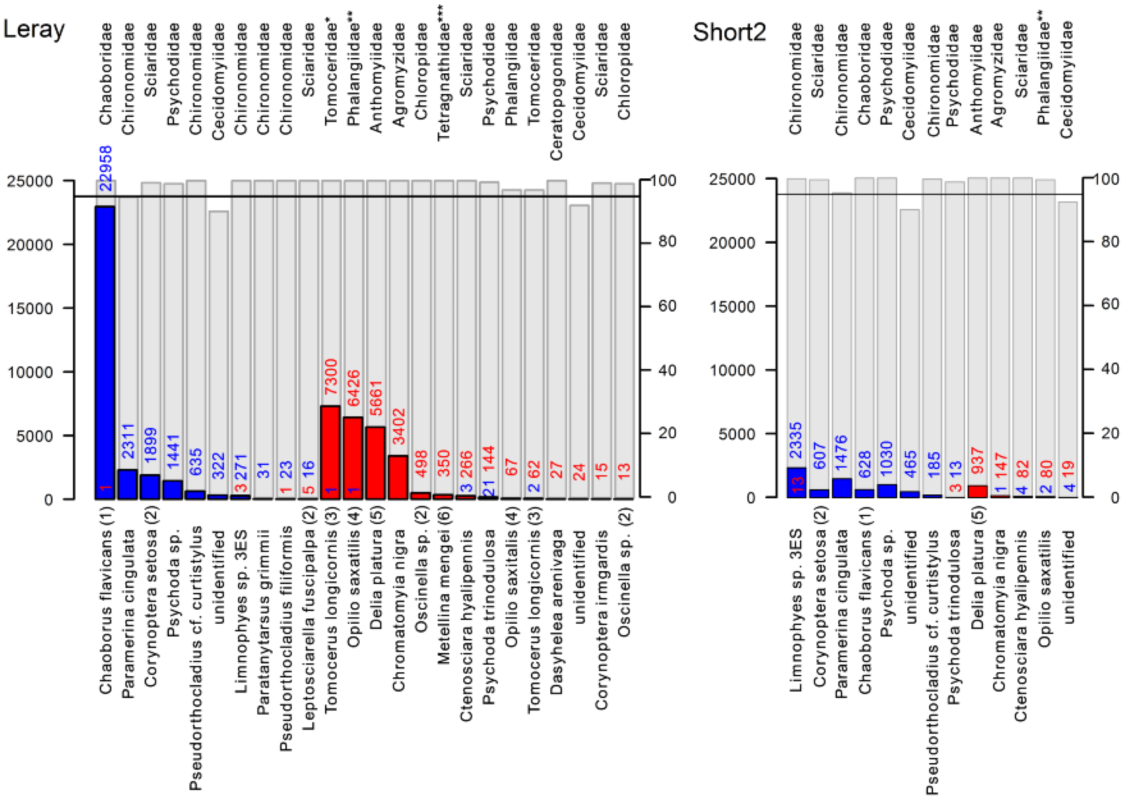


Figure 4: Taxa observed at two sites on Lundy using: Left) Leray (2013) primers and Right) Short2 (NatureMetrics Ltd., pers. comm.) primers. Left vertical axis: Number of sequences observed for a specific taxon. Blue (Pondsbury) and red (Quarry) bars and blue and red numbers on the graph represent number of sequences observed. Right axis: % similarity (grey bar) to a reference sequence in the BOLD database. Horizontal line indicates 97% similarity. Family names are given above graph. All families belong to Diptera, except *) Entomobryomorpha (Collembola), **) Opiliones (Arachnida) and ***) Araneae (Arachnida). Species names (if available) are given below graph. Numbers between parentheses refer to: 1) (Lane, 1978) 2) (Menzel et al., 2006) 3) (Smith and Nunny, 2012) 4) (Parsons, 1988) 5) (Parsons, 1996) 6) srs.britishspiders.org.uk (last accessed 07/07/2017. Note that Tomocerus longicornis, Opilio saxitalis and Oscinella sp. are represented by two Leray OTU

RESULTS

Drosera populations

The Pondsbury quadrat contained 91 *D. rotundifolia* plants and the quarry quadrat 66. Within the two-day sampling period plants in the Pondsbury and quarry quadrats caught totals of 44 and 83 prey items respectively.

Molecular identification of prey items

In total, 234,058 raw paired-end reads were obtained. There were 162,345 paired-end reads for the Pondsbury sample and 71,713 paired-end reads for the quarry sample. Reads were merged and 94.2% of the Pondsbury and 96.8% of the quarry samples could be combined into single contiguous sequences. These datasets were subsequently split by PCR primer sequence (i.e. Leray or Short2), resulting in two datasets for the quarry sample (Leray: 58866 sequences; Short2: 10222 sequences) and two datasets for the Pondsbury sample (Leray: 79316 sequences; Short2: 73110 sequences). Sequences were clustered per primer pair to construct OTUs. OTUs with 10 or more associated sequences are given in Figure 4.

Figure 4 shows that several OTUs are represented by a large number of sequences in one sample and by a very small number in the other (e.g. *Tomocerus longicornis*: 7300 sequences in quarry sample, 1 sequence in Pondsbury sample). It is currently unclear whether such very low numbers are a genuine reflection of the presence of a species at the respective quadrat, or whether they are merely a result of cross-contamination. Cross-contamination between samples is a well-known risk when working with environmental DNA (Thomsen and Willerslev, 2015). To avoid overestimation of the number of prey species at each site, such cases were treated as cross-contamination.

Identifications were obtained using the Barcode of Life Database (http://www.boldsystems.org) search engine. This revealed that all Pondsbury OTUs are dipterans (most from the family Chironomidae). Dipterans were also most abundant in the quarry datasets, but two species of Arachnida and one collembolan species were also observed.

With the Leray primer greater diversity was revealed than with the Short2 primer (Figure 4). All OTUs observed using the Short2 primer, are also observed using the Leray primer, but not *vice versa*. The Leray primer revealed three more species for Pondsbury and six more species for the quarry.

At least 12 different arthropod families were detected as prey items. Almost all of these families consist of relatively ‘small’ species (≤5mm) and the majority have an adult flying stage (Table 1). Three of the 12 families are associated specifically with aquatic/bog environments and two with ‘decaying/rotting organic matter’ (Table 1). It must be noted that several non-arthropod OTUs were observed that are not shown in Figure 4. These included a nematode, two fungi and bacteria (Rickettsiales).

There was a clear distinction between prey items taken by the two *Drosera* populations (Jaccard’s index of Similarity=0.01; ‘dissimilar’), with most (19/21) prey taxa found in only one of the two quadrats examined.

DISCUSSION

This trial suggests metabarcoding permits accurate species level identification of *Drosera* prey items. Reliable identifications (>97% sequence similarity with a BOLD database entry) were obtained for a total of 16 species. Some OTUs could not be identified to species level, because they are currently not represented in the BOLD database. With an ever-growing BOLD database, however, the number of such unidentifiable taxa is likely to decrease over time.

Results indicate that Lundy *Drosera* have an eclectic diet. Analysis of just two days’ worth of prey reveals that at least 10 different arthropod species were caught at each 0.5×0.5 m quadrat. A large proportion of these prey species have been reported to occur on the island (Figure 4). However, for at least some of the species this might be the first Lundy record. This suggests that metabarcoding of *Drosera* prey could be a reliable and

Table 1: Arthropod families detected using the metabarcoding approach. Flying: taxa with flying adult stage. Length data approximate and from a variety of generic sources

Family	**Comments**	**Flying**	**Diptera**	**Length (mm)**
Chaoboridae	Chaoboridae: non-biting, mosquito-like, larvae aquatic and predatory upon zooplankton	Y	Y	≤10
Chironomidae	Chironomidae: non-biting midges; larvae in water/wet habitat or decaying matter	Y	Y	≤10
Sciaridae	Sciaridae breed in all sorts of rotting matter and fungi	Y	Y	≤7
Psychodidae	Psychodidae:owl midges, swarm over breed sites, larvae feed on decaying matter, esp. in water	Y	Y	≤3
Cecidomyiidae	Cecidomyiidae: gall midges, 600+ spp, larvae not all in galls, some eat aphids, for example	Y	Y	≤5
Tomoceridae	Collembola with long antennae	N	N	≤5
Phalangiidae	Harvestman – feed on small invertebrates (perhaps stealing from *Drosera*?)	N	N	≤5
Anthomyiidae	Anthomyiidae: flies; larvae feed on decaying matter	Y	Y	≤3
Agromyzidae	Agromyzidae: like miniature houseflies, larvae=leaf and stem-miners	Y	Y	≤6.5
Chloropidae	Chloropidae: small to minute flies; larvae mainly plant feeders, *Oscinella*=frit-fly ~1.5mm	Y	Y	1.5
Tetragnathidae	Spiders with elongated body	N	N	2-23
Ceratopogonidae	Ceratopogonidae: tiny biting midges, larvae live in water/swamp often with much organic matter	Y	Y	≤5

(relatively) non-invasive technique for community analyses and assessment of taxon presence. It certainly offers significant advantages of accuracy and ease compared to species level identification of semi-digested arthropod fragments via more traditional, morphological techniques.

Dipterans (two-winged flies) dominate the prey samples. Nine of the twelve observed families belong to this Order. This confirms that dipterans form a large proportion of sundew prey, suggesting that the Order forms an important source of nutrients for Lundy *D. rotundifolia*. Similar overrepresentations of dipterans are reported by Ellison and Gotelli (2001) and Foot *et al*. (2014). The latter study investigated the attraction efficiency of *D. rotundifolia* blades and reported that 57% of captured prey items were dipterans. The authors point out that Diptera are most likely not actively attracted (or deterred) by red *D. rotundifolia* blades because Diptera lack red receptors (Foot *et al.*, 2014). Thus, the apparent dominance of dipteran prey might simply reflect their relative abundance in boggy environments.

Our analyses revealed low overlap of prey taxa between the two sites. This could indicate the local invertebrate communities to be very different too, possibly as a result of dissimilar microenvironmental conditions. Pondsbury and North Quarry are, after all, very different environments in that Pondsbury is open and exposed to both sun and wind whilst North Quarry is sheltered from the prevailing wind and receives less sunlight (Figure 2). Even so, although intriguing, the observed prey taxon dissimilarity may simply represent an artefact of only sampling one time-point and the high dipteran diversity on Lundy. More detailed investigations (including replication of quadrats over space and time) are needed to determine whether the two *Drosera* populations feed on genuinely distinct arthropod communities.

Most prey items were heavily degraded. It is probable that this was reflected at the DNA level, with 'older' prey items containing DNA of lesser quality than 'newly' captured ones. Differences in prey DNA quality might have introduced bias, with 'older' prey being underrepresented or even missing from the final sequencing dataset. Metabarcoding is prone to other biases, including relative specimen size (larger specimens contribute more DNA to the pool than smaller ones) and primer efficiency (some specimens in the pool will PCR amplify better than others). Because of such biases the sequence numbers given in Figure 4 cannot be extrapolated to biomass or number of individuals caught. They merely indicate that a taxon is present on the island and in the habitat sampled.

It is also important to note that metabarcoding is an indirect method of community assessment. It is well known that cross-contamination among samples can introduce noise and the method therefore never provides 100% certainty that a species was present, even when uttermost care is taken. Such noise can lead to the incorrect conclusion that a species inhabited a site, whereas it actually did not. This type of error is more likely for species detected with low numbers of sequences. In typical metabarcoding experiments, dozens of samples are run in parallel. To minimise the chance of falsely concluding any of the species reported here stems from contamination from samples run in parallel, sequencing reads were compared among all samples processed in the same sequencing run (NatureMetrics Ltd, pers. comm.). Based on this comparison it seems unlikely that any of the species was absent from the site for which we report it.

This study opens opportunities for future research. Accurate identification of prey to species level will permit high resolution analysis of environmental effects upon *Drosera* diet. Questions that might be posed include: Do diets of *Drosera* populations inhabiting contrasting habitats differ? Do *Drosera* prey taxa vary according to season or even depending on whether it is night or day? Are some arthropod species more attracted by the plants than others and if so, why?

These are some of the questions that might be addressed using Lundy *Drosera* populations as a model system. Whatever the answers may be there is no doubt that these predatory little plants will both invite and repay research for many years to come.

ACKNOWLEDGEMENTS

We would like to thank Tom Dickins (Middlesex University) for organising field trips to Lundy and for useful conversations regarding the evolution of plant carnivory. We thank Kat Bruce and Alex Crampton-Platt (NatureMetrics Ltd) for advice on the analysis of metabarcoding data. This study used the computational resources of the NHM London that are maintained by Peter Foster. Fieldwork was funded by Middlesex University (Faculty of Science and Technology).

REFERENCES

Adamec, L., 2002. Leaf absorption of mineral nutrients in carnivorous plants stimulates root nutrient uptake. *New Phytologist.* 155, 89-100. doi:10.1046/j.1469-8137.2002.00441.x

Adlassnig, W., Lendl, T., Peroutka, M., Lang, I., 2010. Deadly Glue – Adhesive Traps of Carnivorous Plants, in: von Byern, J., Grunwald, I. (Eds.), *Biological Adhesive Systems: From Nature to Technical and Medical Application*. Springer Vienna, Vienna, pp. 15-28

Botany, 1874. *American Naturalist*. 8, 55-57. doi:10.1086/271258

Darwin, C., 1875. *Insectivorous plants*, first edition. ed. John Murray, United Kingdom

Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Natural. Methods* 10, 996-998. doi:10.1038/nmeth.2604

Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics,* 26, 2460-2461. doi:10.1093/bioinformatics/btq461

Ellison, A.M., Gotelli, N.J., 2001. Evolutionary ecology of carnivorous plants. *Trends in Ecology & Evolution*. 16, 623-629. doi:10.1016/S0169-5347(01)02269-8

Foot, G., Rice, S.P., Millett, J., 2014. Red trap colour of the carnivorous plant *Drosera rotundifolia* does not serve a prey attraction or camouflage function. *Biological Letters*. 10

Hebert, P.D.N., Cywinska, A., Ball, S.L., deWaard, J.R., 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences,* 270, 313-321

Hooker, H.D., 1916. Physiological Observations on *Drosera rotundifolia*. *Bulletin of the Torrey Botanical Club*, 43, 1-27. doi:10.2307/2479710

Lane, R., 1978. The Diptera (two-winged flies) of Lundy island. *Annual Report of the Lundy Field Society 1977*, 28,15-31

Leray, M., Yang, J.Y., Meyer, C.P., Mills, S.C., Agudelo, N., Ranwez, V., Boehm, J.T., Machida, R.J., 2013. A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: application for characterizing coral reef fish gut contents. *Frontiers in Zoology*, 10, 34. doi:10.1186/1742-9994-10-34

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet Journal*, 17, No 1 Gener. Seq. Data Anal.

Menzel, F., Smith, J.E., Chandler, P.J., 2006. The sciarid fauna of the British Isles (Diptera: Sciaridae), including descriptions of six new species. *Zoological Journal of the Linnean Society,* 146, 1-147. doi:10.1111/j.1096-3642.2006.00190.x

Millett, J., Jones, R.I., Waldron, S., 2003. The contribution of insect prey to the total nitrogen content of sundews (*Drosera* spp.) determined in situ by stable isotope analysis. *New Phytologist*. 158, 527-534. doi:10.1046/j.1469-8137.2003.00763.x

Parsons, A.J., 1996. Invertebrates (excluding Lepidoptera) on Lundy 1995. *Annual Report of the Lundy Field Society 1995*, 46, 87-91

Parsons, A.J., 1988. Invertebrates on Lundy, 1987. *Annual Report of the Lundy Field Society 1987*, 38, 52-53

Peng, Y., Leung, H.C.M., Yiu, S.M., Chin, F.Y.L., 2012. IDBA-UD: a de novo assembler for single-cell and metagenomic sequencing data with highly uneven depth. *Bioinformatics.* 28, 1420-1428. doi:10.1093/bioinformatics/bts174

Roth, A.W., 1782. Von der Reizbarkeit der Blatter des sogenannten Sonnenthaues (*Drosera rotundifolia, longifolia*), *Beytrage zur Botanik, Erster theil*.

Schmieder, R., Edwards, R., 2011. Quality control and preprocessing of metagenomic datasets. *Bioinformatics* ,27, 863-864. doi:10.1093/bioinformatics/btr026

Smith, P., Nunny, R., 2012. Mapping of sedimentary marine biotopes around Lundy, UK. *Journal of the Lundy Field Society*. 3, 41-74

Thomsen, P.F., Willerslev, E., 2015. Environmental DNA – An emerging tool in conservation for monitoring past and present biodiversity. Special Issue Article: Environmental DNA, *Biological Conservation*, 183, 4-18. doi:10.1016/j.biocon.2014.11.019

Thum, M., 1988. The significance of carnivory for the fitness of *Drosera* in its natural habitat.1. The reactions of *Drosera intermedia* and *Drosera rotundifolia*. *Oecologia,* 75, 472-480. doi:10.1007/BF00376954

Thum, M., 1986. Segregation of habitat and prey in two sympatric carnivorous plant species, *Drosera rotundifolia* and *Drosera intermedia. Oecologia*, 70, 601-605. doi:10.1007/BF00379912

Yang, C., Wang, X., Miller, J.A., de Blécourt, M., Ji, Y., Yang, C., Harrison, R.D., Yu, D.W., 2014. Using metabarcoding to ask if easily collected soil and leaf-litter samples can be used as a general biodiversity indicator. *Ecological Indicators,* 46, 379-389

Zhang, J., Kobert, K., Flouri, T., Stamatakis, A., 2014. PEAR: a fast and accurate Illumina Paired-End reAd mergeR. *Bioinformatics,* 30, 614-620. doi:10.1093/bioinformatics/btt593

CLIFF NESTING SEABIRDS ON LUNDY: POPULATION TRENDS FROM 1981 TO 2017

by
HELEN BOOKER[1], PETER SLADER[2], DAVID PRICE[3], A.J. BELLAMY[4] AND TIM FRAYLING[5]
[1]RSPB, South West Regional Office, 4th Floor (North Block),
Broadwalk House, Southernhay West, Exeter, EX1 1TS
[2]10 Moorland Way, Exeter, EX4 2ET
[3]8 Scattor View, Bridford, Exeter, EX6 7JF
[4]National Trust, Home Farm, Parke, Bovey Tracey, Newton Abbot, TQ13 9JQ
[5]Natural England, Ground Floor, Sterling House, Dix's Field, Exeter, EX1 1QA
[1]*Corresponding author, e-mail: helen.booker@rspb.org.uk*

ABSTRACT

In the first week of June 2017 the breeding population and distribution of seabirds on Lundy (with the exception of *Larus* gulls, Manx Shearwater and Storm Petrel) was surveyed using a repeat of the methodology from the previous surveys that have run approximately four yearly since 1981. The results show an increase in many species, particularly since rat eradication, and indicate that Lundy's importance as a seabird island is gradually being restored.

Keywords: *Lundy, Guillemot, Razorbill, Puffin, rats*

INTRODUCTION

Lundy is one of the most important sites in south west England for breeding seabirds and is a Site of Special Scientific Interest (SSSI) for Manx shearwater (*Puffinus puffinus*), Puffin (*Fratercula arctica*), Guillemot (*Uria aalge*), Razorbill (*Alca torda*) and Kittiwake (*Rissa tridactyla*). It is one of only two locations in England supporting breeding Manx Shearwater and Storm Petrel (the other being the Isles of Scilly), and one of the few where Puffins breed. Lundy's cliff nesting seabirds have been monitored on a four to five yearly cycle since 1981. Herring Gulls (*Larus argentatus*), Lesser Black-Backed Gulls (*L. fuscus*) and Great Black-Backed Gulls (*L. marinus*) have been surveyed at the same time, but in a less intensive way, with an estimated count of nests taken. The first full survey of the island's Manx Shearwaters was undertaken in 2001 and trial surveys for Storm Petrel began in 2016 following confirmation of breeding in 2014.

In June 2017, a repeat survey of the cliff nesting seabirds was undertaken as part of this survey cycle for Guillemots, Razorbills, Puffins, Kittiwakes, Fulmars (*Fulmaris glacialis*) and Shags (*Phalacrocorax aristotelis*).

METHODOLOGY

The survey was conducted between 3 and 10 June 2017, using a direct repeat of methods from previous surveys, the most recent conducted in 2013 (Price *et al.* 2014). The survey method is based on the published standard methods for surveying each species (Walsh *et al., 1995).* Every section of coastal cliff was monitored from vantage points, using a register to record numbers of breeding seabirds at each site.

Auks (Guillemots, Razorbills and Puffins) are difficult to survey accurately and the published methods have been adapted to make a whole island census practical for Lundy. The adapted technique means the results are therefore a representative indication of breeding numbers allowing direct comparison between surveys. For Guillemots and Razorbills the count unit is individual birds occupying breeding sites. Puffins are also counted individually, but including birds on the sea adjacent to breeding cliffs. Walsh *et al.* (1995) suggest at least five counts should be made; however, because of the size of the task on Lundy and the time available for survey, this has been adapted to two counts of the main nesting areas and a single count of others. However, weather conditions during the 2017 survey were not favourable with several days of wet and windy weather, and it was therefore not possible to complete the usual two visits to the busier colonies and each site was only surveyed once.

For Kittiwakes and Shags, which construct an obvious nest, a count of Apparently Occupied Nests (AONs) was made, and for Fulmars (which make no nest, but lay their eggs on suitable ledges), the count unit was Apparently Occupied Sites (AOSs), taking care to avoid including birds just sitting on the ledges but not breeding.

Up to 2013, the register used to identify vantage points and record observations was based on line drawings of the cliffs and an old map base that was hard for the inexperienced eye to decipher and locate the survey vantage points. For 2017, the register was updated to a photographic based document for ease of reference, enabling future surveyors that may be less familiar with the cliffs to locate the sites. A copy of the site register is held by the RSPB at the Exeter office.

Though estimated numbers of occupied nests (AONs) of each *Larus* gull species were recorded when possible, the time pressure due to the adverse weather conditions meant that detailed surveying was not possible, and full coverage was not achieved. As such the results are incomplete and not at all representative, and are therefore not included in this report.

Plate 1: Peter Slader checking the site register at Jenny's Cove. © Lee Bullingham-Taylor

RESULTS

Overview of species totals and trends

Despite the inclement weather and the lack of a second visit to the main west coast sites (from Jenny's Cove to NW point), a full island count was undertaken for all species except the gulls. These results are presented in Table 1, which provides a breakdown of the target species by coastal sections and the pattern of counts, emphasising the importance of the rugged west coast.

Table 1: Overview of results for cliff nesting species in 2017 by survey count section

Section	**Guillemot (ind.)**	**Razorbill (ind.)**	**Puffin (ind.)**	**Kittiwake (AON)**	**Fulmar (AOS)**	**Shag (AON)**
A: South Light to Shutter Rock	10	94	0	0	1	1
B: Shutter Rock to Old Light	31	151	0	0	1	9
C: Old Light to Battery Point	0	20	0	0	0	0
D: Battery Point to Needle Rock	125	67	31	0	38	1
E: Needle Rock to Pyramid	2,727	397	198	59	103	3
F: Pyramid to St James Stone	2,028	366	57	179	10	3
G: St James Stone to NW Point	1,262	532	58	0	29	21
H: NW Point to NE Point	1	8	20	0	0	0
I: NE Point to Gannets Rock	12	12	11	0	39	1
J: Gannets Rock to Brazen Ward	0	31	0	0	0	0
K: Brazen Ward to Halfway Wall	2	11	0	0	6	6
L: Halfway Wall to South Light	0	46	0	0	0	10
Totals	**6,198**	**1,735**	**375**	**238**	**227**	**55**

The total all-island counts for 2017 for each species are also presented in Table 2 along with the count totals from the previous nine surveys, providing an indication of species trends over the past 36 years. For the auks in particular this presents a picture of remarkable increases in numbers, continuing the encouraging improvement in numbers observed in the 2013 survey, and for most species counts now well exceed the figures for the last national seabird census, Seabird 2000.

Table 2: Numbers of cliff nesting seabirds between 1981 and 2017

Year	Guillemot (ind.)	Razorbill (ind.)	Puffin (ind.)	Kittiwake (AON)	Fulmar (AOS)	Shag (AON)
1981	2,197	991	129	933	109	29
1982	1,979	861	87	911	117	43
1986	2,096	761	39	718	185	35
1992	2,628	791	37	407	174	22
1996	1,914	951	15	392	202	37
2000	2,348	950	13	237	190	56
2004	2,321	841	5	148	178	63
2008	3,302	1,045	14	151	170	63
2013	4,114	1,324	80	127	209	112
2017	6,198	1,735	375	238	227	55
Change 2013-2017	+51%	+31%	+369%	+87%	+9%	-51%
Change 2000-2017	+164%	+82%	+2,784%	0%	+19%	0%

Species Accounts

Guillemot and Razorbill

Guillemots are the second most numerous seabird species breeding on Lundy (after Manx shearwater) with an estimated 6,198 individuals in 2017, which represents a staggering 51% increase on the 2013 figure and a continuation of increasing numbers since 2004. Lundy now supports almost three times the number of guillemots recorded in 2004, and the population is currently at a level not seen since the late 1940s (Davis and Jones 2007).

The pattern of site occupancy remained similar between this survey and the last with Jenny's Cove to NW Point (sections E, F and G in Table 1) continuing to support the majority of birds and showing the greatest increase in numbers since 2013. Section F (Pyramid to St James Stone) has seen an increase of 557 birds, whilst numbers in Jenny's Cove have increased by 1,323 birds in this four year period, and interestingly, they have recolonised Devil's Chimney, which was abandoned some twenty years ago in 1996. (It is salutary to recognise that the number of Guillemots now occupying Jenny's Cove exceeds the totals obtained for the whole of Lundy in any of the surveys prior to 2008 (as illustrated in Tables 1 and 2).

Razorbills have also increased steadily since 2004 with 1,735 individuals recorded in 2017 representing a 31% increase on the previous survey. The pattern of change is rather variable around the island. Birds are often exploiting previously unoccupied areas of broken ground and clefts in cliffs and generally colonising new sites, with sizeable increases in numbers along the south coast as well as from Jenny's Cove northwards.

The populations of Guillemots and Razorbills is illustrated in Figure 1 below, showing the relatively stable populations until 2004, followed by marked increases, especially for Guillemots.

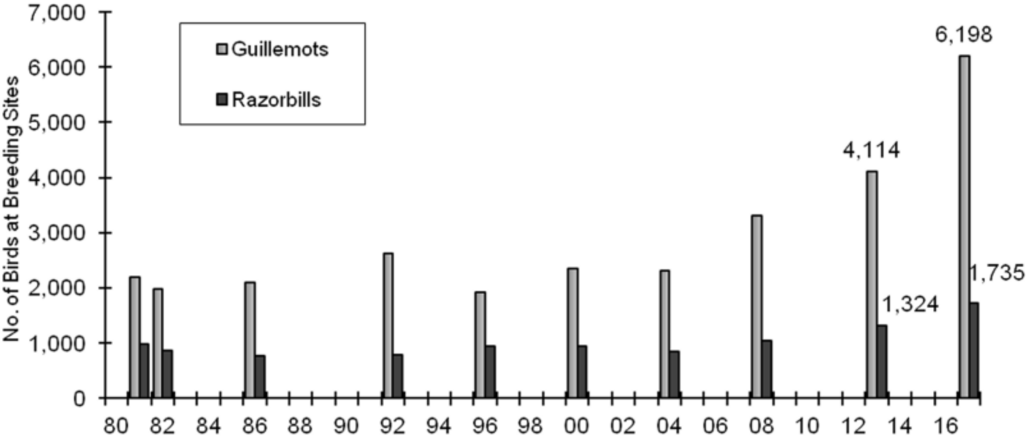


Figure 1: Guillemot and razorbill population change since 1981 (individuals)

Puffin

An amazing total of 375 puffins was recorded in 2017, a population level not seen since the early 1950s. This compares to 80 in 2013 and just 5 birds in 2004. As with the other auks, 2004 was a turning point and their fortunes have radically improved since then, as illustrated in Figure 2.

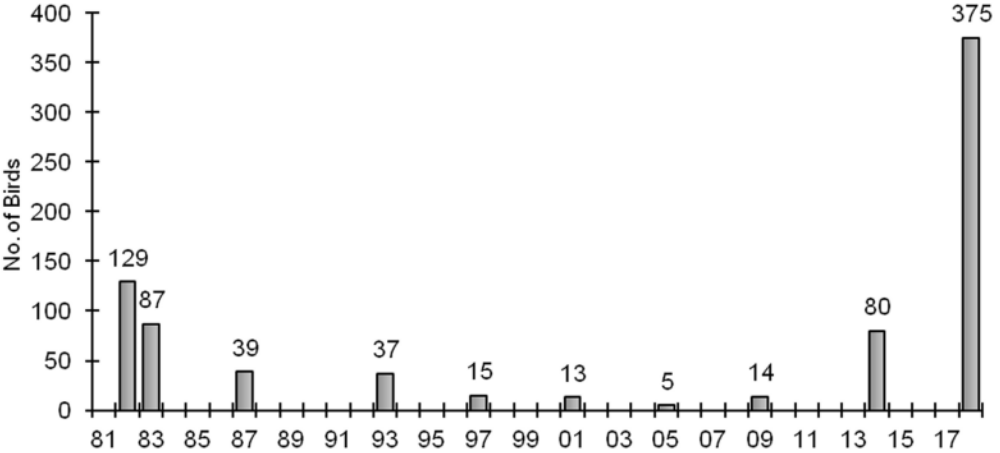


Figure 2: Puffin population change since 1981 (individuals)

Table 3 shows that Puffins now occur in all six of the coastal sections extending up along the west coast from Battery Point northwards and around to Gannets Rock. In 2013, though numbers had increased, all but four of the birds recorded were still confined to Jenny's Cove and the north of St Philip's Point. The most important area is still Jenny's Cove, where numbers have swelled from 61 birds in 2013 to 198 in 2017, an increase of 137.

Table 3: Puffin population change since 2004 by coastal section

Section	**2004**	**2008**	**2013**	**2017**
A: South Light to Shutter Rock				
B: Shutter Rock to Old Light				
C: Old Light to Battery Point				
D: Battery Point to Needle Rock			1	31
E: Needle Rock to Pyramid		6	61	198
F: Pyramid to St James Stone	5	8	15	57
G: St James Stone to NW Point			3	58
H: NW Point to NE Point				20
I: NE Point to Gannets Rock				11
J: Gannets Rock to Brazen Ward				
K: Brazen Ward to Halfway Wall				
L: Halfway Wall to South Light				
Total	**5**	**14**	**80**	**375**

Plate 2: Puffins at Jenny's Cove in 2016. © Elisabeth Price

Kittiwakes

The apparently inexorable decline in kittiwakes since 1981 showed signs of levelling out in 2008 (see Figure 3) and in 2017 actually showed a welcome upturn in numbers from 127 AONs in 2013 to 238 in 2017 (an 87% increase). The huge colony of some 400 pairs crammed into Puffin Gully in 1981 and 1982 had been abandoned along with virtually all other sites by 2004, with just single figure counts in Jenny's Cove and the only significant concentration of birds at two sites between St Philip's Point and St James Stone in Section F. The increase to 59 AONs in Jenny's Cove in 2017, and the improved numbers at the two Section F colonies (from 119 to 179 AONs), is an encouraging sign.

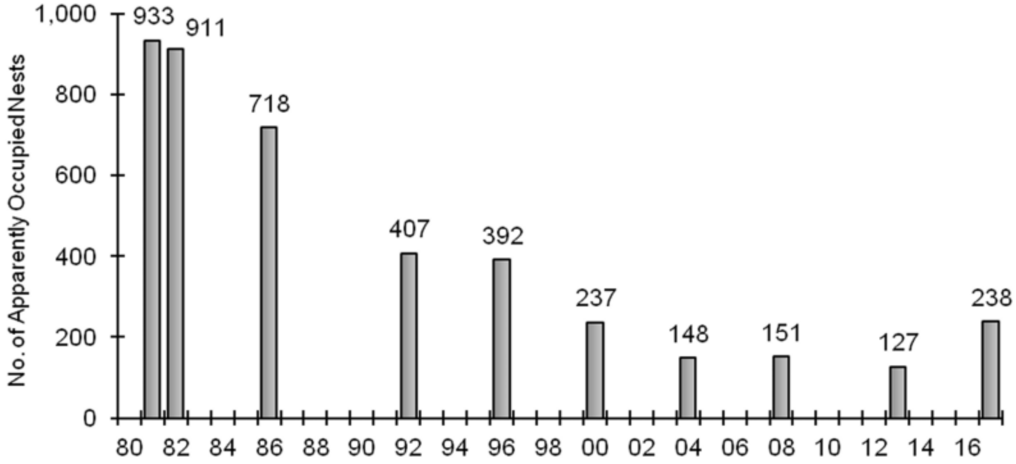


Figure 3: Kittiwake population on Lundy from 1981 to 2017 (AONs)

Fulmar

The 2017 survey produced a further increase in Fulmars to 227 AOSs, the highest count since 1981. Patterns of site occupancy and numbers within these sites were similar to that of the previous survey. However, the long term movement away from the east coast (and from Gannets Rock in particular), and the colonisation of Jenny's Cove and elsewhere along the west coast continues, with an increase of 19 AOSs in Jenny’s Cove, and a small decrease (from 14 to 6 AOSs) between Brazen Ward and Halfway Wall (Section K) on the east coast.

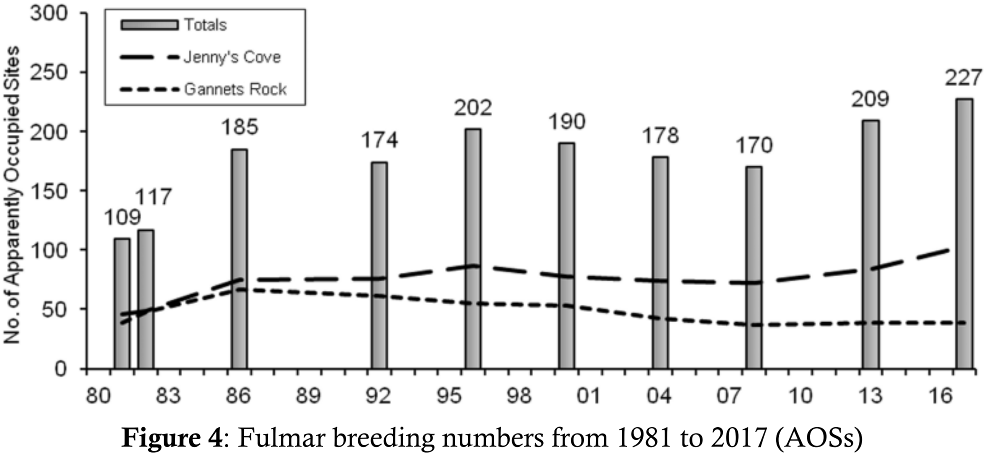


Figure 4: Fulmar breeding numbers from 1981 to 2017 (AOSs)

Shag

The timing of seabird surveys on Lundy (typically late May-early June) has been chosen to obtain best results for counts of auks and does not necessarily favour the surveying of breeding shags. Shags nest earlier than the other seabirds and it is quite possible that breeding at some sites has finished prior to the usual survey period. Also, some birds may choose not to breed at all in some years, particularly if food availability is poor. Nesting shag numbers from the surveys therefore need to be treated with some caution. Though the 2017 figure of 55 AONs is far below the 112 AONs recorded in 2013, it is more in line with that of previous surveys up to 2008, and probably indicates a relatively stable population.

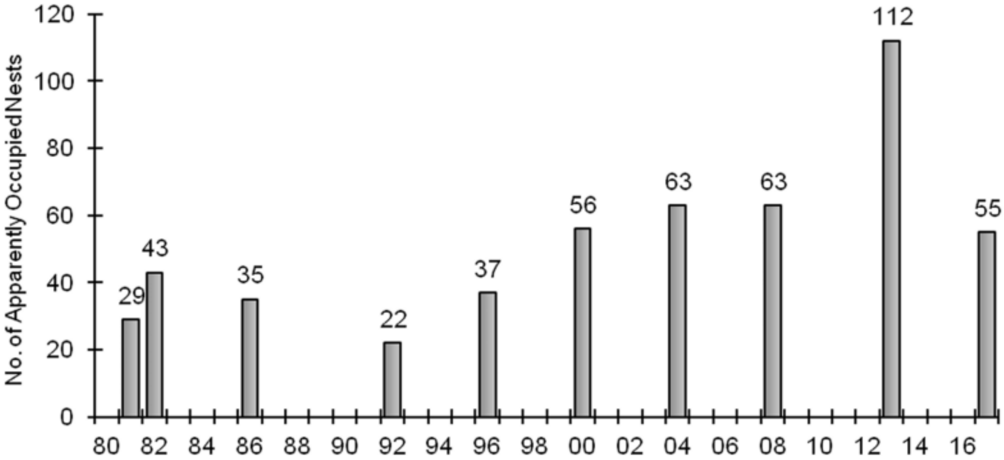


Figure 5: Change in number of recorded shag AONs since 1981

Shags require a relatively large flat area to build a nest and very much prefer it to be inconspicuously sited under a large rock or in a crevice. With sheer cliffs around much of the island such sites are relatively limited and most of the nests found on Lundy are sited along the break in slope at the top of cliffs or in areas of fallen boulders and rocks. The relatively flat-top of Goat Island (near South West Point) is a favoured location, as are some of the more broken cliff faces north of St Philip's Point, with a scattering of birds along the lower cliffs of the east coast around Halfway Wall Bay.

Gulls

It was not possible to accurately survey the *Larus* gulls in 2017 and therefore no results are presented. Further survey for these species will be carried out in 2018.

DISCUSSION

Weather conditions were particularly adverse during the week of the survey and, though full single counts for the target species were obtained, surveying of gulls was compromised. In years when a second count is feasible for auks in the main breeding areas, the maximum count from the two visits is used. If a second visit to the main sites had been possible in 2017, the lower count would have been discarded. Consequently, the 2017 counts are considered a potential under-estimate for these species.

The positive trend for most seabirds on Lundy builds on those reported in 2013 (Price *et al.*, 2014). Despite the constraints of the weather during the survey and as a result being limited to single counts, there are stark changes in numbers that provide a real indication of trend over the last four years. National trends reported by JNCC show that Lundy's seabirds are generally faring well compared to the wider UK. JNCC's trend information is based on a sample of monitored colonies and compares these to the last national census, Seabird 2000. The latest trend information is not available for Puffins; however Guillemots have increased by 5% nationally between Seabird 2000 and 2015 and Razorbills by 32% in the same period (JNCC, 2016). The population increases for Lundy are considerably more for these species at 164% and 82% respectively between 2000 and 2017.

Fulmar numbers have decreased nationally by 31% between Seabird 2000 and 2015, whereas on Lundy they have increased by 19% between 2000 and 2017. Shags have declined nationally by 34% and Kittiwakes by 44% in the same period (JNCC 2016). On Lundy, despite some variability during this period, the populations for Kittiwakes and Shags in 2000 and in 2017 were virtually the same (a difference of just one nesting pair for both species).

The dramatic increase in the Puffin population and substantial increases in Guillemot and to a lesser extent Razorbill, have occurred since 2004. This pattern is also co-incident with the increase in Manx Shearwaters (Booker and Price, 2014) and ahead of the more recent colonisation of Storm Petrels (Taylor, 2014). The absence of rats, which were eradicated from Lundy over the winters of 2002/03 and 2003/04 (Appleton *et al.,* 2006) is probably the main driver for such positive changes. Rat predation of eggs and chicks is most likely to have affected the burrow nesting species, Manx shearwater and Puffin, and be the reason behind the absence of breeding Storm Petrels. It is also probable that rats suppressed the population of Razorbills, which nest in crevices.

Plate 3: Guillemots occupying the broken ground above the cliff in 2016. © Elisabeth Price

Further evidence to support a response to the absence of rats is a shifting distribution of auks, with Guillemots, Razorbills and Puffins now nesting higher up into the broken ground where the cliff top meets the steep grassy coastal slopes and the habitat becomes a complex mix with rock, soil and broken ground providing numerous nesting opportunities. These areas were previously occupied by rats but are now available as safe nest sites. The change is particularly apparent at Jenny's Cove where breeding numbers of most species have seen the biggest increase. Plate 3 was taken in 2016 and illustrates the use of this habitat by Guillemots.

Seabirds require both safe nesting sites and adequate food to be able to breed successfully. Therefore alongside the absence of rats, the increase in so many of Lundy's seabird species has to be supported by adequate prey availability within the species' foraging range from the island. Thaxter *et al.* (2012) provide the following average foraging ranges for auks.

Table 4: Published foraging ranges for Guillemot, Razorbill and Puffin

	Foraging Ranges (km)	
	Mean Maximum	Average
Puffin	105.4	4.0
Guillemot	84.2	37.8
Razorbill	45.8	23.7

Mean maximum=the average of the maximum ranges from all studies

Though the specific foraging ranges of Lundy's auks have not been studied, the increases in the populations of these species suggests that prey is currently plentiful within a few tens of kilometres from the island. Data from Lundy's Manx Shearwaters, a species able to undertake foraging trips of over 300km (Thaxter *et al.,* 2012), indicates that whilst some birds travel long distances, many foraging trips take place in local waters around the island and off the Cornwall coast (Freeman *et al.*, 2012). Such local foraging suggests that the seas around Lundy can be rich in food.

Guillemot numbers are now at their highest recorded by any complete island census since an estimate of 19,000 pairs in 1939 (Perry, 1940). By 1949 numbers had apparently fallen to around 3,500 individuals, and when Barbara Whittaker, warden at the time, carried out the next comprehensive all-island counts in 1955 and 1956 the numbers recorded were 3,850 and 3,910 respectively (Davis and Jones, 2007). By the time of the Operation Seafarer survey in 1969 numbers had declined to 1,647 individuals. Between 1969 and 2004 numbers fluctuated around 2,000 birds, and after this date, coinciding with rat removal, numbers began their substantial increase (Davis and Jones, 2007; Price and Booker, 2008 and Price *et al.,* 2014).

The story is similar, but less pronounced, for Razorbills. Perry estimated 10,500 breeding pairs in 1939 and since then the highest whole island count was in 1962 when 2,130 individuals were recorded (Davis and Jones 2007). After this date, numbers declined to the all-time low of 761 individuals in 1986 (Price, 1986) after which, as with Guillemot, they fluctuated up to 2004 before beginning the steady increase to their current level.

Favourable conditions for foraging, both prey abundance and accessibility, is also the likely reason for the upturn in breeding Kittiwakes, which, until this year, have largely been in decline since surveys began in 1981. It seems highly unlikely rats reached the Kittiwake ledges and most probable that this species has been affected by other factors such as a lack of prey availability. The situation on Lundy is not unique; in addition to the -44% UK trend described above, 58% of colonies from southern English counties (from Kent to Isles of Scilly and including Lundy) have been abandoned between 1986 and 2014 and the remaining colonies have declined by 66% between 2000 and 2014 (McMurdo Hamilton *et al.*, 2016). McMurdo Hamilton *et al.* reviewed the publications suggesting causes of decline in Kittiwakes in southern England, which indicate that weather conditions, frontal system patterns and predation are amongst the reasons for the decline in southern populations.

As already noted, assessing the breeding population of Shags requires survey work over several months to cope with their asynchronous breeding. However, in the absence of any other data, it would seem that the 2017 survey results, which are consistent with the general trend over recent years, indicate there is no major cause for concern. If anything the absence of rats from the areas of broken ground at the top of the cliffs and in the scree slopes may well be a positive factor in providing nests sites with less chance of predation and encouraging occupation of more such areas.

CONCLUSIONS

The importance of Lundy for breeding seabirds continues to grow with many species faring better on Lundy than across the UK generally. The island is home to many thousands of seabirds during the breeding season and has the potential to support many more if conditions remain suitable. Maintenance of the island's rat-free status, combined with well managed seas, is essential to ensure that the island's seabird species can continue to thrive. There is still uncertainty over the latest trends in *Larus* gulls as these could not be adequately surveyed this year and these populations should be fully counted in 2018.

Ongoing regular monitoring of all Lundy's seabirds will help provide a measure of the overall health of Lundy's nesting habitats and the seas around it. The results from the 2017 survey suggest that the future for most species of seabird on Lundy is promising and that the island is gradually regaining its historic importance as a major seabird colony.

ACKNOWLEDGEMENTS

Thanks to Richard Caldow, Bart Donato, Vicky Gilson and Esther Pawley from Natural England for fieldwork assistance.

Thanks also to Derek Green, Lundy General Manager, for supporting the survey through the provision of tickets and accommodation to the RSPB free of charge and to Dean Jones, Lundy warden, for general support and survey help.

REFERENCES

Appleton, D., Booker, H., Bullock, D.J., Cordrey, L. & Sampson, B. 2006. The Seabird Recovery Project: Lundy Island. *Atlantic Seabirds* 8, 51-59

Booker, H. & Price, D. 2014. Manx Shearwater Recovery on Lundy: Population and Distribution Change from 2001 to 2013. *Journal of the Lundy Field Society*, *Vol. 4, 2014,* 105-116

Davis, T.J. and Jones, T.A. 2007. *The Birds of Lundy*. Devon Bird Watching and Preservation Society and Lundy Field Society, Berrynarbor, Devon

Freeman R., Flack, A., Taylor, C., Dean, B., Kirk, H., Fayette, A., Perrins, C. and Guilford, T. 2012. The foraging and migration of Manx shearwaters on Lundy. *Annual Report of the Lundy Field Society 2011, 61,* 104-108

JNCC 2016. Seabird Population Trends and Causes of Change: 1986-2015 Report. Joint Nature Conservation Committee. Updated September 2016

McMurdo Hamilton, T., Brown, A. & Lock, L. 2016. Kittiwake declines in southern England. *British Birds* 109, 199-210

Mitchell, P.I., Newton, S.F., Ratcliffe, N. & Dunn, T.E. 2004. *Seabird Populations of Britain and Ireland*. London: T & AD Poyser

Musgrove, A., Aebischer, N., Eaton, M., Hearn, R., Newson, S., Noble, D. & Parsons, M. 2013. Population estimate of birds in Great Britain and the United Kingdom. *British Birds* 106, 64-100

Perry, R. 1940. *Lundy, Isle of Puffins*. Drummond, London

Price, D. 1986. Lundy Census of Breeding Seabirds: Site Register. Unpublished report to RSPB and Lundy Field Society

Price, D. and Booker, H. 2008. Lundy Census of Breeding Seabirds: 2008. Unpublished survey results to RSPB, JNCC and Lundy Field Society

Price, D., Slader, P. & Booker, H. 2014. Survey of breeding cliff nesting seabirds: 2013. *Annual Report of the Lundy Field Society 2013, 63, 85-9*

Taylor, A.M. 2014. Storm Petrel: first confirmed breeding record for Lundy and Devon. *Annual Report of the Lundy Field Society 2013*, 64, 66-68

Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W. & Burton, N.K.H. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation 156*, 53-61

Walsh, P.M., Halley, D.J., Harris, M.P., del Nevo, A., Sim, I.M.W. & Tasker, M.L. 1995. *Monitoring Handbook for Britain and Ireland.* JNCC/RSPB/ITE/Seabird Group, Peterborough

POLLEN BEETLES AND REPRODUCTIVE SUCCESS OF THE ENDEMIC LUNDY CABBAGE: THE CONSEQUENCES OF AN APPARENT INVASION EVENT IN 2007

by

ROSY J.D. KEY[2], ROGER S. KEY[2], MOHINE ALAM[1] AND STEPHEN G. COMPTON[1,3]
[1]School of Biology, University of Leeds, Leeds, LS2 9JT
[2]Formerly Natural England, Peterborough
[3]*Corresponding author, e-mail: s.g.a.compton@leeds.ac.uk*

ABSTRACT

Lundy cabbage is a yellow-flowered crucifer endemic to Lundy. Pollen beetles (*Brassicogethes* spp.) are present routinely in its flowers, but exceptional numbers were present in 2007, probably as a result of mass migration from the mainland. We used the proportion of flowers failing to set fruit and the proportion of unhealthy flower buds to compare the plant's reproductive success in 2007 with nine subsequent years, when *Meligethes* numbers were much lower. It appears that in 2007, but not others, the nationwide expansion of oilseed rape production may have had negative consequences for this protected plant species.

Keywords: *Brassicogethes, Coincya wrightii, Lundy, Meligethes, migration*

INTRODUCTION

Lundy cabbage (*Coincya wrightii*) is one of the few endemic plants found only in the British Isles. Molecular evidence suggests that it is a post-glacial derivative of the more widespread *C. monensis*, the Isle of Man cabbage (Compton *et al.*, 2007). Lundy cabbage is a short-lived perennial that grows on the cliffs and Sidelands of the eastern side of Lundy. It does not reproduce vegetatively and so relies entirely on sexual reproduction to maintain the size of its populations and to disperse to new ones. The conspicuous flowers are soft yellow and, and grouped into upright raceme inflorescences. Flowering occurs mainly from mid May to mid June, but ones in which buds, flowers or fruits are grazed off will continue to attempt to flower and some plants in flower can be present even in winter. Larger plants produce more flowers and more seeds, and large plants can generate several hundred fruits and thousands of seeds in a season (Compton & Key, 2000). Lundy cabbage fruits ('pods') are typical of less derived members of the cabbage family Brassicaceae. They are elongate and roughly cylindrical in cross section. Each fruit is divided into two parts, with a long basal siliqua that has a central septum running its length and two dehiscent valves, and a shorter terminal beak. Most of the seeds are in the siliqua, with just one or two seeds in the beak (Compton & Key, 2000). The seeds are dispersed mainly when the siliqua dehisces, but seeds in the beak can also be carried by the wind (Compton *et al.*, 2010).

Lundy cabbage is unique among the British flora because it is the only host-plant for endemic insects, the Bronze Lundy cabbage flea beetle (*Psylliodes luridipennis*) and the Lundy cabbage weevil, *Ceutorhynchus contractus* 'var.' *pallipes*, which is considered currently to be an undescribed species (Compton *et al*., 2002). In addition, the plant is eaten by several other insects, most of which are generalist herbivores that feed on a wide range of crucifer species (Compton & Key, 2000). Flies, butterflies, moths, ants, beetles, wasps, sawflies and solitary bees and bumble bees visit the flowers and are potential pollinators (honey bees are absent from Lundy). Wright (1936), after whom the plant is named, suggested that the adults of *Meligethes* spp., (Coleoptera: Nitidulidae) were the major pollinators of Lundy cabbage (Plate 1). These pollen beetles are now placed in a new genus, *Brassicogethes* (Audisio *et al*., 2009). However, although they are frequent floral visitors, and can become covered in pollen, these beetles are unlikely to be efficient pollinators of Lundy cabbage (Chifflet *et al*., 2011). Both their adults and larvae also feed on the petals and flower buds, as well as pollen, so their net effects are negative for the plants. Reflecting this, *Brassicogethes aeneus* and to a much lesser extent *B. viridescens,* are significant pests of cruciferous crops such as oilseed rape (Williams & Free, 1979; Kirk-Spriggs, 1996).

Plate 1: *Brassicogethes viridescens* (pollen beetle) adults are the most common and easily-seen beetles on the flowers of Lundy cabbage. They are often mistaken for the endemic Lundy cabbage flea beetle

Brassicogethes viridescens is usually the more common crucifer-feeding pollen beetle on Lundy, but *M. aeneus* is also present and was common on Lundy cabbage in 2007. Both species feed on a wide range of yellow-flowered crucifers (Kirk-Spriggs, 1996). The life history of *Brassicogethes* species can be summarised as follows: there is usually a single generation each year. Adults emerge from hibernation in the spring, seek out flowers to feed on pollen before visiting a narrower range of plant species to lay their eggs on developing buds, on which the larvae feed. Larval development (at least in *B. aeneus*) takes less than two weeks after which the larvae fall to the ground to pupate. Adults feed on pollen of a wide range of species again in the autumn, before entering the soil to hibernate (Lane, 1984; Kirk-Spriggs, 1996).

Most Lundy cabbage plants grow in areas inaccessible to grazing animals (goats, sheep and rabbits) and have to be viewed from a distance. Using binoculars, annual standardized counts of the numbers of Lundy cabbage in flower have been carried out each spring since 1994. These counts are supplemented by estimates of the proportion of plants that are not flowering that are based on the very limited areas where plants are accessible on foot. The estimated numbers of individuals in flower has varied by about a factor of ten between 1994 and 2017. During the first half of this period the variation in plant numbers was mainly driven by dramatic fluctuations in the numbers of rabbits on the island, which had boom periods ended by periodic outbreaks of myxomatosis (Compton *et al.*, 2004). In more recent years the rabbit population on the island has been relatively stable, but the numbers of flowering Lundy cabbage have continued to fluctuate, though not as dramatically (S.G. Compton, R.S. Key and R.J.D. Key, unpublished data). Much of this variation may be climate-related, but a drop in the numbers of plants with flowers present in 2007 was apparently related to unusually high levels of insect damage to the inflorescences. Every inflorescence we could inspect closely had adult pollen beetles (*Brassicogethes* spp.) feeding on the buds and petals, and almost every flower had at least one adult pollen beetle feeding there. This stimulated us to monitor changes in flowering success, in order to determine whether 2007 was an exceptional year for pollen beetles and for the reproduction of the plants.

Lundy cabbage inflorescences mature from the bottom up, so that basal fruits, more central flowers and terminal flower buds can all be present at the same time. Any flowers that fail to set seed abscise and leave behind the short pedicel. The relative numbers of pedicels and fruits can provide an indication of the proportion of 'successful' flowers (Plate 2) and in the past the proportion of flowers that managed to produce fruits has been used as an index of pollen beetle damage to oilseed rape. However, this needs cautious interpretation, because in addition to insect feeding, climate, soil nutrition and pollination rates can all influence the ratio of successful/unsuccessful fruit set (Williams & Free, 1979; Kirk, 1992; Bartomeus *et al.*, 2015).

Plate 2: Inflorescence of Lundy cabbage showing developing fruits and bare stalks where there has been no fruit set

METHODS

During late May or early June in the years 2007 to 2017 we attempted to assess ratios of fruits to bare pedicels (where fruits had failed to form), and bud damage, on plants growing above and below the Sideland path on the north side of Millcombe and along the road from Millcombe to the Landing Beach, up to about 200m further south. Ten plants with at least three inflorescences displaying open flowers or pods were selected haphazardly in each area if a choice was available. Ten plants at the correct developmental stage were not always accessible in all three areas (17 and 28 rather than 30 plants were sampled in 2016 and 2017 respectively) and in 2012 a late flowering season meant that no suitable plants were available at the time of our survey. Within each inflorescence we counted the numbers of flowers (distinguished from buds if at least part of a petal had started to emerge), fruits, aborted pedicels, apparently healthy buds (green) and unhealthy/aborting buds (which start to turn yellow or brown before falling).

RESULTS

In most years we were able to sample 30 inflorescences. The numbers of buds present on the plants varied greatly, depending in part on the age of the inflorescence (older inflorescences have no buds remaining). 2007 was noteworthy in that it was the only year when the number of aborting buds outnumbered those that appeared to be healthy (Table 1). The relative numbers of flowers to fruits and the pedicels of aborted flowers was also highly variable, reflecting variation in the ages of the inflorescences (later developing inflorescences had a higher proportion of flowers). The year 2007 was again exceptional, with the lowest numbers of flowers and pods per inflorescence and the highest numbers of aborted pedicels (Table 1). Comparisons of between-year differences in the proportion of stalks that had fruits present (Figure 1 upper) and the proportion of buds that appeared to be healthy (Figure 1 lower) illustrate the considerable variation present, but also emphasise that 2007 was an exceptional year for the plant.

Table 1: Annual variation in the numbers of apparently healthy (green) and aborting (yellow or brown) flower buds, open/opening flowers, successful fruits ('pods') and bare pedicels in Lundy cabbage inflorescences. SD=standard deviation

Year	Healthy buds		Unhealthy buds		Flowers		Successful fruits		Bare pedicels	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
2007	3.97 (4.77)	0-23	5.01 (2.98)	0-17	1.68 (1.95)	0-7	1.74 (2.74)	0-14	13.48 (8.63)	0-49
2008	2.67 (4.00)	0-15	0.32 (0.92)	0-5	4.11 (3.72)	0-15	11.16 (9.46)	0-48	6.17 (6.77)	0-36
2009	4.17 (4.01)	0-12	3.53 (2.27)	0-11	4.10 (3.00)	0-12	15.73 (11.88)	1-47	7.53 (6.26)	0-25
2010	3.19 (3.29)	0-12	1.70 (1.70)	0-5	3.93 (2.42)	0-11	14.50 (8.93)	2-53	3.14 (3.48)	0-18
2011	1.97 (3.45)	0-17	0.83 (1.85)	0-10	2.31 (2.36)	0-10	12.52 (6.93)	0-34	9.99 (6.88)	0-46
2012	-	-	-	-	-	-	-	-	-	-
2013	5.98 (5.17)	0-20	1.94 (1.79)	0-6	7.96 (3.49)	0-21	13.48 (7.51)	2-31	2.81 (5.06)	0-28
2014	4.56 (6.35)	0-31	1.53 (1.85)	0-9	1.81 (2.03)	0-10	5.61 (5.42)	0-25	12.58 (7.24)	0-41
2015	3.87 (4.23)	0-18	1.88 (1.27)	0-5	4.84 (2.91)	0-13	8.63 (7.07)	0-36	4.26 (4.52)	0-22
2016	3.25 (2.96)	0-11	1.90 (1.82)	0-7	4.00 (2.84)	0-11	5.80 (5.08)	0-14	7.02 (7.30)	0-44
2017	6.55 (5.26)	0-23	2.49 (2.03)	0-9	3.30 (2.49)	0-13	10.00 (7.60)	0-29	7.70 (6.72)	0-36

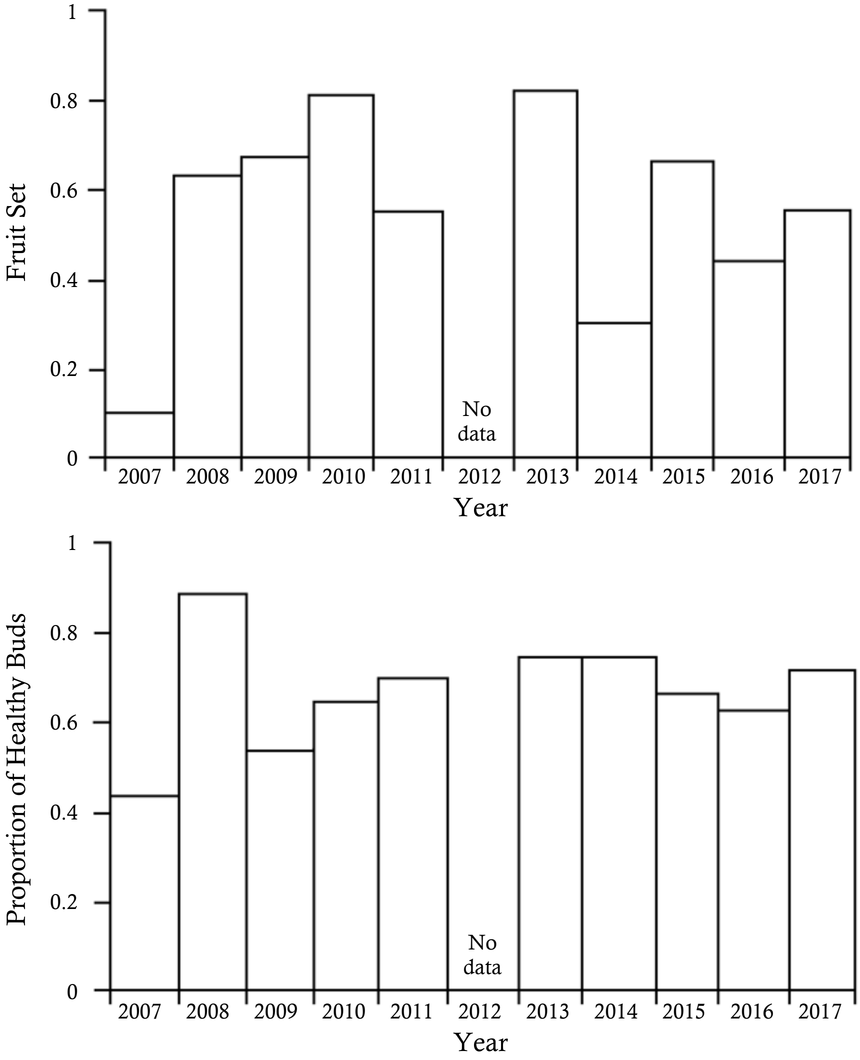


Figure 1: Upper: Annual variation in the proportion of stalks on Lundy cabbage inflorescences that had fruits ('pods') present. Lower: Annual variation in the proportion of buds that appeared healthy

DISCUSSION

The numbers of seeds produced by crucifers such as oilseed rape and Lundy cabbage depends more on the proportion of buds that are successful than the number of buds initiated (Diepenbrock, 2000). Flowers that produce only bare stalks can be common, even in commercial oilseed rape crops, where as few as 40% of the stalks may produce fruits on some plants (Williams & Free, 1979). Our annual estimates of Lundy cabbage reproductive success, based on the proportion of healthy buds and successful fruit-to-empty pedicel ratios, confirm that 2007 was an exceptionally poor year for the plant. In none of the subsequent ten years was there such a high proportion of buds considered to be unhealthy and in all the subsequent years a higher proportion of flowers managed to develop into fruits. The small proportion of stalks that supported the development of fruits in 2007 was even more striking and suggests that damage to the flowers was unusually high. The low flowering success among the plants that year was also reflected in a smaller proportion of plants that had any flowers visible at the time of our visit. This estimate of the proportion of plants with or without any flowers has to be treated with caution because it is based on only a small fraction of the total population area, but in 2007 the proportion of plants with visible flowers was nonetheless the lowest we have recorded in the 24 years when equivalent estimates are available, and almost half the frequency recorded in any other year (S.G. Compton, R.S. Key and R.J.D. Key, unpublished data). It is highly likely that the reduced reproductive success in 2007 was a consequence of damage caused by the exceptional numbers of *Brassicogethes* present on the inflorescences that year. Their feeding damage to the petals was clearly evident; almost every flower had the beetles present and, although their densities were not quantified, we estimated that there was an average of more than one *Brassicogethes* adult per flower. This can be compared with spray threshold guidelines ranging from 15 beetles per plant down to three beetles per plant for control of *B. aeneus* on winter oilseed rape (Lane, 1984; Hansen, 2004). Many of the Lundy cabbage plants had more than 15 beetles on individual inflorescences in 2007.

In most years, our limited collections have found that of *B. viridescens* is by far the more abundant of the two species on Lundy cabbage, and in some years we have failed to record any *B. aeneus.* This was not the case in 2007, when there were very large numbers of *B. aeneus.* Adults of this species utilise a far wider range of host plants than their larvae (Ouvrard *et al.*, 2016). Lundy cabbage is the only large perennial crucifer on the island, and there are only minimal numbers of other yellow-flowered crucifers. It is therefore unlikely that the exceptional numbers of *Brassicogethes* in spring 2007 was the result of exceptional recruitment from within the island. A more plausible hypothesis is that the island received an ‘invasion’ of *B. aeneus* from the mainland in the spring of that year. Significant increases in the UK acreage of oilseed rape from the 1980s led to increased pest problems for this crop, and an increased need for chemical control (Lane & Cooper, 1989). This major increase in the availability of a suitable host plant is likely to have increased the numbers of *B. aeneus* across the country as a whole (Hokkanen, 2000). Adult *B. aeneus* are highly mobile and can disperse over large distances (Tamir *et al.*, 1967; Junk *et al.* 2016; Juhel *et al.*, 2017; Mauchline *et al.* 2017), so the less than 20 kilometres that separate Lundy from mainland England is unlikely to be a significant barrier for this species. Significant invasions are nonetheless clearly rare and *B. aeneus* does not represent a threat to the abundance of the cabbage and its associated endemic insects. The exceptional situation in 2007 presumably resulted from an unusual combination of factors, though the meteorological Office summary of the weather for May that year suggests it was not exceptional (https://www.metoffice.gov.uk/climate/uk/summaries/2007/may).

ACKNOWLEDGEMENTS

We would like to thank Derek Green, the island wardens, and their assistants for all the help they have provided to the ‘cabbage counters’ over the years.

REFERENCES

Audisio, P., Cline, A.R., De Biase, A., Antonini, G., Mancini, E., Trizzino, M., Costantini, L., Strika, S., Lamanna, F. & Cerretti, F. 2009. Preliminary re-examination of genus-level taxonomy of the pollen beetle subfamily Meligethinae (Coleoptera: Nitidulidae) *Acta Entomologica Musei Nationalis Pragae* 49, 341-504

Bartomeus, I., Gagic, V. & Bommarco, R. 2015. Pollinators, pests and soil properties interactively shape oilseed rape yield. *Basic and Applied Ecology* 16, 737-745

Chifflet, R., Klein, E.K., Lavigne, C., Le Féon, V., Ricroch, A.E., Lecomte, J. & Vaissière, B.E. 2011. Spatial scale of insect-mediated pollen dispersal in oilseed rape in an open agricultural landscape. *Journal of Applied Ecology* 48, 689-696

Compton, S.G. & Key, R.S. 2000. *Coincya wrightii* (O.E. Schulz) Stace. *Journal of Ecology* 88, 535-547

Compton, S.G., Key, R.S & Key, R.J.D. 2002. Conserving our little Galapagos – Lundy, Lundy cabbage and its beetles. *British Wildlife* 13, 184-190

Compton, S.G., Key, R.S. & Key, R.J.D. 2004. Lundy cabbage population peaks – are they driven by rabbits and myxomatosis? *Annual Report of the Lundy Field Society 2003* 53: 50-56

Compton, S.G., Craven, J.C., Key, R.S. & Key, R.J.D. 2007. Lundy Cabbage: past, present and future. *Proceedings of the 60th Anniversary Symposium of the Lundy Field Society*, 161-178

Compton, S.G., Norton, R., Straker, R., Walker, C. & Key, R.S. 2010. Lundy cabbage seed dispersal, seed banks and seed germination after rhododendron clearance. *Journal of the Lundy Field Society* 2: 45-52

Diepenbrock, W. 2000. Yield analysis of winter oilseed rape (*Brassica napus* L.): a review. *Field Crops Research* 67: 35-49

Hansen, L.M. 2004. Economic damage threshold model for pollen beetles (*Meligethes aeneus* F.) in spring oilseed rape (*Brassica napus* L.) crops. *Crop Protection* 23, 43-46

Hokkanen H.M.T. 2000. The making of a pest: recruitment of *Meligethes aeneus* onto oilseed Brassicas. *Entomologia Experimentalis et Applicata* 95, 141-149

Juhel, A.S., Barbu, C.M., Franck, P., Roger-Estrade, J., Butier, A., Bazot, M. & Valantin-Morison, M. 2017. Characterization of the pollen beetle, *Brassicogethes aeneus*, dispersal from woodlands to winter oilseed rape fields. *PLOS ONE* 12, e0183878

Junk, J., Jonas, M. & Eickermann, M. 2016. Assessing meteorological key factors influencing crop invasion by pollen beetle (*Meligethes aeneus* F.) - past observations and future perspectives. Meteorologische Zeitschrift 25, 357-364

Kirk, W.D.J. 1992. Insects on cabbages and oilseed rape. Naturalists' Handbooks 18, 1-66. Pelagic Publishing

Kirk-Spriggs, A.H. 1996. *Pollen Beetles.* Handbooks for the Identification of British Insects 5 (6a). Royal Entomological Society

Lane, A., 1984. *Oilseed rape handbook.* The Open University Press, Milton Keynes

Lane, A. & Cooper, D.A. 1989. Importance and control of insect pests of oilseed rape. *Aspects of Applied Biology* 23, 269-275

Ouvrard, P., Hicks, D.M., Mouland, M., Nicholls, J.A., Baldock, K.C.R., Goddard, M.A., Kunin, W.E., Potts, S.G., Thomas, T., Veromann, E. & Stone, G.N. 2016. Molecular taxonomic analysis of the plant associations of adult pollen beetles (Nitidulidae: Meligethinae), and the population structure of *Brassicogethes aeneus*. *Genome* 59, 1101-1116

Mauchline, A.L., Cook, S.M., Powell, W., Chapman, J.W. & Osborne, J.L. 2017. Migratory flight behaviour of the pollen beetle *Meligethes aeneus*. *Pest Management Science* 73, 1076-1082

Tamir, L., Šedivy, J., Bergmannova, E. & Hanker, I. 1967. Further experience obtained in studies on dispersal flight of *Meligethes aeneus* F., marked with P 32. *Acta Entomologica Bohemoslovaca*, 64, 325-332

Williams, I.H. & Free, J.B. 1978. The feeding and mating behaviour of pollen beetles (*Meligethes aeneus*) Fab. and seed weevils (*Ceutorhynchus assimilis* Payk.) on oilseed rape (*Brassica napus* L.). Journal of Agricultural Science 91, 453-459

Williams, I.H. & Free J.B. 1979. Compensation of oilseed rape (*Brassica napus* L.) plants after damage to their buds and pods. *Journal of Agricultural Science* 92, 53-59

Wright, F.R.E. 1936. The Lundy Brassica, with some additions. *Journal of Botany* 74, (Suppl.) 1-8

AN EXPLORATORY STUDY INTO THE BEHAVIOUR OF ATLANTIC PUFFINS *(FRATERCULA ARCTICA)* ON LUNDY

by
PEGGY LIEBIG[1], HENRIETTA PENTONY AND ELEANOR TARRANT TAYLOR
University of Exeter, Animal Behaviour Research Group, School of Psychology,
Washington Singer Laboratories, Perry Road, Exeter, Devon, EX4 4QG
[1]*Corresponding author, e-mail: liebig.peggy@gmail.com*

ABSTRACT

The impact of sea conditions and weather on the behaviours of Atlantic Puffins (*Fratercula arctica*) have not previously been examined on Lundy therefore it was assessed in the current study. It was found that weather, swell size and group size had a significant effect on recorded behaviours, but not tide, wind or time of day. The current research provides insight into specific behaviours Puffins exhibit whilst on the water and the percentage of time spent performing them. The results could be useful for conservation, as well as to researchers and birdwatchers wanting to observe Puffins on the water.

Keywords: *Atlantic Puffins, Lundy, behaviour, environmental conditions, conservation*

INTRODUCTION

Atlantic Puffins *(Fratercula arctica)* breed in vast colonies off both coasts of the Atlantic Ocean (Harris, 1984). They are relatively small predatory seabirds, measuring up to 25 centimetres (Plate 1), and are omnivorous, largely hunting for small fish such as Herring *(Clupea harengus)* or Sand Eels *(Ammodytes tobianus)* in the open ocean or by the shore (Martin, 1989). As agile swimmers, they are able to dive to maximum depths of 60 metres for up to two minutes at a time to optimise foraging yield (Wanless *et al.*, 1988). Puffins are highly social animals, seemingly influenced by conspecific behaviour and activity (Ward & Zahavi, 1973). Furthermore, the

Plate 1: Puffins on Lundy.
© Peggy Liebig

environment has an extensive impact on the birds' behaviours; Puffins have been found to adapt their breeding and hunting behaviours according to their environment, such as water temperature and altitude of the breeding site (Fayet, 2015). Puffins arrive at the island from March to nest in burrows on the west facing cliffs. Lundy was named due to the former high populations of Puffins on the island as the Icelandic word 'lundi' translates to 'Puffin' (Perry, 1940). They depart for the North Atlantic and Iceland in late July or August subsequent to breeding (Lock, 2006). Despite previously high numbers on the island, various factors over the years have led to population fluctuations, the primary factor being Rats *(Rattus rattus)* predating on pufflings and eggs in burrows. Numbers have been steadily decreasing from Perry's first estimate of 3,500 birds in 1940 to an estimate of 15 Puffins in 1996 (Price, 1996). This significant population decline to a low density is known as the Allee effect. It can arise for a number of reasons and can often be linked to changes in the environment (Roques *et al.*, 2008). However this number has since increased to 32 birds in 2010 (Saunders & Wheatley, 2012). Due to harsh winter storms in 2013/14 Puffin numbers drastically decreased on Lundy with few young birds surviving (Osthaus *et al.*, 2017). Currently, there is insufficient data on Puffin behaviour as research tends to focus on population estimates. Therefore, this study focuses on the behaviours of Puffins whilst on the water and the possible influence of sea and weather conditions.

Currently, Puffins are listed by the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species as 'Vulnerable' (Birdlife International, 2016) and populations are in decline. Lundy is an important breeding ground for migratory Atlantic Puffins (Baldwin, 2009). Effective species conservation requires knowledge of natural behaviour such as migratory patterns, interactions with conspecifics and other species, foraging demands and reproductive behaviour (Slater *et al.*, 1997). This knowledge can enable the development of effective protection measures as accurate monitoring can aid conservation attempts (Nichols *et al.*, 2000). Therefore, increasing knowledge of Puffin behaviours may enable a further understanding including interactions and how these may relate to the Puffin population on Lundy, specifically Jenny's Cove.

Social interactions and information centres

Seminal research has indicated that Auk social behaviour and survival are closely linked (Darling, 1952) and other birds can significantly influence Puffins' foraging and general behaviour at sea. Therefore, social behaviours could impact on the survival of Puffins on Lundy. Research into Puffin interactions, particularly with other species, is currently lacking; consequently this study aims to investigate which behaviours Puffins exhibit on the water, looking particularly at social behaviours, such as interactions with other Auks and conspecifics. Puffins often share their habitat with a variety of seabirds, including Skuas *(Stercorariidae)* and Gulls *(Laridae)*. On Lundy, Puffins share their breeding grounds with Guillemots *(Uria aalge)* and Razorbills *(Alca torda)*, but there is limited research into interactions between the species. An observational study by Divoky (1982) found that although single Puffins often reside near Guillemot flocks on both land and sea, few interactions were observed between the species. Research suggests that living in close proximity to other species can promote intra-species as well as inter-species interactions, particularly in Horned Puffins *(Fratercula corniculata)* as they were found to be more social when in close proximity to another species (Bakhturina & Klenova, 2016). One social behaviour occasionally observed between two Puffins both on land and water is billing. It involves one bird nestling the other's breast and throat feathers. Billing can serve as a greeting or celebration following an aggressive encounter with a conspecific, but is mainly linked with courtship (Johnsgard, 1987). Billing has been found to be most commonly displayed during the early breeding season and is a group activity, with up to six birds billing in a group. This behaviour is proposed to be almost contagious, as new billing pairs were observed to begin billing near the originating pair (Conder, 1950). Understanding how Atlantic Puffins interact with conspecifics and other species can help conservation efforts; for instance, when Puffins begin to engage in billing behaviour in groups this may be an indicator that they will soon start to breed (Calvert & Robertson, 2002) and they benefit from limited human interaction.

It has been suggested that social interaction can lead to increased foraging success. Fisher (1954) proposed that living in social colonies can function to benefit feeding in birds. Ward and Zahavi (1973) found that birds congregate in so called 'information centres' to gain access and exchange information regarding the location and density of food sources. This was suggested as large groups of Puffins have been observed congregating outside of their colonies where they preen, rest or display prior to departing to forage (Ward & Zahavi, 1973). This is supported by research which found that food related grouping behaviour was proposed to enhance overall colony fitness (Beauchamp, 1998). Successful use of information centres has been observed in several bird species such as Great Blue Herons *(Ardea herodias)*, Great Egrets *(Ardea alba modesta)*, Carrion Crows *(Corvus carone carone)*, Hooded Crows *(Corvus carone cornix)* and Terns *(Lavidae)* (Mock *et al.*, 1988; Richner & Marclay, 1991; Waltz, 1987). All were observed departing with colony members, following congregation, and were found to have increased foraging success. Successful foragers then return to the 'information centre' and interact with unsuccessful foragers, which then are subsequently observed foraging with enhanced feeding success (Richner & Heeb, 1995). In the current study, it is hypothesized that Puffins will congregate in information centres, interacting with conspecifics or Auks prior to flying out to the open ocean to forage.

Impact of sea and weather conditions on behaviours

Environmental changes may significantly impact on species populations, therefore behavioural flexibility may be a key determinant in species success (Sol & Lefebvre, 2000), with individuals with more generalized adaptations being more flexible than specialists (Brashares *et al.*, 2000). Determining how behavioural shifts occur and are maintained may be essential for species conservation; for example, the Mauritius Kestrel *(Falco punctatus)* experienced a significant decline in population with the introduction of predators to nest sites (Temple, 1986). As a consequence, the remaining birds relocated from tree nesting to inhabiting cliffs; this habitat shift was maintained throughout generations demonstrating how changes in the environment may significantly impact on behaviour and influence population numbers. Understanding behavioural decisions made by individuals during certain environmental conditions can help to predict their behaviours in novel conditions, such as after harsh weather conditions. The consequences of habitat loss or change could then be predicted by behavioural models (Goss-Custard & Sutherland, 1997). Knowledge of Puffin behaviour on the water and the impact of weather conditions could increase investment in the continuation of Puffin populations on Lundy by facilitating both birdwatchers and researchers. Birkhead and Ashcroft (1975) proposed that there was limited information on how the sea conditions could influence diving behaviours in Auks. Therefore, this study aims to investigate the impact of various sea and weather conditions on Puffin behaviours on the water.

Previous investigation into Auk behaviour whilst on the water indicated that Guillemots are active most of the time (64%) and spend only 13% of time resting. The remaining time was spent flying (11%) and diving (12%) (Tremblay *et al.*, 2003). Researchers also have explored whether sea state affects the performance of Auk behaviours. The state of the tide has previously been linked to seabird behaviour; research suggests that high tide causes prey to rise to the surface, resulting in increased diving activity in seabirds (Hunt Jr *et al.*, 1998). Therefore, Puffins may be more likely to be observed on the water and exhibit increased diving behaviours during high tide, as prey may be more plentiful. In addition, swell size could impact seabird activity; research suggests that diving behaviour in seabirds, including Auks, was significantly higher at high swell than at low swell (Burger *et al.*, 1977) suggesting that swell size may also impact on prey availability. Weather has also been found to impact food availability. Cimino *et al.* (2014) found that weather conditions can have an impact on Puffins prey species such as Krill *(Euphausiacea)* and smaller fish which in turn will impact Puffin behaviours; it may change foraging which would impact on Puffin location. Furthermore, studies on weather conditions and the impact they might have on seabirds was conducted on European Shags *(Phalacrocorax aristotelis)* (Bustnes *et al.*, 2013). The researchers found that unfavourable weather conditions in winter increased mortality rates of non-breeding Shags throughout all the age classes. On the other hand, research suggests that time of day does not affect Auk behaviour (Holm & Burger, 2002), although Corkhill (1973) found that Puffins generally forage in the morning or late afternoon. Daily feeding behaviours of Guillemots on the ocean frequently vary due to the changes in weather (Finney *et al.*, 1999). These studies indicate that weather could impact on the behaviours exhibited by other seabirds, including Puffins. Therefore, this study predicts that there is an impact of sea state and weather on the behaviour rates. Due to previous research into Auk behaviour it is also hypothesized that time of day will not significantly impact on Puffin behaviour.

METHODS

Location and subjects

The research was carried out on Lundy which lies in the Bristol Channel, 10 miles off the coast of North Devon, United Kingdom. The Puffins' nesting ground is typically found at Jenny's Cove which is on the west side of the island facing the Atlantic Ocean (Plate 2). The nesting ground is located on cliffs with the burrows situated near

Plate 2: Jenny's Cove, Lundy. © Peggy Liebig

the bottom. The Puffins were observed from a cliff opposite the nesting ground which provided a clear view of the sea using a spotting scope and two pairs of binoculars. Puffins are not sexually dimorphic, therefore a distinction between the sexes was not possible. Additionally, Puffins were easily distinguished from other auk species, Guillemots and Razorbills, by plumage and bill morphology (Plate 3). The Puffins were only observed while on the water at Jenny's Cove and not whilst they were at their burrow sites.

Plate 3: Distinction between Puffins and other Auks.
© Peggy Liebig

Sampling method

Observations started at approximately at 8am and were discontinued after 3pm as Puffins were no longer visible on the water. The observations took place every day from 23-28 April 2017. The two observers used binoculars to observe the subjects. Distance observation sampling was conducted from approximately 200 metres from the focal cliff. Instantaneous focal animal sampling was utilised whereby one individual on the water was observed for a five minute period before changing to the next individual using the method of Altmann, (1974). Two teams observed two different animals, with one researcher constantly observing through binoculars and telling a second researcher the observations, who recorded those on a scoring sheet; the fifth researcher kept track of the time. Verbal communication between the two observers ensured they did not focus on the same bird at the same interval. When observing the same group, the observers would ensure during the first minute that they were watching different individuals. The tasks rotated after every interval to reduce observer fatigue. Inter-rater reliability was assessed by all researchers concurrently watching one individual and comparing recorded behaviours on the first day. The weather condition, wind, swell, tide state and Puffin group size were recorded for every time interval. The behaviours were recorded using an ethogram adapted from Camphuysen, Fox, Leopold & Petersen (2004) (Table 1).

Table 1: Ethogram to determine observed behaviours. Definitions adapted from Camphuysen *et al.* (2004) and the codes were used during observations

Behaviour	**Definition**	**Code**
Billing	Rubbing beaks with another individual	B
Diving	Whole bird under water	D
Flapping	Rapid up and down movement of the wings while on the water	F
Flying	Bird is in the air and moving	FY
Head dip	Head under water	H
Interaction with conspecific	Any contact with other Puffins; inspecting, playing with, grooming, nursing, hugging etc., except billing	IP
Interaction with other Auks	Any contact with other Auk species (Guillemots, Razorbills); inspecting, playing with, grooming, nursing, hugging etc.	IA
Interaction with Gulls	Any contact with predating species (Gulls); inspecting, playing with, grooming, nursing, hugging etc.	IG
Preening	Cleaning and positioning feathers of themselves with beak	P
Resting	Floating, inactive, not purposefully moving	R
Swimming	Moving on the water in a specific direction	S
Others	All other behaviours performed that are not listed above	O
Out of sight	Individual cannot be seen	OU

Statistical analysis

The intervals were re-coded for statistical analysis; the time of day was divided into three categories; early morning (8am-10am), late morning (10am-noon) and afternoon (noon-3pm). Weather was coded as either sunny or cloudy, since it did not rain during the observation period. Tide was coded as low tide or high tide. The swell was recorded as wave height in metres, which ranged between no swell and two metres during the observation period. Tide times, wind and swell estimates for each day were obtained from the BBC weather website. All the behaviours were coded as separate variables as well as the group size, which was defined as the number of individuals around the focal Puffin. It was then analysed whether the Puffins exhibited a specific behaviour more frequently per observational period than another. Therefore, this study looked at rates of the behaviour, rather than frequencies (Altmann, 1974). Multiple multivariate analysis of variances (MANOVA) were used to examine the effects of tide, time of day, weather, swell, group size and wind, which were included as independent variables, on all of the observed behaviours which were entered as the dependent variables.

The data was analysed with IBM SPSS Statistics 24. Results were considered significant when $P<0.05$ with a confidence interval of 95%. Data were checked for normality and homogeneity and initial analyses indicated that the data was normally distributed. Additionally, there were no significant outliers found in the data.

RESULTS

A principal component analysis indicated that the behaviours did not correlate significantly with each other therefore the behaviours were not grouped together for further analysis.

All mean rates per observed times, standard errors as well as the minimum and maximum observed rates for each scale variable were calculated (Table 2). Resting behaviour was exhibited most often and interaction with Gulls was the least often.

Grouping the active behaviours together (billing, flapping, head dip, interactions and preening), descriptive statistics show that Puffins were active the majority of the time whilst on the water (65.82%) and spent the remaining time resting (27.98%), flying (3.32%) and diving (2.88%). (Figure 1).

Social interactions and information centres

To investigate how sociable the Puffins on Lundy are, two new variables were computed. The first variable was called 'interactions' and consisted of billing, interactions with other Puffins, Auks and Gulls. The second variable was called 'single behaviours' and consisted of diving, flapping, flying, head dipping, preening, resting and swimming. Puffins spent only 10% of the observed time interacting with Gulls and Auks and 90% performing other behaviours independently. The most commonly performed behaviour was interacting with conspecifics ($N=246$). They were observed less often interacting with other Auks ($N=36$), billing with Puffins ($N=13$) and, the least, interacting with Gulls ($N=1$).

Looking at all behaviours individually, group size had a significant effect (MANOVA Pillai's $V=1.089$, $F(143,1980)=1.522$, $P<0.001$). Puffins swam more frequently in groups between three and five ($F(11,182)=2.760$, $P=0.002$). Group size also affected

Table 2: Descriptive statistics including mean, standard error, minimum and maximum of the observed behaviours from the ethogram, as well as group and swell size

Variables	Mean	Standard Error	Minimum	Maximum
Group size	3.50	0.19	1	17
Swell size	1.02	0.06	0	2
Billing	0.07	0.03	0	5
Diving	0.44	0.08	0	8
Flapping	1.89	0.18	0	24
Flying	0.51	0.05	0	4
Head dip	2.76	0.30	0	27
Interaction with conspecific	1.26	0.12	0	9
Interaction with Auk	0.18	0.04	0	4
Interaction with Gull	0.01	0.01	0	1
Preening	0.69	0.09	0	6
Resting	4.28	0.27	0	24
Swimming	3.17	0.24	0	16
Others	0.04	0.02	0	2
Out of sight	0.38	0.04	0	1

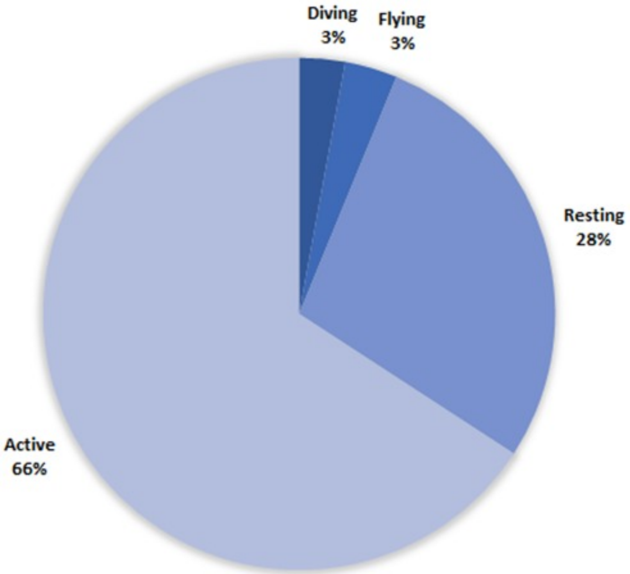


Figure 1: Percentages of Puffin activity on the water
Active behaviours were grouped to include: billing, flapping, head dipping, interactions and preening. Puffins were active the majority of the time whilst on the water, excluding diving and flying. They were found to spend just over one quarter resting whilst on the water

Puffins' interactions with Auks (F(11,182)=2.549, P=0.005) where they preferred to interact with Auks when alone or up to a group of 10 Puffins. Puffin-Puffin interactions were also affected by group size (F(11,182)=5.385, P<0.001). These interactions were highest when group sizes were between two and 10 individuals. Further analysis revealed that group size affected the performance of billing behaviour (F(11,182)=3.422, P<0.001) where a group size of six was the preferred size (Figure 2).

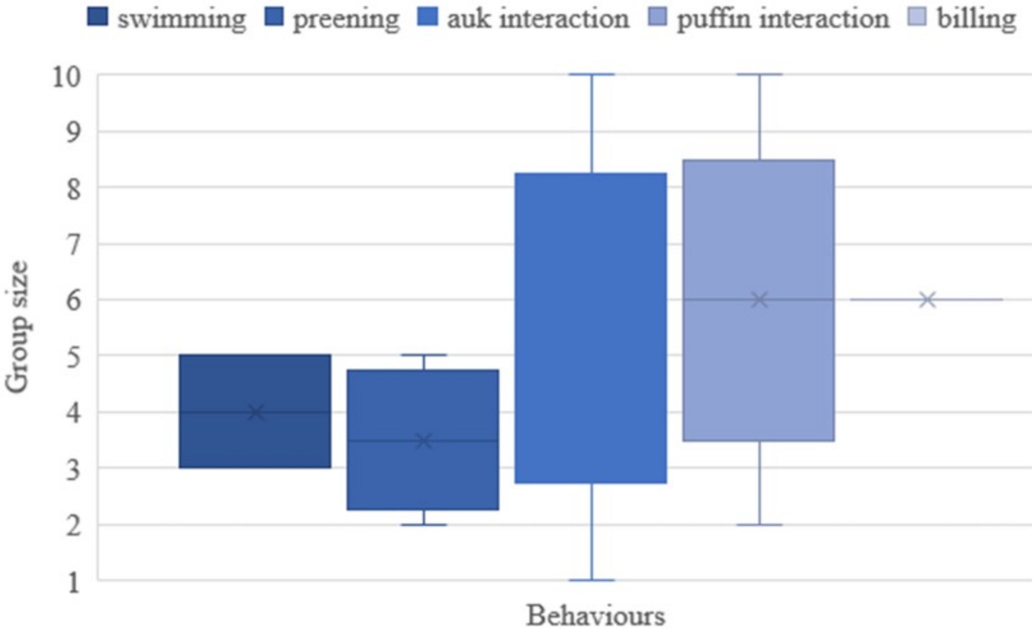


Figure 2: Group size correlating with significant behaviours
Puffins were found to swim more frequently when in groups between three and five. They also preferred to preen in group sizes ranging from one to four Puffins. Puffin-Puffin interactions were highest when group sizes were between two to 10 individuals, furthermore interactions with Auks were most frequent when the Puffins were alone or up to a group of 10 Puffins. Billing behaviour occurred most often in a group size of six

Another new variable was computed, using Auk interaction and Puffin interaction, called 'interaction 2', to determine whether Puffin-Puffin interactions or Puffin-Auk interactions led to Puffins flying off to the ocean. A linear regression analysis was performed with flying as dependent variable and the interaction as independent variable. Puffin-Puffin and Puffin-Auk interactions did not significantly predict flying (F(1,193)=0.041, P=0.839).

Behaviours and environmental factors

Tide state did not have a significant effect on overall behaviours. Although time of day was non-significant on the behaviours overall, it had a significant effect on diving (F(2,191)=3.358, P=0.037). A post-hoc pairwise comparison revealed that the Puffins preferred to dive in the late morning (N=76) than early morning (N=52).

Swell size had a significant effect on the performance of the behaviours overall (Pillai's V=0.587, F(52,720)=2.382, P< 0.001). Individually, swell size had a significant effect on diving (F(4,189)=3.336, P=0.011). Post-hoc pairwise comparisons (Tukey's method, with overall α=0.05) suggested that the Puffins preferred to dive when swell size was between zero and one and a half metres. Swell size also significantly predicted interactions with other Puffins (F(4,189)=3.273, P=0.013) and other Auks (F(4,189)=4.256, P=0.003); Puffins interacted more with other Auks in higher swell sizes, between one and a half and two metres. Swell size significantly affected preening behaviour (F(4,189)=6.009, P<0.001). A post-hoc revealed that the Puffins preferred to preen when there was a one to two metre swell compared to other swell sizes. Swimming was also significantly affected by swell size (F(4,189)=4.078, P=0.003), suggesting that they swam more in one and two metre swells (Figure 3).

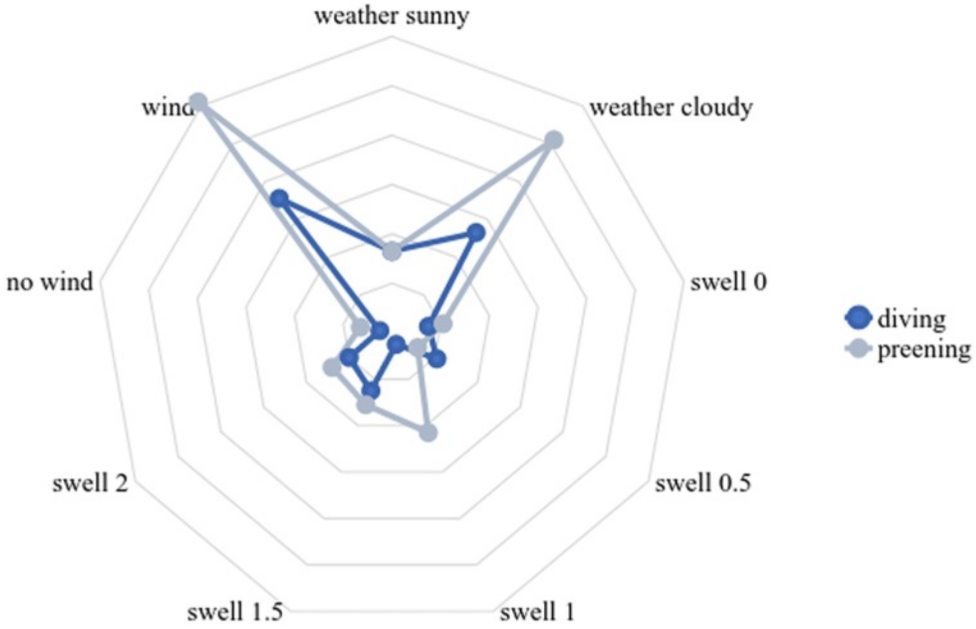


Figure 3: Diving and preening rates performed during different sea and weather conditions Puffins preferred to dive when there was a 1.5 metre swell and when it was cloudy and windy. They also were observed to preen more in one metre swell, when it was cloudy and windy

Weather was found to have a significant effect on the performance of the behaviours (Pillai's V=0.228, F(13,179)=4.072, P<0.001). Wind was not significant on behaviours overall, but results suggest the Puffins were flapping more in windy conditions (F(1,191)=4.223, P=0.041). They were observed to fly more when it was sunny compared to when it was cloudy (F(1,191)=4.530, P=0.035). They also were observed to preen more when it was cloudy (F(1,191)=11.948, P=0.001) and windy. Puffins had more interactions with other Auks in cloudy weather (F(1,191)=9.844, P=0.002). (Figure 3).

DISCUSSION

Currently there is limited research into Puffin behaviour, therefore little is known about how their behaviour changes with differing environmental conditions such as sea state and weather. Due to the increasing population size, studies of Puffin behaviour on Lundy may become more achievable now than they were previously. Having sufficient data on their behaviours can assist various organisations to design relevant conservation projects and help conservationists predict behavioural change (Goss-Custard & Sutherland, 1997). This study focused on Puffin behaviour while on the water; results showed the similar distribution of performed behaviours as previous research on Guillemots (Tremblay *et al.*, 2003). It was found that there was a significant impact of most recorded environmental factors; however Puffins were not found to congregate in information centres, as found in the study conducted by Ward and Zahavi (1973).

Social interactions and information centres

Seminal research indicated that Puffins are highly sociable (Darling, 1952); however, during this study, Puffins spent only 10% of the observed behaviours interacting with other birds. During observations, it was noticed that Puffins frequently interacted with conspecifics and other auks. Puffins appeared to use other auks as a shield towards predatory Gulls by placing their burrows amongst other auks. This could be to avoid having their food taken by the Gulls, as it was found that the arrangement of nests in relation to conspecifics can significantly reduce food theft (Pierotti, 1983). Previous researchers have suggested that interactions with other birds are more frequent if breeding grounds are shared (Grant, 1971). However, on Lundy, although Puffin populations are outnumbered by auks and gulls and they nest in the same vicinity, the Puffins still did not spend significantly more time interacting with other auks. Consequently, this study supports the results found by Divoky (1982) who observed few interactions between Puffins and Guillemots. The current research also does not seem to support the notion that interactions increase with proximity (Bakhturina & Klenova, 2016). The lack of interactions between Gulls and Puffins could be as research was conducted early in the breeding season, therefore Puffins were not bringing fish back to their offspring at the nesting grounds (Pierotti, 1983), therefore the gulls would not have been able to intercept this transportation and steal the fish. This could be an area considered for future research as interactions between Puffins and other sea birds may increase later in the breeding season. Furthermore, the observation of interactions between Puffins and other species, such as Gulls, could aid conservation efforts as Gulls have been observed predating on Puffins and stealing their fish during the breeding season (Pierotti, 1983). Conservation efforts for the Puffin population could aim to monitor and potentially regulate Gull populations on Lundy to protect vulnerable pufflings.

Additionally, information about social behaviours and interactions could aid conservation as restrictions could be placed on the visiting tourists; for instance, not allowing them to go within a specific proximity of the potentially breeding pairs as soon as billing is observed (Calvert & Robertson, 2002). This study confirms Conder's (1950) findings as it was observed that Puffins performed billing behaviour in the early breeding season in groups of up to six individuals. Understanding the behaviours which suggest that the Puffins may be preparing to breed could lead to more successful breeding and rearing of the pufflings and overall increases in populations as human impact could be reduced.

Regarding the information centre hypothesis, there was no correlation found between interaction with conspecifics and increased flying. To support the information centre hypothesis, it would be expected that interactions would lead to an increase in flying behaviour, with Puffins congregating to access information regarding food location, then flying out to forage out in the open ocean (Ward & Zahavi, 1973). However, Richner and Heeb (1995) propose that this information centre hypothesis is redundant and an alternative hypothesis based on individual selection could more successfully serve as an explanation for the observed behaviour. In order to further explore the use of information centres in Puffins, it would be necessary to code the behaviours in the order they occurred, as this research was only able to explore the association rather than the direction. This study also was not designed to look whether Puffins went out to the ocean to forage after interactions occurred; this could be another area for further study.

Behaviours and environmental factors

Although previous literature suggests that time of day does not affect Auk behaviour (Holm & Burger, 2002), the results of the current study found that Puffins dive more frequently in the late morning compared to the early morning or afternoon. This could be explained by the timings that the Puffins were observed; recorded observations did not take place before 8am as the observations made before this time indicated that Puffins were not visible on the water. Additionally, observations did not take place after 3pm because Puffins were again not visible. One could speculate that during these times the Puffins were out foraging and therefore they were not observable on the water. Corkhill (1973) suggests that Puffins usually forage in the morning and late afternoon which coincides with this explanation. Because of this, it could be argued that Puffin behaviour does vary throughout the day; however, the current study could not investigate this due to the constraints of the observation area.

Contradictory to past studies (Hunt Jr *et al.*, 1998), there was no effect of tide found on any of the behaviours including diving. This unexpected result could be related to the location in which the Puffins were observed, as observations were made in the bay and the Puffins may go further out to sea to forage; therefore, there may be less need for the Puffins to dive as food is scarce in the bay. Puffin prey, such as Sand Eels and Herrings, are usually found in the open water (Wright & Begg, 1997), thus the swell observed in the bay may not significantly impact on diving behaviours as these behaviours may be more linked to the open ocean.

Diving was performed more frequently when there was a swell up to one and a half metres. This supports previous research which suggested that diving behaviour in seabirds increases at times of high swell compared to low swell (Burger *et al.*, 1977). Puffins exhibited more preening behaviour when the swell size was one metre high and during cloudy and windy weather. They also displayed preference to preen when there was a group size of one to four individuals. Preening has been associated with enhancing the waterproof quality of feathers in seabirds, by using the oils and waxes that secrete from the preen gland (Chiale *et al.*, 2014), therefore this increase in preening behaviour during cloudy conditions could be a result of the increased diving behaviour seen. This maintenance could be more important in cloudy and windy weather conditions, because feathers may be increasingly ruffled due to the wind. Additionally, increased preening in larger social groups could also be explained by the contagious effect, as found previously with billing (Conder, 1950). As weather conditions were found to significantly impact on Puffin behaviour at Jenny's Cove, knowledge of how behaviour may be impacted by the environment may assist conservationists and help to increase the currently low numbers of Puffins around the British shores.

As considered earlier, environmental conditions have been found to impact behaviours. In the research previously discussed conducted by Temple (1986), the Mauritius Kestrel population was reduced to only two breeding pairs; similar population decline was also found with Puffins on Lundy, with a significant decline from early estimates of 3,500 (Perry, 1940) to an estimate of 15 Puffins (Price, 1996). This Allee effect can be due to various reasons, partly because of environmental factors (Roques *et al.*, 2008); the storms on Lundy were linked with the significant decrease in Puffin population (Lock, 2006). Climate fluctuations have been found to be a key factor in breeding success for a variety of bird species, including Puffins (Durant *et al.*, 2004). Therefore, it is important to study sea and weather conditions in relation to Puffin behaviour to help conservation efforts to determine which conditions are favourable for the successful breeding of Atlantic Puffins and in which conditions the populations may suffer. This is particularly important in current times due to the results of climate change and its possible impact on the environment. Environmental changes may not only influence the populations of the Puffins on the island, but also the behaviours as demonstrated by this observational study (Goss-Custard & Sutherland, 1997). Behavioural changes may link to the rate of reproductive success and survival, thus may impact on populations. As there is limited information on the behaviours of Atlantic Puffins, the insight into the effect of the environment on Puffin behaviour provided by this study may enable further efforts into the conservation of this currently 'Vulnerable' seabird species (Birdlife International, 2016).

CONCLUSION

In conclusion, this research gives further insight into Puffin behaviours, specifically the range of behaviours they display on the water. The first prediction was found to be supported, as the sea state and weather was found to have a significant influence on a variety of behaviours. However, time of day did impact on the frequency of diving behaviours, with Puffins diving more frequently in the late morning. The second prediction was found to not be supported, as Puffins did not necessarily use information centres as they were not observed congregating in meeting places, interacting with conspecifics and/or Auks prior to flying out.

Further research should include the order in which the behaviours occurred which would allow for a closer look into foraging behaviour after interactions took place. Understanding the way in which Puffin behaviour changes in different environmental conditions could be useful to researchers and birdwatchers wanting to observe Puffins on the water; this would also aid conservationists as Puffin behaviours could be predicted during specific environmental conditions, including the impact of harsh weather. Additionally, little has been documented on the behaviours of Atlantic Puffins specifically whilst they are on the water; therefore, this study provides some insight into what behaviours the birds are likely to perform.

ACKNOWLEDGEMENTS

We are very grateful to Linus Juen and Dani Carpendale for assisting with data collection and for help writing the University report. Special thanks to Lisa Leaver for being our tutor, providing us the opportunity to go to Lundy to conduct this study and for helping us edit the report. We used the 'sequence-determines-credit' approach to determine authorship.

REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227-266

Bakhturina, D.S. & Klenova, A.V. (2016). Quantitative analysis of the behavior of three Auk species *(Charadriiformes, Alcidae)*: Crested Auklet *(Aethia cristatella)*, parakeet Auklet *(Cyclorrhynchus psittacula)*, and horned Puffin *(Fratercula corniculata)*. *Biology Bulletin*, *43*(7), 670-684

Baldwin, J.R. (2009). Harvesting seabirds and their eggs on the Irish Sea islands (Part 1: The Welsh islands, Lundy and Scilly). *Folk Life*, *47*(1), 76-96

BBC (2017). Weather tide tables. Retrieved from: http://www.bbc.co.uk/weather/coast_and_sea/tide_tables/10/542#tide-details. Accessed on 23 April 2017

Beauchamp, G.U.Y. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews*, *73*(4), 449-472

BirdLife International (2016). *Fratercula arctica*. The IUCN Red List of Threatened Species 2017: e.T22694927A110638141. http://dx.doi.org/10.2305/IUCN.UK.2017-1.RLTS.T22694927A110638141.en. Downloaded on 09 May 2017

Birkhead, T.R. & Ashcroft, R.E. (1975). Auk numbers on Skomer island. *Nature in Wales*, *14*, 223-233

Brashares, J.S., Garland Jr, T., & Arcese, P. (2000). Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behavioral Ecology*, *11*(4), 452-463

Burger, J., Howe, M.A., Hahn, D.C. & Chase, J. (1977). Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. *The Auk*, 743-758

Bustnes, J.O., Anker-Nilssen, T., Erikstad, K.E., Lorentsen, S.H. & Systad, G.H. (2013). Changes in the Norwegian breeding population of European shag correlate with forage fish and climate. *Marine Ecology Progress Series*, *489*, 235-244

Calvert, A.M. & Robertson, G.J. (2002). Colony attendance and individual turnover of Atlantic Puffins in Newfoundland. *Waterbirds*, 25(3), 382-387

Camphuysen, C.J., Fox, A.D., Leopold, M.F. & Petersen, I.K. (2004). Towards Standardised Seabirds at Sea Census Techniques in Connection with Environmental Impact Assessments for Offshore Wind Farms in the UK: a comparison of ship and aerial sampling methods for marine birds and their applicability to offshore wind farm assessments. *Department for Environment, Farm and Rural Affairs*

Chiale, M.C., Fernández, P.E., Gimeno, E.J., Barbeito, C. & Montalti, D. (2014). Morphology and histology of the uropygial gland in Antarctic birds: relationship with their contact with the aquatic environment? *Australian Journal of Zoology*, *62*(2), 157-165

Cimino, M.A., Fraser, W.R., Patterson-Fraser, D.L., Saba, V.S. & Oliver, M.J. (2014). Large-scale climate and local weather drive interannual variability in Adélie penguin chick fledging mass. *Marine Ecology Progress Series*, *513*, 253-268

Conder, P.J. (1950). On the courtship and social displays of three species of Auk. *British Birds*, *43*, 65-69

Corkhill, P. (1973). Food and feeding ecology of Puffins. *Bird Study*, *20*(3), 207-220

Darling, F.F. (1952). Social behavior and survival. *The Auk*, *69*(2), 183-191

Divoky, G.J. (1982). The occurrence and behavior of non-breeding Horned Puffins at Black Guillemot colonies in northern Alaska. *The Wilson Bulletin*, *94*(3), 356-358

Durant, J.M., Anker-Nilssen, T., Hjermann, D.Ø. & Stenseth, N.C. (2004). Regime shifts in the breeding of an Atlantic puffin population. *Ecology Letters*, *7*(5), 388-394

Fayet, A. (2015). *Long-distance movements in pelagic seabirds: at-sea behaviour and life-history consequences* (Doctoral dissertation, University of Oxford)

Finney, S.K., Wanless, S. & Harris. M.P. (1999). The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot (*Uria aalge). Journal of Avian Biology,* 30, 23–30

Fisher, J.B. (1954). Evolution and bird sociality. *Evolution as a Process*, 71-83

Goss-Custard, J.D. & Sutherland, W.J. (1997). Individual behaviour, populations and conservation. *Behavioural Ecology: An Evolutionary Approach*, *4*, 373-395

Grant, P.R. (1971). Interactive Behaviour of Puffins *(Fratercula Arctica L.)* and Skuas *(Stercorari Us Parasiticus L.). Behaviour*, *40*(3), 263-281

Harris, M.P. (1984). *The Puffin*. T. & A.D. Poyser: Calton, United Kingdom

Holm, K.J. & Burger, A.E. (2002). Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. *Waterbirds*, *25*(3), 312-325

Hunt Jr, G.L., Russell, R.W., Coyle, K.O. & Weingartner, T. (1998). Comparative foraging ecology of planktivorous Auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series*, *167*, 241-259

Johnsgard, P.A. (1987). *Diving Birds of North America.* Lincoln: University of Nebraska Press

Lock, J. (2006). Eradication of brown rats *Rattus norvegicus* and black rats *Rattus rattus* to restore breeding seabird populations on Lundy Island, Devon, England. *Conservation Evidence*, *3*, 111-113

Martin, A.R. (1989). The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. *Bird Study*, *36*(3), 170-180

Mock, D.W., Lamey, T.C. & Thompson, D.B. (1988). Falsifiability and the information centre hypothesis. *Ornis Scandinavica*, 231-248

Nichols, J.D., Hines, J.E., Sauer, J.R., Fallon, F.W., Fallon, J.E. & Heglund, P.J. (2000). A double-observer approach for estimating detection probability and abundance from point counts. *The Auk*, *117*(2), 393-408

Osthaus, B., Farrell, A., Fisher, P. & Heinrichs, P. (2017). Evaluation of two observational methods to assess the numbers of nesting puffins (Fratercula arctica). In: *International Conference in Protecting Biodiversity, 16th-18th February, 2017, Mannampandal, Tamil Nadu, India*

Perry, R. (1940). *Lundy, Isle of Puffins*. London

Pierotti, R. (1983). Gull-puffin interactions on Great Island, Newfoundland. *Biological Conservation*, *26*(1), 1-14

Price, D. (1996). Surveys of breeding Seabirds on Lundy: 1981-1996. *Lundy Field Society Annual Report*, *47*, 28-35

Richner, H. & Marclay, C. (1991). Evolution of avian roosting behaviour: a test of the information centre hypothesis and of a critical assumption. *Animal Behaviour*, *41*(3), 433-438

Richner, H. & Heeb, P. (1995). Is the information center hypothesis a flop? *Advances in the Study of Behaviour*, *24*, 1-46

Roques, L., Roques, A., Berestycki, H. & Kretzschmar, A. (2008). A population facing climate change: joint influences of Allee effects and environmental boundary geometry. *Population Ecology*, *50*(2), 215-225

Saunders, N. & Wheatley, S. (2012). Atlantic puffin *(Fratercula arctica)* population, distribution and productivity on Lundy in 2009 and 2010. *Journal of the Lundy Field Society*, *3*, 111-124

Slater, P. J., Snowdon, C. T., Rosenblatt, J. S. & Milinski, M. (1997). *Advances in the Study of Behavior*. California: Academic Press

Sol, D. & Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, *90*(3), 599-605

Temple, S. A. (1986). Recovery of the endangered Mauritius kestrel from an extreme population bottleneck. *The Auk*, *103*(3), 632-633

Tremblay, Y., Cherel, Y., Oremus, M., Tveraa, T. & Chastel, O. (2003). Unconventional ventral attachment of time–depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *Journal of Experimental Biology*, *206*(11), 1929-1940

Waltz, E.C. (1987). A test of the information-centre hypothesis in two colonies of common terns, *Sterna hirundo*. *Animal Behaviour*, *35*, 1, 48-59

Wanless, S., Morris, J.A. & Harris, M.P. (1988). Diving behaviour of guillemot (*Uria aalge)*, Puffin (*Fratercula arctica)* and razorbill *(Alca torda)* as shown by radio-telemetry. *Journal of Zoology*, *216*(1), 73-81

Ward, P. & Zahavi, A. (1973). The importance of certain assemblages of birds as “information-centres” for food-finding. *Ibis*, *115*(4), 517-534

Wright, P.J. & Begg, G.S. (1997). A spatial comparison of common guillemots and sandeels in Scottish waters. *ICES Journal of Marine Science*, *54*(4), 578-592

THE SECRET LIFE OF THE LUNDY HOUSE SPARROWS

by
JULIA SCHROEDER[1,4], ISABEL WINNEY[2], SOPHIE BENNETT[1],
ALFREDO SÁNCHEZ-TÓJAR[3] AND ANTJE GIRNDT[1,3]
[1]Division of Biology, Imperial College London, Silwood Park Campus, Ascot, UK
[2]Laboratoire EDB, University of Toulouse 3 Paul Sabatier, Toulouse, France
[3]Evolutionary Biology, Max Planck Institute for Ornithology, Seewiesen, Germany
[4]*Corresponding author, e-mail: Julia.schroeder@imperial.ac.uk*

ABSTRACT

The House sparrows (*Passer domesticus)* on Lundy have been the subject of continuous study for 26 years. As an effectively closed population, they permit the testing of hypotheses concerning the evolutionary advantages and disadvantages of extra-pair copulation ('infidelity'). This paper summarises the research of recent years which shows that some hypotheses which seek to account for infidelity in House sparrows are not supported by the Lundy data and that other, novel, hypotheses will need to be tested in the future.

Keywords: *House sparrows, Lundy, extra-pair, infidelity*

INTRODUCTION

The Lundy sparrows have been under scientific scrutiny since 1991, when the first nest boxes were erected on the island. Since then, researchers from UK, German and Australian universities have returned every year to closely monitor the Lundy sparrows' breeding success by counting their eggs and chicks, ringing the chicks, and following their fate through their whole life. House sparrows are ubiquitous across the UK (Summers-Smith, 1963) meaning we could catch them in any farm or city. So why specifically study the sparrows on Lundy? Primarily, the geographic isolation of Lundy, combined with its modest sparrow population size mean that we can capture and sample every sparrow that is born on Lundy, and track these individuals throughout their lives. The lack of dispersal in conjunction with the comprehensive monitoring allow us to learn about a rather secretive, yet common behaviour of passerines: infidelity.

Theoretical background

Social monogamy – where a single female and male pair up together to care for one or more broods – is widespread among birds. Yet, the advent of paternity tests using molecular genetics to find out for sure who are the parents of an individual has shown that many male passerines care for someone else's young in their nests, so called 'extra-pair' offspring (Burke & Bruford, 1987). Many socially monogamous passerines display extra-pair behaviour, meaning they mate with birds other than their social partner (Griffith, Owens & Thuman, 2002). Males that sire extra-pair offspring are thought to increase their breeding success at little or no cost, because they do not provide parental care, incubate the eggs, and bring food to these extra-pair offspring (Schroeder *et al.*, 2016). In addition, males can increase their reproductive output by fertilising more females, because sperm are far less costly to produce than eggs (Birkhead, 2000). So males can fertilise, or attempt to fertilise, a large number of females. Females, however, are limited in the number of eggs they can produce and the number of offspring they can care for. In sparrows, a brood usually has no more than four to a maximum of six eggs. Thus, if females cheat on their social mate, their reproductive output is the same; they produce an offspring sired by their extra-pair partner (an extra-pair offspring) instead of one sired by their social partner (a within-pair offspring). Therefore, female reproduction is inherently limited, but male reproduction is much less constrained.

Even if females were to dump their eggs into a strangers' nest (something we have never observed in Lundy sparrows), the energetic investment that a female puts into the production of an egg by far outnumbers what a male invests into a sperm. Therefore, a basic assumption in evolutionary biology is that males invest in quantity of offspring, while females invest in quality (Kempenaers & Schlicht, 2010).

Hypotheses

The dichotomy in how much each sex can increase their breeding success has inspired more than two decades of research. It seems obvious why males would cheat (to have more offspring at little cost), yet it remains unclear why females cheat. One hypothesis (see Forstmeier, Nakagawa, Griffith & Kempenaers, 2014, for a review and summary of all stated hypotheses), called the 'good genes' hypothesis, states that females who produce extra-pair offspring gain indirect genetic benefits because they choose extra-pair males of higher quality than their social partner. Thus the offspring sired by an extra-pair male with 'good genes' are expected to inherit his higher genetic quality. A second hypothesis – the genetic compatibility hypothesis – states that extra-pair males are not genetically superior to the social partner, but are instead more compatible with the female's own genome. For example, if a female socially mated with a close cousin as a social partner, she could have poor quality offspring, and she might therefore choose an unrelated extra-pair partner to have higher quality extra-pair offspring.

Predictions

The above described two hypotheses clearly predict that within-pair offspring should be of lower quality than extra-pair offspring, and thus we expect within-pair offspring to have lower fitness (e.g. lower survival and reproduction rates) than extra-pair offspring. In addition, the good genes hypothesis predicts that extra-pair males are better than within-pair males. The genetic compatibility hypothesis predicts that extra-pair males are more genetically dissimilar from the female than the within-pair male. To test these predictions, we first need to know which offspring are extra-pair and who the extra-pair father is, which can be determined with a genetic paternity test (Dawson *et al.*, 2012).

The cheating Lundy sparrows

It is relatively easy to show that a social father is not the genetic father of an offspring. If, after accounting for the maternal genotype, the alleles do not fit with the genetic make-up of the social father's genotype, it is clear that the female must have cheated. However, identifying the actual genetic father can only be achieved if the extra-pair father is also DNA-sampled. Herein lies the crux of why we study sparrows on Lundy island. In an open population, birds can fly freely to and from the study area, hence many extra-pair fathers are simply not caught and genotyped by chance. The vast majority of Lundy sparrows stay on the island, and we can capture and sample every bird. Thus, it is unlikely that resident sparrows leave the island, or mainland sparrows immigrate to Lundy regularly (Schroeder, Burke, Mannarelli, Dawson & Nakagawa, 2012). Therefore, in the Lundy sparrows, it is possible to genetically identify each and every extra-pair father. Prof. Terry Burke from the University of Sheffield has, as early as the 1990s, recognized that Lundy is an ideal and unique natural laboratory to test the above-mentioned hypotheses for why females cheat.

RESULTS OF LONG-TERM LUNDY SPARROW RESEARCH

After two decades of research on Lundy, we can rule out some of these hypotheses. The indirect fitness benefits hypothesis predicts that extra-pair males should be of higher quality than within-pair males. Furthermore, it also predicts that extra-pair offspring will do better in life than within-pair offspring, because they received the good genes from the extra-pair fathers. Of the three studies that used lifetime reproductive success to study this question, one supported the indirect fitness benefits hypothesis (Gerlach, McGlothlin, Parker & Ketterson, 2012) while two opposed it (Hsu, Schroeder, Winney, Burke & Nakagawa, 2014, and Reid & Sardell, 2011). Our own long-term data from the Lundy sparrows goes against the indirect fitness hypothesis entirely; our work shows that extra-pair offspring have a lower survival than within-pair offspring (Hsu, Schroeder, Winney, Burke & Nakagawa, 2014), and so are clearly not of higher quality. From the genetic compatibility hypothesis, we can predict that that within-pair males should be more closely related to the female than the extra-pair males. The evidence from other passerine populations is inconclusive (Hsu, Schroeder, Winney, Burke & Nakagawa, 2015, and Arct, Drobniak & Cichon, 2015). On Lundy, extra-pair males and within-pair males do not differ in how related they are to the female (Hsu, Schroeder, Winney, Burke & Nakagawa, 2015). In fact, the only difference is that extra-pair males are older than within-pair males (Hsu *et al.*, 2017). Therefore, Lundy data also does not support the hypothesis that females engage in extra-pair copulation to reduce inbreeding in their offspring (Hsu, Schroeder, Winney, Burke & Nakagawa, 2015). Thus, our data suggests that engaging in extra-pair behaviours is not adaptive for females. Clearly, we need new hypotheses.

A fresh perspective

Recently, other researchers have put forward a number of novel hypotheses that do not require female extra-pair behaviour to be beneficial (Forstmeier, Nakagawa, Griffith & Kempenaers, 2014). These have been called non-adaptive hypotheses. The sexually antagonistic selection hypothesis suggests that a gene for extra-pair behaviour may be beneficial in males but not in females. If the genes are selected for in males, this may lead to female extra-pair behaviour as a by-product (Forstmeier, Nakagawa, Griffith & Kempenaers, 2014). The spill-over hypothesis suggests that female and male infidelity is a spill-over effect for individuals with high sexual activity levels. Females and males with a high sex drive may engage more in mating and thus may be more likely to engage in extra-pair mating attempts too (Forstmeier, Nakagawa, Griffith & Kempenaers, 2014). A similar hypothesis, the opportunity hypothesis, suggests that female and male infidelity is a by-product of socialising. Spending time in the close vicinity of others may have benefits such as greater protection from predators, higher chance of finding food sources etc. However, the same behaviour may also bring with it a weaker pair bond and plenty of opportunities for extra-pair copulations. This is particularly interesting in sparrows that form social groups during and outside their breeding season. In the future, we will continue conducting research on the Lundy sparrows, focusing on these novel hypotheses. We are confident of gaining a fresh perspective on infidelity by studying how these charismatic birds spend time with each other.

REFERENCES

Arct, A., Drobniak, S.M. & Cichon, M. 2015 Genetic similarity between mates predicts extrapair paternity – a meta-analysis of bird studies. *Behavioural Ecology* **26**, 959*968-968

Birkhead, T. 2000. *Promiscuity*. Harvard University Press

Burke, T. & Bruford, M.W. 1987. DNA fingerprinting in birds. *Nature* **327**, 149-152

Dawson, D.A., Horsburgh, G.J., Krupa, A.P., Stewart, I.R.K., Skjelseth, S., Jensen, H., Ball, A.D., Spurgin, L.G., Mannarelli, M-E., Nakagawa, S., Schroeder, J., Vangestel, C., Hinten, G. & Burke, T. 2012. Microsatellite resources for Passeridae species: a predicted microsatellite map of the house sparrow *Passer domesticus*. *Molecular. Ecology Resources.* **12**, 501-523

Forstmeier, W., Nakagawa, S., Griffith, S.C. & Kempenaers, B. 2014. Female extra-pair mating: adaptation or genetic constraint? *Trends in Ecological Evolution* **29**, 456-464

Gerlach, N.M., McGlothlin, J.W., Parker, P.G. & Ketterson, E.D. Promiscuous mating produces offspring with higher lifetime fitness. *Proceedings Royal Society, London, B* **279**, 860-866

Griffith, S.C., Owens, I. & Thuman, K. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* **11**, 2195-2212

Hsu, Y.-H., Schroeder, J., Winney, I., Burke, T. & Nakagawa, S. 2014. Costly infidelity: Low lifetime fitness of extra-pair offspring in a passerine bird. *Evolution* **68**, 2873-2884

Hsu, Y.-H., Simons, M.J.P., Schroeder, J., Girndt, A., Winney, I., Burke, T. & Nakagawa, S. 2017. Age-dependent trajectories differ between within-pair and extra-pair paternity success. Journal of Evolutionary Biology **30**, 951-959

Kempenaers, B. & Schlicht, E. 2010. Extra-pair behaviour. *Animal Behaviour: Evolution and Mechanisms,* 359-411

Reid, J.M. & Sardell, R.J. 2011. Indirect selection on female extra-pair reproduction? Comparing the additive genetic value of maternal half-sib extra-pair and within-pair offspring. *Proceedings Royal Society.* London. *B* **279**, 1700-1708

Schroeder, J., Burke, T., Mannarelli, M.-E., Dawson, D.A. & Nakagawa, S. 2012. Maternal effects and heritability of annual productivity. Journal of Evolutionary Biology **25**, 149-156

Schroeder, J., Hsu, Y.-H., Winney, I., Simons, M., Nakagawa, S. & Burke, T. 2016. Predictably philandering females prompt poor paternal provisioning. American Naturalist **188**, 219-230

Summers-Smith, J.D. 1963. *The House Sparrow.* New Naturalist Series 19. Collins

BLACK RABBITS ON LUNDY: TUDOR TREASURES OR POST-WAR PHONIES?

by
MARTIJN J.T.N. TIMMERMANS[1,2], HANNA ELMI[1], STEPHEN KETT[1]
[1]Department of Natural Sciences, Middlesex University, The Burroughs, Hendon, London, NW4 4BT
[2]Department of Life Science, Natural History Museum, Cromwell Road, London, SW7 5BD
[2]*Corresponding author, e-mail: M.Timmermans@mdx.ac.uk*

ABSTRACT

Lundy is renowned for its feral black rabbits which, according to popular tradition, have inhabited the island since medieval times. Black rabbit fur was valued for much of the Middle Ages, explaining why warreners of Lundy might have favoured them, but genes responsible for feral rabbit melanism remain unexplored. Further potential complicating factors occur in the form of recent (twentieth century) small-scale domestic rabbit introductions to the Lundy feral population. To gain insight into genetic mechanisms underlying melanism on Lundy, rabbit samples were collected and subjected to molecular analysis. The Lundy rabbit population is shown to harbour non-functional copies of the agouti signalling protein (*Asip*) gene, a main determinant of coat colour in mammals. The observed genetic mutation is not unique to Lundy, having been reported to underlie dark coat colour phenotypes in various domestic rabbit breeds. The mutation is recessive and only phenotypically expressed in homozygous individuals. Although presence of this particular allele does not preclude recent genetic augmentation or replacement, simple population genetics show that allele persistence from a medieval introduction is not impossible.

Keywords: *Lundy, black rabbits, DNA analysis, melanism gene, medieval ancestry*

INTRODUCTION

Although there is fossil evidence of rabbits, *Oryctolagus cuniculus* (Linnaeus, 1758), in what was to become the British Isles during the Hoxnian (Yalden, 1999), for the most recent epoch until ~2.3ka before present they were confined to the Iberian Peninsula and, possibly, north-western Africa (Surridge *et al.* 1999). Phoenician and Roman traders transported rabbits across the Mediterranean and they were present in northern and central Europe by the Middle Ages, probably sometime after AD1000 (Lever, 1994). Normans were the first to successfully introduce rabbits to

Britain, often to its sandy or peat-covered offshore islands. There rabbits were effectively confined, could burrow easily and were safe from mainland predators (Williamson, 2007). Lundy was one of the first British locations in which their presence is recorded. Irving *et al.* (1997) cite Exeter City Archives to state that between 1183 and 1219 the tenant of Lundy was entitled to take 50 rabbits a year 'from certain chovls on the island'. By 1274 a report to Edward I (regarding the produce of Lundy) stated 'taking of rabbits is estimated at 2000, £5 10s.' The report also indicates the primary purpose of such a harvest: '5s. 6d. each hundred skins, because the flesh is not sold' (Ritchie, 1920). That Henry III could instruct the constable of Lundy to put the proceeds of the sheriff of Devon's sale of 2,500 Lundy rabbit skins 'towards the expense of building the new tower' (Powicke, 1949) demonstrates the value of such commerce. Moreover, Lundy rabbits were particularly valued because a large proportion provided black fur, for centuries favoured as clothing trim or lining by the wealthy and socially elevated. Henry VI possessed a night shirt lined with black rabbit fur (Mason and Parry, 2010) and Henry VIII was obviously preparing to obtain his own when Hampton Court accounts listed the purchase of 'a great long auger of irne, to make and bore coney holes within the kynges beries new made for blake coneys in the warren' (Williamson, 2006).

Although black rabbit fur was a desirable product (Veale, 2003) it could be one with a legally restricted clientele; Tudor sumptuary laws, for example, dictated who was privileged to wear such 'black coney' (Cox, 2006) and in the majority of mainland warrens common grey rabbits remained most numerous, their fur used for warmth rather than for display and their meat for culinary purposes (Bailey, 1988). On the other hand, in some coastal and East Anglian warrens such as Methwold ('famous to a proverb' for its black rabbits according to Blomefield (1805) and Wretham (known as 'The Black Rabbit' warren), warreners specialised in breeding black rabbits to supply the demands of fine tailoring and, particularly, millinery (Mason and Parry, 2010).

Such specialism implies sophisticated warren management and this indeed occurred. A comprehensive description of methods and equipment employed (Sheail, 1971 and Mason and Parry, 2010 for such) is beyond the province of this paper. Suffice to say, elsewhere in the British Isles warrened rabbits were usually harvested by net or non-lethal trap with assistance from (muzzled) ferret and/or dog so a conscientious warrener could dictate the sex and phenotype of those rabbits killed and those released to produce subsequent generations. Ratios of both could be controlled precisely; in Hertingfordbury (Hertfordshire) in 1634 a warren tenant was bound to leave 'one hundred and twenty female Conyes and twenty male Conyes wheirof the better halfe to be black' (Hertfordshire Archives and Local Studies D/EP T264 cited by Williamson, 2007). It is not, thus, unreasonable to posit that similar methods were utilised on Lundy to manipulate its rabbit population and thus propagate a desirable black rabbit product.

Sheail (1971) and Ritchie (1920) note that by the fifteenth and sixteenth centuries black rabbits had been introduced to several offshore islands in England and Scotland respectively and these introductions founded the black rabbit populations for which such warrens were so prized. Sheail goes on to note 'Even today, there are a few black rabbits on Lundy Island', the implication being they are a legacy of such introductions. That there are 'a few black rabbits on Lundy' is not in doubt but whether this trait was acquired via unbroken inheritance from medieval introductions is a difficult question to address, particularly when it is known that several introductions of domestic rabbits occurred in the twentieth century, bringing potential genetic novelty to the islands feral rabbit population (Linn, 1997).

Two loci play a main role in coat colour pigmentation in vertebrates – the extension locus and the agouti locus (Hoekstra, 2006; Suzuki, 2013). The extension locus encodes the melanocortin 1 receptor *(Mc1r)*, and the agouti locus encodes the agouti signalling protein *(Asip)*. *Mc1r* determines which pigment is synthesized from the melanin precursor dopaquinone. When *Mc1r* is active, brown or black eumelanin is produced, resulting in dark fur. When *Mc1r* is inhibited, yellow or red pheomelanin is produced, giving lighter coloured fur (Hoekstra, 2006). *Asip* is an antagonist of *Mc1r*. It binds to *Mc1r*, and by doing so, inhibits *Mc1r*'s function, resulting in reduced eumelanin synthesis and therefore a lighter phenotype (Suzuki, 2013).

Mutations affecting coat colour in the extension and agouti locus have been described for rabbits. For example, a six base-pair deletion in *Mc1r* is associated with *dominant* black coat colour in this species (Fontanesi *et al.*, 2006). This 6 basepair (bp) deletion seems to hamper effective binding of *Asip* to *Mc1r* and thus prevents its inhibition, resulting in a black phenotype.

A 1bp insertion in *Asip* has been associated with *recessive* black coat colour in rabbits (Fontanesi *et al.*, 2010). This deletion in the 2nd exon of the gene causes a frameshift and introduces preliminary stop codons, i.e. it is a loss-of-function mutation (Figure 1). As with the 6bp deletion in the extension locus, this mutation prevents the inhibition of *Mc1r* and therefore results in a black phenotype.

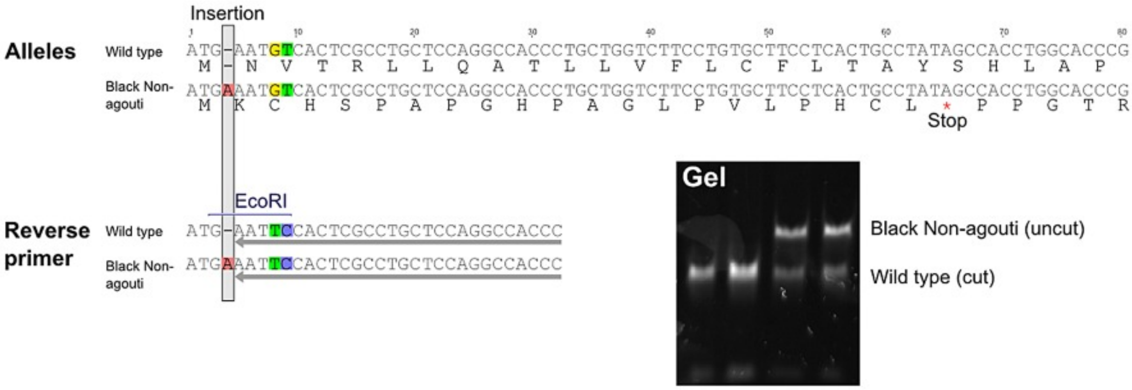


Figure 1: PCR-RFLP essay of Fontanesi *et al*. (2016) applied here.
Alleles: examples of DNA and amino acid sequences of a wild-type and a black non-agouti allele (partial). The 1bp insertion in the black non-agouti allele causes a frameshift that introduces stop codons resulting in a truncated protein.
Reverse primer: the reverse primer Ex2-ART-R (grey arrows) introduces an artificial EcoRI restriction site in the wild-type allele only.
Gel: the gel image shows the banding patterns of the four 2016 samples. Two samples on the left: homozygous wild-type; two samples on the right: heterozygous, carrying a wild-type and a black non-agouti allele

Both black coat mutations have been described for domestic breeds, but, to our knowledge, are currently not known from wild rabbit populations. The low frequency of black rabbits on Lundy might suggest recessive inheritance of the trait. With this in mind, we investigate whether the 1bp frameshift mutation in *Asip* underlies the black rabbit phenotype that is observed on the island.

MATERIAL AND METHODS

Rabbit tissue samples were obtained from dead rabbits found at various locations on Lundy in June 2016 and June 2017 in an *ad hoc* manner (Table 1, Figure 2). Soft tissue was taken from rabbit remains using forceps and dissecting scissors where possible. Where this was not possible, fur was sampled. Eight wild-type rabbits were sampled in 2016; 28 wild-type and 2 black rabbits were sampled in 2017. Carcass location coordinates were noted via GPS for most of the samples collected in 2017. Carcasses were photographed to record phenotype and tissue/fur samples were stored in absolute ethanol until further processing.

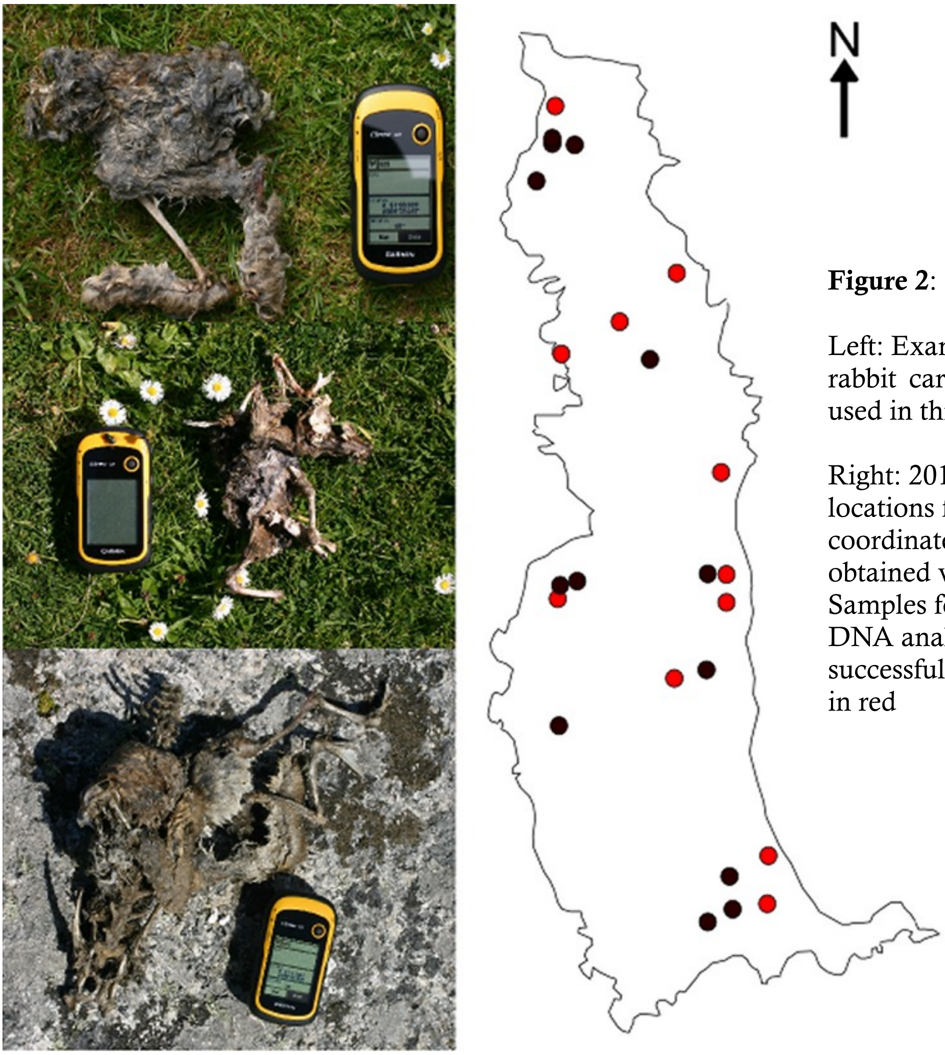


Figure 2:

Left: Examples of rabbit carcasses used in this study

Right: 2017 sample locations for which coordinates were obtained via GPS. Samples for which DNA analysis was successful are given in red

Table 1: Samples collected in June 2016 and June 2017. Data of collection and coordinates of carcasses sampled are given when available. na=not available. Phenotype indicates phenotype of the specimen: W=wild-type, B=black. Genotype indicates the genotype of the specimen: hom. wt=homozygous wild-type, heteroz=heterozygous, hom. na=homozygous non-agouti

Date	Sample	Degree	Minutes	Degree	Minutes	Location	Phenotype	Genotype
na	T1					600m North of North Quarry	W	hom.wt
na	T2					500m North of North Quarry	W	
10/06/2016	T3					Jenny's Cove	W	
09/06/2016	T4					Lundy Village	W	hom. wt
09/06/2016	T5					Lundy Village	W	heteroz.
10/06/2016	T6					Jenny's Cove	W	
na	T7					South east path	W	heteroz.
09/06/2016	T8					900m North of North Quarry	W	
06/06/2017	1A	51	9.807	4	39.659	NW of Castle	W	hom. wt
06/06/2017	1B	51	10.642	4	40.543	E of Earthquake	W	hom. wt
06/06/2017	1C	51	11.283	4	40.166	S of Threequarter Wall	B	
06/06/2017	1D	51	11.373	4	40.290	S of Threequarter Wall	W	hom. wt
06/06/2017	1E	51	11.853	4	40.484	North End	W	
07/06/2017	2A	51	9.936	4	39.655	By Millcombe chairs	W	
07/06/2017	2B	51	9.939	4	39.647	E Coast path just N of Millcombe	W	hom. wt
07/06/2017	2C	51	10.643	4	39.833	E Coast path just N of VC Quarry	W	
07/06/2017	2D	51	10.700	4	39.841	E Coast path between VC and North Quarries	W	hom. wt
07/06/2017	2E	51	10.969	4	39.861	Low E coast path 500+m N of North Quarry	W	hom. wt
07/06/2017	2F	51	10.977	4	39.857	Low E coast path 600+m N of North Quarry	W	
07/06/2017	2G	51	11.508	4	40.050	Low E coast path 100m N of Mousehole and Trap	W	hom. wt
09/06/2017	3A	51	11.950	4	40.561	North End, Long Roost	W	hom. wt
09/06/2017	3B	51	11.290	4	40.546	North End, Long Roost	W	hom. wt
09/06/2017	3C	51	11.868	4	40.587	Just S of Long Roost	W	
09/06/2017	3D	51	11.856	4	40.583	Further S of Long Roost	W	
09/06/2017	3E	51	11.759	4	40.648	Further S of Long Roost	W	
10/06/2017	4A	51	10.672	4	40.475	100m NW of St Helena's Church	W	
11/06/2017	5C	51	10.626	4	39.838		W	
11/06/2017	5D	51	10.626	4	39.838		W	hom. wt
11/06/2017	5E	51	10.442	4	39.920		W	
11/06/2017	5F	51	9.871	4	39.825		W	
11/06/2017	5G	51	9.797	4	39.811		W	
11/06/2017	5H	51	9.760	4	39.912		W	
14/06/2017	6A	51	10.419	4	40.059		W	hom. wt
14/06/2017	6B	51	10.617	4	40.559		W	
14/06/2017	6C	51	10.288	4	40.549		W	
na	7A						W	heteroz.
na	8A						W	
21/05/2017	0P					Lundy Village	B	hom. na

DNA was extracted using the Qiagen Blood and Tissue kit. PCR was employed to amplify small fragments of the ASIP gene. PCR reactions used primers described in Fontanesi *et al.* (2010). PCR was performed on the samples collected in 2016 using primers Ex2-F and Ex2-R (Fontanesi *et al.*, 2010), targeting a fragment of 396bp (397bp if insertion is present) (including primers) that contains part of intron 1, exon 2 and part of intron 2. PCR products were sent to the Natural History Museum London for Sanger sequencing. A second PCR was performed using primers Ex2-F and Ex2-ART-R, targeting a fragment of 94bp (95bp if insertion is present) (including primers). Primer Ex2-ART-R introduces a restriction site for the endonuclease EcoRI (G^AATTC) in the wild-type allele only i.e. when the insertion in exon 2 is absent (Figure 1) (Fontanesi *et al.*, 2010). This latter PCR was performed on all samples and the products were subsequently digested with EcoRI. Reactions were performed at 37°C for one hour in a total volume of 20µl and used the following reaction mixture: 8µl PCR product, 20 units EcoRI-HF (NEB), 40µg BSA. Samples were separated on 5% Mini-PROTEAN® TBE Precast Gels (BioRAD). GelRed was used for staining. Samples were run at 100 volts for 45 minutes and visualised under UV light. Genotypes were scored by hand.

Genotypes frequencies were tested for Hardy-Weinberg equilibrium using a chi-square test available on the OEGE website (www.oege.org/software/hwe-mr-calc.shtml) (Rodriguez *et al.*, 2009).

RESULTS

PCR product was obtained for 3 of the 8 soft tissue samples collected in 2016 using the Ex2-F and Ex2-R primers (the 396/397bp fragment). The products were sent for sequencing and for one sample readable Sanger trace files were obtained (sample T5: wild-type phenotype). The other 2 sequencing reactions failed (i.e. unreadable Sanger trace files were obtained), most likely due to the PCR products being of poor quality. Visual inspection of the T5 trace files revealed the specimen to be heterozygous and to carry a wild-type and a recessive black non-agouti allele.

All 38 samples (Table 1) were subsequently subjected to PCR-RFLP analysis (the 94/95bp fragment). PCR product was obtained for 4 of the samples collected in 2016 and 13 samples collected in 2017, which were digested with EcoRI. Two of the 2016 specimen were homozygous for the wild-type allele and two heterozygous (i.e. carried the recessive non-agouti allele in addition to the wild-type allele) (Figure 1). This observation does not deviate from Hardy-Weinberg expectations (Chi-square test: $\chi^2=0.44$, $p>0.05$). Using the observed allele frequencies 2 homozygous wild-type, 1.5 heterozygous and 0.25 homozygous black rabbits would have been expected for a population that is in Hardy-Weinberg equilibrium. Eleven of the 2017 specimen were homozygous for the wild-type allele, one was heterozygous, and one homozygous for the recessive non-agouti allele. As expected, this latter homozygous specimen had the black phenotype. It was the only black individual for which genotype data were obtained. However, the chi-square test rejected the Ho hypothesis of this sample being in Hardy-Weinberg equilibrium ($\chi^2=5.05$, $p<0.05$). Here, 10.2 homozygous wild-type rabbits, 2.65 heterozygous rabbits and 0.17 homozygous black rabbits would have been expected for a population that is in Hardy-Weinberg equilibrium.

DISCUSSION

This study shows that at least some black rabbits on Lundy derive their black coat colour from a 1bp insertion in the *Asip* gene. This insertion is a frameshift mutation that makes the gene product non-functional (Fontanesi *et al.*, 2010). As a consequence *Asip* will not inhibit *Mc1r* and the relative amount of black eumelanin increases. This mutation is a recessive mutation; the black phenotype is only expressed in individuals that carry two loss-of-function alleles. It is, to our knowledge, the first time that this specific mutation has been reported within a wild rabbit population.

Rabbits have been present on Lundy since medieval times during which black specimens were highly valued. A question arises whether the black rabbits of today are direct descendants of the black rabbits that were bred when Lundy acted as a medieval warren, and how they are related to black specimens in other populations and breeds. The 1bp insertion observed here is identical to the one reported for domestic breeds (Fontanesi *et al.*, 2010) and it seems highly unlikely that the Lundy non-agouti allele arose independently from the one observed in those breeds. It is more likely that Lundy and domestic rabbits obtained the allele from a single common ancestor. The finding of this specific allele on Lundy therefore supports a medieval origin of the black phenotype of present day domestic breeds.

It is also possible, however, that the black non-agouti allele arrived on Lundy in much more recent times. Albeit insular, the Lundy population cannot be considered closed. It has been restocked with specimens from other localities on numerous occasions in the twentieth century. These restocking exercises also involved domestic animals, including for example dark-coloured specimens of the Rex breed (Linn, 1997). Interestingly, recent genetic research has shown that dark coat colour in this specific breed is determined by the same frameshift mutation in *Asip* (Yang *et al.*, 2015). It is therefore not impossible that the black non-agouti allele observed here originated from Rex or other animals introduced on the island only a few decades ago. In that case, another more ancient 'black allele' might still linger within the Lundy genepool. More research, that also for example includes the *Mc1r* locus, is needed to answer this.

On the UK mainland organised warrening eventually fell prey to a variety of changes in agriculture, practices associated with hunting and legislation. Agricultural changes extended the range of habitat available for escaped rabbits to set up their own, feral populations. New game laws enabled farmers to exploit rabbits on their own land whilst selective elimination of 'ground game' predators favoured rabbit proliferation. Localities varied in their susceptibility and timescale associated with such changes (Williamson, 2007) but by the nineteenth century feral rabbit numbers had increased to the extent they exercised significant ecological influence over much of the mainland and were considered a serious agricultural pest by some. In 1840 a Select Committee was set up to look into the matter (Sheail, 1971). Rabbit proliferation continued despite attempts at control and by the 1950s it was estimated (Thompson and Worden, 1956) that the British mainland population was 60-100 million, with densities of up to 35-50ha^{-1}. As warrens declined, their rabbits, where not deliberately eliminated, spread and mingled with feral relatives and previously-selected phenotypic characters were lost via introgression and natural selection. Presumably, the Lundy warren followed a similar fall from grace. Preponderance of black rabbits whilst Lundy was managed as a warren is unlikely to have resulted from a naturally-selected Hardy-Weinberg equilibrium. Evidence from UK mainland warrens indicates intensive management was required to maintain the black phenotype. As warrening decreased and feral populations increased, alleles responsible for black phenotype will have dispersed into the feral genepool to produce a new Hardy-Weinberg equilibrium. It is likely that other anthropogenic influences such as introduction of non-native zoonoses (myxomatosis and haemorrhagic virus), and culling will have produced low population numbers prone to genetic bottlenecking, also with consequences for subsequent Hardy-Weinberg outcomes.

It is not currently possible to establish beyond doubt whether Lundy's black rabbits' alleles result from medieval selection or from twentieth century introductions. One point is, however, worth making. The melanism allele located in this study is recessive. This has two functional consequences, one genetic and one historical. Both might have a bearing on the matter.

In 1992 myxomatosis reduced the Lundy rabbit population to a few hundred animals (Compton *et al.*, 2004), and since then the population has gone through at least three more virus induced bottlenecks (Compton *et al.*, 2007), including that of 2017, yet the melanistic trait persists. Although only a small number of Lundy rabbits express the black phenotype (in the 2017 sample 2 out of 30 rabbits were black), a much larger number will be heterozygous and carry the black non-agouti allele. Assuming the population was in Hardy-Weinberg equilibrium in 2017 (which according to the genotype analysis for currently unknown reasons might not be the case – see results), the model predicts that 38% of the rabbits will have been heterozygous and 26% of the alleles on Lundy will have been black non-agouti. This illustrates an effect of heterozygotic trait possession: although homozygotes may be rare or even absent, heterozygote frequencies are much higher and it is they that are most likely to carry the trait forward for future generations to express. So, depending on allele frequencies, a recessive trait may be rare in expression but robust in the face of genetic bottleneck.

The same characteristic might also determine which type of melanism would be selected (albeit unknowingly) by warreners. For producing pure-breeding melanistic rabbits a recessive trait might be preferred. Dominant alleles mask non-desirable wild-type alleles but recessive traits require both alleles to conform before the trait is expressed and ensures pure-breeding strains will persist.

Neither of these factors can determine gene provenance with certainty but they may aid the suggestion that for medieval melanism genes to have survived to the present day in Lundy rabbits is not entirely unfeasible. Equally, however, it does not preclude the possibility of other, more ancient, genes persisting and it is for these that the search continues …

ACKNOWLEDGEMENTS

We would like to thank Tom Dickins (Middlesex University) for organising field trips to Lundy and for useful discussions regarding melanism in animals. We thank Chris Pawson (University of the West of England) for collecting a black rabbit sample. Fieldwork was funded by Middlesex University (Faculty of Science and Technology).

REFERENCES

Bailey, M., 1988. The Rabbit and the Medieval East Anglian Economy. *Agricultural History Review*. 36, 1-20

Blomefield, F., 1805. *An Essay towards a Topographical History of the County of Norfolk*, Within A History of Norfolk. London Publishers, W. Miller

Compton, S.G., Craven, J.C., Key, R.S., Key, R.J.D., 2007. Lundy cabbage: past, present, future. *Lundy Studies*. 161-178

Compton, S.G., Key, R.S., Key, R.J.D., 2004. Lundy cabbage population peaks – are they driven by rabbits and myxomatosis? *Annual Report of the. Lundy Field Society 2003*, 53, 50-55

Cox, N., 2006. Tudor sumptuary laws and academical dress: An Act against wearing of costly Apparel 1509 and An Act for Reformation of Excess in Apparel 1533. *Transactions of the Burgon Society*. 6, 15-43

Fontanesi, L., Forestier, L., Allain, D., Scotti, E., Beretti, F., Deretz-Picoulet, S., Pecchioli, E., Vernesi, C., Robinson, T.J., Malaney, J.L., Russo, V., Oulmouden, A., 2010. Characterization of the rabbit agouti signaling protein (ASIP) gene: Transcripts and phylogenetic analyses and identification of the causative mutation of the nonagouti black coat colour. *Genomics* 95, 166-175. doi:10.1016/j.ygeno.2009.11.003

Fontanesi, L., Tazzoli, M., Russo, V., 2006. Mutations in the melanocortin 1 receptor (MC1R) gene are associated with coat colours in the domestic rabbit (*Oryctolagus cuniculus). Animal Genetics.* 37, 489-493

Hoekstra, H.E., 2006. Genetics, development and evolution of adaptive pigmentation in vertebrates. *Heredity*. 97, 222-234. doi:10.1038/sj.hdy.6800861

Irving, R.A., Schofield, A.J., Webster, C.J., 1997. *Island Studies*. Lundy Field Society

Lever, C., 1994. *Naturalized Animals*, Chapter 2. T. & A.D. Poyser Ltd., London

Linn, I., 1997. *Wild Mammals of Lundy*, in: Irving, R.A., Schofield, A.J., Webster (Eds.), Island Studies. Lundy Field Society, pp. 107-117

Mason, A., Parry, J., 2010. *The Warrens of Breckland*. The Breckland Society

Powicke, F.M., 1949. *Ways of Medieval Life and Thought*. Chapter 3. Odhams Press Ltd

Ritchie, J., 1920. *The Influence of Man on Animal Life in Scotland: A study in faunal evolution.* Cambridge University Press

Rodriguez, S., Gaunt, T.R., Day, I.N.M., 2009. Hardy-Weinberg equilibrium testing of biological ascertainment for Mendelian randomization studies. *American Journal of Epidemiology*. 169, 505-514. doi:10.1093/aje/kwn359

Sheail, J., 1971. *Rabbits and their History*. David and Charles (Publishers) Limited, Devon

Surridge, A.K., Bell, D.J., Ibraham, K.M. & Hewitt, G.M. (1999) Population structure and genetic variation of European wild rabbits (*Oryctolagus cuniculus*) in East Anglia. *Heredity* **82:** 479-487

Suzuki, H., 2013. Evolutionary and phylogeographic views on Mc1r and Asip variation in mammals. *Genes and Genetic Systems*. 88, 155-164

Thompson, H.V., Worden, A.N., 1956. *The New Naturalist 13: The Rabbit*. Collins, London

Veale, E.M., 2003. V. *The Structure of the London Industry,* in: The English Fur Trade in the Later Middle Ages. British History Online, pp. 78-100

Williamson, T., 2007. *Rabbits, Warrens & Archaeology*. Tempus Publishing Ltd

Williamson, T., 2006. *The Archaeology of Rabbit Warrens*. Shire Publications Ltd

Yalden, D., 1999. *The History of British Mammals*. Chapter 1. T. & A.D. Poyser Ltd, London

Yang, C., Ge, J., Chen, S., Liu, Y., Chen, B., Gu, Z., 2015. Sequence and Gene Expression Analysis of the Agouti Signalling Protein Gene in Rex Rabbits with Different Coat Colours. *Italian Journal of Animal Science*. 14, 3810

MONUMENTAL STANDING STONES IN THE BURIAL GROUND ON LUNDY, BRISTOL CHANNEL

by

CHARLES ELLIS
23 Brynfield Road, Langland, Swansea, SA3 4SX
e-mail: charlesrellis23@btinternet.com

The late Professor Charles Thomas, at the request of the Lundy Field Society, in 1969 examined the Burial Ground and in his book, *And Shall These Mute Stones Speak*, published in 1994, gives much information. He classified the four stones as follows:

1. ref. no. 1400 Optimi
2. ref. no. 1401 Resteuta (British and Feminine)
3. ref. no. 1402 Potiti
4. ref. no. 1403 Tigerni.

There has been much more published since then. Douglas B. Hague in 1982 published a pamphlet called 'The Early Christian Memorials Lundy' which contains much useful analytical information. However, Charles Thomas (1994) emphasises that the subject remains largely unresearched and unclear. This is when he also suggested that the Beacon Hill Burial Ground is the most important one in Western Europe. It might therefore be helpful to consider the context in which these monumental stones appeared on Lundy. It has been suggested that they were erected in the fifth-sixth centuries. We know that at that time the Romans had largely withdrawn and that Christianity was gaining ground amongst the higher echelons of ecclesiastical and secular society. By their very nature the more ambitious monuments reflected the status and enhanced prestige of those named. The act of engraving and setting up the monuments implies performance, status, remembrance in the society at that time. Three of the monuments have crosses at the top. One of them, 1403, does not but that may be because the top appears to be missing. The four monuments are all different which is significant. The language appears to be Latin and would have been used by ecclesiastics at that time and 1401 appears to be feminine suggesting that this was a family unit or part of one. The majority of inscribed monuments were established near ecclesiastical sites and we know that an early 'church' exists within the Burial Ground. The inscriptions are not identical in their format. 1400 and 1403 are vertical and 1401 and 1402 are horizontal. These characteristics are relevant as they can be seen as referring to particular areas and monastic centres. The same applies to the forming of the letters. The actual position of the inscriptions does on these stones, I suggest, relate to the size and shape of the original stone bearing in mind the practical problems that had to be overcome. At this time in 2017 this is broadly about the limit of our knowledge on this subject.

However, many questions remain unanswered. Who were these people? Where did they come from? Where had they hoped to go?

Over the past year I have read many academic papers, books and pamphlets, and endeavoured to obtain a picture of life in the fifth-sixth centuries in western Britain. The dominance of Roman society was largely gone and they had left ruling families/chiefs who were gradually adopting Christianity. Pilgrimage was important and it was seen as a way of ensuring entrance to the ‘after life’ and led large numbers to make long and difficult journeys. One of these routes was down the west coast of Wales to what we now know as St David’s, where in the fifth century David resided with his fellow ecclesiastics, Paul, Samson and Gildas. It is said that his popular name was in English ‘The Aquatic’ as he only drank water. The Pilgrims’ route passed through their community to Caldey and the South coast of Wales. They sailed from there to the coast of Devon and Cornwall. If we take a line from Caldey, where there was an early Christian settlement, to the Camel estuary it will be seen that it passes about ten miles west of Lundy. From the Camel they might have remained in the area – there are Enodoc, Kew, Endellion etc. – or moved on to Falmouth and then to Brittany and even to Rome.

However, they may have been blown ashore on Lundy and never had the means to leave. This would account for our monuments. The implications on the lives of those concerned is beyond our imagination. There must have been a group of them and they may have spent the rest of their lives marooned and lost to their world. Charles Thomas has suggested that the Burial Ground contains a hundred graves.

As we examine this subject it becomes more speculative and open to imaginative indulgences, but I would venture to suggest would lend itself to serious academic research rather than field work. Further digging in the Burial Ground is not realistic bearing in mind the number of people buried there in the last 100 years. To assist any prospective researcher there are already a number of publications that report on the monuments and some are listed in the references below.

In one publication in the National Library of Wales Archives and Manuscripts/ Monuments/the early medieval Church in South West Wales, page 9, there is a reference to Gildas writing in the mid-sixth century about Vortipor as a ‘Christian though sinful ruler’. This name is similar to Vortimer who was the son of Vortigern who was ‘cursed three times’ by Germanus for incest and who ‘fled south’. Could this relate to stone 1403?

After many hours of research this is the limit of my findings but it poses the questions that I have referred to earlier. Therefore, I am happy to leave it to others to take up the challenge and answer the questions.

REFERENCES

Archaeologia Cambrensis The Journal of the Cambrian Archaeological Association, 1930, 1932, 1941 volumes

Gardner, K.S., 1963. Archaeological Investigations on Lundy 1962. *Annual Report of the Lundy Field Society 1962,* 15, 22-33

Hague, Douglas B., ARIBA, FSA, 1982. *The Early Christian Memorials Lundy*. Pamphlet.

Langham, A.F., 1989. Observations at Beacon Hill Cemetery 1988. *Annual Report of the Lundy Field Society 1988,* 39, 46-49

Thackray, Caroline, 1997. *The Archaeology of Lundy*. In Irving, R.A, Schofield, A.J. & Webster, C.J. Island Studies Fifty Years of the Lundy Field Society. Lundy Field Society

Thomas, Charles, 1992. Beacon Hill Re-visited: A Reassessment of the 1969 excavations. *Annual Report of the Lundy Field Society 1991, 42, 43-54*

Thomas, Charles, 1994. *And Shall These Mute Stones Speak? Post-Roman Inscriptions in Western Britain*. Cardiff. University of Wales Press

Thomas, Charles, Fowler, Peter & Gardner, Keith. 1970. Beacon Hill–Early Christian Cemetery. *Annual Report of the Lundy Field Society 1969*, 20, 14-17

Plate 1 (above): The early Christian memorial stones in Beacon Hill burial ground on Lundy.
Photo © Jennifer Ellis

Plate 2 (right): The Tigerni memorial stone, showing some of the lettering.
Photo © Jennifer Ellis