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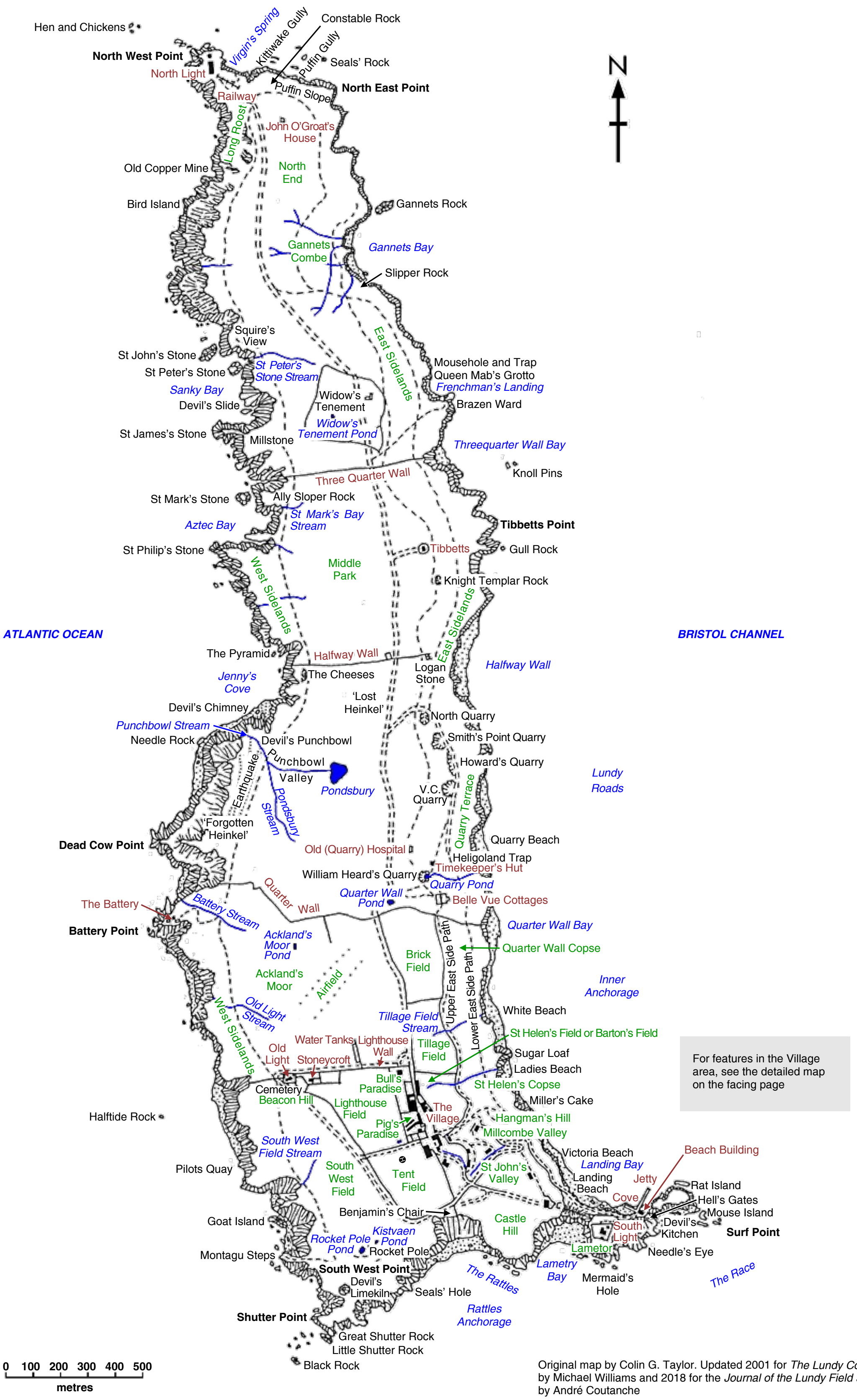
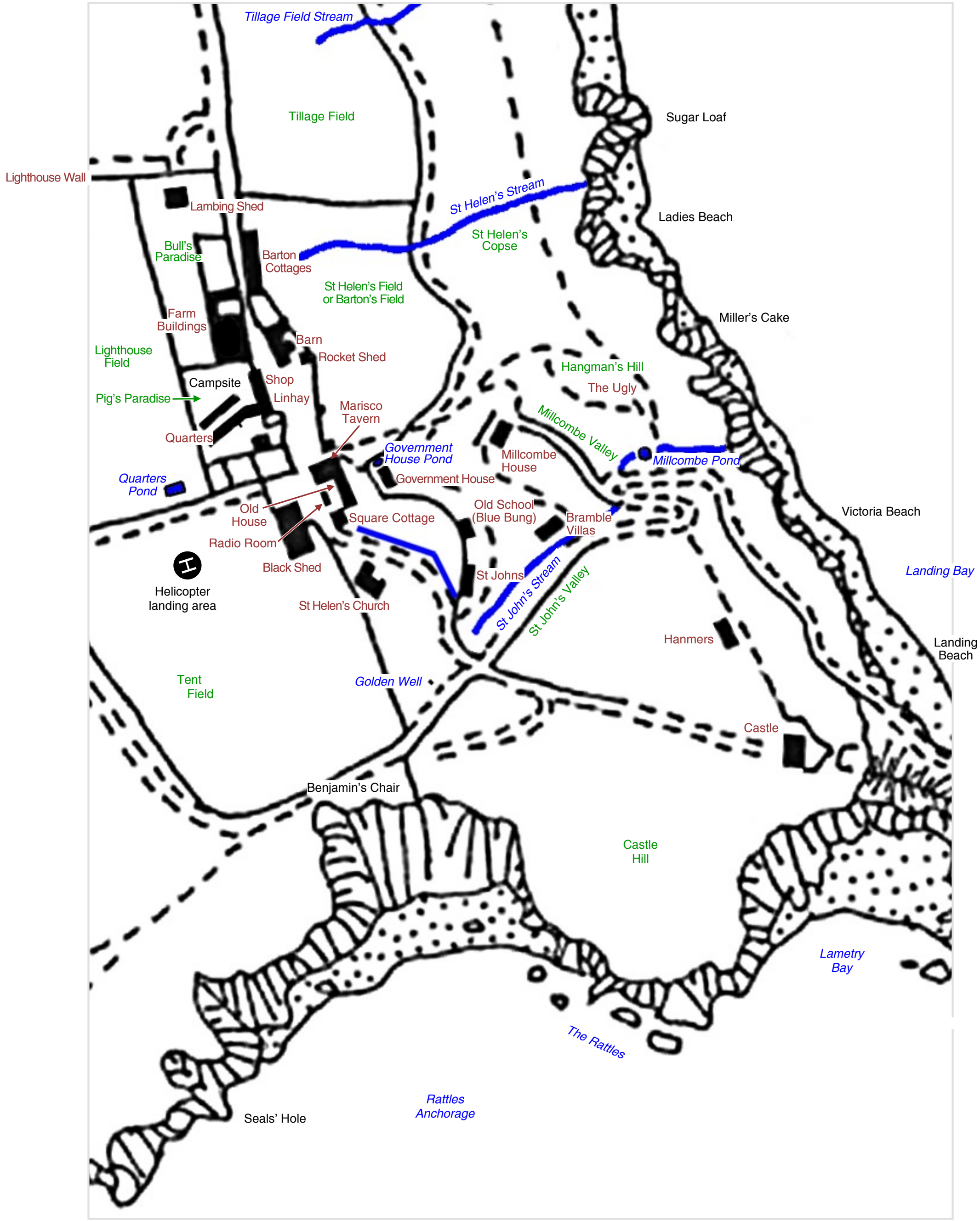


For features in the Village area, see the detailed map on the facing page

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 this larger-than-normal volume of the Journal of the Lundy Field Society. This seventh volume is the last one to be edited by myself and the Technical Editor, André Coutanche. Editing this biennial Journal has been a joint effort with André checking all the technical details submitted in the papers and ensuring consistency of data as well as producing the excellent layout. I would like to thank the many authors who have contributed papers over the years and the referees who have given their time to read them.

It is pleasing to see that this volume has a paper on Lundy's archaeology, only the second to be submitted in twelve years. *Chris Webster* has reviewed all the earlier work carried out in the 1960s, mainly by Keith Gardner and Trevor Miles.

This paper is followed by two papers on Lundy's insect life. A fascinating study of Dung Beetles by *Linda Losito and Bob Cowley* reveals a large increase in recorded numbers of species on the island, aided by bird pellet analysis as well as observation. A paper on Moths by *Steph Ford, Peter Kidd, Kay Nash and Angeline Rietveld* examines the effect of artificial light on Moth diversity in various Lundy habitats.

Alan Rowland has continued his research on Lundy's freshwater habitats and his paper deals with the importance of two of the temporary ponds on the island.

Even the Lundy Fungi have succumbed to DNA analysis in recent years and the paper by *Gareth Griffith, John Hedger and Alan Rowland* use DNA analytical methods to compare fruit body surveys and mycelia in the soils of the grassland and heather.

Grant Sherman has been studying Guillemots on Lundy ledges for over eleven years and it is good to see a paper on chick provisioning and parental attention by Guillemots on the same cliff ledge for the last ten breeding seasons.

The three following bird papers use the existing extensive bird-ringing data and recorded bird lists that have accumulated on Lundy for many years. *Tony Taylor* analyses the ringing data and biometrics of the Goldcrests between 1990 and 2018. Ringing data are used by *Yen Yi Tan, Tony Taylor and Julia Schroeder* to assess migration strategies of the Chaffinch since 1972. Lastly Avian abundance on Lundy from 2008 to 2016 is analysed for diversity and similarity by *Thomas Dickins and Layla Twigger*.

The nine papers are followed by a short communication elaborating the meaning of the word 'Plowers' that was mentioned in the paper on the Clayton Manuscript (LFS Journal, Volume 6) and book reviews of the Lundy Fungi Guide and the book on the work of the archaeologist *Charles Thomas*.

The next volume, the eighth, in 2022, will be edited by Professor Tom Dickins and I hope that he will receive the same support that I have received over the last twelve years.

Jennifer George
Editor
January 2020

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THE LUNDY FIELD SOCIETY'S ARCHAEOLOGICAL WORK IN THE 1960s

by
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ABSTRACT

From the late 1950s to the early 1970s the Lundy Field Society undertook a large number of excavations and surveys on the island, led by Keith Gardner. Very little of this was published but Gardner's records, and those kept by his co-worker Trevor Miles, have now been studied and reports prepared for the smaller excavations. Two larger sites remain to be completed.

Keywords: *Lundy, archaeology, Keith Gardner, Trevor Miles, excavation, survey, prehistoric, medieval, post-medieval*

INTRODUCTION

The Lundy Field Society has been involved in two main phases of archaeological work, firstly in the 1960s led by Keith Gardner and secondly in the 1980s by A.J. Schofield and the author. The later work has been published (Schofield, 1988, Schofield & Webster, 1989, 1990, Schofield, 1994) but the earlier campaigns have only been the subject of brief annual notes and occasional more discursive pieces. Gardner's work came to an end when the island was bought by the National Trust who carried out their own detailed survey work from the late 1980s. Keith Gardner died in 2008 leaving archive materials in the North Devon Record Office (NDRO) but further material has recently come to light in the possession of his collaborator, Trevor Miles. Miles worked principally on the medieval site in Bull's Paradise but reports and some finds from other sites are present in the material that, due to increasing bad health, he provided to the author.

It is intended to bring the two medieval sites, Bull's Paradise and Pig's Paradise, in the village, to full publication but the purpose of the present paper is to record the work on the other sites and provide further details where these exist.

SOURCES

This paper was stimulated by the discovery of large amounts of archaeological archive material by Trevor Miles's relatives while helping him as he became frail. They contacted the author who agreed to pass the material on to the relevant museums and record offices, and to bring the Lundy material to publication. As work on this progressed it was decided to check Quinnell's (2010) assertion that the Gardner archive in the North Devon Record Office contained 'only occasional plans and sections without any contextual explanation.' The Gardner archive (NDRO B/867) proved to contain large numbers of maps, drawings, photographs and record cards that complement the Miles archive and allow much more to be said about the excavations, although the records still appear to be incomplete, especially of textual descriptions.

Gardner and Miles had met in Somerset through their work with respectively the Clevedon and Bridgwater archaeological societies (Gardner, 2006, 9) and Miles went on to specialise in medieval pottery studies for the (then) Ministry of Works before becoming a teacher. Despite Miles mostly working at Bull's Paradise, there is no obvious logical split between the Gardner and Miles archives as both contain items relating to this and other sites. Gardner's archive also contains large quantities of paperwork relating to the organisation of the work on the island, together with correspondence and working versions of his publications.

Gardner also had a collection of photographic slides which were not originally deposited with the archive although a set of duplicates was given to the National Trust (Gardner, 2006, 9). Most are not clearly identified on the slide mounts but comparing those that are with the reports, and also relocating the positions from where they were taken on the island, has allowed most to be identified. The slides have now been scanned and will join the archive in the NDRO; the numbers used here were sequentially added to the scans and have been added to the slide mounts. Gardner published an account of his work on the island, *An Archaeologist on Lundy* (Gardner, 2006), which is primarily autobiographical but does contain some information on the chronology of the fieldwork.

Following Gardner's work, the National Trust undertook two surveys: an initial catalogue (Thackray, 1989) followed by a detailed topographical survey from 1990-94. The survey work is described by Blaylock (2010) who notes that 'more interpretative work needs to be undertaken before the survey can be published' but that the information has been incorporated into the National Trust Sites and Monuments Record (available online via the Heritage Gateway at www.heritagegateway.org.uk). NT SMR numbers will be used to identify sites below but it should be noted that these do not coincide with the numbers used by Thackray (1989) in the initial survey. Many of the prehistoric finds from Gardner's work made their way into the National Trust's collections and have been identified and published in detail by Quinnell (2010).

TIMELINE

Gardner first visited Lundy in 1955, having been directed there by the well-known Somerset naturalist and caver, Harry Savory (Gardner, 2006, 7, 12). He spent the next few seasons getting to know the island and surveying; publishing on the Gannets' Combe settlement (Gardner, 1956), Mesolithic flintwork (Gardner, 1957), speculating on the early medieval period (Gardner, 1960a) and stray finds in Bristol Museum (Gardner, 1960b). An investigation of a building at Puffin Slope was also noted (Dyke, 1960).

In 1961 the field known as Bull's Paradise was surveyed and two trenches opened across the earthworks (BP I and II). Further trenches were opened over other earthworks in the field in 1962 (BP II, III, IV and V) but no work is recorded the following year. In 1964, work was concentrated on BP III as it would be for the rest of the decade but other 'classification' excavations were carried out in Middle Park (MP I) and Widow's Tenement. After a year gap, work resumed in 1966 at BP III and other sites: Middle Park (MP II), Benson's Cave, a hut on Beacon Hill, and a platform at Jenny's Cove (JC I). In 1967 trenches were opened on Acland's Moor (AM I and AM II), a hut at the North End (Hut 6) and a building above Jenny's Cove (JC IV). Lundy was put up for sale in 1969 and realising that a new owner might not permit work to continue, plans were made for what might (and eventually proved to) be a final season. That year excavations were undertaken in the cemetery on Beacon Hill, directed by Charles Thomas, with the aim of discovering a context for the early Christian inscribed stones (Thomas, Fowler & Gardner, 1969a, 1969b; Thomas, 1992, 1994) and there is evidence for work at Tibbetts and Acland's Moor (AM III).

Gardner's excavations ended following the purchase of the island by the National Trust but some other work continued. Slides show casts being taken of the Beacon Hill stones which Gardner (2006, 30) describes and dates to 1972; the slides are dated 1971 except for one showing the casts crated up in the church ready to be taken to Bristol. Their whereabouts are now unknown. In 1973 the Western Archaeological Trust excavated in Pig's Paradise which Gardner photographed while running an adult education course on the island. Gardner and his team continued surveying in Bull's Paradise in 1974 and 1975, though it is not clear to what end.

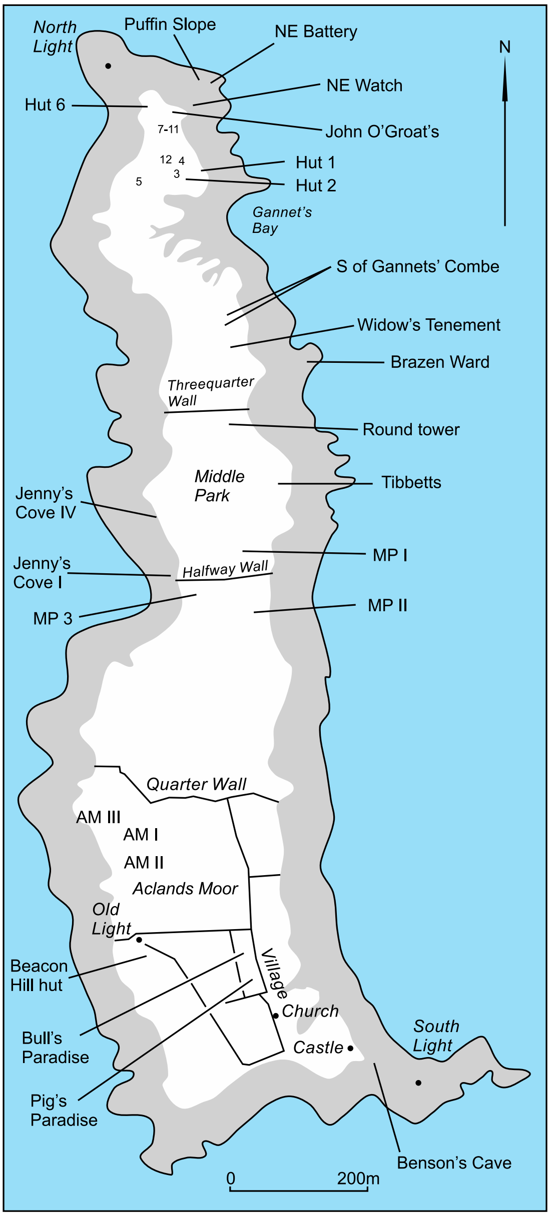

Figure 1: Map of Lundy showing sites mentioned in the text. Small numbers are Gardner's for other huts at the north end. Grey indicates steep sidelands or cliffs

Prehistoric sites

The aim of much of the work on the prehistoric sites, particularly at the North End, was to recover dating evidence and Gardner describes the work as 'classification'. There was an assumption at this time that Bronze Age pottery was only found in funerary contexts and so most of the pottery recovered from roundhouse excavations was believed by Gardner to be Iron Age in date. Excavation of settlements on the mainland associated with the introduction of calibrated radiocarbon dating shows that parallels for most of the Lundy pottery are earlier, with much of the Lundy pottery now seen to be Late Bronze Age Plain Ware dated to the eleventh to ninth centuries BC (Quinnell, 2010). There is also some earlier biconical ware, a long-lived pottery style dating from the eighteenth to eleventh centuries BC, and a few pieces of Trevisker ware, again of the Middle Bronze Age.

North End

Gardner refers to two areas at the North End, A and B, and these seem to be separated spatially and chronologically. North End A seems to include the prehistoric hut circles, at least two of which were excavated, while B may have referred to the later sites. The best recorded excavation is at Hut 6, described as 'Elliptical hut c. 25 ft×30 ft; bed recess formed by a chord of orthostats; pottery of late bronze age type' (Gardner, 1968a, 41). Gardner gives the grid reference as SS13254790, which equates to NT SMR 108003. The Miles archive contains a plan (Figure 2) that shows the elliptical shape, a possible entrance to the east and a subsidiary smaller hut circle (6A) to the south east. A trench 10 feet long and 3 feet wide is shown running east-west including part of the 'bed recess' at its western end. The section drawings, which are 9 feet long, show two layers beneath the topsoil but neither is described. The pottery is now interpreted as belonging to the Middle Bronze Age Biconical tradition but the flintwork is non-diagnostic (Quinnell, 2010, 24, 31). When visited in 2019, the site was almost completely overgrown with heather and only the tops of the larger stones were visible.

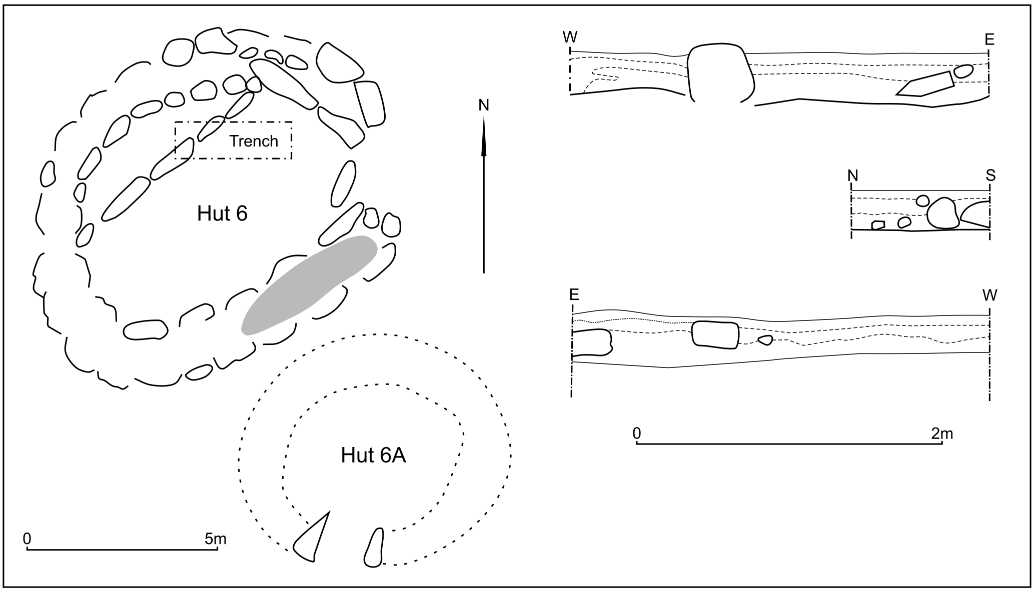

Figure 2: North End, Hut 6. Based on plan and sections in Miles archive (2/29, 2/34). The grey area is shown dotted in the original which may indicate small stone infill. The section drawings are unlabelled

The other hut recorded as excavated is Hut 2, which Blaylock (2010) identifies as NT SMR 108025 and says was excavated in 1967 citing Gardner (1968). However, the only hut circle excavations recorded in Gardner's report are Hut 6 and two on Acland's Moor. In the Miles archive is a drawing titled 'Lundy North End "A" Hut Ref 2' (Figure 3) which can be identified as NT SMR 108025 and there are slides in the Gardner collection (006, 010, 066) showing this hut but not naming it. The plan shows a hut circle with fieldwalls leading from it and a rectangular enclosure formed on one of these. There is also a trench plan and section (NDRO B867/5/2/1) but the location of the trench is not identified on any of the plans. The pottery from Hut 2 is described as prehistoric in character and the flintwork is non-diagnostic (Quinnell, 2010).

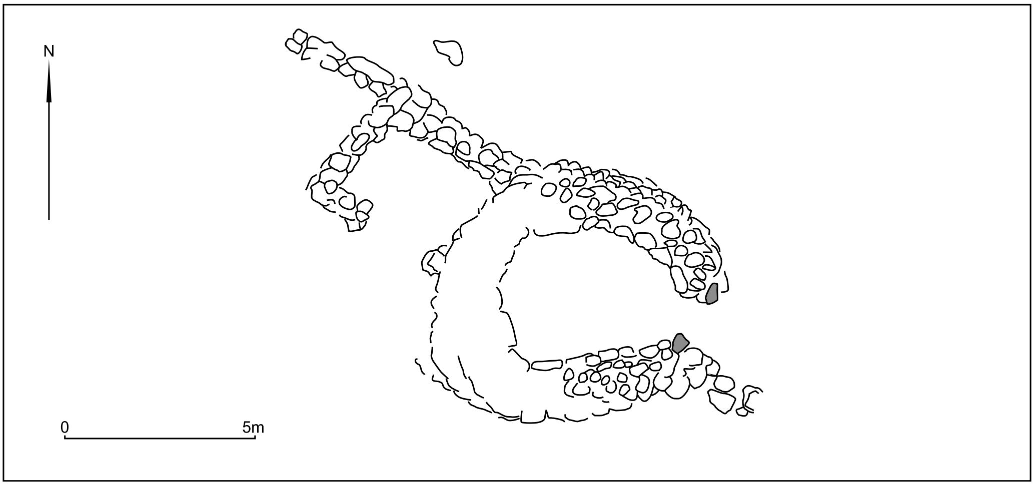

Figure 3: North End, Hut 2. Based on plans in Miles archive 2/33 and NDRO B867/1/19/13. Comparison between the plans shows that most of the stones were sketchily drawn at this and other sites

The only other detailed plan is a companion to that noted above and titled 'Lundy North End "A" Hut Ref 1'. Again, this seems to show two conjoined structures, one clearly a roundhouse with doorposts. This is NT SMR 10818 and has been redrawn as Figure 4.

Gardner's published plan of the huts and field system (Gardner, 1956) does not identify them but an annotated Ordnance Survey map in the Gardner archive (NDRO B867/5/1/3) shows twelve numbered huts (locations shown on Figure 1). Not all of these were identified by the NT survey or can be found today. It seems likely that they were not accurately surveyed but that the map showed rough locations of discoveries and potential sites.

Gardner's number	Grid reference	NT SMR number	Comments
1	SS13464764	108018	See text. Shown by Ordnance Survey
2	SS13394760	108025	See text. Shown by Ordnance Survey
3	SS13354762	108024	Shown by Ordnance Survey. Interpreted by the NT as a very small hut
4	SS13374737	Probably 108020	Interpreted by the NT as a clearance cairn
5	SS13194759	108031	Shown by Ordnance Survey. Suggested by the NT to be a cairn
6 and 6a	SS13244791	108003	See Text. Shown on Ordnance Survey map
7	SS13324784	108011	Shown by Ordnance Survey. Interpreted by the NT as a robbed cairn
8	SS13364783	Not recorded	Shown by Ordnance Survey
9	SS13324781	Possibly 108012	Shown 25m south of NT SMR grid reference
10	SS13344781	Possibly 108013	Shown 15m south of NT SMR grid reference
11	SS13364781	Not recorded	Photographic slides in Gardner collection 313, 314
12	SS13314766	Possibly 108023	Suggested by NT to be natural enhanced by clearance

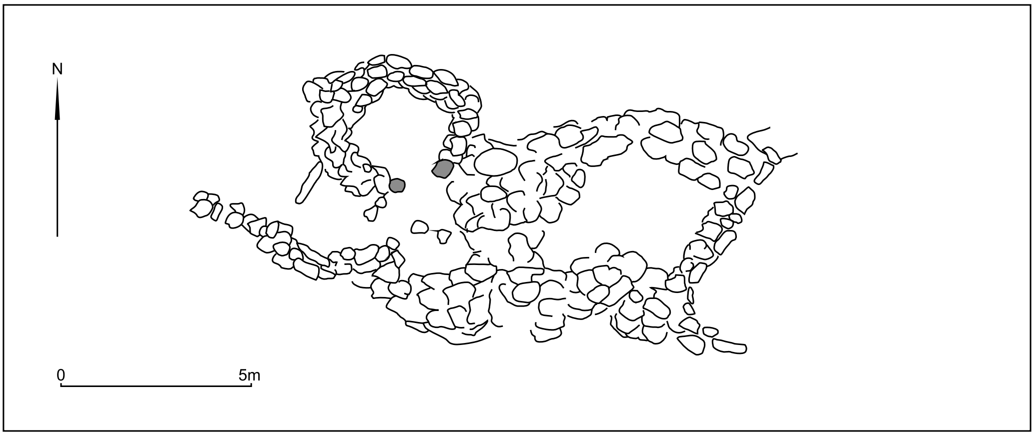

Figure 4: North End, Hut 1. Based on plans in Miles archive 2/32 and NDRO B867/1/19/13

Quinnell (2010, 24) says that there are other sherds from the North End in the collection but that it is not clear if these were from excavations or were surface finds. Many of the sites appeared to the NT surveyors to have been excavated in some fashion but this could have happened at any date; A.T.J. Dollar is recorded as having 'investigated' several (Dollar, 1930).

South of Gannets' Combe

Two hut circles are shown being surveyed in Gardner's slides (210 and 299), which can be identified as NT SMR 108045 and 108071. Both are interpreted in the NT SMR as natural hollows or extraction pits. The second is described as having its centre below the surrounding ground level, possibly robbed out. This is likely to be the site 'sectioned' in 1969 but which was devoid of dating evidence (Thomas *et al.*, 1969, 17). There is a photocopy of a section drawing titled 'Hut circle, S of Gannetts [sic] Combe' in the Gardner collection (NDRO B867/5/2/1) that is presumably this site. It shows a mound of 'Mixed bedrock with traces of peat and grey granular old ground surface' lying on the peat layer. There are no structural components and this appears to be a simple mound, unless it shows a section across a bank. The locations of soil samples for pollen analysis are shown.

Widow's Tenement

The excavation intended to investigate the medieval settlement (see below) also recovered 'presumably on the old land surface […] several flints and a sherd of much coarser pottery [than the medieval]. Further examples of this latter were forthcoming from rabbit scrapes outside the NE corner of the E enclosure and proved to be similar in fabric to the Early Iron Age "A" pottery currently being found in Middle Park.' (Gardner, 1964, 30). The NT collection contains four sherds from the excavation and four sherds as surface finds. Only one of these is diagnostic as Late Bronze Age Plain Ware (Quinnell, 2010, 25, 34, 35). The only artefact in the Miles archive is catalogued (1/18) as '[196] small flint end scraper from medieval occupation layer'.

Jenny's Cove IV

Survey work in 1967 around the west end of Halfway Wall discovered a rough rectangle of orthostats. A trench 24ft×6ft was excavated across the western end which recorded a thick (8-10ft) rubble wall supported by orthostats and containing a circular chamber. A larger trench (28ft×16ft) was opened in the following year which recorded the remainder of the rectangular enclosure, which Gardner describes as 'not as clearly defined as the thick western wall' (Gardner, 1968b, 44). No dating evidence was recovered. Gardner suggested parallels, in style if not in date, with Neolithic houses in Shetland on the basis of the thick walls and intramural chamber but also suggested to Trevor Miles (Miles archive 1/7a, dated 6/2/1968), a similarity to the Iron Age courtyard houses at Chysauster in Cornwall. Gardner's photographs and most plans (e.g. NDRO B867/5/2/2), however, fail to show the packing stones around the chamber as clearly as the published plan (Gardner, 1968b, 45), although they might have been removed by the excavation.

Both Gardner's interpretations were made before the second season, as can be seen from the plan prepared at the end of the first season (Miles archive 1/7b) which shows a large sub-circular structure surrounded by a 'conjectural wall line' containing the small chamber towards the north west. In the event the larger trench, which Gardner describes as 'further clearance', did not conform to expectations, exposing a rectangular structure with walls formed of a double row of orthostats. Gardner (1968b, 44-48) seems to have been reluctant to modify his interpretation and suggested that a low rock outcrop might have been incorporated in the conjectural wall, which might also have had an intramural passage to the east side, explaining the outer face of the square room and the lack of stone infill. A simpler explanation might be that more than one phase is present: an earlier structure with a circular, possibly intra-mural, room and a later rectangular structure formed from the partial demolition of the earlier structure. As Gardner did not excavate west of his original trench it is hard to be certain if the stones drawn poking through the grass in a curving line give a true representation of any walls below; the evidence from the eastern extension would suggest caution in any interpretation. The absence of artefacts leaves any proposed phases undated, but a prehistoric date for the earlier phase seems reasonable with a medieval or later date for the square structure.

Middle Park

Survey work in 1963 recorded a field system associated with two buildings, one (NT SMR 108210) of which was excavated in 1964 (MP I). Gardner's photographs (301, 302) show a single trench 12ft by 3ft with stone rubble at the SW end. The only known drawing is a section (NDRO B867/1/19/17, photocopied as Miles archive 2/35) which shows a layer (4) of 'grey-brown soil' between the topsoil and decayed granite natural. This terminates at the heap of stone visible at the end of the trench. The key to the drawing states that layer 4 contains pottery and flints. Gardner describes the site as 'a circular hut 30ft in diameter with an occupation layer producing flints and pottery of Early Iron Age "A" type.' (Gardner, 1964, 30). Blaylock suggests that the site might have originated as an Early Bronze Age ring cairn reused for domestic purposes in the Later Bronze age (Blaylock, 2010, 25). The pottery is now identified as Late Bronze Age Plain Ware (Quinnell, 2010, 34-35) and it is not clear why Blaylock introduces a hypothetical earlier phase.

Another site (MP II) was excavated in 1966, producing 'abundant' pottery of the first few centuries BC (Gardner, 1966, 30). Gardner's grid reference locates this to NT SMR 108264 and plans survive in the archives (Miles 2/37, NDRO B867/1/19/13). These show a sub-rectangular enclosure about 40ft by 30ft with a semi-circular enclosure annexed to one side. An excavation trench 18ft by 3ft is shown across the wall of the main enclosure on the Miles archive plan; the NDRO plan is more detailed (Figure 5). Trench plans and section drawings together with index cards giving some layer details are also in the Miles archive (2/36). The drawings show that the trench was originally only 12 feet long but was extended by 3 feet at each end to explore the area away from the wall. Two layers were recorded beneath the turf, an upper 'Black ? occupation' layer containing 'small pieces of pot, slates, charcoal [and] one pebble with a bruised faces' and a lower 'occupation layer' which also contained pottery. The section drawing shows a wall with vertical faces 0.75m high.

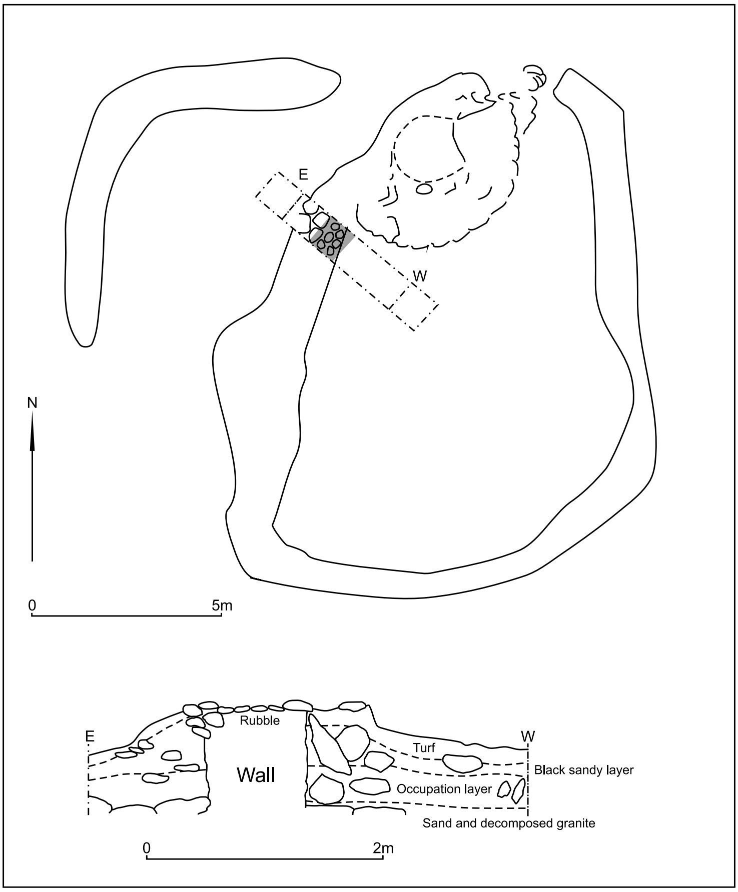

Figure 5: Middle Park II. Based on the site plan (2/37), trench plan and section (2/36) in the Miles archive and NDRO plan (B867/1/19/13). The grey area on the plan is the location of the wall as shown on the trench plan (2/36), which is narrower than the stones shown on the site plan and crosses the trench at right angles. Note that the section drawing does not show the full length of the trench which was subsequently extended by three feet at each end. The direction of north appears to be incorrectly indicated on the trench plan and sections

Blaylock (2010, 25), following the NT SMR, says that Gardner excavated in both enclosures but provides no evidence for this. She suggests that the larger enclosure is a medieval longhouse, partly destroying an earlier hut circle, which seems to be a slight misreading of the NT SMR which suggested it was a 'a stock enclosure to a long-house, which sits within a much bigger tenement enclosure, similar in form and shape to Widow's Tenement'. The pottery is prehistoric and includes Late Bronze Age Plain Ware (Quinnell, 2010, 25, 35); the absence of medieval pottery would argue against domestic use at this date, although the survival of the vertical wall faces might suggest that it is more recent than the Bronze Age.

One of Gardner's maps (NDRO B867/5/1/8) shows a third site in Middle Park (MP III) 50m south of the west end of Halfway Wall. This appears to be a trench but is 44m long and nearly 9m wide, which is clearly too large. The site is shown as an earthwork on the NT survey with its east end coinciding with a field bank that is also shown as a pencil line on Gardner's map. The NT SMR (108252) describes the foundations of a rectangular building and suggests that it might be a longhouse. There does not appear to be any evidence that Gardner excavated here; it may have been planned.

There is also a detailed plan of a 'round tower' (NDRO B867/1/19/18). This gives the grid reference 136446 which locates it to NT SMR 108128, a prominent mound just south of Threequarter Wall. There is no indication that Gardner excavated here and early descriptions (Chanter, 1877, 45) suggest that the central depression is an old feature. Chanter (1877, 45) suggested in the 1870s that 'the descriptions that have been handed down' say that the ruin was the remains of a round tower similar to those of early medieval Ireland. He says the inner diameter is 15 feet (4.5m); the NT survey says 3m by 5m, and the Gardner drawing shows it about 6.5m. Gardner (1972, 21) suggests that 'current opinion is divided between its being a robbed burial cairn and the base of a windmill'.

Acland's Moor

Two sites were investigated in 1967 but their locations are confused. Gardner (1968, 44) describes the first (AM I) as 'remains of rough cobble foundations' at SS132446 and the other (AM II) as a 'hut circle (?) within larger circle of stones. Fallen orthostats with traces of cobble backing' at SS13154475. Gardner's marked Ordnance Survey map (NDRO B867/5/1/9) shows the two locations at the grid references given (i.e. AM I to the south and AM II to the north) and his photographs show both excavations: AM I as a square excavation full of rubble and AM II as a deeper rectangular trench with two large stones, although some of the more distant shots titled AM I are clearly of AM II.

The NT SMR identifies these as their site numbers 108390 (northern) and 108406 (southern) but states that Gardner 'must be mistaken' in his published description of the sites (NT SMR 108406) and that the AM numbers are transposed. They thus describe the northern site (NT SMR 108390) as that with the cobbles. This seems to be correct as examination of the northern site in 2019 identified the rocks visible in the background of Gardner's photographs of AM I. It is difficult to explain this discrepancy as Gardner worked on both sites in the same year and it is hard to believe that he did not realise that the site with the cobbles lay to the north of the other. Locating AM II in 2019 was harder as Gardner's photographs show it in an area of bracken with few distinctive rocks. The Old Light is visible in the background of several photos and by aligning the buildings in the same relative positions on site it is suggested that it lay at SS13204463 which is NT SMR 108406. The pottery from AM II was identified by Quinnell (2010, 25) who correlates this to NT SMR 108390 but to the grid reference of NT SMR 108406. No closer dating than of prehistoric type was possible.

All Gardner's excavation records and photographs are consistent in their description and depiction of AM I and AM II so that in the account that follows these numbers will be used to identify the excavations irrespective of confusion about the locations.

Acland's Moor I is recorded on a single record card and three copies of an overall site plan (NDRO B867/1/19/9, B867/5/2/1, Figure 6). There are no known excavation plans or sections, probably as little considered significant was encountered. The card is dated August 1967 and records that an area 9 feet square was stripped of turf revealing a scatter of stones. These were removed from a 3ft wide section on the west side of the square which revealed larger stones suggested to be a wall foundation, although no wall faces were apparent. Slate and one piece of coal were recovered but no pottery. The rubble was then removed from the remainder of the excavation which again revealed larger stones 'in situ' but no pattern was evident. A fragment of flint was found. The trench was then extended by a 12ft long, 3ft wide cutting sited to cross a low mound suspected as being a buried wall. Larger stones appeared to match this location with less stone to the north of the wall than to the south where it is described as 'suggestive of tumble'. The only finds here were two small pieces of charcoal and two foreign stones.

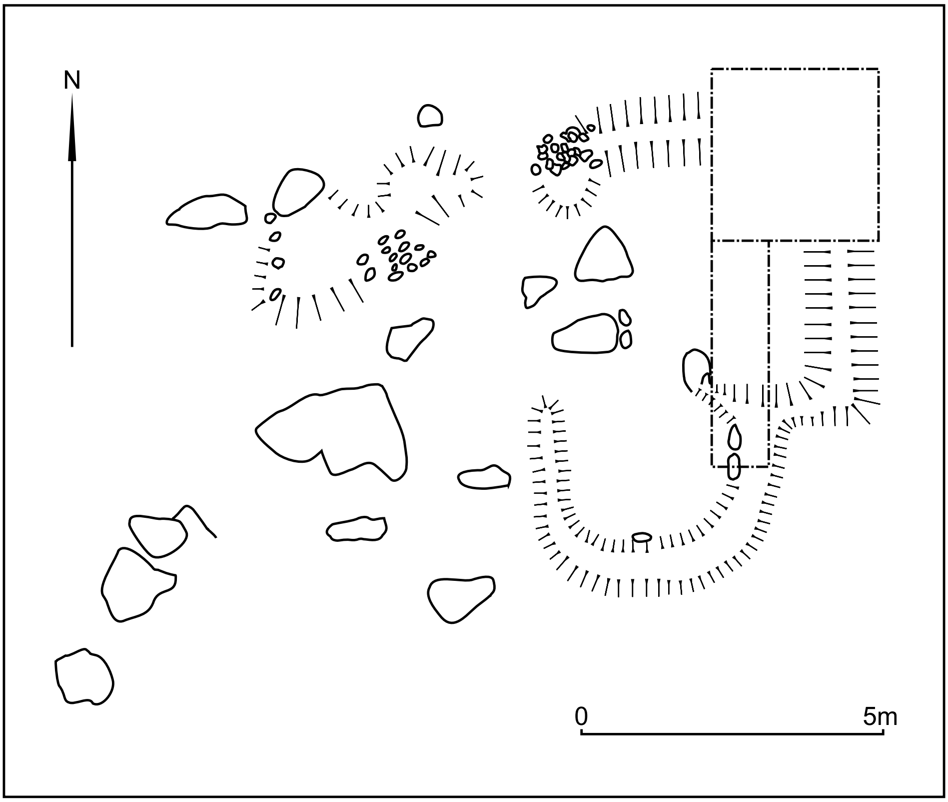

Figure 6: Acland's Moor I. Based on NDRO B867/5/2/1. Only the initial 9ft square trench is shown on the plan; the position of the later extension is inferred from the description

The 1967 season at Acland's Moor II is recorded on four record cards with copies of plans and sections (NDRO B867/1/19/9, Figure 7). The cards record are dated August and report the removal of turf over a 9ft by 3ft area 'between oval ?arrangements of stones'. Removal of the layer beneath this recovered small fragments of slate, pottery and daub, and revealed more stones. The trench was extended by 3ft eastwards to reach 'a fallen orthostat'. Beneath this was a black layer (3) which appeared 'to be changing to rough sandy granite' but still contained charcoal and burnt granite fragments with small fragments of pottery. Layer 4 was a sandy dark brown layer with granite fragments; 'several fragments of chert, one small stone axe and thick rough pot fragments' were on this layer. There were also slates with 'fabricated notches'. The 'occupation layer ended in grey sandy substance and disintegrated granite. 2 rough granite artefacts found in this layer. Trench cleaned down to bedrock and section drawn'.

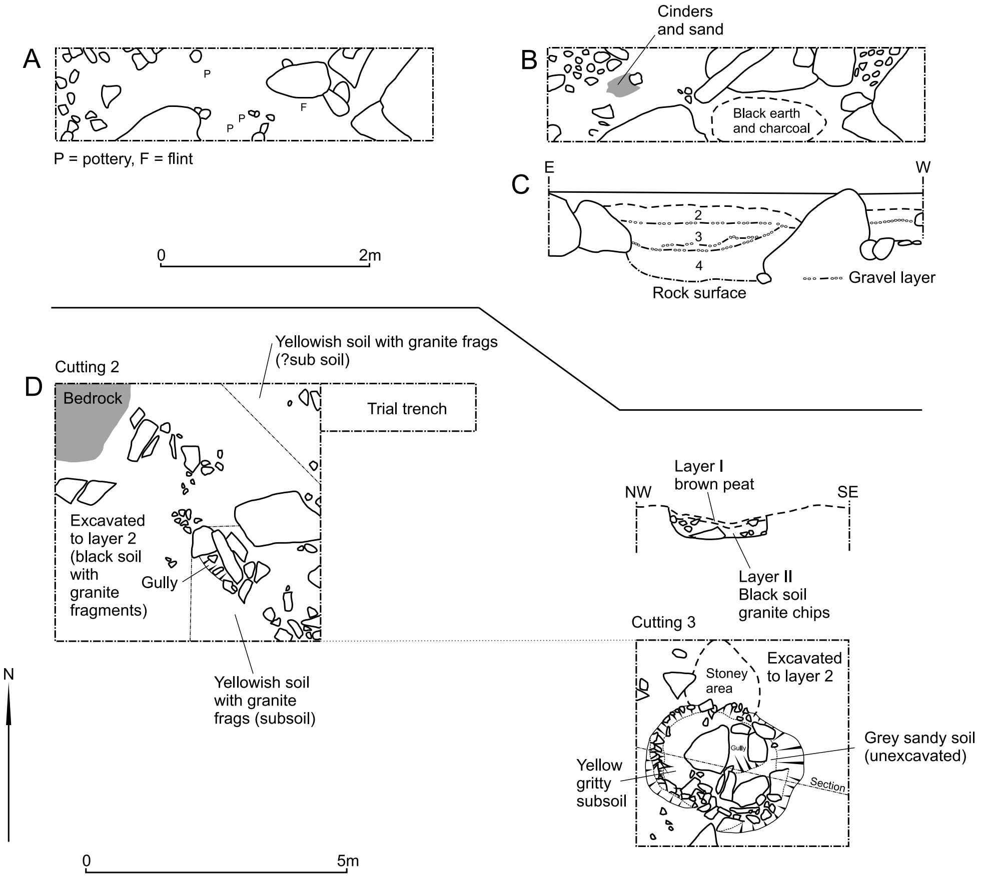

Figure 7: Acland's Moor II. A) Plan at surface of layer 2. B) Plan at surface of layer 3. C) drawing of the south side of the trench. Based on several, sometimes contradictory, copies of plans in NDRO (B867/1/19/9). The differences between the plans clearly show that most stones were drawn sketchily. D) Plan and section of 1969 trenches 2 and 3. Based on plans in NDRO (B867/1/19/9)

The site was revisited in 1969 but the only evidence is plans of two large (5m and 4m square) trenches near the 1967 trench. There are also undated plans, lists and diagrams that suggest the site was being considered as a stone circle. This hypothesis may have led to the extension of the excavation with the aim of assessing if any of the stones were artificially positioned and Trench 3 appears to show an excavated stone hole. No written materials are known to survive so it is hard to assess the thinking behind this or the results.

Gardner's annotated Ordnance Survey map (NDRO B867/5/1/9) also shows the location of AM III at SS12994485 and there is a plan of the site with a trench marked (NDRO B867/1/19/9, Figure 8). The plan shows a survey of a 'boundary wall' with a possible hut incorporated into it. A detailed plan of the trial trench shows the stones of the wall but does not appear to have confirmed the presence of the hut. The site plan is located relative to two of the telegraph poles which formerly linked the North and South lighthouses. These have been removed and the exact location of the plan is uncertain as there is a single slide (276, dated 1969) showing the 'AM III', but no excavation. This can be located to SS13004480, some 50m from the mapped location, south along the west side path. The NT SMR and survey plan are devoid of records in this area.

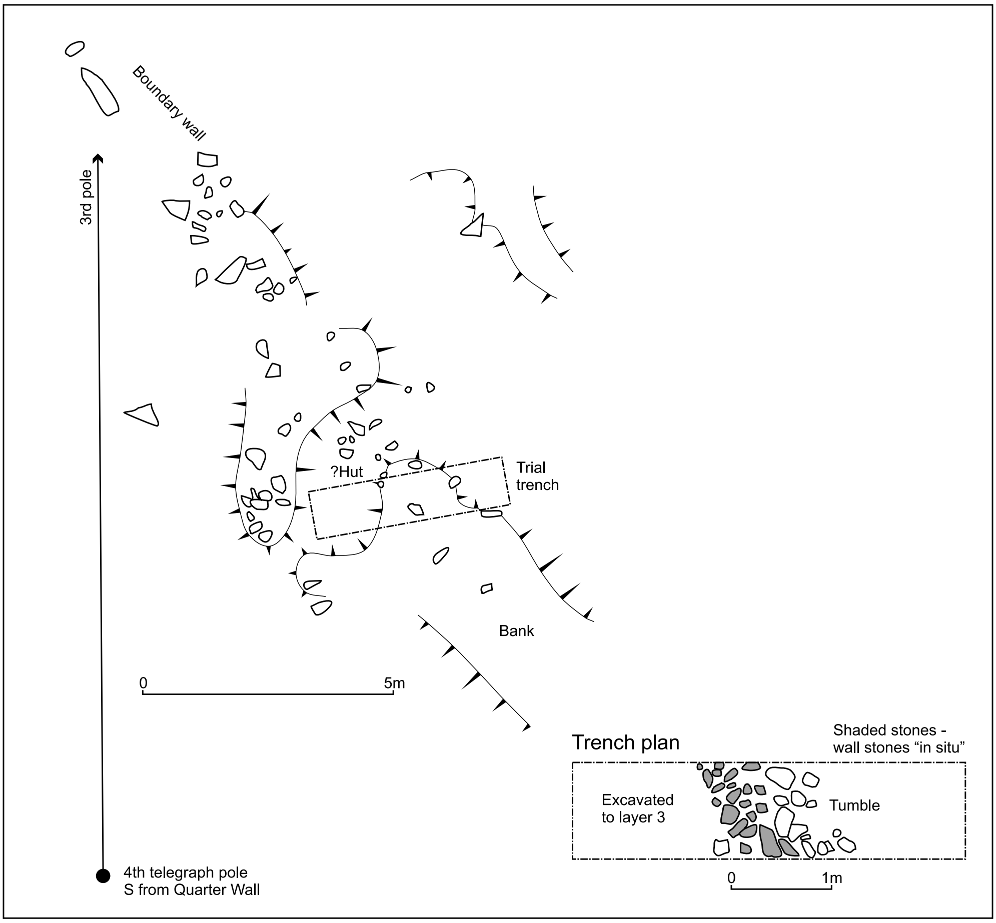

Figure 8: Acland's Moor III. Plan of earthwork survey and trial trench. The plan is related to a base line running between telegraph posts that have now been removed

Beacon Hill hut circle

The largest of several hut circles to the south of the Old Light was excavated in 1966. Gardner (1965-66, 30) describes it as 'a circular hut with 9ft thick cobble wall lined on the inside with granite slabs'. Finds included 'a poor barbed and tanged arrowhead and a quantity of coarse pottery, again of the same broad SW type of the first few centuries BC.' A plan and a section drawing survive in the Miles archive (2/27, 2/28, Figure 9), together with a catalogue of the stone finds, a box of the stone finds and three photographs (Plate 1). There are also copies of plans in the Gardner archive (NDRO B867/1/19/8, B867/5/2/1). The pottery is described by Quinnell (2010, 36) as Late Bronze Age Plain Ware. Similar material was recovered from Thomas's excavation in the cemetery, suggesting a Late Bronze Age settlement of several houses in the area (Quinnell, 2010, 43).

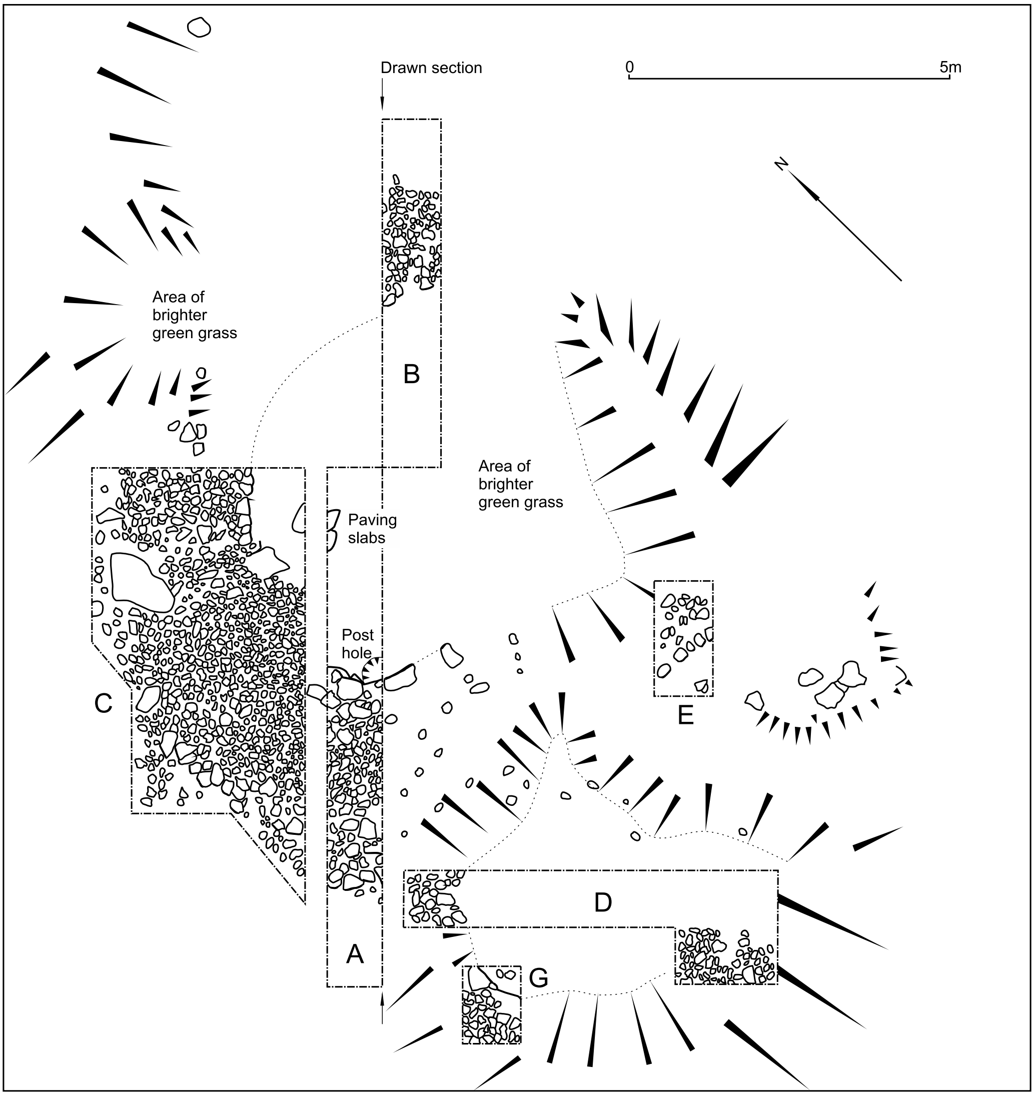

Figure 9: Beacon Hill hut excavation. Composite of two plans (NDRO B867/5/2/1 and Miles 2/27). Trench F is indicated to be 'across field bank' off the top of the plan

Plate 1: Beacon Hill Hut excavation. View of excavation looking south.
Photo: Miles archive 1/3

The plans and section seem to show a more complex structure than described by Gardner, with what appears to be a subsidiary structure to the S (Figure 9, trench D and G) and little evidence of walling to the east. The section appears to show a layer (Figure 10, Layer 3) within the walls, possibly derived from occupation though this is not suggested, which is cut by a posthole (9) adjacent to the wall. There are also two very thin layers, one of charcoal overlying one of sand, shown below the topsoil. The extent of these are not shown on any of the plans.

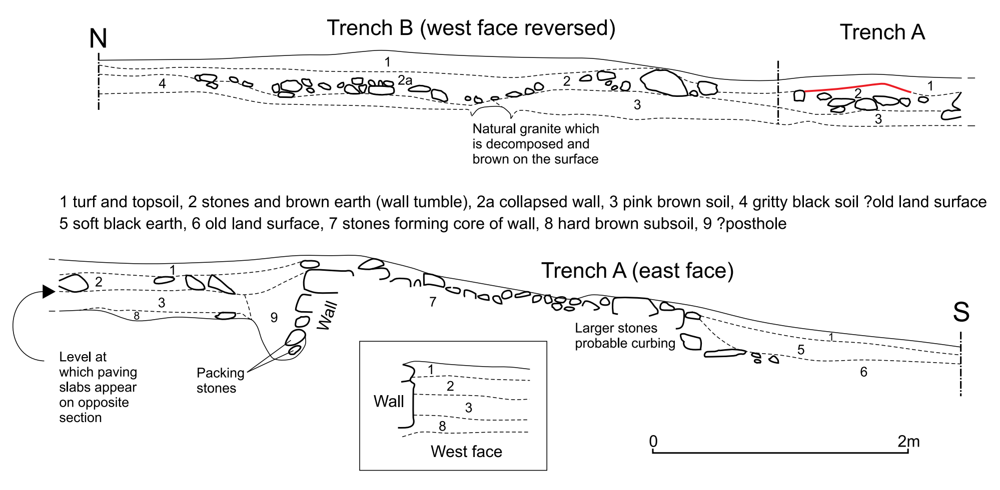

Figure 10: Beacon Hill hut excavation. Composite section of trench A and B. The inset shows the west face with layers uninterrupted by the post hole. The red line indicates the location of a thin layer of charcoal above one of sand that are too thin to draw.
Based on Miles 2/28

Two other trenches (Sites II and III) are shown on a plan of the area (NDRO B867/5/2/2) which also shows the hut circle excavations and a section across a lynchet (see below). These appear to be sited to target hut circles (Site III, NT SMR 108510 and Site II, probably 108513 or 108511). An index card and three photographs (NDRO B867/1/19/8) may refer to one of these trenches although the orientation of neither trench matches the location of the church shown in the background. The card is captioned 'Beacon Hill X' and dated September 1967 and describes the finding of a 'rough wall with no inner face' but that no 'signs of habitation' were encountered. The photographs show the excavators working immediately after the removal of turf.

In 1969, Peter Fowler excavated a trench across a lynchet to the south of the cemetery. This receives only a brief mention (Thomas *et al.*, 1969, 17); no dating evidence was obtained but the soil had collected beside and over a stone field wall probably relating to the hut circles. A possible location is shown across a lynchet (NT SMR 108506) running NE from the hut circle to the cemetery wall on the plan (NDRO B867/5/2/2). This is referred to as Trench F on the plan in the Miles archive (2/17).

Medieval

Large quantities of medieval pottery are present in the Miles archive from the sites of Bull's Paradise and Pig's Paradise in the village. It is intended to publish a full account of these excavations subsequently and only the other medieval sites on the island are described below.

Widow's Tenement

A cutting 6ft square was made in the south-west corner of the rectangular main building in the settlement at Widow's Tenement. As well as the prehistoric pottery described above, medieval pottery of thirteenth century date was recovered from below the wall collapse (Gardner, 1964, 30). A photocopy of a plan of the farmstead and the section drawing from the excavation survives in the Miles archive (2/16, 2/42, Figure 11) but there are no medieval finds. There are some overall plans of the settlement in the NDRO (B867/1/19/4, B867/5/2/4) and a published plan by Philip Rahtz (Gardner, 1972, 24; Gardner, 2006, 74).

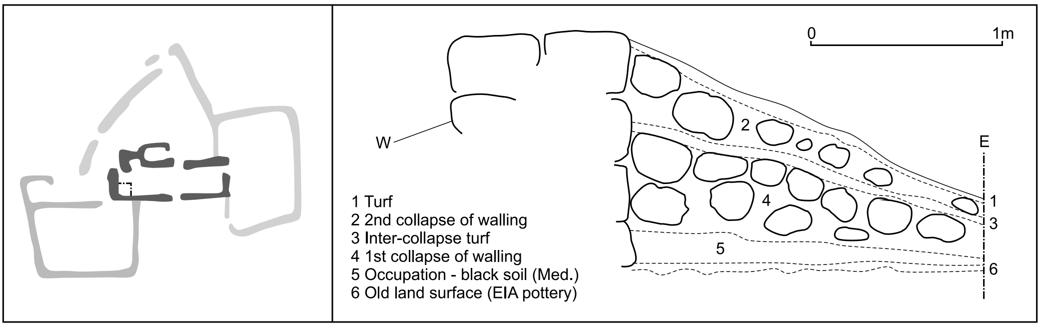

Figure 11: Widow's Tenement. Left, plan based on that by Rahtz (reproduced in Gardner, 1972, 24; Gardner, 2006, 74) with added trench location. Right, section based on Miles 2/42 showing north side of trench. It is clear from photographs that this is highly stylised. The EIA pottery is now considered to be late Bronze Age (Quinnell, 2010, 25, 34, 35)

Jenny's Cove I

In 1966 a revetted masonry platform (NT SMR 108223, Plate 2) was being tidied for photography and sherds of 'thirteenth-century pottery' were recovered (Gardner, 1966, 31). This led to a small excavation which 'produced nothing of later date'. The pottery is described as comparable to that from the Bull's Paradise excavation and further work on finds from there may provide a better date. Perhaps surprisingly there are no records or finds from this site in the Miles archive but three plans and an index card survive in the NDRO (B867/1/19/1, Figure 12). The card is dated August 1966 and describes: 'Topsoil removed from trench 3ft wide from interior of wall along west side. Very friable and much burrowed by rabbits and bees. Pieces of thirteenth-century pot found on a level 3" down. Yellow ?clay subsoil at 10 inches down, solid, one small pottery fragment and broken granite bits. Bedrock at 1 ft 4 inches, present depth of wall at corner 1 ft 9 inches'.

Plate 2: Jenny's Cove I. The west face of the 'mangonel battery' platform showing the walls built on the natural granite outcrop. Photo: author

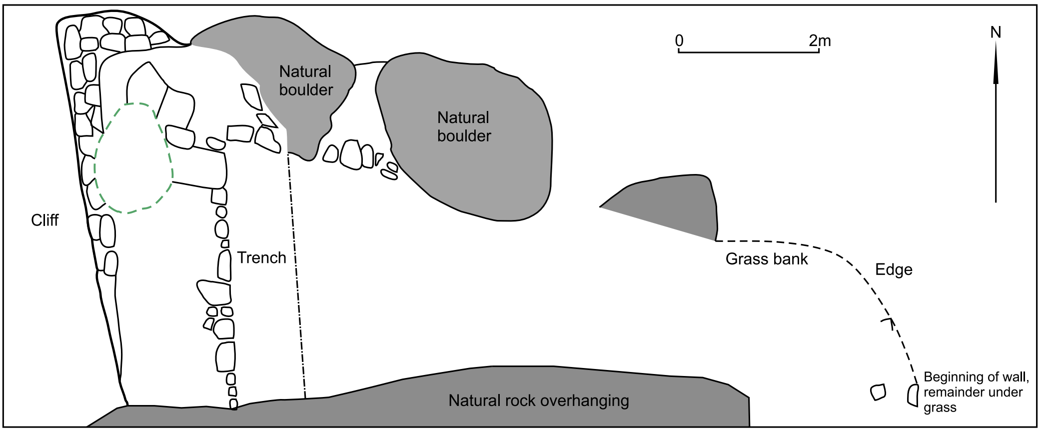

Figure 12: Jenny's Cove I. Plan of the 'mangonel battery' platform showing location of trench. On the original pencil drawing the area enclosed by a dashed green line is believed to be intended for vegetation. Based on two sets of plans in NDRO B867/1/19/1

Gardner identified the site as a defence work and given the evidence of the medieval pottery suggested that it could have been used as the standing for a mangonel, for which there is documentary evidence in 1222 (Gardner, 1966, 31). The location however seems rather precarious for a large siege engine and getting the engine onto the platform would not have been easy (Figure 12). The description of the scheduled monument (National Heritage List for England entry 1016032) considers that 'It seems to have been designed as a platform for musketeers rather than cannon.' The compilers of the schedule entry seem unaware of the medieval date provided by the pottery but are certainly correct that the site is too high above the water for effective cannon use. As they note, the site, and another similar one (NT SMR 108224) lower down to the south-west, overlook the path from the landing place in the cove so the interpretation as a musketry, or archery, position seems most reasonable. It is also possible that the pottery might be residual from a destroyed medieval structure on the site or nearby.

The other platform (NT SMR 108224) mentioned above does not seem to have been investigated in detail by Gardner although a slide (483) labels it as JC II. It is described by the NT SMR as 'roughly square in shape (c.6m×c.6m) and has been raised. Dry stonework is visible on the north side, c.2m high and extending from the base of a rock buttress seawards to the edge of a deep gully.' Examination in 2014 and 2019 showed a feature somewhat different in character at the location on the NT survey: a wall c.10m long running west from the rock buttress to meet the natural rock again at a deep rift. There was no indication of a platform behind the wall where the ground sloped up naturally and, as it blocks a route around the buttress, an interpretation as a western completion of Halfway Wall seems more plausible. It is also possible that the 'platform' lies elsewhere, though clearly not at the location mapped by Historic England (NHLE 1016033) as this faces the wrong way.

Two further sites are recorded only by the slides. JC III appears to be one of the small dams across a valley designed presumably to create stock ponds. JC V is a small patch of walling filling a gully on the sidelands.

Post-medieval and industrial

Four sites are listed as being recorded in detail at the North End in 1967 (Gardner, 1968, 41), and plans for all survive in the archives.

Puffin Slope

The site known as Puffin Slope is recorded as being explored in 1960 and described as a rectangular room with a large fireplace and adjacent granite seat (Dyke, 1960). It is suggested that it served as a 'guardroom for the North East Fortification and was possibly of the Civil War period'. Gardner later (1972) stated that there was a 'rough track' to the battery platform (NT SMR 108006, below). Two things hint at more recent use: Dyke, presumably relying on information from Gardner, says that the fireplace still showed traces of ash and that there was a collapsed sloping roof 'thatched with thrift'. It is not clear what the evidence for this roof was as he later says that 'all timber had been removed for kindling'. In 1967 when the site was planned, all this had presumably gone; the plan only shows the walls with the fireplace in the east wall and the door and seat to either side (Miles archive 2/30b, Figure 13, Plate 3). The description in the NT SMR

(108004) says that most of the 'building's horizontal surfaces are buried under a thick layer of overhanging thrift' which is presumably what was interpreted as thatch. Both Gardner (1972) and the NT liken the structure to John O'Groat's House (below). When visited in 2019 the site was in good condition under a thick blanket of thrift which had filled the room to the depth of the north wall and buried the 'seat'. The location of the entrance was similarly covered. The building is cut deeply into the hillside with its south wall about 2m high and a much lower wall to the north which continues down on the exterior as a retaining wall for the floor. The only real point of similarity to John O'Groat's House would appear to be the presence of a well-constructed fireplace, although the design is not similar.

Plate 3: Puffin Slope. From the west, showing the fireplace with the site of the door to the left and the top of the retaining wall in the left foreground. Photo: author

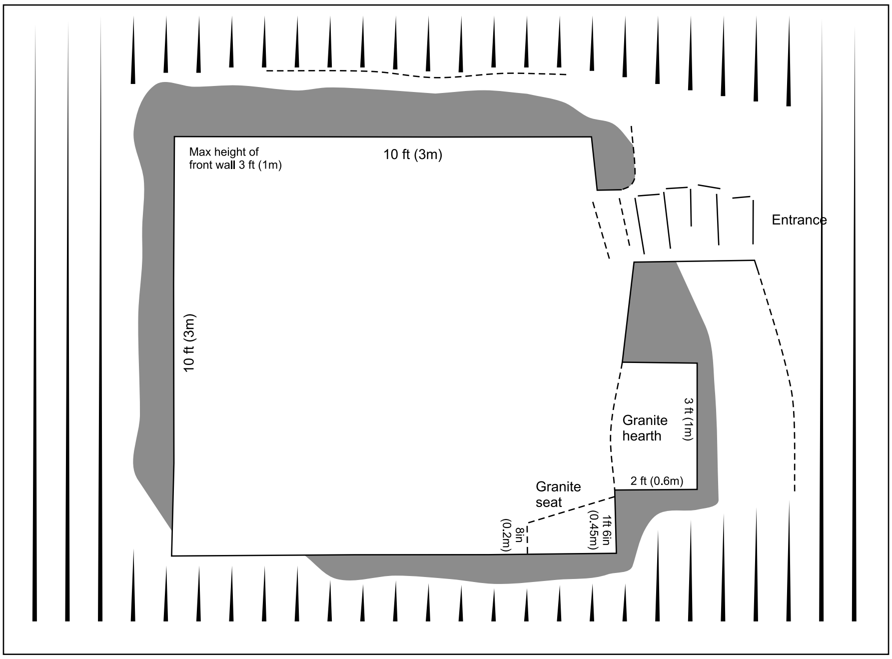

Figure 13: Puffin slope. Plan (not to scale) based on Miles 2/30b. North to top

North East Battery

About 50m to the east of the Puffin Slope building lies the NE Battery (NT SMR 108006), described as an earthen gun platform about 5m square revetted by a drystone wall (Thackray, 1989). Two plans, one a copy of the other, survive in the Miles archive (2/30, Figure 14) together with three photographs and a note explaining the difficulties encountered when surveying. It is clear from the differences between the plans that the rubble is shown schematically and they do not give a good impression of the structure though they do show it as 16ft by 12ft (5×3.5m). The NT SMR says the site is 3m square and likens the site to the 'mangonel battery' (NT SMR 108223, above), though the Miles photographs show the walling here as rougher rubble than the well-laid masonry at the other site (Plate 2). The NT SMR also notes the presence of a rough track between the Puffin Slope building and the battery and also a length of wall (NT SMR 108005) but does not say if the two are coincident. When visited in 2019, the site survived in good condition with rough walling retaining the platform. There were few signs of the supposed trackway, particularly at the platform end where rock outcrops had to be negotiated for access, and the wall could not be found. Both sites are about 30m above the water, so may be related though this would be too high for effective cannon fire. It seems more likely that the Puffin Slope building is later and connected, perhaps, with seabird harvesting.

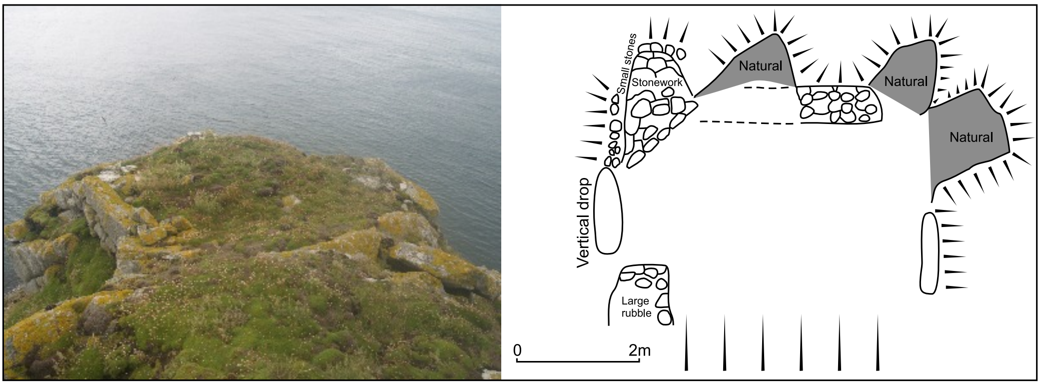

Figure 14: NE Battery. Left, in 2019. Right, plan based on Miles 2/30c. NNE to the top

North East Watch

Above the NE Point just below the edge of the plateau is a third structure, called the NE Watch by Gardner (1968, 41). Two plans, four photographs and a note survive in the Miles archive (2/31a-d). The plans, although clearly titled, are very sketchy and at first sight appear to show two different structures, one (2/31c) an irregular platform and the other (2/31d) a rectangular walled structure with a door at the south end of the east wall. The note describes the east wall: 'where clearly visible, [it] is "stepped" as shown on the plan. But it is not clear over much of its length, externally. At its north end it does not, I think, return westward, and may only serve as a revetment to the natural slope.' Plan 2/31d shows a westward return of the wall that fades to its west end and no western wall is depicted. There is no indication of the rectangular structure on plan 2/31c but it must be the same site as the drawing also shows the upper and top faces of the stepped wall.

The NT SMR (108007) provides yet another description: 'A rectangular building platform with an internal partition, [which] consists of tumbled wall, c.1m wide by 0.2m high. Possible bank on southern edge and cut into the slope on the western side'. In 2019 the site was partly overgrown with bracken and the only obvious feature was a ruined wall running north-south across what appeared to be a natural platform in the granite. To the west of this was a sunken area with a bank along the northern side. It is possible that the NT survey saw the whole terrace as artificial with the surviving wall as the partition but this is clearly not what Gardner's plans show. Although it is difficult to reconcile them, they both show a nearly square room 2.9 or 2.7m by 2.25m and describe a step along the base of the east wall. This could not be found in 2019 but the site is much more overgrown than shown in 1967 photographs.

John O'Groat's House

This (NT SMR 108008) lies about 90m to the west of the North East Watch on a slight rise in the plateau; it appears to have been built on a cairn (NT SMR 108009). The 1966 plan shows a rectangular, single-roomed structure, internally 5.5 by 3.2m, with a door in the east wall, a fireplace towards the east end of the north wall and a possible window cill in the west wall. A long stone is shown below the window and annotated 'bench' with another stone at an angle in the north-west corner. This site is much visited and has undergone some changes since the plan was drawn; the south-east corner has been disturbed and the window is now blocked up by crude walling. Some of these changes are apparent in the NT survey drawing (reproduced in Thackray & Blaylock, 2002) where the south-east corner is less disturbed and the diagonal stone at the north-east has been turned to form part of the bench.

Steinman (1836) calls it Johnny Groats House and describes it as a small cottage at the north point, which suggests that it was roofed at that date. The Ordnance Survey six-inch map of 1820 also shows it roofed but in 1787 it had been described as the remains of a house or room 23ft by 10ft (Chrymes, 1824). The name is suggested to have originated when the building was let for shooting to some Scotsmen but it is probably just a jocular name for somewhere 'far' to the north.

The NT SMR describes additional features recorded in the survey in 1990: 'a protruding wall from the western wall face and possibly the remains of a terrace associated with this feature. This may indicate the presence of a stack.' It is not clear what relationship was proposed between this and the fireplace evident in the north wall. The north wall fireplace is not centrally positioned as described by the NT survey but lies closer to the door, possibly suggesting the former presence of an internal partition dividing the building into two rooms of equal size. There is an appropriately located change in the opposite wall which may support this interpretation. The building has been associated with the various defence works nearby but the NT survey suggests that it may have been a seasonal shelter for shepherds. Neither suggestion is particularly convincing, and others are possible such as the processing of collected seabirds.

Brazen Ward

This is the most complex and complete of the defensive sites and was surveyed in 1967 (Gardner, 1968, 41-2). The plan was redrawn for publication by John Dyke, misinterpreting and simplifying some features of the original, which was prepared by Norman Quinnell of the Ordnance Survey Archaeology Division with Gardner (Figure 15). The plan in the Miles archive (1/4) shows the wall in the northern part of the site with a structure of at least two rooms towards its northern end. To the south, just beyond a spur, are further structures built of drystone walling between natural boulders around a revetted platform. These appear to continue further southwards for some distance. The coast to the north of Brazen Ward is shown with a further section of walling 150m to the north, which is known as the Mousehole and Trap battery (NT SMR 108046).

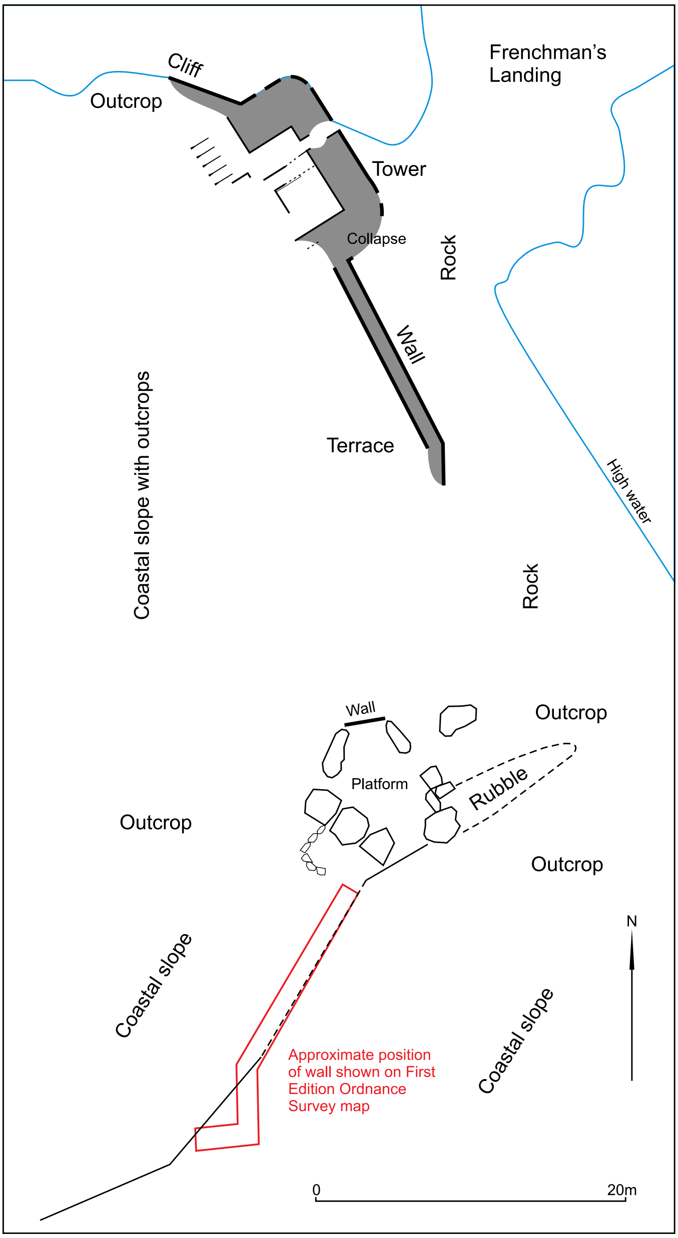

Figure 15: Brazen Ward. Based on plan by Norman Quinnell and Keith Gardner (Miles archive 1/4) with details from site survey (2019) and Ordnance Survey first edition mapping

The southern room was excavated by Gardner who notes 'S. room cleared: pebble floor at 7ft. form [sic] top of wall? Store room for powder: Pottery of ? 16th cent' (Gardner, 1968a, 44). The plan shows that only the northern half of the room was excavated and it remains in this state today. A section drawing (NDRO B867/1/19/11) shows a single stony infill and there is a letter in the Miles archive (1/33) which explains Gardner's reasoning for the suggestion of gunpowder storage. Some of the sherds recovered were covered with a 'black, pitch-like residue' that Gardner suggested could have been produced by burning sulphur and he enclosed two sherds on which he had experimented. He does not seem to have been convinced as the letter ends: 'although it is probably only ships tar'.

The pottery survives in the Miles archive and has been re-examined by David Dawson who identifies two ware types, both probably from north Devon and dating to the sixteenth or seventeenth century, see Appendix. The pottery is in three numbered bags but in the absence of any recording of stratigraphy it is not known what differentiates them, although the third bag contains the sherds with the 'sulphur' deposits. As no distinction can be seen in the pottery types it seems possible that they were simply collected on different days.

The defences seem to have been based on a wall, over 1.5m high on the inside and over 4m on the outside, intended to prevent access to the island from the large flat rock that acts as a natural quay and is known as Frenchman's Landing. The wall is built off a natural rock terrace and is characterised in its lower parts by the use of very large unshaped stones that have been carefully chosen to fit together. These appear to have been brought to course, above which the wall stones tend to be smaller, squarer and sometimes coursed. The southern end is problematic as it would have made more sense to continue the wall to the next outcrop, as noticed in the NT SMR whose compiler wonders if the defences were incomplete. Quinnell's plan however, shows the wall curving inland before fading away which would argue against this. From below, however, this turn can be seen to have been forced by an inturn in the natural rock and there is no visible evidence that the wall continued. It makes little sense for the wall to end here as this is the easiest place to climb up from below and it is possible that the wall did continue and has been entirely removed by wave action in this less protected location.

The structure at the northern end may be the base of a tower as it projects from the wall line. If it is as late in date as the pottery suggests, bastion might be a more appropriate term but if so, it is much less formally designed than the outer defences of the castle. The walls of this tower are about 2.5m thick and built of small stones like the top section of the main wall. The room inside is 6.5m by 3.2m and is divided by a partition 1.1m thick that is not jointed to the outer wall and probably not to the inner. The wall appears to have collapsed on its south side at the eastern end although this could be a product of the excavation that has removed half the fill of this compartment. The northern compartment has an opening in the east wall 0.8m wide on the inside; the sides do not seem to be splayed which would suggest a narrow door rather than a window or embrasure. The inner side has been walled up with roughly laid squared stone and filled with rubble walling that has partly eroded outwards. The room behind seems to have no rear (west) wall, just a very steep grass slope that appears artificial and forms an entrance into the structure. The junction between the tower and wall is obscured by a great deal of collapse but one area of face survives to show the join but not enough to confirm any temporal relationship. If this structure is to be interpreted as a tower, it is curious that the tops of all the walls survive to the same height but this may be explained, as with the main wall, because it was unfinished.

Behind the wall is a flattened area, containing large boulders and outcrops, that continues towards a buttress of natural rock before the coast turns inland. Part of the north side of this buttress has been walled in similar large fitted blocks to that of the lower part of the main wall and this supports a platform, partly retained by natural boulders and partly by low stone walling. Projecting east from this is another platform bounded by low stone walls with a slightly domed rubble fill. This seems too narrow for guns or archers and may be the lower courses of another piece of walling. To the south-west, Quinnell's plan shows a line of stone and careful examination in 2019 shows that this represents an intermittent wall, occasionally of up to three courses, running along the slope for an unknown distance. The steep slope of the ground is the same above and below this wall face, which presumably must have revetted a now-lost infill, perhaps with a wall-walk on the top. One of Keith Gardner's slides (467) shows a more substantial section of masonry and the 1886 Ordnance Survey map (Devonshire sheet IVA.6) shows a wall here with what appears to be a small angle bastion at the south end which is not shown on more recent maps.

The pottery cannot be used to date the construction of the structures as it is all from a phase of infilling, or possibly collapse of upper storeys, but does indicate use of the site in the early post-medieval period.

Tibbetts

An excavation near the Admiralty lookout on Tibbetts Hill is mentioned in 1969 when a small rectangular feature was trenched and found to be of nineteenth century date (Thomas *et al.*, 1969, 17). A single photograph in Gardner's slide collection (209), shows the trench to the south of the lookout and aligned on its west wall. There are also plans (NDRO B867/1/19/9, B867/1/19/17), captioned 'Tibbets A', which may be this site and appear to show the north end of a stone-walled rectilinear building with a curving earth bank over, or forming, the southern end. No excavation trench is shown. Gardner suggested that the excavated structure was a stonemason's lodge associated with the building of the lookout but there has clearly been a lot of ground disturbance here and in the absence of any recorded evidence for a date, the structure could be of any, or several, dates. This disturbance continues, with prehistoric pottery being picked up from the area in 1989 (Schofield & Webster, 1989, 43) and 2017 (author).

Benson's Cave

Benson's Cave is an artificial chamber driven into the Morte slate geology below and to the east of the castle. A small excavation was undertaken in 1966 (Gardner, 1966, 31) and an overall plan survives in the Miles archive (2/26, Figure 16) with trench plans, sections and survey notes in NDRO B867/1/19/15 (Figure 17). The overall plan shows the level approach cutting dug WNW into the hill which widens sharply to form two square areas to north and south.

The southern one is brick-lined with a brick wall and doorway facing into the approach. The bricks appear to be local to the island with granite inclusions visible and have been laid in a hard, white mortar which also survives as a thick render in places. The roof is a brick barrel vault running north-south with a layer of slate above it. A parapet of edge-laid bricks retains the slates at the west end and has probably fallen from elsewhere. The whole roof has been filled to recreate the natural slope and is now grass covered. Inside, the only features are two slots at the east end of the north and south walls which will have held a wooden bench. The northern is empty but the southern retains a piece of sawn timber. There is a mortar scar marking the position of the bench on the wall. The door has a cement mortar scar for a recent door frame.

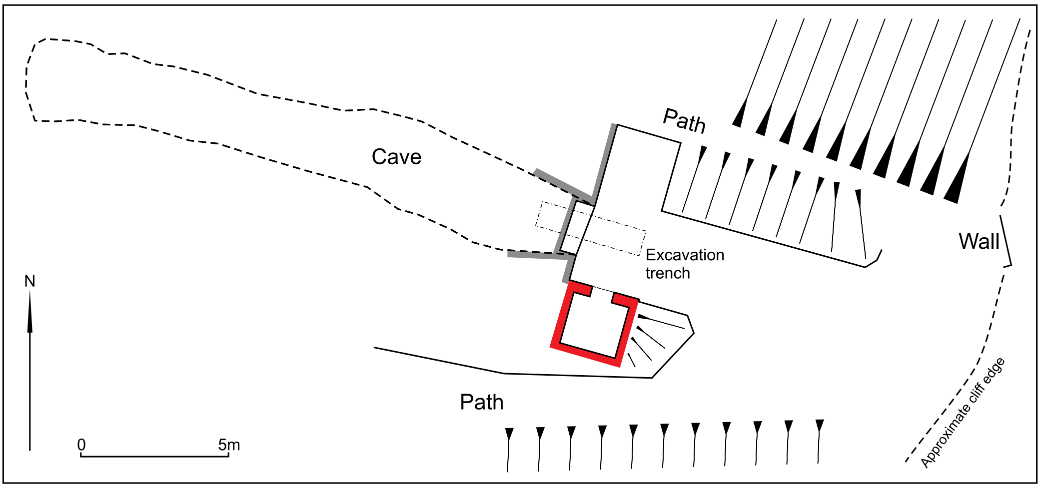

Figure 16: Benson's Cave. Based on plan in Miles archive (2/16) and site survey (2019)

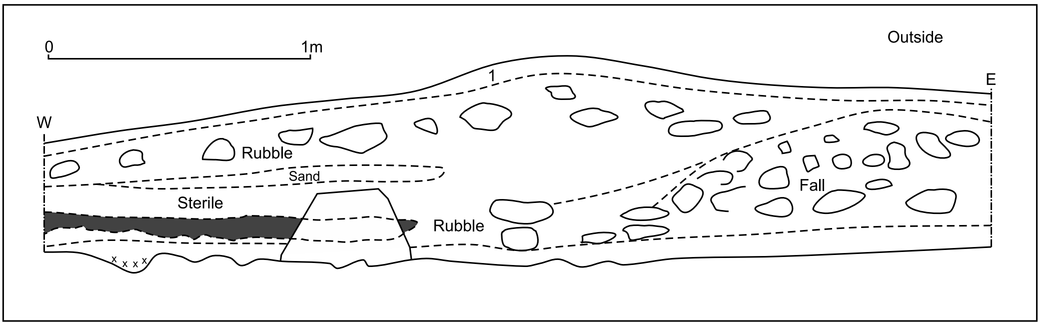

Figure 17: Benson's Cave. Section drawing of N side of trench. Only layer 1 is numbered and several of the dividing lines are very sketchily drawn. The dark layer is clearly the black mud and the clay pipes in a depression are probably marked with ×. Based on a drawing in NDRO B867/1/19/15

Plate 4: The entrance to Benson's Cave in 2019. Part of the brick structure can be seen on the left. The castle is visible on the hilltop above. Photo: author

The opposite side may have been intended to match and be unfinished. It is currently rubble filled but natural stone seems to be visible extending into the area at the base of the eastern side. The western side is retained by a squared granite block wall which also extends behind the brick room to the south. The low entrance to the cave interrupts this wall and has a large irregular granite lintel (Plate 4). Above the lintel the wall face is set back while to either side the wall face appears to have been carried up giving the appearance of buttresses. The lower part of the wall returns into the cave until it meets the rock faces. The cave is much higher than the entrance; the upper part of the wall is visible from inside the cave above the lintel. Beyond this the cave widens and the roof rises until it comes to a sudden end at 19m.

Outside the cave the entrance cutting runs east for 13m before a vertical drop formed by a geological dyke; small paths lead north and south from here turning back up the hill on either side of the cave. Below the east end of the northern path is a masonry wall eroding out of the cliff face possibly with a right-angled turn or end. This is best seen from below or across the gap from the South Light. The upper part of the wall is composed of three courses of squared granite blocks above a levelling course of thinner slabs of dyke material. Below this the wall is poorly coursed rubble including both types of stone.

The earliest plan of the castle (Grose, 1776) shows the cave, described as ‘Subterranean vault’, with the two paths, and a capstan shown and labelled on the cliff top. Instead of the current vertical cliff face, a ridge is shown running from the east which is labelled ‘Lametry Neck’. The two wider areas in front of the cave entrance are shown but the brick building is not, and there is no indication of the wall on the cliff edge.

The 1966 plan shows a trench 12ft by 3ft dug through the entrance. Gardner (1966, 31) reports that the excavation ‘revealed a disturbed section producing coal, shells, bones, iron, clay pipe fragments or pottery of 17th-19th century’. The note and record cards in NDRO B867/1/19/15 are confusing but seem to show that the excavation was based on overall ‘layers’ with notes of where these were not consistent. There are plans of the surface of these layers that are mostly uninformative since the layers were uniform, and on the section drawing only layer 1 is labelled (Figure 17). The note gives the following sequence; the two components to layers 1 and 2 may be inside and outside the cave.

1a) Rough topsoil mixed with pieces of shale and broken brick. 2 inches
1b) Texture of layer same. 19th-century pottery. Rabbit and bird bones.
2) +8". Rubble – pot, coal, rabbit bones
+5". Rubble – sterile.
3) Close blackish mud.
W -> 4'8" Mud / 5'3" Rubble (4) / Rock fall (5) and brick debris, coal and limpet and oyster and bird bones. Glazed pot 17c 18c.
6) +3". Floor and OL [Occupation layer]. Pipe stem, glass, iron, bones, shells, pottery Shale and patch of mortar.
7) Bed rock 18/19c pipe in depression.

The record cards give descriptions of layers 2 and 3:

> Layer 2. Inside the cave at 15" depth rubble gave way to close blackish mud, from the limit of excavation to 4'8" towards the mouth of the cave. Rubble leading there from to [sic] rock fall at 9'11" mixed with brick debris and shell (?period when brick edifice was built).
>
> Rock fall removed. Fair amount of anthracite mixed in. Bird bones limpet shells and 1 oyster shell. Fragments pottery (glazed) and brick. Fragment metal 18" down. 1'6" from S edge, 10" from S [overwritten, possibly has E underneath] edge. ?Floor and occupation level, pipe stem, glass fragments, metal. Note – this occurs 6ft down from underside of 'capstone' [lintel].
>
> Layer 3. ?Floor taken down to bedrock approx. 3" below. Found to be merely decomposed shale with few bird-bones, limpet shells and fragments of brick and pottery. ? Patch of mortar towards back of cave (plan level 3).
>
> In depression in bed-rock fragments of 19th-C pipe were found (?early archaeologists?).

Unfortunately, none of the finds is known to survive and it is probable that they were not retained in view of their modern date. The rock fall was presumably caused by the partial collapse of the structure above the entrance lintel, but there is no record of whether the fall was granite as used in the structure or the local bedrock slate. The presence of anthracite might support the appearance of the structure above the entrance as a fireplace, but again there is no record of whether the coal is burnt or not. The black layer may also suggest the storage of coal.

The depth of deposit in the cave is surprising. When originally cut the cave floor would have been bare rock and the dates of the finds within and below the fill suggest that this material has been imported to make a fairly level floor some 0.5m above the rock floor in the nineteenth century. This infilling continues outside the cave, and presumably into the brick building.

Gardner also notes that there were graffiti in the cave dating to 1726-50 but believed that the origins of the cave were more likely to be associated with Thomas Bushell in the Civil War, who was, amongst other things, a mining engineer. There is a list of the initials and dates in the Miles archive (1/73) which runs from 1709 to 1891 but it is not known when this was compiled or how it relates to Langham's record taken in about 1960 (Langham, 1989).

Benson's cave is an enigmatic structure and the excavations have added to the questions rather than provided answers. The cave itself is very tall and would have been taller before the infilling; while providing a large volume of storage most of it would have been out of reach. The low entrance would have prevented anything large being taken in, although this entrance may be a later alteration.

The brick building appears to post-date Grose (1776) and has the appearance of a gunpowder magazine, which might explain the late date of the finds found in the excavation. Apart from the design, the interpretation as a magazine seems unlikely as access would be difficult and exposed unless for a gun mounted on the edge of the cliff. Brick is an unusual material for Lundy, though the fieldname Brick Field suggests a location for their manufacture. Three brick buildings were found in the castle excavations where they seem to have been of seventeenth century date (Thackray, 1985). Finally, the structure above the cave lintel is enigmatic. As noted above it has the appearance of a fireplace, which would imply a building above the level of the cave but none of the historical sources suggest this.

CONCLUSIONS

Overall, the LFS excavated over 26 sites in the 1960s under the leadership of Keith Gardner but in common with most 'old' excavations the records are frustrating for the next generation of scholars, armed as they are with new questions and techniques. Gardner's work happened just before a major shift in excavation strategy when a belief in the primacy of the section drawing requiring the excavation of small trenches was replaced by area excavations recorded primarily in numerous plans. There was also a tendency to have fixed ideas before excavation that were proved or, less often, disproved by the digging. An example of this is the work at Jenny's Cove IV where it is clear from the records that Gardner had already decided what it might be and then excavated more and more as it didn't conform to these ideas.

Many of these excavations were described by Gardner as 'characterisation' which appear to have had the aim of recovering dating evidence and seeing if any internal structures could be determined, and these must be considered a success as we now have dating evidence for occupation on the island for most periods. Where Gardner did fail, and he was certainly not alone in this, was his failure to publish the results promptly. This together with the dispersal of the site records has meant a 50-year gap when little was known of the work. Part of the cause of this this may have been the change of ownership that stopped the excavations but there must be a suspicion that Gardner would have continued in the same fashion for several more years, rather than publishing and planning his next research objectives.

The primary aim of this paper has been to bring to light the records that survive in a convenient form that will allow future analysis and the formulation of research questions. Several questions do occur immediately, however. In the prehistoric period, the evidence is overwhelmingly of Late Bronze Age hut circles and fields, with only scattered finds of earlier and later material; the only other dated structure is Hut 6, of Middle Bronze Age date. This may suggest long-term trends in population on the island driven by climate change or other factors. The Iron Age seems almost completely absent, although the castle ditch at the south end might hint at an origin as a defended enclosure of this date. Gardner never excavated here and subsequent work showed little stratigraphy survived in the interior (Dunmore, 1982; Thackray, 1985) so questions about the origins of the castle site remain.

Roman material is limited to the area of the Beacon Hill cemetery with none recorded from elsewhere by Gardner's work or the 1980s test pitting (Schofield, 1988, Schofield & Webster, 1989, 1990). This may suggest a single farming settlement in that period and have relevance for the location of the post-Roman cemetery.

The medieval period will be covered in the report on the excavations at Bull's and Pig's Paradises but in the post-medieval period, there are a large number of structures that are not easily explained. Many of these are described as batteries and comprise levelled platforms on the steep sidelands to the island but most do not sit easily with that interpretation. Most seem too high above the water level to serve as good locations for cannon and the difficulties of emplacing large weapons on them would be serious. A very large number of weapons would be needed to equip all the sites unless they were moved around, when the difficulties of emplacement would be multiplied. Some of those in more defensive locations, such as at Jenny's Cove, might serve better as infantry positions – either for archers or, later, musketeers – but there seem few signs of any walling to protect them. It may be that most, and the small buildings that are associated with some at the North End, are related to the seabird industry as collection or storage locations. In the absence of dates for all except Brazen Ward (which does fit the criteria for a battery) it is not possible to be more definite.

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APPENDIX: The pottery from Brazen Ward by David Dawson

Three bags of heavily abraded sherds were examined. All appear to be of early post-medieval, that is sixteenth/seventeenth-century. Two fragments of clay tobacco-pipe stem appear to be of similar date. This report is a superficial examination based on visual observation. It should be noted that the soft red earthenware fabric (type A) as examined by John Allen, Oliver Kent and the author and which may be attributed to North Devon is very similar to that from the two kilns producing a form of Dyfed gravel-tempered ware at Newport, Pembrokeshire (Dawson & Kent, forthcoming). Scientific analysis would be required to help settle the point. The forms however have affinities to North Devon not Pembrokeshire.

CJW bag 496, original number [48]

14 sherds, rather abraded, of red earthenware and two pieces of clay tobacco-pipe stem. 12 of the sherds are of the fine fabric type A (three of these exhibiting an internal brown glaze) and two of the coarser fabric type B.

Fabric type A: wheel-thrown, soft-fired oxidised red earthenware sometimes exhibiting a light grey reduced core; inclusions are scarce angular particles of white and translucent quartz <1mm and a more abundant speckling of black particles which bleed dark brown in the glaze <0.2mm. Related to Exeter fabric types EX 63 and 64 (Taylor, 2005, 74-75)

Forms of type A: One sherd (1) is from a distinctive baluster jar related to those described as type 10 at the Exeter Inn, Barnstaple, assemblage (Morris, 2017, 289-290), and sherd (2) is a rim almost identical to globular jar (4) in the catalogue below.

Fabric type B: wheel-thrown, soft-fired oxidised brown earthenware; inclusions are <1mm abundant angular and waterworn quartz and fragments of sedimentary rock typical of the earlier North Devon gritted wares.

Forms of type B: probably globular jars.

CJW bag 499, original number [82]

45 sherds, rather abraded, all the same earthenware fabric type A.

Forms of type A: the jars may be related to those described as type 14 at the Exeter Inn, Barnstaple, assemblage, the handle (6) to jug type 2N/P and the neck (7) to costrel type 21A (Morris, 2017, 288-290).

CJW bag 497, original number [255]

Two body sherds of fabric type B with internal dark green glaze, probably from the same vessel.

Catalogue of selected sherds

1. Baluster jar, single body sherd of fabric type A; internal brown glaze.
2. Globular jar, single rim sherd almost identical in form and diameter to (4) below, Slight traces of an internal glaze.
3. Jar (Figure 18: 1), diam. 170mm represented by 3 rim sherds. Everted rim, external collar at junction of neck and shoulder; two vertical strips of reduced speckled green glaze running down from the rim outside and remains of an all over speckled green glaze inside.

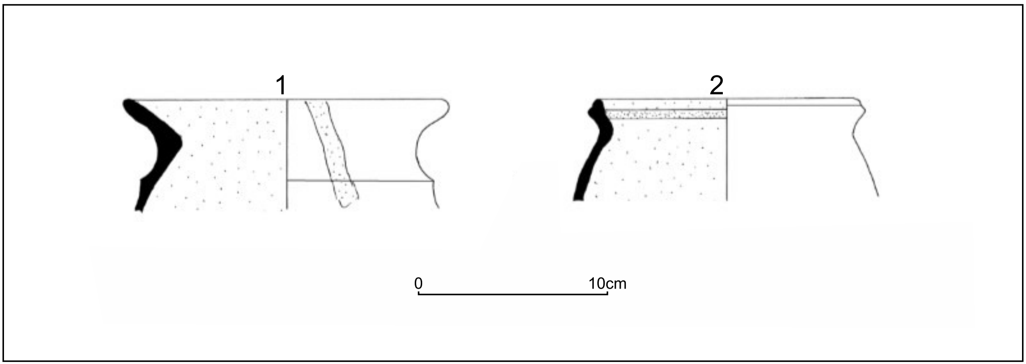

Figure 18: Pottery from Brazen Ward. Drawing: David Dawson

4. Jar (Figure 18: 2), diam. 140mm represented by 4 joining rim sherds and one body sherd from the neck. Everted rim with a rill round the top; traces of internal glaze.
5. Probable jar represented by a body sherd with an external diagonal strip of brown/green glaze and traces of a similar glaze inside.
6. Probable jar represented by a body sherd with a possible spot of glaze outside and traces of internal brown/green glaze within.
7. Probable jar represented by a body sherd with a vertical strip of brown/green glaze outside and traces of glaze within.
8. Sherd of a plain oval-section bar handle; unglazed.
9. Neck of a small bottle; unglazed.

A SURVEY OF DUNG BEETLES (AND OTHER *COLEOPTERA*) ON LUNDY AND AN INVESTIGATION OF THE ANALYSIS OF BIRD PELLETS AS A BEETLE SURVEY TECHNIQUE

by

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ABSTRACT

Forty corvid pellets were collected on Lundy over a three day period in July 2017. The pellets were later dissected and beetle fragments were identified to species. A comparison was made between the numbers and species found in the pellets and those found alive or dead, in or around dung, over the same three days. Subsequently, our survey results were compared with the results of historical surveys.

Keywords: *Lundy, Coleoptera, dung beetles, bird pellets, corvids*

INTRODUCTION

To understand the nature of an ecosystem, the maximum amount of data on the type and nature of organisms present in a habitat must be collected. Beetles (Coleoptera) form a key part of all terrestrial ecosystems because they are such a functionally diverse group. However, apart from the large colourful ones which feed on flower heads, most beetles prefer to stay out of sight and are not easy to find. Insectivorous birds and mammals know where to find them, and their waste products often contain the hard indigestible parts of beetle exoskeletons. Mammals such as foxes and hedgehogs egest these in their faeces. Birds regurgitate insect remains from their crops in dry pellets. Analysis of both types of waste can be a rich source of information about the local beetle fauna.

Barn Owl *(Tyto alba)* pellets are reasonably well-studied by naturalists because they are comparatively large and easy to find, occurring below owl roosts inside dry buildings. In particular, it has become common practice to analyse the contents of Barn Owl pellets as a means of surveying the small mammal fauna of a locality.

Little Owl *(Athene noctua)* pellets can also be found at regular haunts, on fence posts and below nesting sites. A paper written in 1937 by Alice Hibbert-Ware contained details of an extensive long term analysis of Little Owl pellets (Hibbert-Ware, 1937). She showed that their diet consisted mainly of insects and hence that they were innocent of the charge of mass slaughter of young game birds. An analysis of Little Owl pellets from Gloucestershire that we carried out in 2017 provided data in line with Hibbert-Ware's findings (Crofts, 2017). These birds are large consumers of dung beetles, particularly of the larger species.

Despite these examples, Philip Miles pointed out over 60 years ago that there has been surprisingly little research into the insect content of bird pellets, describing it as a 'practically virgin field of investigation' (Miles, 1952). He would be even more surprised (and no doubt very disappointed) to discover that this is still true.

In fact, in their 2004 study of Hooded Crow *(Corvus corone cornix)* pellet content in the Lough Hyne area of County Cork, Ireland, Horgan and Berrow state that theirs is the first study 'to specifically address the occurrence of dung beetles in the diet of any crow species' (Horgan & Berrow, 2004). However, the focus of their study was the impact of the Crows' predation on the invertebrate assemblage living in the dung.

But Corvids (a group containing Rooks, Crows and Ravens) are opportunistic feeders, taking whatever they can find. So we believe that their pellets have the potential to yield valuable information about the nature of the broader local ecology.

Rook (*Corvus frugilegus*) pellets build up below rookeries so they are easy to locate in large quantities, but apart from the odd elytron of the weevil *Sitona lineatus,* they are rarely a good source of insect remains. However, we have recently found Rook pellets in Orkney containing three species of the smaller dung beetles (Aphodiini).

Carrion Crow (*Corvus corone corone*) and Raven (*Corvus corax*) pellets are bigger, denser and usually much richer in beetle remains, particularly of the larger dung beetles (Plate 1). On Lundy, Rooks are only rare migrants, but Crows and Ravens are always around, stalking through fields which contain sheep, Highland cattle or ponies, looking for the insects in dung. They are also fond of standing on the top of dry-stone walls, and hence this is where they produce many of their pellets (Plate 2). If the pellet falls into a crevice in the wall, it will be protected and its contents may remain intact, forming a time capsule of what beetles have been eaten.

Plate 1: Some pellets are more obviously 'beetley' than others. The size of this one suggests it comes from a Raven. © Bob Cowley

Plate 2: This wall by the sheep field is a favourite of the Crows, which makes it a good place to look for their pellets. © Bob Cowley

We were originally alerted to Lundy's potential as a site for bird pellet research by reading an online version of Alan Rowland's 2014 paper in the *Journal of the Lundy Field Society* (Rowland, 2014). He had had the vertebrate content of various pellets analysed by Alasdair Love, but the insect content was not fully considered. When we contacted him, he sent some remaining pellets collected on Lundy in 2012 for us to investigate. Subsequently, we were put in touch with Steve Kett from Middlesex University, who supplied us with some additional pellets collected on Lundy in 2015. All of the pellets which we received from them (selected because of their 'beetley' surface) appeared to be from Crow and Raven.

As a result of these investigations, we decided to plan our own expedition, and this paper deals with the analysis of bird pellets we collected over three days on Lundy in July 2017.

One purpose of our current study was to see whether the contents of the pellets, specifically the dung beetle remains, were a true reflection of the occurrence of the live dung beetles currently in the dung pats. If this could be shown, then past and future analysis of corvid pellets could be used as a method for gathering a lot of data on the beetle fauna of Lundy (and subsequently, elsewhere). It sidesteps the problems of collection of live material from an SSSI. Photography of live specimens in the field is fraught with problems if the beetle is tiny, covered in dung and very similar to related species. Even under a powerful microscope, the crucial details may be impossible to see in a live, moving specimen. Corvid pellets can be collected in quantity throughout the year, stored and then analysed to provide a window into annual changes in beetle populations on the island.

METHOD

The method of collecting data was straightforward. We covered as much of the island as we could on foot in the time available.

On arrival on Thursday 6 July 2017, we completed a circuit through the sheep pasture in the south-west of the island. On Friday 7 July, we followed the main track to the northern tip of the island, returning along a western coastal route. On Saturday 8 July, we explored in detail the dry-stone walls around the sheep pasture to the north-east of the village, and then followed the paths through the wooded area to the east of the island.

Any live beetles on the ground or on the heads of flowers were noted and photographed if necessary. Any dead beetles or parts of beetles were collected (Plate 3). The dung of Highland cattle, ponies and sheep were examined for the presence of live dung beetles (Plate 4). These were identified, photographed if necessary, and their numbers noted (Plate 5). Dry stone walls and the surfaces of single large stone blocks were searched for pellets or pellet remains (Plate 6); these were bagged separately along with their grid reference (Plate 7).

Once back in Oxford, Linda Losito undertook the pellet analysis. Each pellet was soaked in a mixture of disinfectant and washing-up liquid and then broken apart under a microscope. Any beetle fragments were sorted out from the stones, plant material, and other debris. Fragments of bone, snail shells, seeds and larval forms were also removed for potential identification.

The beetle fragments ranged in size from whole heads and complete large elytra (wing cases) to tiny pieces a few millimetres long. These had to be cleared of adhering debris. Any hollow structure (like a weevil thorax) has to be emptied out because it might contain a beetle head or pieces of elytra. Legs are fairly robust and often survive the crushing process in a bird's crop, but they are not very useful, except to give some estimation of numbers. Sometimes, very distinctive legs, like those of *Typhaeus typheous*, are present without any other remains.

Rarely, fragments of an unusual beetle may appear in two different pellets, and separate fragments of elytra can be matched to form a complete whole. One must conclude that the two pellets were produced by the same bird. Hence the contents of pellets from the same place should always be checked against each other to aid difficult identifications.

On the other hand, a pellet will occasionally contain a virtually perfect uncrushed specimen, complete with intact legs and antennae. The insect is likely to be from the top of the food mass when it is ejected from a full crop. This tends to occur with smaller beetles, which may be eaten in large numbers.

Once isolated and cleaned, each beetle fragment was dried, carded and stored (Plate 8). It then had to be identified. Unfortunately, identification keys are designed for use with whole specimens. They may refer to features present on the abdomen when all that you have are the head and elytra. Identification can only be achieved by comparison with a named specimen. This was facilitated by owning a large personal collection, as well as having regular access to the world-class collections in the Oxford University Natural History Museum. Even so, weevils present a particular problem. Bird crops are full of tiny stones which have a very abrasive effect, rubbing off most of the diagnostic scales, but careful searching will usually reveal a few scales left around the edges of the thorax.

Plate 3: Many beetle fragments were found by thorough searching of tracks and bare places. © Bob Cowley

Plate 4: Although other techniques are available, getting hands-on with the dung maximises our chances of locating and identifying dung beetles, while causing them minimum disturbance. © Bob Cowley

Plate 5: After removing this beetle from the dung, we put it in a collecting tube where it was photographed and identified as *Agrilinus ater*. It was returned to the same dung in less than a minute. (Note the use of a Lundy map as background!) © Bob Cowley

Plate 6: A typical corvid pellet, in a typical location. This one is probably from a Raven. © Bob Cowley

Plate 7: Every pellet and specimen was bagged or photographed, and listed (with its grid reference) on our daily log sheet. © Linda Losito

Plate 8: Many of the beetle fragments extracted from the pellets for identification were less than 2mm long. © Bob Cowley

It must always be understood that this method of analysis can only provide information about what is there. Absence in the pellet is not proof of absence in the diet. For instance, one might expect that soft bodied or very small organisms leave no trace, and beetles with particularly robust exoskeletons like scarabs and weevils may be over-represented in the pellets. However, this does not appear to be the case as some pellets contained very large numbers of fairly fragile but intact elytra of Elateridae (click-beetles). Having said that, it is improbable that corvids would bother with anything much smaller than a weevil, so pellets would not be a good tool for investigating the presence of very small beetles such as Latridiidae.

RESULTS AND DISCUSSION

Table 1 shows the range of species found either live in dung, on the ground (dead or alive), or as fragmentary remains identified in pellets. The nomenclature used accords with the most recent edition of the Checklist of Beetles of the British Isles (Duff, 2018).

You can see from Table 1 that there was a broad correspondence between the range of beetle species found in our pellets and those found by direct inspection of the ground and animal dung. However, our pellet analysis revealed the presence of 33 species, compared to a total of only 18 species observed directly in the wild. More particularly, the pellet analysis revealed the presence of 20 species not found by other means, while missing only five that were. This suggests that the pellet sampling process was actually more thorough than directly surveying the ground and dung.

The 33 species found in the pellets are representatives of just 10 families which is quite a limited spread, given that there are 102 families of Coleoptera. It is a similar list to those found in our analysis of the 2012 and 2015 samples; they had contained 26 species from eight families, but the overall content was very similar. All of the beetles are of a type likely to be found at ground level. Weevils are plant feeders but tend to throw themselves to the ground when disturbed. Chrysomelids and other large plant-eating beetles may be under-represented. This is just what you would expect to find in the pellets of ground-feeding corvids.

The pellets contained six species of dung beetle and five of the same species were also found as live or recently dead specimens whilst surveying the island. The sixth species *Melinopterus sphacelatus* avoids the months of July and August, and is replaced by other Aphodiini species. We have previously found it in one of the June 2015 pellets. Its presence in ten of the samples we collected suggests that these were older pellets, which was confirmed by their hard, dry nature and mite infestations. Comparison with previous pellets shows the expected change in Aphodiini species due to seasonal change. There were no *Acrossus rufipe*s or *Agrilinus ater* in the pellets from 2012 and 2015.

Three types of dung (pony, sheep and Highland cattle) were present in large quantities on Lundy. During our three day visit, we investigated samples from all over the island. None were very productive in terms of live dung beetles present when compared to similar places on the mainland. The largest numbers found at one site were 18 *Agrilinus ater* in sheep droppings and eight *Acrossus rufipes* in cattle pats. A lot of dung was completely devoid of dung beetles. This may reflect the presence of anthelmintics such as Ivermectin which are frequently fed to domestic animals as a prophylactic against internal parasites.

Table 1: Coleoptera species found during our survey either living in dung, elsewhere on the ground (alive or dead), or identified from remains found in corvid pellets

FAMILY	SPECIES	DUNG	GROUND	PELLET
CARABIDAE	Carabus granulatus L.		Y	Y
	Carabus nemoralis Mull.		Y	
	Poecilus versicolor (Sturm)			Y
	Pterostichus niger (Schaller)		Y	Y
	Pterostichus melanarius (Ill.)		Y	Y
	Abax parallelepipedus (Pill. & Mitt.)			Y
	Calathus fuscipes (Gze.)		Y	
	Harpalus rufipes (De Geer)			Y
HYDROPHILIDAE	Sphaeridium bipustulatum F.	Y		
HISTERIDAE	Margarinotus striola (Sahl.)			Y
LEIODIDAE	Ptomaphagus subvillosus (Goeze)			Y
SILPHIDAE	Thanatophilus rugosus (L.)			Y
	Phosphuga atrata (L.)		Y	Y
	Silpha tristis Ill.		Y	Y
	Nicrophorus investigator Zetters.		Y	Y
STAPHYLINIDAE	Ocypus olens (Mull.)			Y
	Philonthus marginatus (Mull.)			Y
	Philonthus decorus (Grave.)			Y
GEOTRUPIDAE	Typhaeus typhoeus (L.)		Y	Y
	Anoplotrupes stercorosus (Scriba)	Y	Y	Y
	Geotrupes stercorarius (L.)		Y	Y
SCARABAEIDAE	Acrossus rufipes (L.)	Y		Y
	Agrilinus ater (De Geer)	Y		Y
	Melinopterus sphacelatus (Panzer)			Y
	Cetonia aurata (L.)		Y	Y
BYRRHIDAE	Byrrhus pilula (L.)			Y
ELATERIDAE	Agrypnus murinus (L.)			Y
	Agriotes lineatus (L.)			Y
	Agriotes obscurus (L.)			Y
	Agriotes sputator (L.)			Y
	Athous haemorrhoidalis (F.)			Y
CANTHARIDAE	Rhagonycha fulva (Scop.)		Y	
TENEBRIONIDAE	Cteniopus sulphureus (L.)		Y	
CURCULIONIDAE	Rhinoncus pericarpius (L.)			Y
	Otiorhynchus sulcatus (F.)		Y	Y
	Sitona obsoletus (Gmelin)			Y
	Sitona waterhousei Walton			Y
	Brachypera zoilus (Scop.)			Y

The larger dung beetles, *Typhaeus*, *Geotrupes* and *Anoplotrupe*s are more likely to be in tunnels under the dung itself so are less likely to be found without serious digging. One *Anoplotrupes* was found in dung, but mostly they were found walking along the edge of paths (Plate 9).

Plate 9: *Anoplotrupes stercorosus* is the dung beetle you are most likely to see on the footpaths of Lundy. © Bob Cowley

One hydrophilid species, *Sphaeridium bipustulatum*, was present in Highland cattle dung in some numbers but was not present in any pellet. In fact, although we have found this and other *Sphaeridium* species on the mainland in dung many times, we have only ever found one in a pellet, which could either reflect their ability to move fast and evade predation, or possible rejection by birds.

Pellets seem to give a better indication of the numbers of large dung beetles than could be obtained by searching for live specimens. When present in pellets, they can be in large numbers, especially considering the size of the pellet. In pellets from this study, two contained evidence of nine *Anoplotrupes*. In one of the 2015 pellets there were 22 *Anoplotrupes*, eight *Typhaeus* and one *Geotrupes* as well as other large beetles. One 2012 pellet was composed almost entirely of *Anoplotrupes* remains.

The collection and examination of pellets has provided insight into both the range and number of dung beetle species on the island and it seems to correlate with the beetles actually present during a specific time window.

In the 1970s, Martin Brendell compiled a comprehensive list of Lundy's Coleoptera from all known records, going back over some 130 years (Brendell, 1976). Of the 16 Geotrupidae and Scarabaeidae on his list, we found seven in pellets and four in dung. Ten Aphodiini species have been found on the island in the past and the six which we did not find could potentially have been around in June and July. They tend to be in smaller populations, so their absence from the samples may be chance or due to a population decline as is happening elsewhere.

The Rose Chafer (*Cetonia aurata*), while a scarab, is associated with flowers not dung, but ground feeding birds would find the adult in large numbers when it emerges from the ground in the spring. In some of the 2012 pellets it was very abundant, making up almost 100% of one pellet. *Anoplotrupes* and *Cetonia* are major components of the corvid diet along with ground beetles.

Although Geotrupidae and Scarabaeidae were the original focus of our study, once we had analysed the fragments from our pellets, we found two other families were particularly well represented.

Silphidae are associated with dead matter. There are six silphids on Brendell's list, of which our pellets produced four. *Phosphuga atrata* and *Silpha tristis* were found in over a third of the samples but in small numbers, presumably because they do not have mass emergences like the geotrupids and scarabs. *Nicrophorus investigator* is a beetle which lives in and around the small corpses which it buries. A carrion-feeding bird is ideally placed to find such specimens. So one might be surprised that it was not found in any of the 2012 and 2015 pellets. But then, although *Nicrophorus investigator* was found by Brendell himself in 1972, his is the only Lundy record between Wollaston in 1845 and our own.

Another notable result from our pellet analysis was the number of Elateridae (click-beetles) species which were found to be present. We had observed no click-beetles during our time on Lundy, and yet our pellets yielded five species out of the 14 on Brendell's list.

Looking more closely at the four families discussed above, Table 2 compares the species found by our current pellet survey with all those listed by Brendell.

As you can see, from our pellet survey alone, we succeeded in finding four out of the six Silphidae on Brendell's list, three out of four Geotrupidae, four out of 12 Scarabaeidae, and five out of 14 Elateridae (for a total of 16 out of 36 species).

But there is an additional column in Table 2, which one could argue offers an even more relevant and impressive comparison. This middle column restricts our attention to only those species on Brendell's list that have been recorded more than once in the last 100 years. After all, any species that has been recorded once or less in the last 100 years is certainly very rare, and may by now be locally extinct (always assuming that one can rely on the accurate identification of such a rare specimen).

Comparing the results of our pellet survey against this arguably more representative list, you can see that we recorded four of four Silphidae, three of three Geotrupidae, four of seven Scarabaeidae, and five of 10 Elateridae (for a total of 16 out of 24 species).

CONCLUSIONS

Despite having only a small amount of time in the field (about 20 hours), we have been able to add considerably more data records for the Coleoptera of Lundy. But of course, this could only be achieved by subsequently spending a disproportionately large amount of time analysing our collected beetle fragments under a microscope.

All our records have been added to the Biological Records Centre's online database iRecord, and so are freely accessible to anyone who may be interested. More specifically, anyone with a particular interest in the natural history of Lundy is encouraged to explore our data through the Lundy Sightings Group section of the iRecord site.

If you do so, looking at all recorders of flora and fauna, you will see that Linda Losito is now second only to Alan Rowland in the overall number of Lundy records submitted, and third in the number of distinct species recorded. In terms of Coleoptera, we have increased the number of records by 969%, our 281 new records raising the total from 29 to 310.

Table 2: Comparison of Silphidae, Geotrupidae, Scarabaeidae, and Elateridae appearing on Brendell's list of all beetles recorded during 129 years on Lundy (1844-1972) with those detected by our analysis of the corvid pellets we collected during three days in July 2017. The middle column shows those species on Brendell's list that have been recorded more than once in the last 100 years

FAMILY	**SPECIES**	**BRENDELL**	**>1/100 YEAR?**	**PELLET SURVEY**
SILPHIDAE	Thanatophilus rugosus (L.)	Y	Y	Y
	Aclypea opaca (L.)	Y		
	Phosphuga atrata (L.)	Y	Y	Y
	Silpha tristis Ill.	Y	Y	Y
	Nicrophorus humator (Gled.)	Y	Y	
	Nicrophorus investigator Zetters.	Y		Y
GEOTRUPIDAE	Typhaeus typhoeus (L.)	Y	Y	Y
	Anoplotrupes stercorosus (Scriba)	Y	Y	Y
	Geotrupes mutator (Marsh.)	Y		
	Geotrupes stercorarius (L.)	Y	Y	Y
SCARABAEIDAE	Acrossus depressus (Kugel.)	Y	Y	
	Acrossus luridus (F.)	Y		
	Acrossus rufipes (L.)	Y	Y	Y
	Agrilinus ater (De Geer)	Y	Y	Y
	Aphodius fimetarius (L.)	Y	Y	
	Colobopterus erraticus (L.)	Y		
	Esymus pusillus (Hbst.)	Y		
	Melinopterus sphacelatus (Panzer)	Y	Y	Y
	Rhodaphodius foetens (F.)	Y		
	Teuchestes fossor (L.)	Y	Y	
	Serica brunnea (L.)	Y		
	Cetonia aurata (L.)	Y	Y	Y
ELATERIDAE	Agrypnus murinus (L.)	Y	Y	Y
	Agriotes acuminatus (Steph.)	Y	Y	
	Agriotes lineatus (L.)	Y	Y	Y
	Agriotes obscurus (L.)	Y	Y	Y
	Agriotes pallidulus (Ill.)	Y	Y	
	Agriotes sputator (L.)	Y		Y
	Dalopius marginatus (L.)	Y	Y	
	Adrastus pallens (F.)	Y		
	Melanotus villosus (Geoff. in Four.)	Y		
	Athous haemorrhoidalis (F.)	Y	Y	Y
	Athous vittatus (F.)	Y		
	Prosternon tessellatum (L.)	Y	Y	
	Selatosomus aeneus (L.)	Y	Y	
	Cardiophorus vestigialis Erich.	Y	Y	

In addition, this study has contributed 135 new records to the Dung Beetle UK Mapping Project (DUMP) and 155 new records to the National Recording Scheme for Scarabaeoidea.

According to Brendell's list, only 16 different species of Geotrupidae and Scarabaeidae were recorded on Lundy in 129 years. Set against this, it is encouraging that we were able to find seven of those species in only 20 hours of field work. But as noted in the discussion of Table 2 above, restricting our attention to only those species on Brendell's list that have been recorded more than once in the last 100 years gives an arguably more enlightening comparison. By that measure, our pellet survey succeeded in finding seven of the 10 species from these two families.

But in addition, our pellet survey turned out to be very successful at finding Silphidae and Elateridae. We recorded four Silphidae compared with the four species on Brendell's list that have been recorded more than once in the last 100 years, and five out of 10 Elateridae.

One can also interrogate the iRecord database to get a good idea of how common a species is in the UK (by looking at the total number of records of that species on the database). Applying that metric to the 16 species of Geotrupidae and Scarabaeidae on Brendell's list, it is interesting to note that the nine species that we failed to find have each been recorded fewer than 90 times nationally, so may be considered comparatively rare. On the other hand, we succeeded in finding all seven of the more commonly occurring species on his list. One might hope that this implies that there has been no great change to the range of dung beetle species present on Lundy.

However, of course this tells us nothing about any possible change of population numbers of each species. The amount of (unoccupied) dung observed on the surface of the pasture certainly suggests the numbers of dung beetles are not adequate to their task.

By simultaneously collecting bird pellets and surveying beetles on the ground and in dung, we sought to investigate whether bird pellet analysis could be a useful technique for the survey of Coleoptera.

Our results clearly indicate that it is – at least for certain birds and certain beetles. Specifically, we believe the pellets of Crows and Ravens could be very useful for the study of ground-living beetles.

Looking specifically at the dung beetle families, Geotrupidae and Scarabaeidae, Table 1 shows that only three species were found in dung and only four were found on the ground. Given that there was one species in common, the two techniques together found a total of six species. However, the pellet analysis succeeded in finding not only all these six species, but an additional one, *Melinopterus sphacelatus*, making a total of seven (Plate 10).

The presence of this additional species is particularly interesting, as it illustrates both a strength and a potential weakness of the pellet analysis technique. The typical season for *Melinopterus sphacelatus* comes to an end during June. So at the time of our visit to Lundy in early July, one would not have expected to find surviving individuals. It is likely that the pellets containing these specimens had been regurgitated some weeks before our visit.

This illustrates that pellets act as time capsules of the species active at the time they are deposited. So the only way to get reliable data of when each species is present is to inspect the same locations on a regular basis, and collect all the pellets you find on each visit. Only by doing this, can you be reasonably confident of the date of deposit of each pellet.

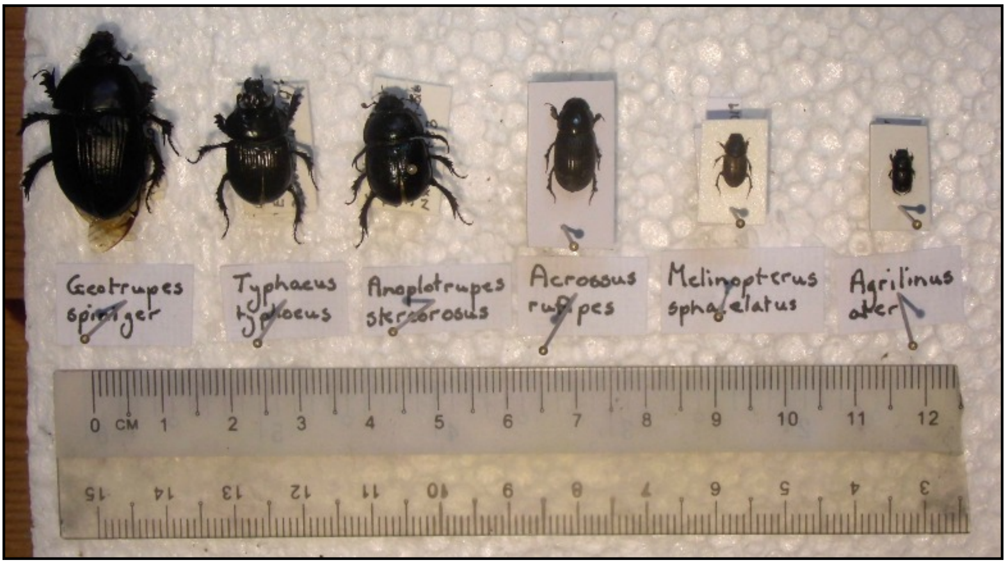

Plate 10: A line-up of the dung beetle species we found on Lundy. (Although *Cetonia aurata* is also classified as a scarab, the adult beetle is not found in dung.) © Bob Cowley

With this caveat, we believe that the analysis of bird pellets does indeed have the potential to be a very useful additional technique for the study of Coleoptera.

More specifically, we conclude that the analysis of Crow and Raven pellets could have exceptional value in the study of Silphidae, Geotrupidae, Scarabaeidae and Elateridae.

Crows and Ravens consume a large number of ground-living beetles, and both birds produce fairly large and cohesive pellets in fairly predictable locations. This means that their pellets are comparatively easy to collect, which could provide new opportunities for surveying.

For example, since the fieldwork of collecting pellets can be undertaken by a non-specialist, pellets could be collected from a variety of sites on a regular monthly or weekly basis by somebody living nearby. The pellets could then be dispatched by post to a specialist coleopterist for analysis, allowing one to efficiently monitor the pattern of changes of beetle species month by month (or indeed, year by year).

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ARTIFICIAL LIGHT AND MOTH BIODIVERSITY: A COMPARISON OF MOTH DIVERSITY ACROSS DIFFERENT HABITATS ON LUNDY TO INVESTIGATE THE EFFECT OF ARTIFICIAL LIGHT

by
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ABSTRACT

Moths perform important roles within ecosystems. Behavioural responses to artificial light disrupt adaptive behaviours, causing population declines. Island populations can assess moth population attracted to artificial light, distinct from urbanisation. Here we present results from day counts of moth larvae and nocturnal Skinner light-traps from Lundy. Findings reveal a significant difference between moth population dynamics and species at differing locations. Overall, numbers of individuals and species caught with the UV-light trap were significantly greater than LED sources. These findings can be applied to potential artificial light changes on Lundy, as well as further changes throughout the United Kingdom.

Keywords: *Lundy, light-pollution, artificial light, moths*

INTRODUCTION

The Earth is currently experiencing substantial biodiversity decline with extinction rates greatly exceeding the long-term average (May, 2010). Insects represent a vital component of terrestrial ecosystems and form a substantial proportion of terrestrial biodiversity (Conrad *et al.*, 2006). They are under-represented in current assessments of biodiversity loss and our knowledge of insects lags behind that of vertebrates and plants (Fox *et al.*, 2011). Common and widespread species undergo dramatic population changes that go largely undocumented, despite playing an important role in supporting the ecosystem (Conrad *et al.*, 2006). Within insect research, there is a bias toward ‘charismatic’ diurnal pollinating insects (Fox *et al.*, 2011) with butterflies firmly established as model organisms for research (Boggs *et al.*, 2003). Nocturnal insects have been relatively ignored.

Nocturnal moths form an ecologically diverse and species-rich group more representative of terrestrial insects than butterflies and bees (Wolfling *et al.*, 2016). Moths are crucial pollen vectors for a diverse range of plant taxa across the globe, are strong indicators of ecosystem quality and environmental change, and are a critical food source for bats and birds (Truxa & Fiedler, 2012; Fox, 2013). Population declines of moths in the UK are equivalent to the IUCN threshold levels for Red List threat categories (Conrad *et al.*, 2006; Fox, 2013).

Many factors have been implicated in this decline, including habitat loss and urbanisation (Bates *et al.*, 2014). Within urbanisation, light-pollution has been speculated as a causal factor of moth declines (Fox, 2013). Light-pollution affects almost 20% of the earth's land surface across the globe, with a predicted rise of 6% annually (Holker *et al.*, 2010). Light levels are critical for many species, acting as a cue for behaviour patterns. Organisms have evolved circadian rhythms, which are now disrupted by artificial lighting (henceforth AL; Gaston *et al.*, 2015).

A wide variety of taxa are likely affected by light-pollution (Davies *et al.*, 2012). Moths are thought to be most at risk due to their 'flight-to-light' behaviour (Truxa & Fiedler, 2012). AL acts as an ecological trap that attracts large aggregations of moths to sub-optimal environments (Bates *et al.*, 2014). It inhibits normal behaviour, detrimental to the pollination, foraging and life cycle of nocturnal moths (see Shimoda & Honda, 2013). This includes direct mortality, disruption of crypsis and biological development, and increased exposure to predators (Bruce-White & Shardlow, 2011). For instance, AL reduces reproductive behaviour in the winter moth (*Operophtera brumata*) due to reductions in female activity and male responsiveness to female pheromones (van Geffen *et al.*, 2015). This can alter ecosystem services through cascading effects from higher to lower trophic levels (Davies *et al.*, 2012).

However, light-pollution typically occurs alongside other anthropogenic stressors such as urbanisation and habitat loss (Bates *et al.*, 2014). AL must be independently quantified from effects of urbanisation and habitat loss to fully comprehend its influence (Fox, 2013). Lundy represents a model environment, with evidenced moth population and self-maintaining ecosystems (Vitousek *et al.*, 1995). The anthropogenic effects of urbanisation have remained minimal with the majority of its landscape comprising undisturbed rural habitats. Small areas with differential levels of AL emitted from man-made constructions permit the study of artificial night lighting in isolation from urbanisation.

Previous research on Lundy has assessed moth biodiversity, but to our knowledge, no research has considered which species on the island are most at risk of behavioural disruption through flight-to-light behaviour (see Beavan & Heckford, 2014). Specifying the biodiversity on the island in varying locations with pre-existing light pressures will indicate if moths are more prevalent in anthropogenic environments and thus at risk of negative effects of AL. Conventional methods of moth-light-trapping will be used to assess the impact of artificial night lighting on the population dynamics and biodiversity of moth species on the model habitat of Lundy. Cloud cover will also be considered as this may influence the efficacy of light sources (Kyba *et al.*, 2011).

Our findings have the potential to disseminate the direct impact of AL on moth populations and species variation. Our hypotheses are presented in Table 1.

Table 1: Hypotheses to be tested

Number	Hypothesis
H_0	There will be no difference in population dynamics of moths at different sites across Lundy
H_1	There will be a difference in the number of individual moths found at different sites across Lundy. We predict that more moths will be captured in locations where there are higher levels of surrounding artificial lighting
H_0	There will be no difference in species diversity of moths at different sites across Lundy
H_2	There will be a difference in the amount of species of moths found at different sites across Lundy

METHODOLOGY

Study Site

Lundy is situated 12 miles from the coast of North Devon, the UK, where the Atlantic Ocean meets the Bristol Channel (51.1781° N, 4.6673° W). Using Skinner moth traps, five different study sites were sampled for moths (see Table 2 for descriptions). The locations were specifically chosen to understand the effect of varying AL levels across the island's different habitats on moth population densities and species diversity. Quadrats were used to systematically identify species of flora in the surrounding area of each site (see Table 4).

Materials and Procedure

Night-time moth traps

Each location was sampled for five nights (28/04/19-02/05/19) from c.20:00 to c.04:00/05:00. Windspeed, temperature, cloud-cover, precipitation levels and lunar phase were recorded for each night of sampling. The trap locations were randomised (see Table 3) as the traps varied in design and spectral composition. It was not possible to standardise trap designs due to availability of equipment. Traps were collected before dawn to maximise trap efficacy and retention. Moths near but not inside the traps were also sampled. Moths collected were placed into plastic containers to be photographed, identified, and recorded onto data collection sheets before being released after dusk.

Daytime surveys

Each location, and an additional location (see Table 2), were sampled for five days (29/04/19-03/05/19) from c.11:00 to c.16:00. Coupled with moth trap sampling at night, day surveys of moths and larvae day provided a comprehensive picture of moth distributions and potential breeding preferences in terms of habitat. The moths and larvae were surveyed by four researchers at each of the five locations for 30 minutes. Sampling methods involved one researcher sweep-netting, whilst others conducted visual observations for moths and larvae. The order of locations surveyed was randomised to avoid sampling bias. Moths found were photographed and placed into plastic containers for identification and released after dusk at the location where they had been obtained.

Table 2: Description of each location sampled on Lundy (see also Figure 1).

Location	**Description**	**Keywords**
Farm*	Situated inland along the main path through the island, near a lambing shed and pigsty, with plant lift around the stone wall along the path (- 51.1678° N, -4.6664° W)	Stone wall, path, farm animals
Garden	Situated on the south coast of the island sheltered behind a small house. Lit with artificial light from 6.30pm to 12.30am. Trap placed in the garden of the holiday home surrounded by plants (51.1640° N, -4.6605° W)	Coastal, artificial light, vegetated, building
Hospital	Situated on the east coast of the island where there was an old ruined hospital chosen for its sheltered rural location within the old walls, overgrown with plants. Chosen due to the lack of artificial light and plant life outside the building. Trap was placed in the centre of the ruined building (51.1700° N, -4.6628° W)	Coastal, dark, building
Tavern	An anthropogenic location with higher density of buildings, light, and people. Trap was placed in an open field behind a barn in the village to capture moths coming from across the field towards the artificial night lighting (51.1649° N, -4.6657° W)	Exposed, artificial light, visitors, buildings
Woodland	A rural location with shelter from trees and bushes and considered a traditional location as a moth habitat. Trap was placed on a small open path in the centre of the woodland (51.1651° N, -4.6613° W)	Sheltered, dark

Note: Locations marked with * represent sites sampled for moth larvae only and were not sampled using light traps. This should be acknowledged when making cross-site comparisons.

Table 3: Moth trap schedule for each location on each night of sampling

Date	**Moth Trap ID**			
	P1	P2	L1	W1
28/04/2019	Woodland	Hospital	Garden	-
29/04/2019	Garden	Hospital	Woodland	Tavern
30/04/2019	Garden	Woodland	Hospital	Tavern
01/05/2019	Hospital	Garden	Tavern	Woodland
02/05/2019	Tavern	Hospital	Woodland	Garden

Note: P1 and *P2* comprised moth traps using low or medium powered LED light sources in a basic form of a Robinson moth trap. *L1* used a high powered LED source within a Skinner moth trap design whereas *W1* used a UV light source within a Skinner trap.

Ethical Considerations

Several ethical issues were considered. Identification was predominantly accomplished through photographs to reduce handling time. When handling was necessary, surgical gloves were worn to reduce disturbance to individuals and prevent the spread of potentially harmful chemicals or disease. Individuals were housed in separate clear plastic containers with surrounding vegetation from where they were sampled. Individuals were released at dusk from where they were sampled to reduce predation risk.

Figure 1: Map indicating locations of moth traps

Key: H=Old Hospital, F=Farm, T=Tavern, W=Woodland, G=Garden

Table 4: Species of vegetation identified at each location sampled

Species of vegetation	**Location**				
	F	**G**	**H**	**T**	**W**
Bluebell *(Hyacinthoides non-scripta)*	-	-	-	-	Yes
Broad-leaved dock *(Rumex obtusifolius)*	-	Yes	Yes	-	Yes
Cat's ear *(Hypochaeris radicata)*	-	-	Yes	-	-
Clover *(Trifolium)*	-	-	Yes	-	-
Common daisy *(Bellis perennis)*	-	-	Yes	-	-
Common dandelion *(Taraxacum officinale)*	Yes	Yes	-	Yes	-
Common gorse *(Ulex europaeus)*	Yes	-	-	-	-
Creeping buttercup *(Ranunculus repens)*	-	-	Yes	-	-
Goosegrass *(Galium aparine)*	-	-	-	-	Yes
Ground ivy *(Glechoma hederacea)*	-	-	Yes	-	-
Meadow-grass *(Poa pratensis)*	-	Yes	-	-	-
Wall pennywort *(Umbilicus rupestris)*	-	Yes	-	-	Yes
Red campion *(Silene dioica)*	-	-	-	-	Yes
Brambles *(Rubus)*	Yes	-	Yes	-	-
Ryegrass (*Lolium perenne*)	Yes	Yes	Yes	Yes	-
Moss *(Sphagnum)*	Yes	Yes	Yes	Yes	-
Stinging nettle *(Urtica dioica)*	Yes	-	Yes	Yes	Yes
Daffodil *(Narcissus)*	-	Yes	-	-	-

Note: Location *F*=Farm, *G*=Garden, *H*=Hospital, *T*=Tavern, *W*=Woodland

RESULTS

Statistical Analysis

All data were analysed using SPSS. Residuals were examined for assumptions of normality and homogeneity of variance, revealing that both were violated for night-time moth trap and daytime count analyses. Accordingly, Generalised Linear Models (GLMs) were computed to investigate differences in moth trap population densities and species across different locations (*N*=4; woodland, garden, tavern, and hospital) and across different light sources (*N*=4; UV and LED [lumens: low, medium, high]). Cloud-coverage was entered as a covariate within the models to account for the effects of cloud-coverage on light dispersal. The 1-Simpson's Index was used to obtain species diversity indices (SDIs) at each location for both adult moth and moth larvae data. The formula for the 1-Simpson's Index is given as: $1\text{-SI} = 1\text{-}\sum ni(ni\text{-}1)/N(N\text{-}1)$. Where *N* is the cumulative number of individuals recorded overall, and *ni* is the cumulative number of species recorded that helps make up *N* in total. Scores nearing 1 indicate high diversity and scores nearing 0 indicate low diversity. Differences in daytime population densities and species diversity across location (*N*=5; additional location of the farm) were investigated using Friedman's tests.

Night-time Moth Trap Survey

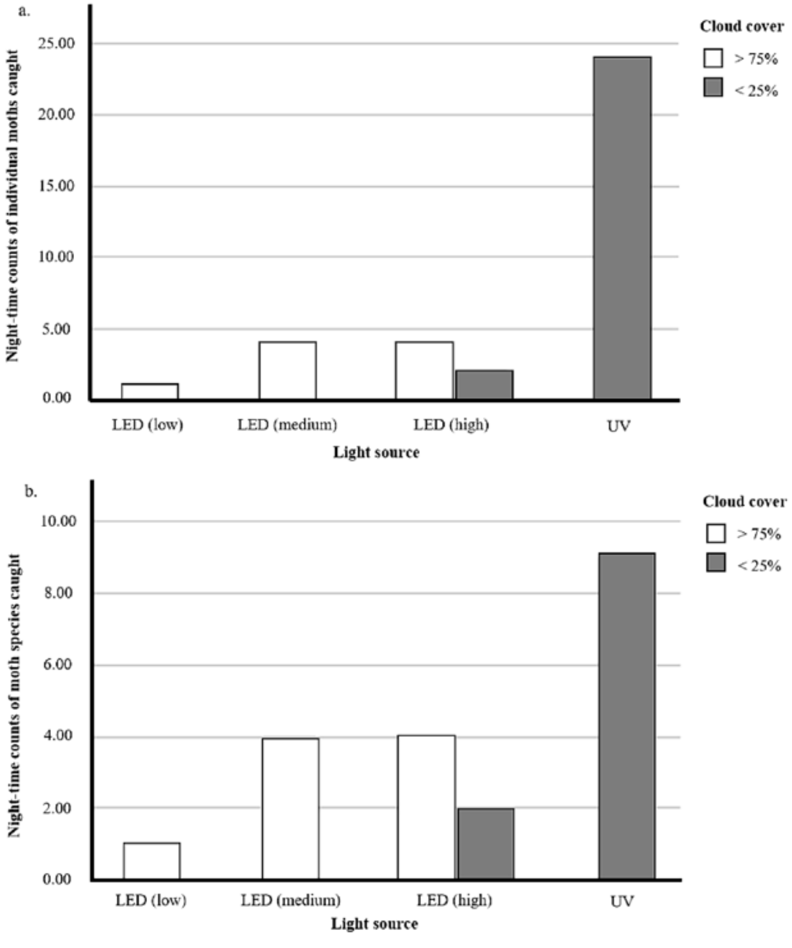
Location and moth population density

Cloud-cover did not influence moth numbers caught across locations when included as an interaction term (Wald $X^2_3=7.20$, $p=0.066$). Main effect of location on the number of moths caught was significant (Wald $X^2_3=17.78$, $p<0.001$; Figure 2a). Parameter estimates revealed that significantly more individuals were caught in the woodland location than all other locations (Wald $X^2_1=12.08$, $p=0.001$, $B=14.96$, $SE\pm=4.30$). All other effects were not significant (Wald X^2’s<0.02, p’s>0.886, B’s<0.62, SE’s$\pm=4.30$).

Location and moth species diversity

Cloud-cover did not influence moth species caught across locations when included as an interaction term (Wald $X^2_3=2.43$, $p=0.49$). Main effect of location on species diversity of moths caught was significant (Wald $X^2_3=16.92$, $p=0.001$; Figure 2b). Again, parameter estimates revealed that significantly more species were caught in the woodland location than all other locations (Wald $X^2_1=11.93$, $p=0.001$, $B=5.69$, $SE\pm=1.65$). All other effects were not significant (Wald X^2’s<0.14, p’s>0.707, B’s<0.62, SE’s$\pm=1.65$).

Figure 2: The number of individual moths caught (a) and the number of species caught (b) by different light sources as a function of cloud-cover



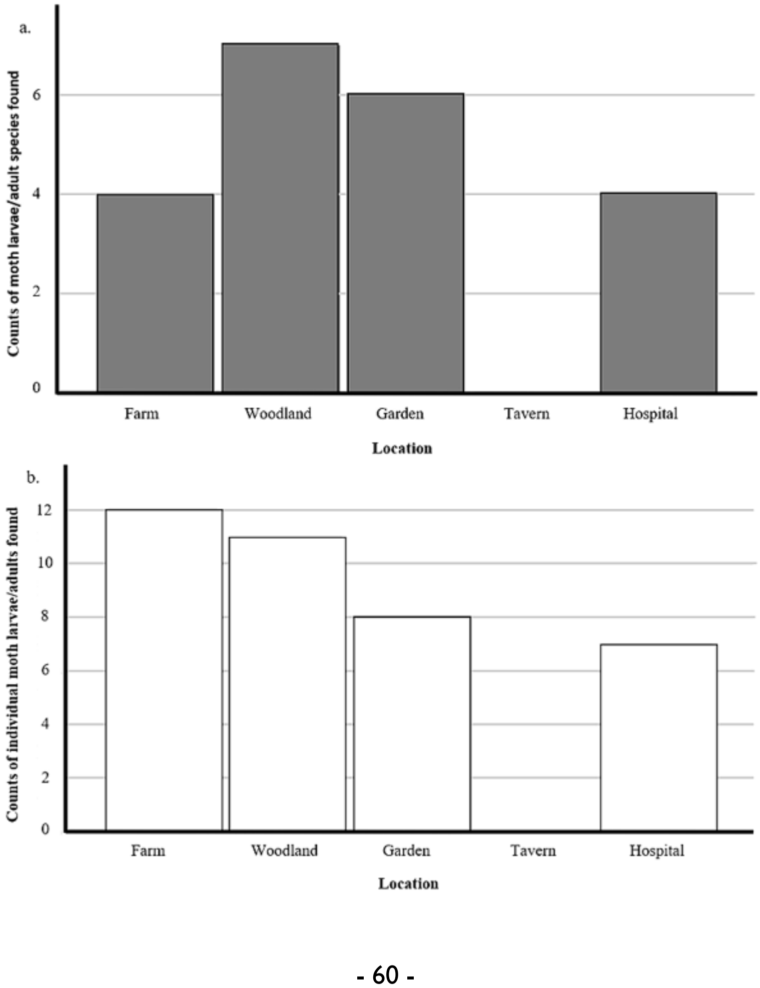
Light source and moth population density

Cloud-cover influenced the number of moth individuals caught across light sources when included as an interaction term (Wald X^2_3=11.28, p=0.010). Parameter estimates revealed that the number of individuals caught by the UV-light source significantly differed from the number caught by all other LED light sources, and that this relationship is dependent on cloud-coverage (Wald X^2_1=8.53, p=0.004, B=-0.21, SE±=0.07; Figure 2a). All other effects were not significant (Wald X^2's<0.39, p's>0.530, B's<-0.04, SE's±< 0.08).

Light source and moth species diversity

Similarly, cloud-cover influenced the number of moth species caught across light sources when included as an interaction term (Wald X^2_3=3.46, p=0.004). Parameter estimates also revealed that the number of species caught by the UV-light source significantly differed from the number caught by all other LED-light sources, but this relationship was dependent on cloud-coverage (Wald X^2_1=12.49, p=<0.001, B=-0.11, SE±=0.03; Figure 2b). All other interactive effects were not significant (Wald X^2's<2.196, p's>0.139, B's<-0.04, SE's±<0.03).

Figure 3: Bar graph showing the difference in the number of moths (a) and the number of species of moths (b) found at each location during daytime surveys



Daytime Surveys

Daytime survey density between locations

There was no difference in the number of moth larvae/adults found between locations (X^2_4=6.49, Asymp. *p*=0.165; see Figure 3a; see Table 5 for means and standard deviations).

Daytime survey species diversity between locations

However, there was a significant difference in the diversity of moth larvae/adult species found between locations (X^2_4=9.81, Asymp. *p*=0.044; see Figure 3b; see Table 5 for means and standard deviations).

Table 5: Means and standard deviations of the number of individuals and number of species of moth and moth larvae found

Location	**No. Individuals Found**		**No. Species Found**	
	M	***SD***	***M***	***SD***
Farm	2.40	2.88	0.80	0.84
Woodland	2.20	1.79	2.20	1.79
Garden	1.60	1.52	1.20	1.30
Tavern	0.00	0.00	0.00	0.00
Hospital	1.40	1.52	0.80	0.84

Simpsons Diversity Index

SDIs of adult moths and moth larvae caught in both night-time trapping and day-time surveys varied from 0 to 0.921 between locations; where low scores represent low diversity and high scores high diversity (see Table 6).

DISCUSSION

AL has been implicated as a causal factor of global moth declines due to its negative effects on moth life cycles and behaviours (Bruce-White & Shardlow, 2011). In addition, moths are under-represented in assessments of biodiversity loss (Fox *et al.*, 2011). Where research has been conducted, it is difficult to discern the effects of AL from the influence of urbanisation since the two typically co-occur (Bates *et al.*, 2014). Our study aimed to shed light on the population dynamics and species diversity of nocturnal moths within the model environment of Lundy to isolate the effect of AL from that of urbanisation.

The effect of location and pre-existing AL levels

Consistent with our hypothesis, analyses revealed that the number of moth individuals and species caught in light traps significantly differed across the 4 locations, independent of cloud-coverage. Contrary to our prediction that more moths would be captured in areas of higher surrounding AL, counts of moths caught in the lowly lit woodland location were significantly higher than all other locations. This unexpected finding contrasts with previous literature proposing that high densities of AL act as ecological traps that result in large aggregations of moths to that area (Bates *et al.*, 2014). Our results instead suggest that moths are aggregating in areas abundant in vegetation, shelter and darkness, away from these artificially lit areas.

Table 6: Adult moth and moth larvae species found at each location with Simpsons Diversity Index (SDI)

Species	**Location**				
	F*	**G**	**H**	**T**	**W**
Bright-line brown-eye (*Lacanobia oleracea*)	-	-	-	-	3
Brimstone (*Opisthograptis luteolata*)	-	-	-	-	1
Brown silver-line (*Petrophora chlorosata*)	-	-	-	-	1
Common quaker (*Orthosia cerasi*)	-	-	-	-	4
Dark sword grass (*Agrotis ipsilon*)	-	-	-	-	1
Dogs tooth (*Lacanobia suasa*)	-	-	-	-	1
Dotted border (*Agriopis marginaria*)	-	1	-	-	2
Emperor (*Saturnia pavonia*)	-	1	-	-	-
Garden tiger (*Arctia caja)*	9	1	-	-	1
Hebrew character (*Orthosia gothica*)	-	-	-	-	1
Marbled coronet (*Hadena confusa*)	-	-	-	-	10
Muslin (*Diaphora mendica*)	-	3	-	-	3
Oak eggar (*Lasiocampa dodneata*)	-	-	6	-	2
Oak tree pug (*Eupithecia quercus*)	-	-	-	-	1
Pale tussock (*Calliteara pudibunda*)	-	-	-	-	1
Powdered quaker (*Orthosia gracilis*)	-	-	-	-	2
Red chestnut (*Cerastis rubricosa*)	-	-	-	-	1
Red twin-spot carpet (*Xanthorhoe ferrugata*)	-	-	-	-	1
Twin spotted quaker (*Perigrapha munda*)	-	1	-	-	-
Unknown Species 1	-	-	-	-	1
Unknown Species 2	-	1	-	-	-
Unknown Species 3	-	1	-	-	-
Unknown Species 4	-	-	-	-	1
Vapourer (*Orgyia anitqua*)	-	-	1	-	2
Total	9	9	7	0	40
Simpsons Diversity Index (SDI)	0.00	0.92	0.29	NA	0.92

Note: Location *F*=Farm, *G*=Garden, *H*=Hospital, *T*=Tavern, *W*=Woodland. Locations marked with * represent sites sampled for moth larvae only and were not sampled using light traps. This should be acknowledged when making cross-site comparisons.

However, the number of moths caught by light-traps has been shown to decrease in the presence of other light sources, including AL (Eisenbeis, 2006). It is plausible that the floor effect in the artificially lit setting of the tavern/village does not represent a true picture of how AL influences moth populations. Rather, it represents how AL influences light-trap efficacy. The observed effects of AL on total abundance and species richness may merely be artefacts of the method used to sample these assemblages.

Although this may be the case for night-time trap data, it does not explain why no adult moths or moth larvae were found during day-time surveys at the tavern when competition between light sources did not occur. If our light-traps were simply being outcompeted by stronger surrounding AL, we would still expect to find large abundances of larvae during the day at these sites, if light is to act as an ecological trap as proposed by Bates *et al*. (2014). It may be that although AL draws moths towards it, it also disrupts and inhibits reproductive behaviour. Van Geffen *et al*. (2015) experimentally demonstrated that artificial night-lighting negatively affects natural moth reproductive behaviour. Such impacts likely lead to detrimental cascading effects on biodiversity, trophic interactions, and ecosystem function (Longcore & Rich, 2004). Thus, a lack of adult moth of moth larvae samples in areas with high AL may represent the inhibitory effect of AL on reproduction.

It was also noted that Common starling (*Sturnus vulgaris*) were observed frequently during the daytime survey at the tavern location. Being known to predate on moth larvae, reduced larvae in this area could therefore be related to increased predation risk from these starlings (Cook *et al*., 2012). Records have shown that birds can predate moths, removing from 20% and in extreme cases 100% of the population (Barbaro & Battisti, 2011). This a known problem as stated by the Warden of Lundy; during previous studies on the island birds learned to predate near the traps, requiring a change in location (D. Woodfin Jones, personal communication, 30 April 2019). In future, surveying the species and frequency of birds and bats present in the area surrounding traps is advised to indicate potential predation rates. Both may influence species counts by learning to predate on the aggregations of moths to these light traps (Fox *et al*., 2013).

In support of the argument that AL inhibits reproduction, an emperor moth was identified in the garden light-trap (high AL) and had laid multiple eggs inside the trap. Although this can initially be interpreted as functional reproductive behaviour, it instead indicates the disruptive effect of AL on moth life-cycle since emperor moths traditionally lay their eggs in sheltered locations on plants (Butterfly Conservation, 2019). The increased AL appeared to have disrupted the moth's natural behaviour of laying in a suitable location due to an overriding flight-to-light response. Although anecdotal, we believe this to be an interesting avenue for future research to assess the frequency of egg-laying in light traps.

Species diversity

The number of individual insects found from day-time insect surveys did not differ across location, but the number of species was found to significantly differ. The most species-diverse location for both night and day surveys was the woodland, probably due to the increased natural vegetation and shelter at this location. This included the discovery of a novel species to the island, the Red chestnut moth (*Cerastis rubricosa*).

Although these woodland moths may be less at risk of behavioural disruption from the AL at the tavern, they may still be attracted to smaller, local buildings that use AL until midnight. Merckx & Slade (2014) found that the distance that moths were attracted to artificial light depended on the macro-moth family. Erebidae were attracted up to 27m, geometridae from 23m and noctuidae 10m. 2 erebidae, 5 geometridae, 6 noctuidae and 1 nepticulidae were caught in the woodland. Millcombe House accommodation was <30 metres from the woodland; some moths caught at this location may be at risk of attraction to this AL. Indeed, the laying female emperor moth was trapped at the garden location which had pre-existing artificial light levels and no suitable food plants, suggesting accommodation light may attract species from other nearby areas such as woodland and grassland.

It is worth noting that seasonality impacts different species in different ways (Sinu *et al.*, 2013). This study only takes a sample of the species diversity in April-May. For a more accurate representation, trapping during various seasons throughout the year would be advised for future study.

The effect of cloud cover and UV light sources

UV and LED light sources differed in their trapping efficacy and this relationship was influenced by cloud-cover. At high levels of cloud-cover (>75%) the UV light-trap caught significantly more individuals and species than all of the LED-light sources. Our work also demonstrates the importance of incorporating cloud-cover as an influencing factor when using light-traps since cloud coverage amplifies luminance (Kyba *et al.*, 2011). The results from our study contradict the results from a study by Castrovillo & Carde (1979), who showed that when the cloud-cover increased, the number of moths captured decreased. However, our study the first to our knowledge to investigate the influence of cloud-cover when using different sources of light in moth trapping. As such, to allow for unbiased comparisons between traps, lamp-type should be identical if their locations cannot be randomised. When planning future work portable UV traps are advised as the large size of the trap restricted the locations it could be placed at, however, the ethical considerations previously mentioned should be taken into account when considering the use of the UV-light (see Table 7).

Our work corroborates with work by Cowan & Gries (2009) who demonstrated how the Indian meal moth (*Plodia interpunctella*) were preferentially attracted to UV light over the LED. Worryingly, the attraction of moths to UV light has been shown to cause damage to retinas, alter behaviour, and disrupt circadian rhythms (van Ooik *et al.*, 2008). For instance, exposing *Orgyia antiqua* moths to UV-light for one hour caused permanent eye damage (Mishra & Meyer-Rochow, 2008). Interestingly, van Ooik *et al.* (2008) also demonstrated how plants irradiated with UV-B-light were the preferred food of *Epirrita autumnata* moth larvae, demonstrating the attractiveness of this light source to this species. Happily, the use of LEDs is continually increasing in urban areas due to their energy-saving properties (Yoon *et al.*, 2012). The lack of attraction to this light source during our research suggests that a continuation of this trend could result in a more positive outcome for moth populations.

Table 7: Strengths and limitations of the study

Strengths	**Limitations**
Light trapping method: This allowed data gathering at community and population level. Different sources of lighting can be used (e.g. LED, UV, and coloured) with a large capacity for high numbers of moths. **Sweep netting & visual survey method**: Cost-effective methods applicable across a range of habitats and environmental conditions. Ease of use enables multiple researchers to utilise these methods, helping to reduce researcher fatigue and enable inter-researcher reliability. A strategic approach using these methods also helps minimise risk of pseudoreplication.	**Light trapping method**: Despite displaying signs to warn the public, UV lighting is harmful to human eyes and so it may not be ethical to place in areas with high human populations and densities. Light trapping may also increase predation risk of moths as well as disrupting their behaviour. A cost-benefit analysis should be run before implementing light trapping. **Sweep netting & visual survey method**: Sampling bias against species of burrowing moth larvae (e.g. leaf miners) may have been encountered. Abundance and diversity of food-plants differed across locations which would likely influence distribution and frequency of moth larvae species. As such, varying temporal patterns in food-plant availability will also be related to the distributions of moth larvae over time. Longitudinal research is required to understand these fluctuations.
Future studies: The findings and implications from this current study present interesting further explorations for moth studies on Lundy. The affordability and clarity of methods allow replications of this study procedure to be conducted easily on Lundy which would help inform the reliability of the present findings.	**Future studies**: effects of time of day, lunar phase, weather, and season could not be adequately assessed due to the short nature of the study and so these factors should be investigated more in-depth. A consistent trapping method using identical design and light sources may be preferred in the future, as it may prove more reliable in yielding population and species distribution data.
Applicability: this study is the first to our knowledge to compare the effectiveness of different light sources used in moth trapping on Lundy, offering insights into the influence of the widespread and increasing use of LED lighting.	**Ethical issues**: use of various light sources overnight has the potential to disrupt the natural behavioural patterns of other local fauna and flora.

Conclusions

Our research of the effects of urbanisation and AL on moth species diversity by light trapping and daytime surveys show that the locations without artificial light contained most species diversity and the greatest number of moths. This result contradicts our hypothesis that high populations and species diversity would be found at locations with higher pre-existing AL levels. However, the pre-existing AL may have detracted from the effectiveness of our light-traps; therefore, future work should incorporate pre-existing lights into trapping methods. Additionally, the time of year and weather conditions may have influenced our results as most species of moth are not yet in the flying stage of their life cycle. UV-light shows a greater capability for moth attraction when compared against the results for the LED light sources. The current trend for the use of LED lights in urban environments could, therefore, be of great benefit to the moth populations as it lowers the risk of urban areas becoming ecological traps. Considering the importance of moths and their larvae to the ecosystem, this could help to prevent the global decline in species populations.

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Plate 1: Red chestnut moth (*Cerastis rubricosa*), novel sighting to Lundy, captured during this study © Peter Kidd

Plate 2: From left to right: Peter Kidd (Researcher), Kay Nash (Researcher), Dean Woodfin Jones (Lundy Island Warden), Steph Ford (Researcher), Angeline Rietveld (Researcher)

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THE IMPORTANCE OF TWO OF LUNDY'S TEMPORARY PONDS

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ABSTRACT

The species composition and habitats of two of Lundy's temporary ponds and their importance as reservoirs of short-lived and unique species is investigated. The type of temporary pond and the composition of species is further determined. Current management of these habitats is explored and their importance as habitats in both their wet and dry phases.

Keywords: *Lundy, Lentic water, freshwater invertebrates, autumnal pond, temporary pond*

INTRODUCTION

The plateau of Lundy is in effect a giant sponge which sits in a region that receives much rainfall throughout most of the year. After prolonged rain every hollow becomes a temporary pond and every permanent pond increases in depth considerably. The first Ordnance Survey maps of Lundy included five temporary ponds at the north east of the island (OS 1886) although between 20 and 25 were recorded after a particularly wet winter (pers. notes).

These north east temporary ponds are quite ephemeral and shallow, forming in slight depressions on bare granite and providing habitat for highly mobile and quick breeding species of Coleoptera and Diptera. There is an exception in Long Roost Pond which, unusually, contains water in its granite basin for considerable periods of the year.

Most permanent ponds occasionally dry up in years of prolonged drought (1976, 1981, 1995 and 2006) but in most years they can be relied on to hold water all year round (George, 2012).

The average number of rainy days throughout the year varies from 12.7 in June to 19.5 in December (Lundy Warden, pers. comm.).

At the southern end of Lundy there are two temporary ponds that have a regular periodicity: Government House Pond (GHP) and Kistvaen Pond (KP).

Definition of a Temporary Pond

A temporary pond is formed by water collecting in an isolated basin that has neither inlet nor outlet and from which water is entirely absent for part of the year (Wiggins *et al.*, 1980).

Brönmark and Hannson (1998) define two distinct types of temporary pond: Temporary Vernal or Temporary Autumnal ponds (see Box 1).

It is important to note that these definitions are not necessarily permanent. For example a particular pond could be vernal one year and autumnal in another year and occasionally, in a very wet year, permanent for that the whole twelve months. It is highly likely that species may in fact determine the designation of the pond (Wiggins *et al.*, 1980).

According to Brönmark and Hannson (1998) both KP and GHP are Temporary Autumnal Ponds with eight to nine month wet and three to four month dry periods; autumnal because the drought is terminated in autumn.

Box 1: Definition of Temporary Ponds

a) Temporary vernal pool

Fills in April from melting snow/rain, levels decline to none by June/July, remains dry until spring. Typically
3-4 months wet
8-9 months dry

b) Temporary autumnal pool

Has impermeable soils and has water into autumn. Typically
9 months wet
3 months dry

Despite this regular drying out, both types of temporary ponds are long-lived. Due to their annual dry phase, any build up of macrophytes dies off. Exposure to the elements means that any remains oxidise and disperse thus preventing the build up of silt. (Brönmark and Hansson, 1998)

Box 2: Species of Temporary Ponds

Group 1 Year round residents

Species that escape desiccation either by resistant stages or by burrowing into sediments.

Group 2 Spring recruits

Species that oviposit in water then spend the winter in aestivating in the dry basin or survive in another life stage.

Group 3 Summer recruits

Species that oviposit in the dry basin then overwinter as eggs or larvae.

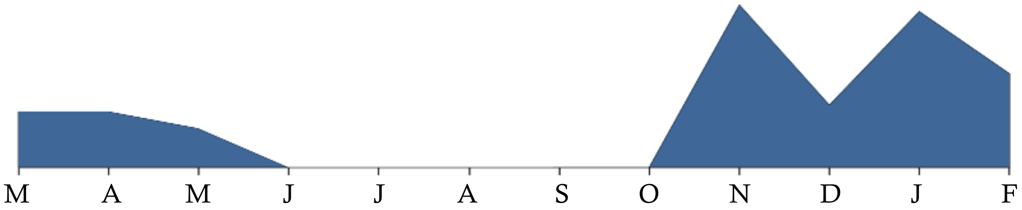
Group 4 Non-wintering migrants

Species that leave the pond before the dry phase and then spend time in a permanent pond before returning to breed in the spring.

Group 5 Terrestrial species

Figures 1 and 2 are adapted from Wiggins *et al.* (1980). The vertical scale in blue is the presence and relative depth of water against the horizontal axis of months from March to February. The year is shown in this arrangement to keep the seasons together: Spring (March/April/May); Summer (June/July/August); Autumn (September/October/November); Winter (December/January/February).

Figure 1: Government House Pond Depths (y axis) by month (x axis)



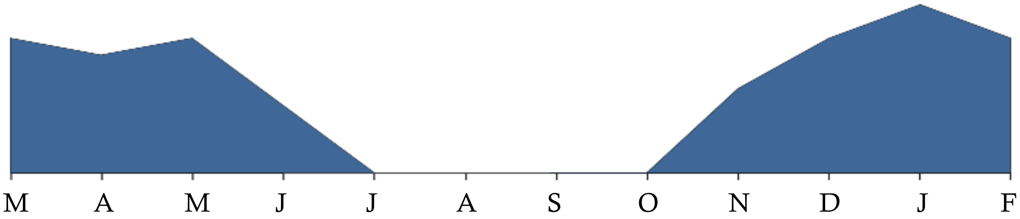
Records of water depths were commenced when Government House Pond was first surveyed in 2010 and continued irregularly until 2016 when records were made more regularly. The pond dries out from May to October/November when it stays wet usually around November through to April although occasionally, as in June 2017 and July 2012 some water was recorded. When it contains water it is around 0.3 to 0.5 metres in depth although this falls rapidly during periods of no rain when surveys are not undertaken. Figure 1 consolidates these depth readings which broadly conform to that of a Temporary Autumnal Pond.

GHP begins to fill around September/October when rainfall increases and continues to fill up to its maximum depth of around 0.5m. This continues until spring when rainfall and groundwater flow decreases until all water has drained or evaporated away at the end of May or beginning of June when the dry phase extends until autumn.

Plate 1: GHP Wet Phase showing the pond covered with *Lemna minor* November 2011

Plate 2: GHP Dry Phase albeit with a small amount of damp mud August 2019

Figure 2: Kistvaen Pond Depths (y axis) by month (x axis)



Depth records exist for Kistvaen Pond from April 2005 when the maximum depth in the western sub pond was as much as 0.35m. Records were made sporadically until 2017 when biotic and abiotic surveys were made on a much regular basis. The pond began to collect water between September and November and retained this at various depths until late May or early June when it dried out for the summer until rain began to collect again in autumn. Figure 2 consolidates these depth readings which broadly conform to that of a Temporary Autumnal Pond.

KP begins to fill in late autumn, around October, and continues to collect rain and ground water throughout the winter until it reaches maximum depth of up to 0.35m. The pond continues with this depth until late spring/early summer when water levels quickly fall leaving three isolated smaller ponds in the west, south and north-east areas when the pond enters its dry phase.

Plate 3: Kistvaen Pond
Wet Phase
February 2010

Plate 4: Kistvaen Pond
Dry Phase
August 2019

Plate 5: Aerial view of Kistvaen Pond showing the western, southern and north-eastern receding wet sub-ponds

Species of Temporary Ponds (see Box 2)
The species that inhabit temporary ponds can be separated into five groups. The strategies they have developed to inhabit this niche habitat defines them. In this paper the fifth group – invertebrate species that inhabit the dry phase – are not discussed although some exploration of the value of the habitats during this phase is made.

In addition to the various species that inhabit temporary ponds, there is also a succession of the species that comprise each group:

Group 1 comprises the permanent residents, those species that are not capable of active dispersal during the dry phase and have developed strategies to aestivate either as drought resistant cysts and eggs either as juveniles or adults. Typical species are Flatworms (Turbellaria), Segmented worms (Oligochaeta), Leeches (Hirudinea), the various planktonic Water Fleas, Copepods and Clam Shrimps (Crustacea), Freshwater Shrimps (Gammaridae), Water Slaters (Isopoda) and Snails, Limpets and Mussels (Mollusca).

Group 2 comprises those taxa that must reproduce in the pond before the water disappears then aestivate as eggs or larvae or, in the case of beetles, leave the pond as adults. They appear immediately after the pond begins to fill and typically have a 4-6 week life cycle. Typical species are Mayflies (Ephemeroptera), Beetles (Coleoptera), Caddis Flies (Trichoptera), True Flies (Diptera), Water Spiders and Mites (Acari).

Group 3, the summer recruits, do not need water for ovipositing and use the basin after the water has gone and overwinter as eggs or as larvae. They appear 2-5 weeks after water appears and typically have a 5-week life cycle and are predominantly Dragonflies and Damselflies (Odonata), Trichoptera, and Diptera.

Group 4, the non-wintering spring migrants, enter temporary ponds in spring about 10 weeks after water appears, breed, develop into adulthood then leave the pond for permanent water until water reappears. Typical species are Ephemeroptera, Odonata, True Bugs (Hemiptera), Coleoptera, Diptera, Acari and Frogs and Toads (Amphibia).

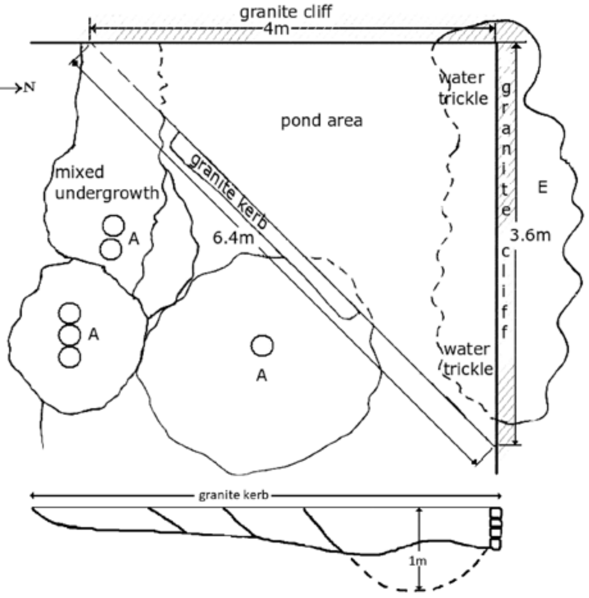
Group 5 species are the terrestrial species not covered in this paper (Williams, 2006, Wiggins *et al.*, 1980).

In summary, Drake (2001) describes the prerequisites for survival in temporary ponds as: an ability to reach maturity before it dries out; a mechanism to survive the dry period; and the ability to re-colonise. The two ponds in this paper are home to a subset of these species which are detailed more fully in the Results section.

Descriptions of the Ponds
Government House Pond is located at Ordnance Survey Grid Reference SS 13808 44067, east of the Tavern, through the arched Trafalgar blue doorway leading to Government House where there is a sheltered area excavated from the rocks and protected by trees on the north side of the path.

The pool is triangular in shape and bounded on two sides by overhanging granite cliffs of up to 3m in height. The third side has a cut granite edging bordered by luxuriant undergrowth and grass. The northern cliff has a large shrub descending from it, Japanese Spindle tree *Euonymus japonicus*, from which much of the leaf debris originates. There are also Sycamore *Acer pseudoplatanus* on the south-eastern periphery. The pool has neither inlet nor outlet but is fed from visible, and audible, water seepage from the northern cliff, and presumably some rain water.

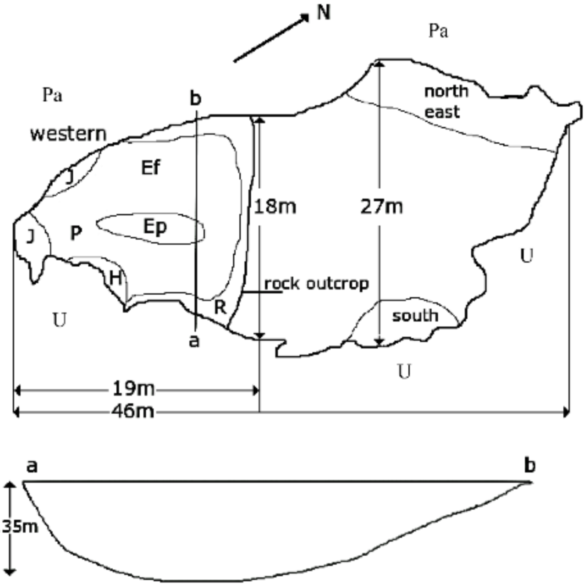
Figure 3: Government House Pond – plan and elevation along the granite kerb



Key
A - *Acer pseudoplanatus*
Sycamore
E - *Euonymus japonicus*
Japanese spindle tree

Kistvaen Pond is located on the southern coast of Lundy, due east of Rocket Pole Pond at Ordnance Survey Grid Reference SS 1355 4369. It is a large shallow depression roughly oblong running east-west and measuring some 46.3m long by 27m wide. It too has neither inlet nor outlet and depends for its water on rain and to some extent ground water. It is bordered by Common Rush *Juncus effusus,* Western Gorse *Ulex galli* and Bracken *Pteridium aquilinum.*

Figure 4: Kistvaen Pond – plan and elevation across section a-b. Typical plants growing in the western sub-pond, one of three of the longest-lasting wet areas, are mapped. The rock outcrop that divides the depression is home to Chaffweed



Key
Ef - *Eleogeton fluitans*
Ep - *Eleocharis palustris*
H - *Hydrocotyle vulgaris*
J - *Juncus effusus*
P - *Potamogeton polygonifolias*
Pa - *Pteridium aquilinum*
R - *Ranunculus lingua*
U - *Ulex sp*

Origins and History

Government House Pond

This pond does not feature in Langham's 1969, otherwise comprehensive, listing of all Lundy's ponds and streams. It is first referred to as 'Pond in the Quarry' in the Heaven archives when Cecilia Heaven relates how she and her brother Walter, aged 9 and 5, played there:

> '… But the pond in the Quarry – now planted with trees, close to the site of the Iron Church – proved irresistible, and I can still vizualise Walter in his old velvet suit plunging in up to his waist!' (Heaven Archive, 1870).

It is also referred to by Langham (1993) in a later unpublished article where he mistakenly attributes the granite as slate in the 'Garden Quarry':

> 'Immediately through the "Gothic Gate", to the east, is a little "Garden Quarry" from which slate was dug and which, when abandoned, quickly filled with water to provide a sheltered pond beloved by dragonflies.'
>
> 'The "Old House" of Sir John Borlase Warren dates, we believe, from about 1775 and stands at what is the extreme head of Millcombe Valley. The large amount of stone required seems to have been quarried from what later became the hotel garden. There is no direct evidence of quarrying here but the sunken contours of the garden (although much modified and landscaped since) suggest that this site is the Old House's stone quarry. Immediately north of the modern Government House is an old quarry from which stone may have been quarried at this time.'

It may have developed as a pool naturally once the quarry had ceased use, but at some stage, there was a deliberate attempt to formalise the pond when the hypotenuse of its triangular shape was delineated by the placing of granite kerb stones along it.

Ternstrom (1999) locates and describes it in her gazetteer 'G343 Pond in the Quarry NGR 1380 4409'. Other than these references to its existence, no attempt has been made to survey or record the fauna and flora of this pond.

Reg Lo-vel (pers. comm.) recollected that there had always been a wet patch in the quarry adjacent to Government House, but could not remember any previous work being done there by Landmark Trust.

Dyke (1971) provided an illustration of the area which 'once sheltered a little church with a spire and bell … dedicated in 1885 … dismantled …. in 1896.' The foundations are clear and were reportedly used as foundation for a greenhouse, but at the time of writing '… has reverted back to nature and become a pleasant open space.' The Quarry and pond obviously predates all building works and was outside the Manor House grounds and apart from its recent excavation has remained undisturbed for much of its existence.

Kistvaen Pond

This pond, originally designated as Rocket Pole Temporary Pond 2 and more recently as Kistvaen Pond, is the large depression to the east of Rocket Pole Pond. It contains some water at some times of the year. At other times there is no water at all.

All winter it holds some water but dries out in late spring, around May remains dry until late autumn which is variably between October or November (Langham, 1969).

In light of Ternstrom's (2000) description of the site of this chambered tomb, it has been renamed from Langham's (1969) original designation, as one of the Rocket Pole complex of ponds, to Kistvaen Pond.

The whole area was originally excavated in 1852 and later in 1887 filled and altered to be much as it is seen today. It continues to be 'variously dry, marshy, or a pond'. It was measured at 242 feet long (Ternstrom, 2000) and is scheduled monument No. 27625.

METHODS

Abiotic

Both ponds have been surveyed occasionally from 2010 in the case of GHP and from 2005 in the case of KP. More regular surveys on both ponds commenced in 2016. Where equipment has allowed, Total Dissolved Solids, pH and depths have been recorded. Inputs for both are ground and rain water and output is evaporation.

Government House Pond:Total Dissolved Solids: 249 to 277 averaging 268, well within the definition of freshwater. pH between 6.3 (May) and 8.0 (Apr) with an average of 7.4. Maximum depth recorded was 0.29m with silt of up to an additional 0.15m in May.

Kistvaen Pond: Total Dissolved Solids: between 206 and 319 (Apr to June) with average of 251, well within the definition of freshwater. pH ranges between 5.9 (March) and 7.8 (June) with an average of 7. Maximum depth was reached in April at 0.44m. There is no silt in this weedy pond.

Despite the regular reduction in volume of water as the ponds dry out, pH and TDS remain within tolerable limits and for the whole of the wet periods these ponds fall within the definition of freshwater and do not restrict their flora and fauna in any way.

Biotics

Surveys have been carried out in most months of the year when there has been water in either of the ponds.

KP has been surveyed in every month with the exception of July, August and October

GHP has been surveyed in every month with the exception of January, June, August and October.

Government House Pond: The initial survey of this pond was made by request of the then Lundy Warden, Nicola Saunders and Lundy Ranger, Chris Flower (pers. comm. 2010). The pond was almost full of silt with only millimetres depth of water on the surface of the accumulated silt. The Conservation Team wanted advice on excavating the pond and returning it to being a body of water. Advice on how to do this was given but only after an initial survey was carried out. Due to the extremely shallow depth of water, the standard net method of surveying was not possible and water was scooped up into a container sampling all areas as well as some of the silt. The resulting mix was allowed to settle and species and abundance ascertained. Ten species were recorded and with the exception of three (*Carchesium, Hydra* and Freshwater Shrimp) all have since been recorded on frequent occasions.

Kistvaen Pond: Standard method surveying was carried out with standard hand net 250mm wide with 1mm mesh with 3 minutes sampling divided between all areas and habitats. Tables 2 and 3 of results includes surveys from April 2005 (George, pers. comm.).

In July 2019 both ponds were expected to be dry. In the event, GHP consisted of damp mud whereas KP had small but decreasing pools in the three areas where water remains for the longest period (Plate 5). These dried around the middle of the month. A stainless steel hand coring tool was used to extract cores of approximately 6cm in length and 1cm in diameter. In KP some areas were too close to bedrock to achieve this and lesser depths were extracted but GHP had sufficient soft silt to achieve this. One core was taken from dry areas adjacent to each of the three areas in KP and two from GHP. The five cores were re-hydrated with a few ml of cooled, but boiled, water and left to infuse for 24 hours.

Government House Pond core samples

Core 1: Damp and muddy with slightly wet surface. *Lumbriculus variegatus* × 5 (2 were partial worms only), Nematode × 1.

Core 2: Drier area with no surface water. *Lumbriculus variegatus* × 8 (two had chalky-white epidermis indicating they were about to aestivate).

Kistvaen Pond core samples

Core 1: North-eastern sub-pond - Nematode × 2.

Core 2: Southern sub-pond - Psychodid larva *Pericoma* sp × 2.

Core 3: Western sub-pond - Nematode worm × 1, *Staphylinidae* beetle larva × 1 (a common predator of Nematodes and Diptera larvae).

RESULTS

A total of 36 species occur in these two ponds: 20 in GHP and 24 in KP. There are only five species that are common to both ponds, Cyprididae, *Cyclops*, *Proasellus meridianus*, Chironomidae and Psychodidae, leaving a further 31 species. Of these, three have been found nowhere else on Lundy: *Phagocata vitta* in GHP and *Dalyellia viridis* and *Rhynchosostoma rostratum* in KP, all flatworms Platyhelminthes. The remaining species can be found in other ponds on the island although the three Mollusca species of GHP are restricted in their distribution, requiring calcium in the water to produce their shell. Water chemistry depends on whether water originates from precipitation or groundwater (van der Valk, 2006) and in this case much of it percolates through the surrounding cliff faces.

One example of *Dalyellia viridis* was found in Ackland's Moor Pond (Rowland, 2014) but this was an isolated example which must have been chance dispersal and has not been found in any subsequent surveys of this or other ponds.

The majority of species are mobile except for the worms, leeches and Isopoda. However their distribution is by means of resistant eggs dispersed by wind or animals.

Government House Pond has three species that were only found on a single occasion: *Carchesium*, *Cholorohydra viridissima* and a Gammaridae species. All three were found in the initial survey of GHP before the accumulated silt was removed and have not, so far, re-colonised. Although *Gammarus duebeni* has been found in Pyramid and Punchbowl streams (Long, 1994), it has not been found in a water body on Lundy since and may have been a misidentified species. The other two species are not uncommon in other Lundy waters. Tipulidae larvae have been found on two occasions; one was recovered in 2018 as a pupa and reared to adulthood. *Philidorea ferruginea* and may be classed either as a freshwater or a terrestrial species.

KP pond has three species that have only been found once: *Polycelis nigra* and *Helobdella stagnalis* which occur in abundance in other ponds. A Tipulidae which was found towards the end of a wet period in 2018 as a pupa was reared to adulthood *Tipula oloracea* and may be classed either as a freshwater or a terrestrial species.

Carchesium and *Hydra* species have not been recovered in GHP and are not typical species of temporary ponds. They are unable to disperse without a host. Both depend on submerged substrates such as roots, aquatic plants, pilings and in the case of *Carchesium* the shells of snails on which they anchor. Thus, they may not return without introduction from other water bodies on the island.

Platyhelminthes: Flatworms (Group 1)

Three species have been recorded in KP and one in GHP. *Polycellis nigra, Dalyellia viridis* and *Rhynchosostoma rostratum* in KP and *Phagocata vitta* in GHP. *P. nigra* is ubiquitous, but the other two species have not been found in any other of Lundy's waters.

All Platyhelminthes lay eggs in cocoons and can regenerate from being cut into several pieces. Fragmentation can be induced by high temperatures which caused them to secrete slime which hardens into a cyst to resist desiccation. Regeneration of *.P vitta* can take up to 10 days once the basin becomes flooded, although *D. viridis* may take 25-40 days to accomplish this (Wiggins *et al.*, 1980).

Nematoda

Nematodes are adapted to survive in the moist substrate. These have been found in both ponds.

Annelida: true worms and leeches (Group 1)

Representative of both families have been found in both ponds*, Lumbriculus variegatus, and Helobdella stagnalis*, although *H. stagnalis* has been found only once in each. Both are common on Lundy. Leeches are known to be able to survive the dry phase by secreting a protective mucous layer after burrowing into the moist substrate. *H. stagnalis* reproduce by fragmentation after encystment although they are thought by (Cook, 1971) to survive as adults in a drought-resistant cyst.

Chelicerata: spiders and mites (Group 4)

Hydracarina sp. have been found in KP and feed on Hemiptera and Coleoptera which appear at the same time as those species. They are not uncommon in Lundy's other freshwaters.

Mollusca: snails, limpets and mussels (Group 1)

Species of this Phylum were only found in GHP represented by *Hydrobia (Potamopyrgus) jenkinsi, Pisidium personatum* and *Galba truncatula*.

H. jenkinsi has been previously recorded in all streams that were surveyed by Long (1994) but are expanding their range into ponds. Similarly, *P. personatum* has been found in most streams and some ponds (Long, 1994, Clabburn, 1994, George & MacHardy, 2004). *G. truncatula* has only been recorded in Quarter Wall Pond North (George & Sheridan, 1987) so this is a useful additional habitat.

Mollusca need calcium to produce their shell which would indicate that KP is deficient in calcium whilst GHP is not. *H. jenkinsi* is an operculate snail in that it has a horny plate with which it can seal itself into its shell producing an epiphragm which reduces moisture loss and enables the species to survive long periods without water.

Table 1: Species that occur in Government House Pond with an indication of abundance, the group to which they belong and in which season they can be found.
* denotes a not counted presence and *1 a single occurrence.
Abundance: 5>500; 4=200-499; 3=50-199; 2=5-49; 1<5

Name	**Spring (M/A/M)**	**Summer (J/J/A)**	**Autumn (S/O/N)**	**Winter (D/J/F)**	**Group**
PROTOZOA: Periticha: *Carchesium* sp.		*	*		n/a
CNIDARIA: Hydra *Chlorohydra viridissima* (Pallas)		*1			n/a
PLATYHELMINTHES: Flatworms *Phagocata vitta* (Duges)			3	3	1
NEMATODA: *Nematode* worm		1		2	
ANNELIDA: true worms and leeches					
Oligochaeta *Lumbriculus variegatus* (Muller)	3	2	2	3	
Hirudinea *Helobdella stagnalis* (L.)			*1		
MOLLUSCA: snails, limpets and mussels					
Hydrobia (Potamopyrgus) jenkinsi (Smith)		2	3	3	
Pisidium personatum (Malm)	3	2	2	4	
Galba truncatula (Muller)	1	2		2	
CRUSTACEA: shelled arthropods					
Copepoda: *Cyclops* sp		*	*	*	
Ostracoda: Family *Cyprididae* sp.	2			1	
Isopoda *Proasellus meridianus* (Racovitza)		3	3	3	
Amphipoda Family *Gammaridae* sp.		*1			
INSECTA: insects					3
Trichoptera Caddis flies *Notidobia ciliaris l*arva (L)				1	
Diptera: two-winged flies					2
Ceratopogonidae sp. larva				2	
Dixidae sp. larva				1	
Chironomidae larva	2		2	2	
Culicidae sp. larva				*	
Tipulidae Philidorea ferruginea (Meigen)			1	1	
*Psychodina*e *Pericomini sp.*				2	
Total=20 species including 3 singles	5	10	10	16	

Table 2: Species that occur in Kistvaen Pond with an indication of abundance, the group to which they belong and in which season they can be found.
* denotes a not counted presence and *1 a single occurrence.
Abundance: 5>500; 4=200-499; 3=50-199; 2=5-49; 1<5

Name	**Spring (M/A/M)**	**Summer (J/J/A)**	**Autumn (S/O/N)**	**Winter (D/J/F)**	**Group**
PLATYHELMINTHES: Flatworms					1
Polycellis nigra (Muller)			*1		
Dalyellia viridis (Shaw)	2			1	
Rhynchosostoma rostratum (Muller)	1			2	
NEMATODA: *Nematode* worm				1	
ANNELIDA: true worms and leeches					
Oligochaeta *Lumbriculus variegatus* (Muller)	1	1		1	
Hirudinea *Helobdella stagnalis* (L)			*1		
CHELICERATA: spiders and mites *Hydracarina sp*	1			1	4
CRUSTACEA: shelled arthropods					1
Cladocera:					
Simocephalus vetulus (Muller)	4	4	*	*	
Chydorus sphaericus (Muller)	5				
Ostracoda: Family Cyprididae	2			1	
Copepoda:					
Cyclops sp.	3	1	1	1	
Harpaticoidea	2				
Isopoda *Proasellus meridianus* (Racovitza)		3	2	2	
INSECTA: insects					
Ephemeroptera: *Cloeon dipterum* (L.)		1	1		2
Collembola					
Podura aquatic (L.)	1			1	
Isotomurus palustris (Muller)	1				
Hemiptera:					4
Corixia panzeri (Fieber)	1	3			
Gerris sp.	1	2			
Notonecta viridis (Delcourt)		1			
Coleoptera:					
Dytiscid sp.	2	2	1	2	
Colymbetes fuscus (L.)		*1			
Diptera: two-winged flies					2
Chironomid sp.		2		1	
Psychodidae sp.	1				
Tipulidae *Tipula oleracea* (L.)			*1		
Total=24 species including 4 singles	15	11	8	12	

No males have yet been found, but the females can contain 30-40 fully developed young within her shell making them ideally suited to survive the dry phase of a temporary pond.

Galba truncatula in an aquatic pulmonate which can breathe air and survive out of water for between 6 weeks and 4 months in its aestivated state.

Pisidium personatum can survive for up to 8 or 9 months in damp leaves.

Chelicerata: spiders and mites (Group 4)

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Pisidium personatum can survive for up to 8 or 9 months in damp leaves.

Crustacea: shelled arthropods (Group 1)

Cladocera

The water fleas *Simocephalus vetulus* and *Chydorus sphaericus* were only found in KP.

Copepoda

Cyclops sp. were found in both ponds.

Both these plankton species have been recorded since freshwater records began when Galliford began surveying (1954). Eggs can only survive as encysted eggs in bottom sediments or dry mud but have been reactivated after up to three (Wiggins *et al.*, 1980).

Cladocera can produce eggs parthenogenetically or at certain times of the year by male fertilisation. These eggs are kept in the brood chamber of the female until the ephippium is shed when she moults. These eggs are hard and thick and can remain dormant through drying and freezing until suitable conditions for development occur make them ideally suited to temporary ponds.

Harpaticoidea were found in KP only.

Ostracoda (Group 1)

Family *Cyprididae* were found in both ponds.

Eggs are highly resistant to desiccation having double-walled chitinous shells. They may have several generations a year. In temporary ponds this is restricted to one generation when diapause eggs are triggered to hatch when the pond floods.

Isopoda (Group 1)

Proasellus meridianus was found in both ponds. This is a ubiquitous species found in most of Lundy's waters. It is highly likely that this species aestivates in the ground once water has all evaporated. Adults reappear immediately after water begins to collect in the pond.

Insecta: insects (Group 2)

Ephemeroptera:

Cloeon dipterum was only found in KP; this species is common in the ponds of Lundy.

Collembola

Podura aquatic and *Isotomurus palustris* were only found in KP but these not uncommon species are probably under-recorded.

Trichoptera Caddis flies

Notidobia ciliaris larva was only found in GHP and not recorded on Lundy previously.

Insecta: insects (Group 4)

Hemiptera

Corixia panzeri was only found in KP but Corixids can be found in most other open ponds on Lundy.

Gerris sp. only found in KP which is a highly mobile species that will locate any suitable body of water and can be found widely elsewhere on Lundy.

Notonecta viridis was only found in KP, another highly mobile species that will locate any suitable body of water and can be found widely elsewhere on Lundy.

Coleoptera

Dytiscidae sp. were only found in KP both as larvae of various sizes and adults. *Dytiscidae* are a highly mobile species that will locate any suitable body of water and can be found widely on Lundy.

The most abundant larvae and adults were 3-4mm diving beetles of *Hydrophorus* sp. However occasionally much larger larvae are seen, probably of *Colymbetes fuscus*, an adult of which has been recorded on one occasion.

Diptera: two-winged flies (Group 2)

Chironomidae, *Psychodidae* and *Tipulidae* species have been found in both ponds. GHP is also host to *Ceratopogonidae*, *Dixidae* and *Culicidae* larvae.

Long (1994) recorded some of these families in the streams of Lundy that he surveyed, but despite there being little or no other records, there is no reason to believe the records of *Diptera* found in these ponds are unique.

Larvae of most *Diptera* are air breathers and therefore restricted to shallow waters; either margins or very shallow ponds. Although mosquito larvae (*Culicidae*) break this rule being able to swim, they are at greater risk in open water and so tend to favour shallow pond margins. Rat-tailed larvae (*Syrphidae*) have telescopic posterior spiracles so they can live in sediments several centimetres under water. *Eristalis*, *Holophilus* spp. are known to inhabit sites that are dry in summer. They have been seen in KP but on only one occasion by casual observation. Dipteral larvae are able to survive freezing in pond margin sediments (Drake, 2001). Mosquitoes are known to lay eggs in dry places that will be later submerged.

Diptera are highly mobile and able to colonise new sites with a long flight periods and short life-cycles. It is no surprise that both ponds are hosts to a range of Diptera species.

DISCUSSION

No comprehensive survey of either flora or fauna of the dry phase had been attempted, but a list of plants and vertebrates observed during the dry phase is worth recording.

During its dry phase, GHP is dry or at best damp mud with only ruderal plants invading from the periphery. Typically, nettles, brambles hogweed and dock stray across the area, but nothing really can achieve full succession as the regular refilling of water inhibits this. The pond is heavily shaded by shrubs and trees which may also inhibit growth.

The damp rock face on the northern edge where water can be heard and seen trickling during the wet phase does bear abundant growth of a Liverwort, Bifid Crestwort *Lophocolea bidentata* and on occasion the water surface has been covered with Lesser Duckweed *Lemna minor*.

In contrast, KP has a regular dry phase flora, when the area becomes completely grassed over with Rushes and Sedges remaining. The margins of the drying pond attract Greater Spearwort *Ranunculus lingua* whilst Marsh Pennywort *Hydrocotyle vulgaris*, Bog Pimpernel *Anagallis tenella* and Tormentil *Potentilla erecta* spread across the drying sward. Once the area is as completely dry as is possible on Lundy, Chaffweed *Cenunculus minimus* becomes established (pers. comm. Andrew Cleave). All these plants can survive inundation during winter and the dry summer phase.

Fungi are also to be found during the dry phase in the basin of KP. Scarlet Waxcaps *Hygrocybe coccinea* can be seen and the Sphagnum Brownie *Hypholoma elongatum* was seen for only the second time on Lundy in 2013. This species is known to like wet conditions and can obviously tolerate complete immersion during the winter (John Hedger, pers. comm.).

During its wet phase, KP should attract waders, but the shallow depth of mud overlying the bedrock is not conducive to there being a large number of invertebrates on which they could feed. It is exposed on the south coast with almost no cover in which to shelter from patrolling gulls and Peregrines *Falco peregrinus*. The usual range of common birds are seen, typically Meadow Pipit *Anthus pratensis*, Skylark *Alauda arvensis*, Pied Wagtail *Motacilla alba*, Wren *Troglodytes troglodytes* and warblers. More unusual species have occasionally been seen such as Dunlin *Calidris alpina*, fairly regularly, and Semipalmated Sandpiper *Calidris pusilla* in 1980 and Pectoral Sandpiper *Calidris melanotos* in 1985, both Lundy rarities (Tim Davis, pers. comm.).

KP continues to thrive in both its dry and wet phases. It provides a valuable resource to spring and autumn migrant birds and one of the few places where Chaffweed can be reliably found. It too has flatworm species unique to Lundy ponds in *Dalyelia viridis* and *Rhynchosostoma rostratum*.

Hover flies *Syrphidae* are common on Lundy. An early informal survey of KP recorded many Syrphidae larvae, rat-tailed maggots, but subsequent surveys have not recovered any examples. The larvae are known to prefer dirty and polluted waters. KP would seem to no longer be a suitable habitat.

Both these ponds whilst temporary are long-lived, GHP since at least 1870 and KP since 1852, and provide special habitats particularly for flora as well as freshwater fauna.

CONCLUSION

Compared to permanent ponds, temporary ponds are host to a smaller number of species which may be less common that those in permanent ponds. They also provide habitats for more common species that disperse from more permanent ponds once they have attained adulthood. Temporary pond specific species typically have a short life cycle – although any extended wet season allows predators to migrate into temporary ponds to take advantage of this life. This can be seen in KP when surveys late in the wet phase finds ranging Coleoptera and Hemiptera, Heteroptera taking advantage of the abundant prey in its waters. GHP has not attracted these predators but does provide an additional valuable habitat to molluscs and to the flatworm *Phagocata vitta* that has not previously been recorded on Lundy.

In 2010 GHP had completely filled in with only a few millimetre deep puddles on an infilling of mud and debris. The Lundy Conservation Team asked for advice on restoring GHP. It would appear that clearing out the silt was not a disastrous decision since almost all species have returned. It is one of the few ponds in which Mollusca occur and is an additional reservoir of this family. The difference in fauna of the two ponds can be accounted for by the substratum and cover. GHP is bounded by granite cliffs and heavily shaded by overhanging trees making it less obvious to flying insects than the open weedy location of KP.

In late autumn, both ponds benefit from increased rainfall and begin to fill. This stimulates the aestivated adults of group 1 species to emerge into the water where they complete their life cycle in a staggered sequence. Group 2 species having mated then see this newly formed water body as an attractive place in which to lay their eggs. They are followed by Group 3 species which have been dormant and are now ready to either hatch from or develop into adults from larvae. Group 4 species identify these bodies of water teeming with life as potential hunting grounds until summer dries it up and the cycle repeats.

These two temporary ponds have survived since 1852 and at least 1870 with minimal intervention. The original deepening of KP carried out by destruction of the Kistvaen (Ternstrom, 2000) gave it its current shape and depth. Any attempt to deepen it, for example to make it more attractive to waders, is impractical as the bedrock is mere centimetres below the soil level and would never retain water longer than it does now. The excavation and subsequent natural filling of GHP proved to be successful with almost all species returned. Originally it was thought that the excavation had caused it to leak, but subsequent surveys proved this to be a temporary pond which has its wet and dry phases.

Both ponds are doing well providing a home attractive to species that depend on temporary waters and benign neglect should continue to ensure their future.

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A COMPARISON OF FRUITBODY AND E-DNA SURVEY APPROACHES FOR ASSESSING THE DISTRIBUTION MYCELIA OF MACROFUNGI IN THE GRASSLAND AND HEATHLAND OF LUNDY

by

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ABSTRACT

Results of surveys of species of fungi in selected areas of Lundy which used fruitbodies to assess distribution and abundance are presented in comparison to data derived from identification of taxa from DNA sequences in extracts of soils (eDNA) from six sites on the island. Two sites were within acid grassland, four from heathland areas of *Calluna vulgaris* (Heather). The apparent restriction of *Cuphophyllus (=Hygrocybe) lacmus* (Grey Waxcap) to the Maritime heath on the North End as determined by past annual fruitbody surveys was confirmed by the abundance of its DNA in the two soil samples from the North End. *C. lacmus* DNA was absent in the soil samples from the two acid grassland sites and in one of the 'southern' *Calluna* sites, though it was present in the soil sample from the other 'southern' *Calluna* site, perhaps indicating a wider distribution on Lundy than that found by fruitbody surveys. The DNA sequence data for the soil sample from acid grassland on the Airfield are also compared with the fruitbody counts made over the past eleven years for this site and shows that for some taxa fruitbody abundance is reflected in the proportion of their DNA in the samples, for others it is not. In addition, some taxa found in the DNA profiles have yet to be found in any survey and may represent new records for Lundy. CHEGD scores derived from the DNA profiles and fruitbody surveys are compared with those of high diversity grassland sites on the mainland and confirm the high conservation status of Lundy grasslands.

Keywords: *Lundy, Macrofungi, eDNA in soil, CHEGD scores, Cuphophyllus lacmus, heathland, grassland, mycorrhizas, endophytes*

INTRODUCTION

Annual, usually week-long, surveys of the fungi have been carried out by ourselves and members of the Lundy Field Society (LFS) since 2003, usually in October and/or November, and the accreted records have been published (Hedger & George, 2004, Hedger *et al.* 2007, Hedger, J.N. 2016) and are also available on the Lundy Field Society website (www.lundy.org.uk>About Lundy>Wildlife on the island>Fungi). The recent publication of an account of the fungi of Lundy by Hedger & George (2018) lists 573 species but the total continues to rise, given that there are many common mainland fungi yet to be recorded on Lundy. These surveys indicated that distribution patterns appeared to exist for some species of fungi which may relate to Lundy habitats.

Using fruitbodies of macrofungi to assess the presence of a species, although easy to do, is widely acknowledged to be flawed, since the mycelium may be present and active, for example within the soil or wood, but may fruit rarely. Even abundant fruitings are often ephemeral and can be missed unless a site is visited frequently over a period of years. This problem has been addressed by eDNA-based survey methods in which sampling of soil or wood is used to identify the presence of mycelia of species of fungi and even to give some estimates of their relative abundance. The approach is dependent upon the existence of DNA barcodes (short tracts of DNA sequence from a specific locus obtained from identified reference fungarium samples) for the taxa. The genes used as DNA barcodes for fungi differ from those used for animals and plants. For fungi it is the ribosomal RNA locus that is used, notably the Large SubUnit (LSU) and internal transcribed spacer (ITS) regions. DNA barcodes for the waxcaps are readily available, since they have been used to determine presence of CHEGD (**C**lavariaceae, **H**ygrophoraceae, **E**ntolomataceae, **G**eoglossaceae, **D**ermoloma/Porpoloma) species in soil samples. These selected grassland fungi are used as indicators to estimate the conservation status of sites both by fruitbody surveys and by DNA profiling of soil samples (Griffith *et al.*, 2004, 2013).

Plate 1: *Cuphophyllus lacmus* (Grey Waxcap) fruiting on peaty soil with *Calluna vulgaris* (Heather) and the Lichen *Cladonia* cf. *arbuscula* on the North End of Lundy

In particular, large numbers of fruitbodies of the Grey Waxcap (*Cuphophyllus lacmus*) occur in late autumn (November and early December) on the peaty soil in the *Calluna vulgaris* (Heather) and *Cladonia arbuscula* (Antler Lichen) dominated Maritime Heath (NVC H13. jncc.defra.gov.uk) on the North End. The example shown in Plate 1 was fruiting within short Heather and the lichen close to John O'Groat's House. The ecology of this waxcap, which is found in both Europe and North America seems to be poorly understood. It is not common and is considered by some to be a grassland or even woodland species (Boertmann, 2010), whilst other field guide authors place it in poor meadows and acid heaths and moors, sometimes mentioning Heather. The strong habitat preference it appears to exhibit on Lundy thus gives the opportunity to better define the autecology of this species, especially its relationship to the Maritime Heath plant community.

The study aimed to compare the fruit body distribution of fungi on Lundy, especially that of the Grey Waxcap, with the results of fungal DNA profiling of soil samples. Six sample sites were selected: two in Maritime Heath areas dominated by *Calluna vulgaris* (Heather) at the North End, where fruitbodies of the Grey Waxcap can be abundant; two under Heather elsewhere on Lundy where it seems to be absent; two in acid grassland sites where it had also not been seen but other waxcaps were frequent. In addition at two sites, the North End and the Airfield, more detailed annual counts of fruitbodies had been made in the past, so enabling comparison with the DNA based species profiles of the soil samples from these sites.

METHODS

Field Surveys of Fruit Bodies

North End

Surveys of the Maritime Heath were usually carried out in the first week of November. Recorders using tally counters walked in a line separated by a gap of 5-10 m. The first sweep was along the west side north from St Peter's Stream to the North Light steps. This sweep was then repeated to the east across the north coast passing over John O'Groat's House. Finally, a third sweep was made down the east side south to Gannets' Coombe. Data were amalgamated as total numbers of fruit bodies recorded, nearly all of them the Grey Waxcap.

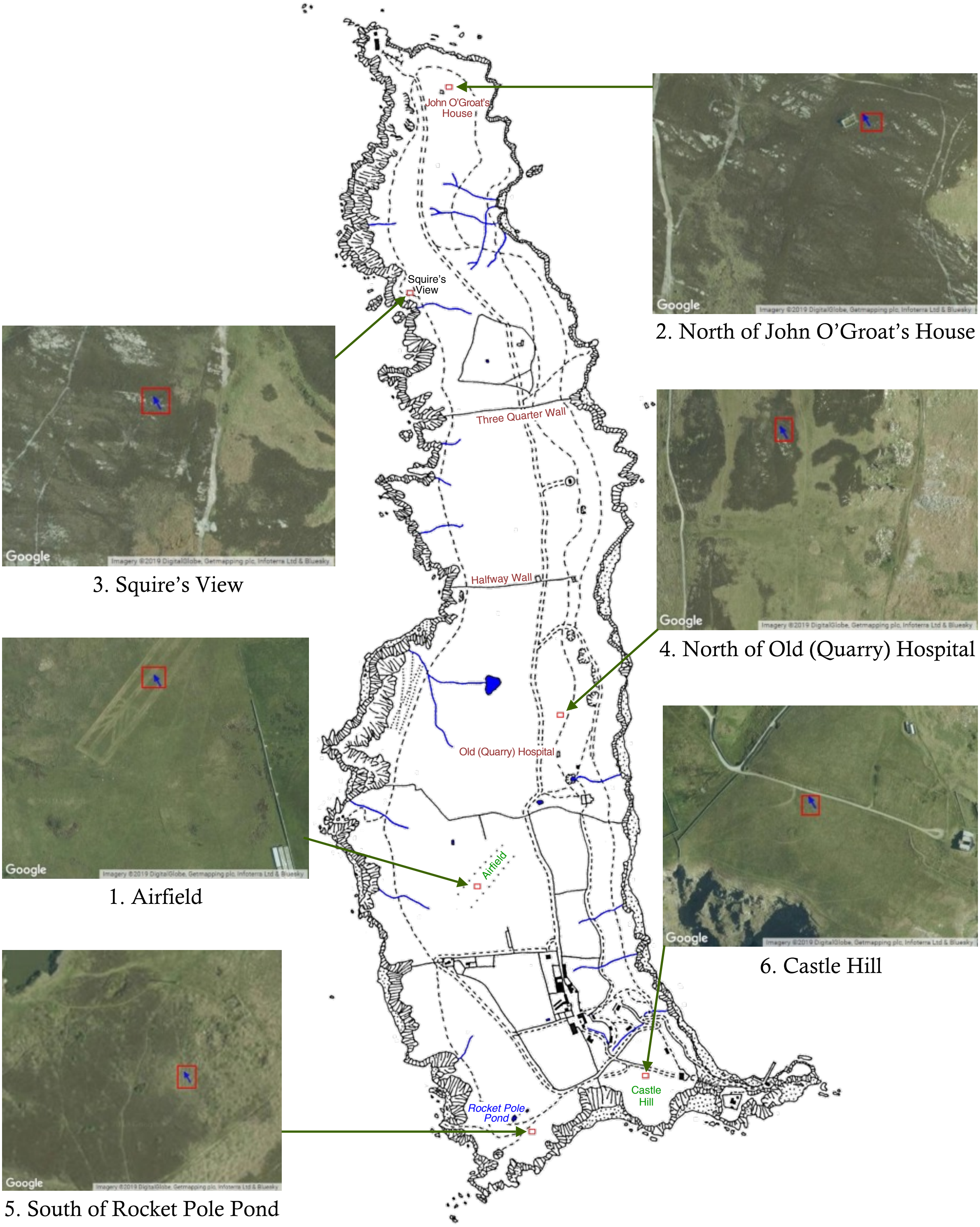
Airfield

This acid grassland site, also surveyed in the first week of November, offered the useful feature of the lines of white-washed stones on either side of the 60m wide mown landing strip. These were used to position a series of ten 6m wide transects beginning in the SW corner (Grid Reference SS132684476) and progressing along the runway for 60m, creating a sample quadrat of 60×60m (3600m^2). For each transect a centre line was walked and the species of fungi and numbers of fruit bodies recorded for approximately 3m on each side. The data were used to calculate the fruit body total for each species for the entire quadrat area.

Soil Sampling

Locations of the sampling sites

Soil sampling was conducted on 15, 16 and 17 February 2016. Air temperature was 2-5°C with no rain. Six sites were selected: two in the Maritime Heath at the North End, south of John O'Groat's House, LU2, and near Squire's View, LU3; two in apparently similar Heather dominated areas in the south of Lundy, north of Old (Quarry) Hospital, LU4, and south of Rocket Pole Pond, LU5; two from acid grassland areas, on the western end of the Airfield, LU1, within the 60×60m annual fruitbody survey quadrat, and on Castle Hill, LU6. The positions of the sites on Lundy are shown in Figure 1 and the National Grid References and longitude and latitude are given in Table 1.



2. North of John O'Groat's House

3. Squire's View

4. North of Old (Quarry) Hospital

1. Airfield

6. Castle Hill

5. South of Rocket Pole Pond

Figure 1: Map of Lundy with inset photographs of the soil sampling sites

Table 1: Details of quadrat locations and sampling dates

Site	Location	Habitat	Sample Date	UK Grid Ref	Lat.	Long.
LU1	Airfield	Acid Grassland	15/02/2016	SS1328844569	51.1698	-4.6715
LU2	North of John O'Groat's House	Maritime Heath	16/02/2016	SS1333447895	51.1997	-4.6731
LU3	Squire's View	Maritime Heath	16/02/2016	SS1317947589	51.1969	-4.6753
LU4	North of Old (Quarry) Hospital	Maritime Heath	16/02/2016	SS1375045422	51.1776	-4.6660
LU5	South of Rocket Pole Pond	Maritime Heath	17/02/2016	SS1351743624	51.1614	-4.6684
LU6	Castle Hill	Acid Grassland	17/02/2016	SS1397343830	51.1634	-4.6620

Soil Coring

Apple corers (20mm diameter) were used to take soil cores to a depth of c.5cm across a 30m×30m quadrat (900m^2) laid out using a 30m tape following a grid pattern with a spacing of c.5m between cores (see Figure 2), giving a total of 36 cores per quadrat. The size of the quadrat and pattern of sampling were as previously used in similar studies of acid grassland sites in Wales and England (Griffith *et al.*, 2018). The positions of the corners of the quadrats were recorded with GPS, photographs and other nearby landmarks. Cores from each quadrat were pooled in a plastic bag (fresh weight of c.300-500g/sample) and placed in a freezer 2-6 hours later. They were transported off Lundy in a cold box and re-stored in a freezer on the mainland prior to transport to Aberystwyth in a cold box where they were kept at -80°C before processing by freeze-drying and finely grinding by passing through a 0.5mm wire sieve. The moisture content of the samples varied from 44-72%. Following grinding, samples were thoroughly mixed and stones and larger fragments of plant material were removed. A subsample (250mg) was taken for DNA extraction using a Qiagen DNeasy PowerSoil Kit, according to the manufacturer's instructions.

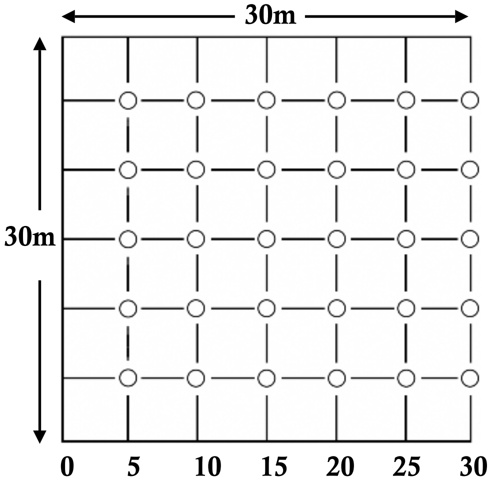


Figure 2: Grid layout of soil sampling points in the 30×30m quadrat

Plate 2: Soil sampling within a 30×30m quadrat near John O'Groat's House (photograph by Sandra Rowland)

Laboratory Methods

Genetic analysis

A 230bp portion of the Large Ribosomal Subunit (LSU) of ribosomal RNA locus was amplified with the primers GBD1-F2 and GBD1-NLC2-AF (Detheridge *et al.,* 2016, 2018). These primers are specific to fungi and bind to highly conserved regions which flank the D1 variable region of the LSU. In order to allow several samples to be sequenced in a single sequencing run, the GBD1-F2 primer contained a 10bp identifier tag. Following PCR amplification, PCR products were cleaned using Spin Column PCR Purification kit (NBS Biologicals) and the yield of DNA was quantified (Nanodrop). The samples were then pooled to give equimolar concentrations. Agarose gel electrophoresis (E-gel) was used to further purify the samples and remove any non-full length PCR products and then quantified once more using an Agilent Bioanalyser. The pooled sample DNA was then diluted to a concentration of 15nM amplified using emulsion PCR, followed by loading onto a 316 Ion Torrent chip. All the steps from emulsion PCR onwards carefully followed the instructions provided with the Ion Torrent PGM (Personal Genome Machine). The full method for DNA extraction, PCR amplification and bioinformatics analyses is published in Detheridge *et al.* (2016 and 2018).

Bioinformatic Methods

Following the sequencing run, the quality of sequences was assessed and short reads not covering the whole barcode region, sequences of poor quality, singletons/doubletons (unique sequences found only once or twice) and non-fungal sequences were removed. These sequences were then split using the 10bp identifier index tag to separate the six samples. Examination of the fungal communities (all the fungi detected) was undertaken with two ordination methods, detrended correspondence analysis (DCA) and also Non-metric Multi-Dimensional Scaling (NMDS) using the PAST3 program (http://folk.uio.no/ohammer/past/). These methods are widely used in ecology, for instance to analyse plant communities based on quadrat data, with points closer together being more closely related.

RESULTS

Fruitbody Surveys

Quantitative annual surveys of fruitbodies of species of fungi were only carried out in two of the areas where soil-sample sites were located, the North End and the Airfield. However, some qualitative data for the other sampling sites was also available, based on species location lists made over the whole island during annual visits, and is used in the discussion of the DNA profiles.

North End Survey

Large numbers of *Cuphophyllus lacmus* (Grey Waxcap) fruitbodies were found in the autumn surveys of the North End from 2013 to 2018 (Figure 3) emphasising its abundance in the Maritime Heath habitat. The size of the 'flush' of fruitbodies during the November survey week varied, most likely due to the amount of rainfall, with high numbers in damp Novembers such as 2015 and very low numbers in dry ones such as 2018. The one set of figures for December (2016) also shows that flushes can occur very late in the autumn, perhaps delayed by a dry November. However, fruitbodies of this species were never found south of St Peter's Stream on the west coast or further south than the north slopes of Gannets' Coombe on the east side, even in apparently similar Heather areas such as above the Quarries on the East Side, the slopes below Rocket Pole and above the West Coast cliffs in Middle Park.

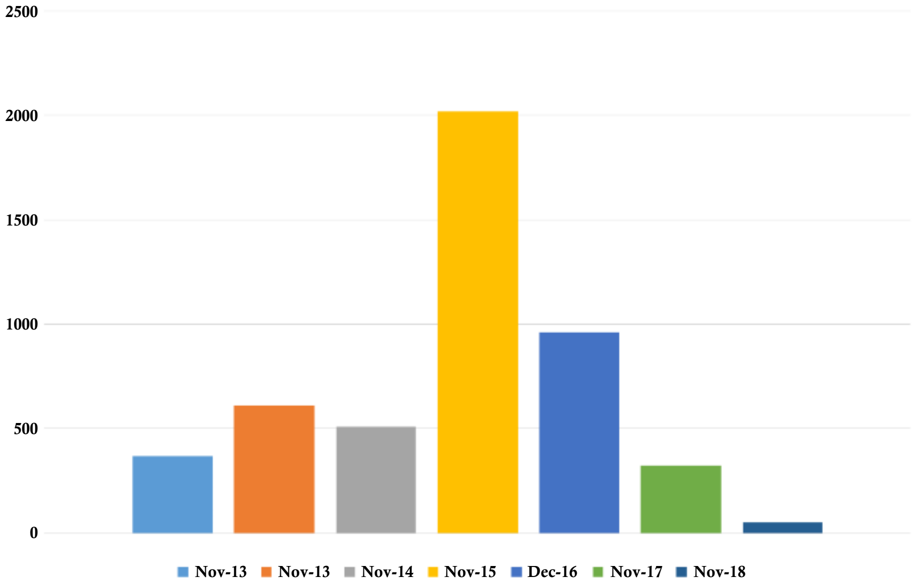


Figure 3: Totals of *Cuphophyllus lacmus* (Grey Waxcap) fruitbodies recorded in surveys of the North End from 2013 to 2018

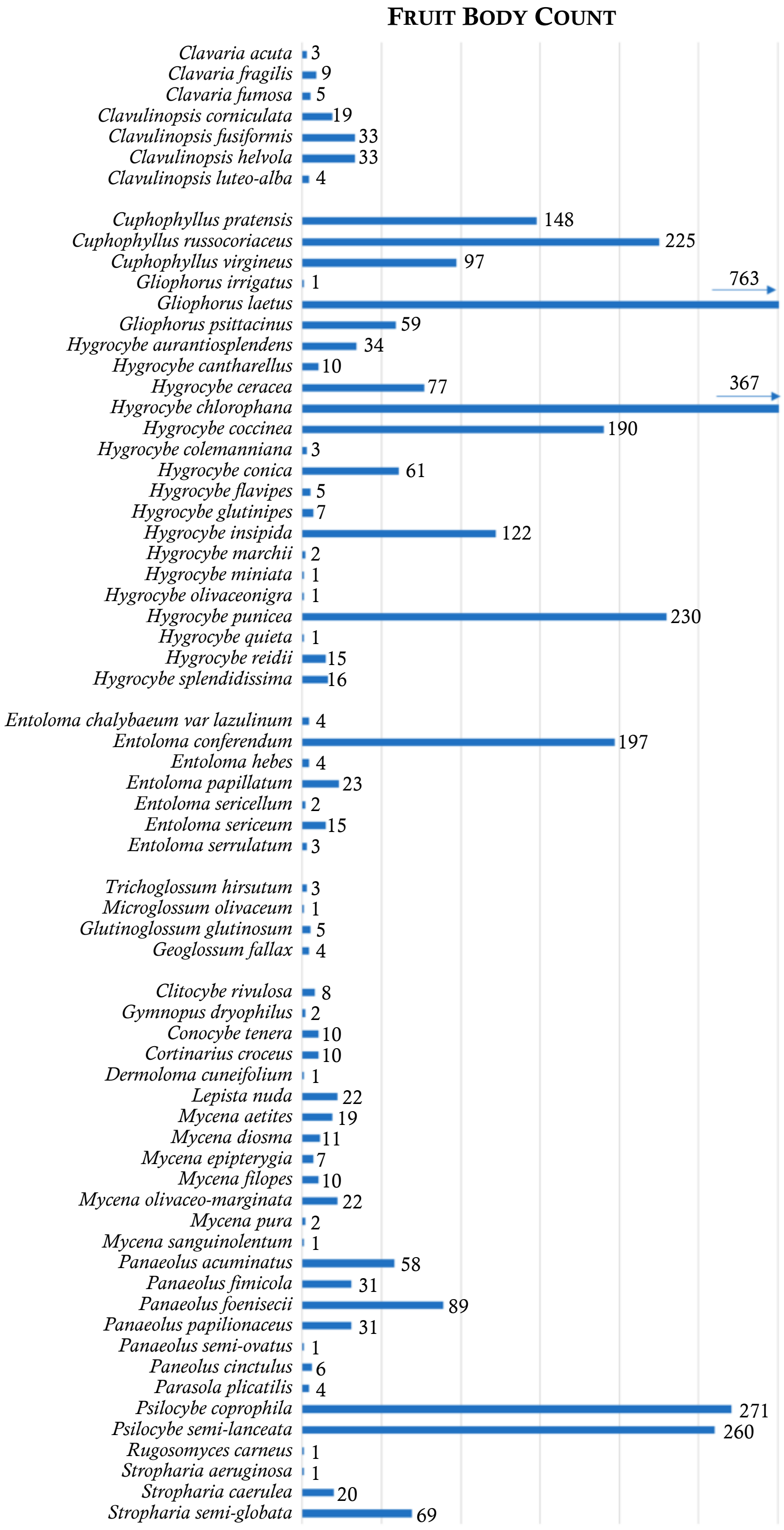


Figure 4: Numbers of fruitbodies of species of macrofungi recorded on the Airfield quadrat 2009-2018

Airfield Survey

The histogram (Figure 4) shows the totals of fruitbodies recorded by the survey on the Airfield quadrat from 2009 to 2018. The species are grouped from top to bottom in the same order as the CHEGD system: **C**lavariaceae; **H**ygrophoraceae; **E**ntolomataceae; **G**eoglossaceae; ***D**ermoloma/Porpoloma* followed by a group of 'non-CHEGD' gilled fungi.

Seven members of the Clavariaceae (Fairy Clubs) were recorded, of which *Clavulinopsis fusiformis* (Golden Spindles) and *C. helvola* (Yellow Club) were the commonest. In practice these two are difficult to distinguish without microscopy so the field distinction made on the survey may not be reliable. A detailed re-survey in November 2019 in fact showed that *C. helvola* fruit bodies were likely to have made up most of the records made in the survey. The family Hygrophoraceae has recently undergone taxonomic revision (Lodge *et al.*, 2014) and several waxcap species formerly placed in the genus *Hygrocybe* now reside in different genera, for example *Cuphophyllus* and *Gliophorus*, both of which are well-represented in the data. A total of 23 species in the Hygrophoraceae were found during the survey. The most abundant fruitbodies were of *Gliophorus laetus* (Heath Waxcap) followed by *Hygrocybe chlorophana* (Golden Waxcap) and *H. punicea* (Crimson Waxcap), all three running into hundreds over the survey period. Other species were comparatively rare, with only one or two fruitbodies found, for example *Hygrocybe miniata* (Vermilion Waxcap) and *H. quieta* (Oily Waxcap). Of the Entolomataceae (Pink Gills) *Entoloma conferendum* (Star Pinkgill) was by far the commonest species, the other six much less frequent. The Geoglossaceae were infrequently found, the four species only amounting to a total of 11 fruitbodies found over 11 years of search. *Dermoloma cuneifolium* (Crazed Cap), was only found once.

The most abundant components of the final grouping of 'non CHEGD' gill fungi in Figure 4 are species which are associated with or grow on the sheep dung on the Airfield such as *Psilocybe semilanceata* (Liberty Cap), *P. coprophila* and species of *Panaeolus*, *Panaeolina* and *Stropharia*. Grassland fungi, often found in meadow surveys in association with the CHEGD fungi, include the seven species of *Mycena* (Bonnets), *Lepista nuda* (Wood Blewit) and *Clitocybe rivulosa* (Fool's Funnel).

Analysis of Sequence Data

A total of 251,436 sequence reads for the LSU D1 locus were obtained across the six quadrat samples (range 29,971 to 71,805 per sample). For the initial analyses, sequences were classified to genus level using the RDP database (Ribosomal Database Project; http://rdp.cme.msu.edu/classifier/). The RDP analysis uses a Naïve Bayesian Classifier to classify sequences to genus level but where suitable matching DNA barcodes are absent, sequences are classified to higher taxonomic orders (Table 2). Green highlighting means the sequence is >5% of the fungal DNA, a white background 0.1-5.0% and a pink background <0.1%. The CHEGD taxa make up a high proportion of the sequences. Clavariaceae are highlighted in yellow, Hygrophoraceae in orange, Entolomataceae in purple. Geoglossaceae are present but none were ranked higher than 64th, so do not appear on Table 2.

Phylum	Class	Order	Family	Genus	Ecology	Count	Cumul. Total	Mean	Median	Max	Min	Lu1	Lu2	Lu3	Lu4	Lu5	Lu6
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	Cuphophyllus4_lacmus	MR CHEG	5	96.85%	16.14%	2.83%	73.76%	0.00%	0.00%	73.76%	17.41%	0.05%	5.61%	0.02%
Ascomycota	Leotiomycetes	Helotiales	Leotiaceae	Rhizoscyphus ericae	MR DSE	5	55.67%	9.28%	3.58%	26.62%	0.00%	0.00%	6.05%	26.62%	21.88%	1.11%	0.01%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	Hygrocybe_sgPS1_punicea	MR CHEG	2	47.08%	7.85%	0.00%	47.06%	0.00%	47.06%	0.03%	0.00%	0.00%	0.00%	0.00%
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	OTU 6: unknown	MR DSE	6	41.53%	6.92%	7.33%	12.79%	1.09%	1.09%	4.22%	12.79%	10.43%	10.69%	2.31%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavulinopsis_CPFU	MR CHEG	4	30.84%	5.14%	3.44%	16.10%	0.00%	6.88%	0.00%	0.00%	0.01%	16.10%	7.85%
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	Dermoloma_cuneifolium	MR CHEG	1	22.68%	3.78%	0.00%	22.68%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	22.68%
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	Mycena	SAP SOIL	6	15.00%	2.50%	1.89%	5.36%	0.63%	0.63%	1.12%	1.51%	5.36%	4.12%	2.27%
Basidiomycota	Agaricomycetes	Trechisporales	Trechisporaceae	OTU 11: unknown	SAP SOIL	6	12.03%	2.00%	1.46%	5.07%	0.86%	1.13%	0.86%	2.05%	1.48%	1.43%	5.07%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	Cuphophyllus1_pratensis	MR CHEG	5	11.46%	1.91%	0.12%	7.74%	0.00%	3.46%	0.00%	0.11%	0.03%	0.13%	7.74%
Ascomycota	Leotiomycetes	Helotiales	Leotiaceae	OTU 12: unknown	MR DSE	4	11.39%	1.90%	0.06%	9.18%	0.00%	0.00%	0.02%	2.09%	9.18%	0.11%	0.00%
Ascomycota	Eurotiomycetes	Chaetothyriales	Cyphellophoraceae	OTU 10: unknown	MR DSE	6	10.91%	1.82%	1.76%	3.76%	0.01%	0.01%	2.26%	3.76%	1.25%	3.62%	0.01%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	Hygrocybe_sgPS2_reidii	MR CHEG	1	9.31%	1.55%	0.00%	9.31%	0.00%	9.31%	0.00%	0.00%	0.00%	0.00%	0.00%
Ascomycota	Leotiomycetes	Helotiales	Helotiaceae	OTU 9: unknown	MR DSE	5	9.07%	1.51%	1.22%	4.70%	0.00%	0.01%	0.56%	1.91%	4.70%	1.89%	0.00%
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	OTU 13: unknown	MR DSE	2	9.02%	1.50%	0.00%	7.86%	0.00%	0.00%	1.16%	0.00%	7.86%	0.00%	0.00%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavulinopsis_CPCO	MR CHEG	4	8.35%	1.39%	0.06%	6.65%	0.00%	6.65%	0.00%	0.11%	0.00%	0.01%	1.58%
Ascomycota	Leotiomycetes	Helotiales	Leotiaceae	OTU 23: unknown		6	8.14%	1.36%	0.83%	3.75%	0.01%	0.03%	0.92%	2.68%	3.75%	0.75%	0.01%
Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	Hyaloscypha	MR DSE	4	7.25%	1.21%	0.97%	2.89%	0.00%	0.00%	0.47%	1.47%	2.89%	2.42%	0.00%
Basidiomycota	Agaricomycetes	Trechisporales	Trechisporaceae	Trechispora	SAP SOIL	6	7.11%	1.18%	0.60%	4.50%	0.05%	0.20%	0.11%	1.01%	0.05%	4.50%	1.24%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	OTU 310	MR CHEG	6	6.54%	1.09%	0.01%	6.45%	0.00%	0.01%	0.00%	0.01%	0.01%	0.04%	6.45%
Ascomycota	Leotiomycetes	Helotiales	X	OTU 16	MR DSE	5	6.26%	1.04%	0.72%	3.65%	0.00%	0.03%	0.54%	1.15%	3.65%	0.90%	0.00%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavulinopsis_CPLA	MR CHEG	6	5.54%	0.92%	0.14%	3.41%	0.01%	1.83%	0.01%	0.12%	0.01%	0.16%	3.41%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavaria_CVAR	MR CHEG	6	5.36%	0.89%	0.40%	3.70%	0.04%	0.71%	0.24%	0.55%	0.04%	3.70%	0.12%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	OTU 22	MR CHEG	3	5.29%	0.88%	0.00%	5.27%	0.00%	5.27%	0.02%	0.01%	0.00%	0.00%	0.00%
Ascomycota	X	X	X	OTU 18		5	5.24%	0.87%	1.02%	1.76%	0.00%	0.00%	0.65%	1.39%	1.76%	1.39%	0.05%
Ascomycota	Leotiomycetes	X	X	OTU 17		4	5.14%	0.86%	0.47%	3.22%	0.00%	0.00%	0.46%	0.48%	0.97%	3.22%	0.00%
Ascomycota	X	X	X	OTU 37		5	4.87%	0.81%	0.85%	1.80%	0.00%	0.05%	0.50%	1.21%	1.80%	1.31%	0.00%
Ascomycota	Leotiomycetes	Helotiales	X	OTU 26	MR DSE	4	4.61%	0.77%	0.14%	3.74%	0.00%	0.00%	0.02%	0.27%	3.74%	0.58%	0.00%
Fungi incertae sedis	Mortierellomycotina	Mortierellales	Mortierellaceae	Mortierella	SAP	6	4.12%	0.69%	0.54%	1.95%	0.11%	0.58%	0.11%	0.34%	0.50%	0.64%	1.95%
Ascomycota	Archaeorhizomycetes	Archaeorhizomycetales	Archaeorhizomycetales	Archaeorhizomyces	SAP SOIL	5	3.99%	0.66%	0.27%	2.58%	0.00%	0.03%	0.13%	2.58%	0.83%	0.41%	0.00%
Basidiomycota	Agaricomycetes	X	X	OTU 20		4	3.75%	0.62%	0.43%	1.65%	0.00%	0.00%	0.76%	1.23%	1.65%	0.10%	0.00%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	Hygrocybe_sgH5_glutinipes	MR CHEG	4	3.58%	0.60%	0.04%	3.31%	0.00%	0.19%	0.00%	0.07%	0.00%	3.31%	0.01%
Basidiomycota	Agaricomycetes	Trechisporales	X	OTU 32		3	3.51%	0.58%	0.09%	3.12%	0.00%	0.20%	0.00%	0.00%	0.00%	0.18%	3.12%
Basidiomycota	X	X	X	OTU 21		2	3.19%	0.53%	0.00%	3.15%	0.00%	0.04%	0.00%	0.00%	0.00%	0.00%	3.15%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Camarophyllopsis_atrovelutina	MR CHEG	4	2.81%	0.47%	0.02%	2.75%	0.00%	2.75%	0.00%	0.00%	0.01%	0.03%	0.03%
Basidiomycota	Agaricomycetes	Agaricales	Entolomataceae	OTU 36	MR CHEG	5	2.66%	0.44%	0.12%	2.11%	0.00%	0.22%	0.00%	0.02%	0.02%	2.11%	0.29%
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	OTU 44		5	2.52%	0.42%	0.20%	1.60%	0.00%	0.51%	0.00%	0.03%	0.01%	0.36%	1.60%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavulinopsis_CPCR	MR CHEG	3	2.50%	0.42%	0.04%	2.01%	0.00%	0.40%	0.00%	0.00%	0.00%	2.01%	0.08%
Ascomycota	Leotiomycetes	Thelebolales	Thelebolaceae	Thelebolus	SAP DUNG	4	2.25%	0.37%	0.05%	2.03%	0.00%	0.08%	0.00%	0.00%	0.02%	0.11%	2.03%
Basidiomycota	Tremellomycetes	Filobasidiales	Piskurozymaceae	Solicoccozyma		6	2.18%	0.36%	0.26%	0.94%	0.01%	0.43%	0.01%	0.09%	0.09%	0.63%	0.94%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Ramariopsis_RMKU	MR CHEG	6	1.82%	0.30%	0.07%	0.91%	0.01%	0.74%	0.01%	0.03%	0.02%	0.91%	0.11%
Ascomycota	Leotiomycetes	Helotiales	Helotiaceae	Cudoniella	MR DSE	6	1.82%	0.30%	0.30%	0.60%	0.09%	0.09%	0.14%	0.34%	0.26%	0.38%	0.60%
Ascomycota	Eurotiomycetes	Eurotiales	Trichocomaceae	Penicillium	SAP SOIL	6	1.73%	0.29%	0.18%	0.62%	0.05%	0.05%	0.14%	0.56%	0.62%	0.13%	0.23%
Ascomycota	Leotiomycetes	Helotiales	Sclerotiniaceae	Torrendiella	MR DSE	6	1.62%	0.27%	0.22%	0.52%	0.04%	0.04%	0.15%	0.46%	0.29%	0.52%	0.16%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavaria_CVAC	MR CHEG	4	1.45%	0.24%	0.04%	0.69%	0.00%	0.69%	0.00%	0.04%	0.00%	0.69%	0.03%
Ascomycota	Leotiomycetes	X	X	OTU 51		4	1.45%	0.24%	0.10%	1.12%	0.00%	0.00%	0.10%	0.09%	0.14%	1.12%	0.00%
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	OTU 40	MR DSE	5	1.40%	0.23%	0.08%	1.06%	0.00%	0.15%	0.00%	0.01%	0.02%	0.16%	1.06%
Basidiomycota	Agaricomycetes	Agaricales	Tricholomataceae	OTU 291		6	1.34%	0.22%	0.09%	0.59%	0.02%	0.06%	0.05%	0.11%	0.02%	0.59%	0.51%
Ascomycota	Leotiomycetes	Helotiales	X	OTU 62	MR DSE	5	1.31%	0.22%	0.09%	0.62%	0.00%	0.14%	0.00%	0.04%	0.00%	0.62%	0.50%
Fungi incertae sedis	Mortierellomycotina	Mortierellales	Mortierellaceae	OTU 323		6	1.30%	0.22%	0.19%	0.55%	0.05%	0.05%	0.06%	0.10%	0.27%	0.27%	0.55%
Ascomycota	X	X	X	OTU 347		5	1.24%	0.21%	0.04%	1.04%	0.00%	0.04%	0.03%	0.04%	0.08%	1.04%	0.00%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	Cuphophyllus3_roseascens	MR CHEG	1	1.19%	0.20%	0.00%	1.19%	0.00%	0.00%	0.00%	0.00%	0.00%	1.19%	0.00%
Basidiomycota	Agaricomycetes	Agaricales	Hygrophoraceae	Hygrocybe_sgPS4_cantharellus	MR CHEG	2	1.14%	0.19%	0.00%	1.13%	0.00%	1.13%	0.00%	0.00%	0.00%	0.01%	0.00%
Basidiomycota	Agaricomycetes	Sebacinales	X	OTU 45		5	1.12%	0.19%	0.11%	0.50%	0.00%	0.00%	0.17%	0.37%	0.50%	0.06%	0.02%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Ramariopsis_RMPU	MR CHEG	3	1.10%	0.18%	0.06%	0.68%	0.00%	0.30%	0.00%	0.00%	0.00%	0.12%	0.68%
Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Clavulinopsis_CPX1	MR CHEG	4	1.10%	0.18%	0.18%	0.42%	0.00%	0.26%	0.00%	0.11%	0.00%	0.42%	0.31%

Table 2 (opposite page): Raw output from RDP analysis of the DNA metabarcoding data for the six Lundy quadrats. Taxa are ranked by cumulative percentage abundance over all six quadrats, with the top 55 (of the 607 taxa) shown here. On the left side, key taxonomic groupings are highlighted in orange (waxcaps), yellow (fairy clubs), pink (pink gills), cracked caps (brown) and dark septate endophyes (green). On the right side, percentage abundance of each taxon (as percentage of the total fungal community) is shown with most abundant taxa highlighted in green (>5%) and least abundant (<0.1%) in red

The DNA barcode sequences present in the RDP database analyses are mostly derived from publicly available sequence data submitted to the GenBank database (http://www.ncbi.nlm.nih.gov/nuccore/EF537888.1). For the CHEGD fungi (waxcaps and associated taxa) Griffith (unpublished data) has previously undertaken extensive DNA barcoding from reference samples (i.e. fruitbodies identified to species level by microscopic analysis), in addition to the reference DNA sequence available on GenBank. These sequences have been added to our in-house version of the original RDP database and the standard generic classifications in RDP have been modified to allow classification at species level. For CHEGD fungi there is sufficient variation at the LSU D1 locus to allow this to be undertaken for all the species of CHEGD, thus allowing better identification than the original RDP database. However, for Entolomataceae (Pink Gills), limited DNA barcode data from reference samples, and various other taxonomic uncertainties relating to this group, make it difficult to link sequences to recognised species.

For some other taxonomic groups, there are fewer DNA barcode sequences available and not all distinct DNA sequences have to date been linked to named species (or possibly relate to species not yet known to science); this results in less precise identification (i.e. only to family or order level). These taxa are listed as numbered OTUs (operational taxonomic units). Analysis of the entire fungal community in the six quadrats revealed the presence of 607 taxa across all the samples (a range of 244-443 OTUs per sample).

Summary data derived from Table 2 are presented in Table 3, showing relative abundances of the various CHEGD fungi as well as abundances of major mycorrhizal groupings. CHEGD species comprise the majority of fungal biomass in the two grassland quadrats LU1 (Airfield) and LU6 (Castle Hill) but also in LU2 (north of John O'Groat's House), due to the predominance of *C. lacmus* at this site.

Table 3: Summary data for the fungal communities in the six Lundy quadrats

Site	**CLAV**	**HYG**	**ENT**	**GEOG**	**DERM**	**Total CHEGD**	**AMF***	**DSE**-Helotiales**	**DSE**-Chaetothyriales**
LU1	22.0%	67.6%	0.5%	0.2%	0.0%	**90.3%**	0.21%	0.80%	1.24%
LU2	0.3%	74.0%	0.0%	0.1%	0.0%	**74.4%**	0.00%	7.80%	4.32%
LU3	1.0%	18.2%	0.1%	0.4%	0.0%	**19.7%**	0.02%	33.82%	13.77%
LU4	0.1%	0.6%	0.1%	0.4%	0.0%	**1.2%**	0.02%	45.20%	10.55%
LU5	25.8%	10.9%	2.4%	0.9%	0.0%	**40.0%**	0.16%	9.32%	11.05%
LU6	16.2%	15.1%	0.4%	0.3%	22.7%	**54.7%**	0.42%	4.09%	3.41%

* AMF=Arbuscular Mycorrhizal Fungi (Glomeromycota)
** DSE=Dark Septate Endophytes

The most numerous non-CHEGD taxa were members of the ascomycete orders Helotiales and Chaetothyriales, together known as dark septate endophytes (DSE; highlighted in green on Table 2) These fungi are commonly found associated with the roots of higher plants and several have been shown to form mycorrhizal associations with their hosts. The most abundant DSE taxon was *Rhizoscyphus ericae*, which forms ericoid mycorrhizal associations with *Calluna* and related ericaceous hosts (Read, 1983; Hambleton & Sigler, 2005). This was most abundant in the Heather-dominated quadrats. Other DSE (OTU6; OTU9; OTU10; OTU12; OTU13) were also abundant in the Heather-dominated quadrats. However, the taxonomy of these fungi remains poorly understood and these five taxa could only be classified to family level due to the absence of closely related DNA barcodes.

It is commonly stated that grassland habitats are dominated by arbuscular mycorrhizal fungi (AMF) belonging to the phylum Glomeromycota (Smith & Read, 2010). However, whilst AMF were more abundant in grassland compared to heathland habitats (see Table 3), they comprise only a small amount of the total fungal DNA (<0.5%). Despite being present at only low levels, it is possible that they are highly active and may thus ‘punch above their weight’ in ecological terms. DSE are also known to be associated with grasses and herbs (Wilberforce *et al.*, 2002) and thus were also present but at lower abundance in the grass-dominated quadrats (LU1/LU6 in Table 3).

Further Analysis of the Data

Further analysis sought to examine the whole fungal community in comparison to other grassland soils we have analysed (mostly from Wales) and more specifically to determine the presence of CHEGD target species in comparison to records of their fruitbodies on Lundy.

Ordination analysis

Initial analysis of the fungal communities in the six Lundy quadrats (LU1-6) by either NMDS or DCA ordination (Figure 5) was undertaken alongside similar community data from ‘top quality’ waxcap grassland sites in Wales (coded as CCW). In such analyses, samples which ordinate closely together have similar fungal communities. LU1 (The Airfield) is clearly close to the most diverse Welsh waxcap meadow sites. LU6 (Castle Hill), although grassland, is much more of an outlier. Of the four Lundy heathland sites, LU2 and LU3 from the North End show greatest separation from the grassland sites, with LU4 and LU5 occupying an intermediate position. LU5 (south of Rocket Pole Pond), was the closest and also had a more diverse plant community of grasses and forbs as well as Heather.

Detailed analysis of CHEGD fungi

For more detailed analysis of CHEGD fungi, BLAST analysis of the sequence data against the curated database on CHEGD sequences was undertaken (Table 4).The most abundant 55 fungal taxa across the six Lundy sites ranked by cumulative numbers of sequences are shown. Columns on the right hand side indicate the percentage of all fungal sequences for each taxon at each site. This yields similar data to the RDP analysis but taxonomic resolution is more accurate. For each CHEGD species, the number of sequences detected for each species in each quadrat is shown. In some cases, many

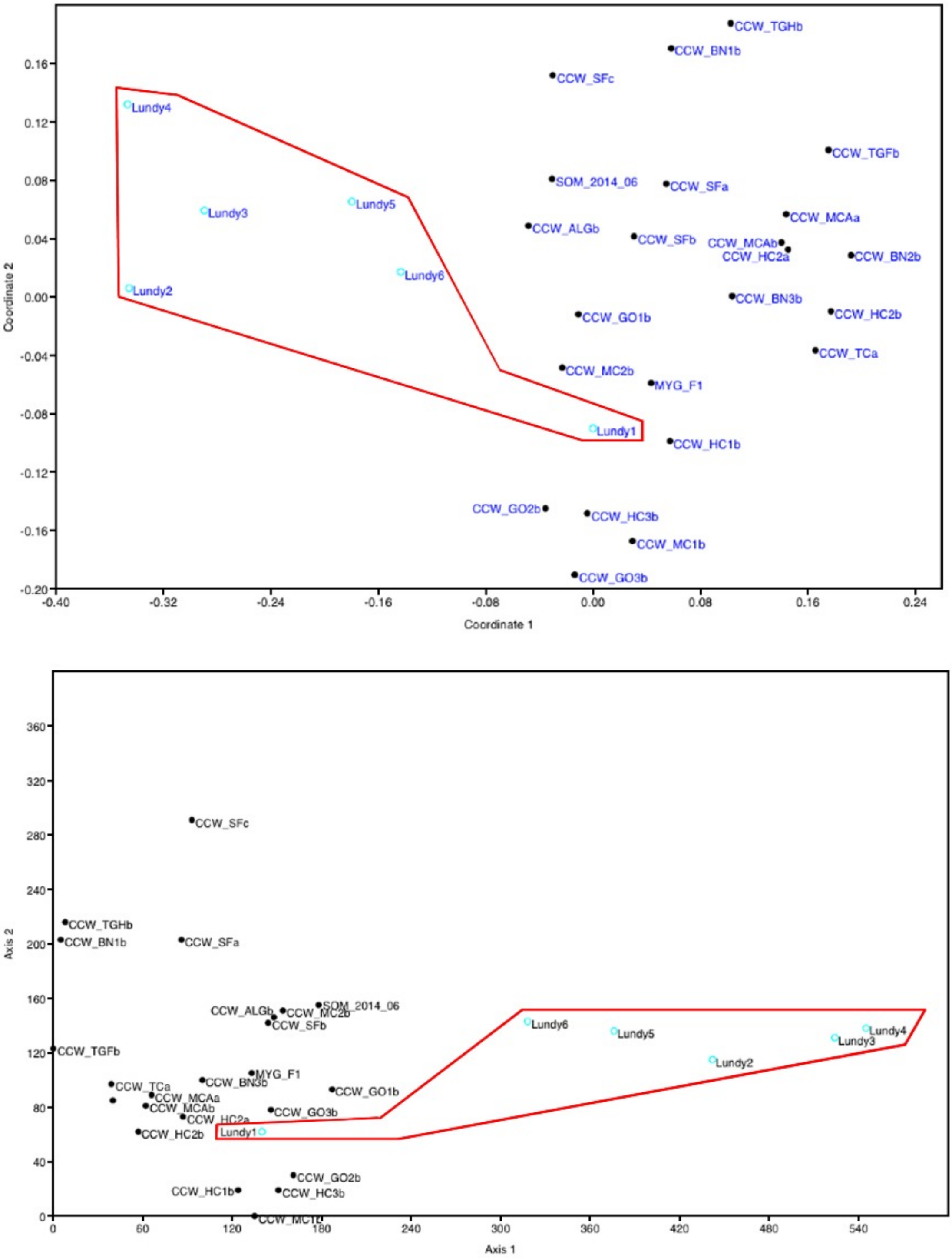


Figure 5: Non-metric MultiDimensional Scaling (NMDS; upper) and Detrended Correspondence Analysis (DCA; lower) ordination of Lundy fungal community data (encircled in red polygons) alongside data from 'top quality' waxcap grasslands in Wales. Samples ordinated more closely together have more similar fungal communities

Table 4: BLAST analysis of fungal sequence data for CHEGD fungi, showing number of sequences for each species found in each quadrat soil sample. CHEGD totals are for species with >50 eDNA sequence reads. *Cuphophyllus lacmus* (Grey Waxcap) reads are shown in bold font

		Lu1	Lu2	Lu3	Lu4	Lu5	Lu6	Total Sequence Reads	Total Quadrats (/6)
C	*Camarophyllopsis atrovelutina*	1052	.	.	3	9	10	1074	4
C	*Clavaria acuta*	264	.	17	.	246	11	538	4
C	*Clavaria argillacea*	.	167	188	.	6	.	361	3
C	*Clavaria fragilis*	5	6	20	.	71	12	114	5
C	*Clavaria guilleminii*	178	.	.	3	28	.	209	3
C	*Clavaria straminea*	264	8	31	11	1095	11	1420	6
C	*Clavulinopsis corniculata*	2544	.	45	.	5	853	3447	4
C	*Clavulinopsis helvola*	170	.	.	.	.	742	912	2
C	*Clavulinopsis laeticolor*	500	7	47	3	35	391	983	6
C	*Clavulinopsis luteoalba*	2686	.	.	4	5828	2844	11362	4
C	*Ramariopsis biformis*	285	9	13	5	326	38	676	6
C	*Ramariopsis pulchella*	61	.	.	.	.	93	154	2
	Clavariaceae spp. unknown	366	.	51	.	1433	551	2401	4
H	*Cuphophyllus fornicatus*	.	48	.	.	.	.	48	1
H	*Cuphophyllus lacmus*	.	**52829**	**7079**	**15**	**2008**	7	61938	5
H	*Cuphophyllus pratensis*	1323	.	43	9	47	2687	4109	5
H	*Cuphophyllus roseascens*	.	.	.	.	426	.	426	1
H	*Cuphophyllus russocoriaceae*	5	3	6	3	16	2270	2303	6
H	*Cuphophyllus virgineus*	.	.	.	.	.	55	55	1
H	*Gliophorus irrigatus*	19	.	.	3	.	4	26	3
H	*Gliophorus psittacinus*	51	.	10	.	10	.	71	3
H	*Hygrocybe cantharellus*	431	.	.	.	4	.	435	2
H	*Hygrocybe ceracea*	3	.	.	.	.	18	21	2
H	*Hygrocybe chlorophana*	14	.	.	.	.	96	110	2
H	*Hygrocybe conica*	343	42	45	12	150	3	595	6
H	*Hygrocybe contrictospora*	.	.	.	.	.	10	10	1
H	*Hygrocybe glutinipes*	71	.	30	17	1208	4	1330	5
H	*Hygrocybe helobia*	2016	13	3	.	.	.	2032	3
H	*Hygrocybe mucronella*	.	.	.	.	.	101	101	1
H	*Hygrocybe pseudoconica*	5	.	.	.	.	.	5	1
H	*Hygrocybe punicea*	17994	20	.	.	.	.	18014	2
H	*Hygrocybe quieta*	9	.	.	9	7	.	25	3
H	*Hygrocybe reidii*	3565	.	.	.	.	.	3565	1
E	*Entoloma conferendum*	85	.	7	5	757	101	955	5
E	*Entoloma porphyrophaeum*	.	6	38	7	8	.	59	4
E	*Entoloma sp.*	.	.	.	4	75	24	103	3
E	*Entoloma serrulatum*	31	.	.	.	3	.	34	2
E	*Inocephalus sp.*	85	.	.	.	4	.	89	2
G	*Geoglossum fallax*	17	.	.	.	43	97	157	3
G	*Geoglossum umbratile*	.	.	.	.	6	.	6	1
G	*Glutinoglossum glutinosum*	46	.	9	.	72	16	143	4
G	*Glutinoglossum heptaseptatum*	.	.	.	.	18	.	18	1
G	*Glutinoglossum pseudoglutinosum*	.	.	.	.	3	.	3	1
G	*Trichoglossum hirsutum*	.	.	.	.	5	.	5	1
G	*Trichoglossum walteri*	.	.	5	.	138	.	143	2
G	*Geoglossaceae spp. unknown*	27	.	.	.	16	.	43	2
"G"	*Microglossum olivaceum*	.	3	.	.	55	.	58	2
D	*Dermoloma cuneifolium*	.	.	.	.	.	7874	7874	1
	Total no. fungal sequences	38278	71805	40754	29971	35903	34725	251436	
	Total no. CHEGD sequences	34515	53161	7687	113	14161	18923	18923	

Clav	10	1	2	0	6	6	13
Hyg	8	1	1	0	4	5	14
Ent	2	0	0	0	2	1	4
Geo	0	0	0	0	3	1	4
Derm	0	0	0	0	0	1	1
CHEGD total	20	2	3	0	15	14	36

thousands of sequences of a single species are detected in a single quadrat indicating the large amount of mycelium of these species in those particular quadrats (e.g. 17,994 sequences of *H. punicea* in the soil sample from quadrat LU1 on the Airfield). However, other species are present at only low abundance in the sequence data and could represent much smaller colonies, potentially indicative of the presence of only spores or small mycelia which might not be large enough to form fruitbodies. This issue makes it difficult to draw direct equivalence between the numbers of species found by eDNA analysis and fruitbody surveys. In deciding how many sequences should be detected in a quadrat for a particular species to be added to the CHEGD total, we have opted to use a threshold of 50 sequences (Table 4). Thus, quadrat LU1 (Airfield) had the highest CHEGD species count (20) followed by quadrats LU5 (below Rocket Pole Pond) and LU6 (Castle Hill) at 15 and 14 respectively. The high CHEGD score at LU5 would indicate that this area, in spite of its selection as a *Calluna* site for the soil survey, has strong affinities with acid grassland.

Across all the quadrats, 14 waxcap species were detected at >50 eDNA sequence reads and a further six species at lower (<50 sequence reads) abundance. Comparing the data in Table 4 for species of fungi detected in the soil sample from the Airfield site (LU1) with the species found over the Airfield fruitbody survey period (Figure 4) some patterns emerge. Firstly in terms of numbers of Hygrophoraceae, eight taxa were recorded at >50 e DNA reads and a further six at <50 reads i.e. a total of fourteen. 23 species were recorded from the annual fruitbody surveys and included twelve of the taxa appearing in the sequence data, the exception being *H. acutoconica*, recorded on Lundy as *H. persistens* (Persistent Waxcap) but not yet found on the Airfield, and *H. helobia* known only from Quarter Wall Cottages. For some species there was a good fit between abundance of fruitbodies in the survey and proportion of its DNA in the sample: *Hygrocybe punicea* (Crimson Waxcap) DNA was over 40% of sequences in the Airfield soil sample and its fruitbodies were one of the most abundant recorded in the survey (a total of 230), as well as some of the largest, so presumably having a large supporting mycelium in the soil (compare Table 3 and Figure 4). A weaker correlation is seen for *Cuphophyllus pratensis* (Meadow Waxcap) (2.8% of the DNA sequences/148 fruitbodies recorded).

For others, the fit between DNA profiles of samples and the survey data was less good. *Hygrocybe reidii* (Honey Waxcap), accounting for over 7% of the sequences in the sample, was only found 15 times and *Hygrocybe cantharellus* (Goblet Waxcap), 0.77% of the sequences, was only found ten times. On the other hand, fruitbodies of some species absent or at <0.15% of the fungal DNA, such as *Hygrocybe chlorophana* (Golden Waxcap), *Gliophorus laetus* (Heath Waxcap) and *Hygrocybe coccinea* (Scarlet Waxcap), were abundant in all years of the Airfield survey. These contradictions may be related to the smaller area of the soil sampling grid compared to the fruitbody count area, perhaps missing localised mycelia of some species and over-emphasising the presence of others.

The second component of the CHEGD system for which we feel some confidence in the DNA barcoding data is the family Clavariaceae with nine taxa at >0.15% of the fungal DNA in the Airfield soil sample. Seven taxa were identified in the fruitbody survey (Figure 4) but only two of these, *Clavulinopsis helvola* (Yellow Club) and *Clavulinopsis (=Ramariopsis) corniculata* (Meadow Coral), were detected from soil eDNA (Table 4). As noted earlier, field identifications of another *Clavulinopsis* species, *C. fusiformis* (Golden Spindles) do not separate it with certainty from *C. helvola*, so records made in the fruitbody surveys of the Airfield were probably of *C. helvola* not *C. fusiformis*. The taxonomy of this family is difficult so the exact status of taxa in databases remains uncertain. However the data suggest that the Airfield grassland has a number of Clavariaceae yet to be recorded as fruitbodies from Lundy.

Sequence data for Geoglossaceae (Earthtongues) are also presented in Table 4. Two species, *Geoglossum fallax* (Black Earthtongue) and *Geoglossum* (=*Glutinoglossum*) *glutinosum* (Slimy Earthtongue), were also found as fruitbodies (Figure 4) so may be more widespread on the Airfield than the low fruitbody numbers suggest.

Seven species of *Entoloma* were found in the Airfield survey, of which one, *E. conferendum* (Star Pinkgill), was abundant in most years (Figure 4) and also occurred as the greatest number of sequences in the soil extracts (Table 4). *E. serrulatum* (Blue Edge Pinkgill) fruitbodies were much less frequent but it was also detected as DNA sequences. Recovery of Entolomataceae DNA sequences from soil samples is usually much lower than for the other CHEGD components, perhaps reflecting lower mycelial biomass in the soil or low DNA content.

The other grassland site from which a soil sample was taken, Castle Hill, LU6, has not had any systematic annual counts of fruitbodies but has had brief species surveys every autumn. The tall rank grass, due to undergrazing for many years following the crash in the Rabbit population in 2005, makes it difficult to find fruitbodies of fungi. Fourteen CHEGD species sequences were detected at >50 eDNA sequence reads of the fungal DNA (Table 4). Four were Clavariaceae, all of them species of *Clavulinopsis* (=*Ramariopsis*) – *C. corniculata* (Meadow Coral), *C. helvola* (Yellow Club), *C. laeticolor* and *C. luteoalba* (Apricot Club). Of these only fruitbodies of *C. helvola* and *C. corniculata* had been found to be common in surveys of Castle Hill, together with *C. fusiformis* (Golden Spindles), which, as in the Airfield site, does not appear in the sequence data. *C. luteoalba* (Apricot Club) has been recorded for Lundy (Hedger & George, 2018), but not on Castle Hill. *C. laeticolor* would be a new record, now confirmed by the finding of fruit bodies of this species on Castle Hill in November 2019. Of the Hygrophoraceae, *Cuphophyllus pratensis* (Meadow Waxcap) was well represented in the DNA sequences and is the only waxcap regularly seen on Castle Hill, possibly because its large size makes it easier to find in the long grass. The much smaller *H. russocoriacea* (Cedarwood Waxcap) sequences have almost the same value but the fruitbodies have never been found. Of the Entolomataceae *E. conferendum* (Star Pinkgill) is the only species regularly recorded from Castle Hill and is also the only representative in the DNA profile. As with the Airfield site Geoglossaceae were a small percentage of the fungal DNA but the same two species, *Geoglossum fallax* and *G. glutinosum,* were detected though never found in the field. The one surprising feature of the Castle Hill data is the abundance of DNA of *Dermoloma cuneifoleum* (Crazed Cap), a CHEGD species not found in the profiles of any of the other five sites but fruitbodies have never been seen on Castle Hill though recorded from the nearby St John's valley.

In contrast, as expected, *Calluna* sites at the North End LU2 (John O'Groat's House) and LU3 (Squire's View) and in the south at LU4 (north of Old (Quarry) Hospital) had CHEGD species counts of 0-3 of which one component, *Cuphophyllus lacmus*, accounted for over 73% of the total fungal DNA at LU2 (John O'Groat's House) and over 17% at LU3 (Squire's View) (as bold figures in Table 4). Both quadrats are within the areas where the annual surveys found fruitbodies of this species. *C. lacmus* DNA was also detected in the soil samples from the two 'southern' *Calluna* sites. It was a trace (0.05%) at LU4 (north of Old (Quarry) Hospital) but accounted for over 5% at LU5 (below Rocket Pole Pond), although its fruitbodies have never been found in either place. It is clearly a much less important component of the soil mycota here. Its DNA was not detected in any of the grassland soil samples on Lundy, LU1 (Airfield) and LU6 (Castle Hill).

DISCUSSION

Up to now the study of the distribution of fungi on Lundy has been by assessment of presence (and absence) of fruitbodies in different areas of the island. This has enabled assignment of species to different terrestrial habitats, an approach used by Hedger and George in their 2018 account of the fungi of Lundy. The relatively new use of eDNA profiling to identify fungi in the habitat can directly prove the presence and even abundance of the mycelium of each species. To date only one study of this kind has been carried out on Lundy, by Monk *et al.* (2014) who used DNA profiling to investigate colonisation of *Rhododendron* stumps on the east side by sampling wood at different stages of decomposition. Their data were rich in sequences of wood rotting taxa, for example species in the family Polyporaceae, some of them new to Lundy.

Our study has focused on sequences of taxa likely to be found in grassland, the CHEGD species, with especially rich information on the waxcaps. It has confirmed that restriction of the fruitbodies of one these fungi, the Grey Waxcap, *Cuphophyllus lacmus*, to the Maritime Heath on the North End of Lundy reflects the real distribution of its mycelia, although it may be present at low levels in soil at other Heather sites. This habitat preference may be because of a mycorrhizal relationship with Heather and/or as a mycobiont partner. Several lines of evidence suggest that waxcaps (and likely other CHEGD) are not saprotrophs, as previously suspected, but rather mycorrhizal with grasses and/or herbs (Griffith *et al.*, 2014). Halbwachs *et al.* (2018) presented isotopic evidence consistent with a mycorrhizal habit, and the hyphae of waxcap have been detected within the roots and shoots of putative plant hosts (Halbwachs *et al.*, 2013; Tello *et al.*, 2014). However, association with ericaceous hosts has not previously been observed. Another possibility is that *C. lacmus* forms an association with lichens such as the foliose *Cladonia arbuscula,* another major component of the Maritime Heath. Both are novel ideas, requiring further supporting evidence. More soil DNA profiling of a range of Heather sites on Lundy, together with evaluation of their plant communities and soil characteristics, is needed as well as a search for *C. lacmus* DNA in samples of Heather roots and in lichen thalli.

The CHEGD system was developed to help evaluate the conservation status of grassland sites. Of the six Lundy sample sites, two were from grassland, the Airfield and Castle Hill. The DNA profiles of the former ordinated close to data from known 'high quality' meadow sites on the mainland. The CHEGD value derived from the DNA data for the Airfield site was 20 (see Table 4), from fruitbody count it was 40 (see Figure 4); the fruitbody count must be higher both due to the eleven-year monitoring period and the much larger sampling area. CHEGD counts using fruitbody surveys on other unimproved grassland sites on Lundy since 2003 have often been in the region of 10-20 species and the island 'total CHEGD' score, derived from the current species total of fungi, is 72 (Hedger & George, 2018). These figures show that the current management of Lundy has created short turf habitats that are rich in species of grassland fungi and underlines the value of Lundy grasslands for conservation of fungal diversity.

The question as to whether DNA sequence data can be used as new records of fungal species in the absence of fruitbody identifications remains open and depends upon the reliability of the databases used. Table 4 includes six highlighted (>50 eDNA sequence reads) species of Clavariaceae (Club Fungi) not yet seen on Lundy, although we are not confident as to the exact current status of some of them. There is also a possible new waxcap record for Lundy. *Cuphophyllus roseascens*, 0.8% of the fungal sequences from the site below Rocket Pole Pond (LU5), is a small pinkish capped waxcap which was first described in Sweden in 2004 and is rare in the UK.

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ECOLOGY OF COMMON GUILLEMOTS ON LUNDY: CHICK PROVISIONING 2008-2019

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ABSTRACT

Provisioning activity of Common Guillemots (*Uria aalge*) was studied at the same ledge on Lundy over ten breeding seasons between 2008 and 2019. Parental attendance decreased and productivity increased over the study period. The increased population of Guillemots on Lundy could be the cause of these changes, but changes in the food-web of the Celtic Sea could also be a factor. Parental attendance was significantly lower in the latter part of the 2012 season associated with the only time that a chick was abandoned.

Keywords: *Lundy, Common Guillemot*, *parental attendance, productivity, chick provisioning, breeding phenology*

INTRODUCTION

The Common Guillemot (*Uria aalge* Pont) or Common Murre is a large (c.950g), long-lived seabird of the auk family (Gaston & Jones, 1998). They occur in the north of the Pacific and Atlantic Oceans and in the Arctic Ocean. Guillemots breed on sea-cliffs in tightly-packed ledges or in rocky crevices, often in mixed colonies with other seabirds. Breeding adults make no nest but instead their egg or chick is sheltered under the body or wing of one parent. In the southern areas of their range, they return to these breeding colonies from mid-October onwards.

Breeding phenology varies with sea temperature; the start of egg-laying in Arctic colonies can be a month later than those in Britain or California. A single egg is laid and parents take turns in incubating, with one parent present except in times of food shortage. Egg-laying is more synchronised within a ledge than between different ledges of the same colony. Eggs are lost to predators or accidentally knocked from ledges due to high breeding density. A replacement egg (or occasionally second replacement egg) can be laid if the first egg is lost. Only one chick is raised per season, although Harris *et al.* (2000) reported a case where a pair successfully raised an orphan as well as their own chick to fledging age. That pair increased their foraging time at the expense of time spent at the colony.

Hatching is a long process; from the first hole appearing to the final emergence of the chick can take around two days. The chick and its parents learn each other's calls during hatching which allows behavioural separation on the physically crowded ledge. Calls from the chick encourage the brooding adult to roll the egg which allows the chick to extend the hole around the wide end of the egg. Calls from the adults encourage the chick to continue to chip away at the egg (Tschanz, 1968).

Newly hatched chicks are carefully protected by their parents and are difficult to see. The presence of a chick can sometimes be confirmed by changes in the behaviour of its brooding parent. The most obvious change in parental behaviour is returning to the ledge with a fish. This is not always conclusive, as Guillemots will occasionally attempt to feed their egg. Parents take turns in brooding their chick, again with one parent present in all but exceptional times. The off-duty parent will either spend time at the ledge or away from the ledge (flying, washing, and foraging for themselves and for their chick). Guillemots can vary their foraging effort to compensate for variations in food availability, either by switching to alternative prey fish, or by increasing the amount of time spent foraging (Burger & Piatt, 1990). Decreased attendance at times of low food availability has been seen in Norway (Tschanz, 1979), eastern Canada (Birkhead & Hatchwell, 1984, Burger & Piatt, 1990), Scotland (Uttley *et al.*, 1994, Monaghan *et al.* 1994, Wanless *et al.*, 2005, Ashbrook *et al.*, 2008), and Alaska (Zador & Piatt, 1999, Harding *et al.*, 2007). Parental attendance reached a plateau of 12 minutes per hour in Cook Inlet, Alaska, at moderate to high fish abundance (Harding *et al.*, 2007b). The Isle of May recorded mean parental attendance of 16.7% over 17 seasons from 1981.

Pairs that have lost their egg or chick will sometimes brood a neighbouring chick (Tschanz, 1968). This allobrooding can be beneficial to the chick, especially in times of low food availability when chicks may by left unattended while both parents forage (Birkhead & Hatchwell, 1984).

Foraging adults return to their chick with one fish at a time (single-prey loading), usually held lengthways in their bill. The returning adult half-opens its wings to ‘tent’ its chick whilst the fish is transferred. Older chicks will take the fish directly from their parent. Younger chicks will wait until the fish is dropped and then take it from the ground. Provisioning rates count the number of fish delivered per chick in a given time. Different colonies have different feeding areas, so normal provisioning rates vary from colony to colony. When combined with the size and species of fish, provisioning rates can give an estimate of the total energy intake of a chick. Fish fed to chicks at UK colonies are mainly Sandeels, clupeids (Sprats and Mackerel) or gadioids (Whiting, Cod) (Anderson, 2014).

At times of severe food shortage, adults may abandon their chick to feed themselves. This behaviour allows long-lived seabirds to maximise their breeding success over their life time at the expense of a single chick. Unlike large Gulls, adult Guillemots will only kill neighbouring chicks in times of extreme food stress (Ashbrook *et al.*, 2008). In these cases, it is only birds feeding their own chick that will kill neighbouring chicks; failed breeders still show alloparental behaviour towards unattended chicks.

Guillemot chicks fledge after two to three weeks of being fed on the breeding ledge. At this age they can regulate their own temperature but are unable to fly. They go to sea with the male parent who continues to feed his chick until it is able to feed itself. Captive chicks were able to pick up fish from the bottom of a tank a week after ‘fledging’. Fledging can fail through predation, or through communication failure between the chick and adult (Greenwood, 1963 & 1964).

Female Guillemots stay on the breeding ledge after their chick and partner have departed. They may stay for another two weeks in normal conditions, but can leave after a few days in times of low food availability. Their partners may return to the ledge if fledging fails.

STUDY SITE

Lundy is a three-mile long granite island located where the Bristol Channel meets the Atlantic Ocean. It is the largest seabird colony in south-west England. Guillemot numbers increased from 3,302 birds on breeding ledges in 2008 to 6,198 birds in 2017 (Booker *et al.*, 2018). This increase was after the RSPB-led Seabird Recovery Project. The count of 4,114 birds in 2013 (Price *et al.*, 2014) was the then highest number recorded on Lundy since the Second World War when seabird numbers in the Bristol Channel were decimated due to increased oil pollution from shipping losses (Birkhead, 2016). The previous highest post-war count was 3,910 in 1956 when Barbara Snow was the LFS warden (Davis & Jones, 2007).

The first major study of Guillemots on Lundy was by Richard Perry in 1939 (Perry, 1940). Perry made detailed descriptions of the breeding behaviour of Guillemots as well as Razorbills, Puffins and Kittiwakes. He estimated that the population of Guillemots was 19,000. Since then Guillemot research has concentrated on ringing (LFS 1940s-1960s), first-flighting (Greenwood, 1963), breeding success (Taylor, 1970s), population (David Price, RSPB, 1980s-present), comparative feeding ecology (Birkhead *et al.*, 1986, Hatchwell *et al.*, 1992) and productivity (various wardens, 2007-present e.g. Dalrymple, 2008, Wheatley & Saunders, 2010, 2011).

The feeding ecology of Guillemot chicks on Lundy (specifically chick diet, provisioning rates and feeding trip duration) was compared with nearby islands in the mid-1980s. In 1985, Lundy was compared with Skomer and Great Saltee (Birkhead *et al.* 1986). In a continuation of that study in 1986, Lundy was compared with Skomer (Hatchwell *et al.*,1992). These studies showed Guillemots from the Lundy and Skomer colonies had different feeding areas: feeding-trip durations were too short for birds from each colony to fly to the same feeding area. Relative proportions of Sprats and Sandeels in the diet of chicks were also different in each colony.

Although feeding areas are different, there is movement of non-breeding birds between these three islands. An immature Guillemot ringed on Skomer was later seen on Great Saltee (Birkhead & Hudson, 1977). Birds ringed as chicks on Skomer have been recorded on Lundy (Taylor, 2015), and one of these was re-sighted on Skomer five days after being seen on Lundy (Tim Birkhead, pers. comm.). One of the adult birds for this study was ringed as a nestling on Great Saltee in 2000.

METHODS

Provisioning data were collected on Lundy over ten breeding seasons from 2008 to 2019, using a video recorder. Data were not collected in 2009 and 2017 due to injuries. Data collected for this study were from a site that has been recorded since 23 June 2008 near St Philip's Stone on the west coast of Lundy (SS130462). This ledge is part of colony F4 on the Lundy Seabird Colony Register and was viewed from location Fe (SS1318046354, Price *et al.*, 2008) and from a location near Ff in 2018 and 2019. Up to 19 pairs of adults have been recorded on this ledge in any one year with a maximum of 15 chicks seen in any one year. The ledge was mostly observed in the morning, but afternoon and evening sessions were also recorded. Only morning sessions were used for this study as provisioning rates can vary with the time of day and there were insufficient afternoon or evening sessions to give significant comparisons. Lower air temperature in morning sessions also leads to stable air and less air turbulence which gives better recordings at high magnification.

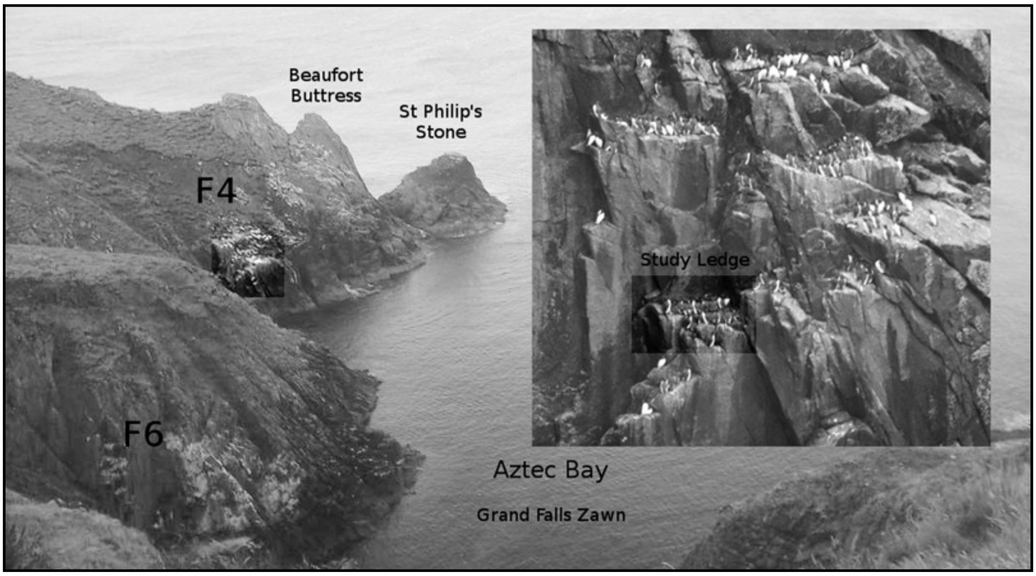

Plate 1: Position of the survey ledge on the west coast of Lundy. Different people have named features on Lundy. St Philip's Stone is attributed to Barbara Snow, Aztec Bay is in Williams (2001). Beaufort Buttress and Grand Falls Zawn have been named by the climbing community (Harrison, 2007). The most consistent method of labelling seabird sites is to use the Seabird Colony Register. This survey ledge is in F4 highlighted with increased contrast. The inset photograph shows the position of the survey ledge within F4

The camera was a Canon XL2 video camera which allows Canon SLR lenses to be used with an effective increase in focal length of around 7×. The site was first recorded with a Sigma 70-300mm APO lens, and later with a Canon 100mm-400mm L lens. In 2015, a 1300mm focal length telescope was attached to the video camera which allowed one of the birds to be identified from its metal leg ring. The camera records Standard Definition 25p PAL video on to 60-minute miniDV tapes; in practice these tapes produce just over 62 minutes of usable video. The tapes were captured onto computer using Sony Video Capture 6.0e and edited using Sony Vegas Pro 8.0c. Corrupt video at the beginning or end of a recording was deleted. Only the first 60 minutes of video was used to calculate provisioning rates and parental attendance. In 2018 a Canon 1100D DSLR camera was used to record 720p HDV on to an SD card in 15-minute segments. In 2019 a Canon 200D DSLR camera was used to record 1080p HDV on to an SD card in 29m 59s segments.

Focal sites were identified by the presence of an incubating or brooding adult, or by the presence of a pair of birds. Pairs were identified by mutual interactions, particularly by mutual preening, although adults also preen neighbouring birds (Lewis *et al.*, 2007). Adults returning to the ledge engage in greeting behaviour with their partner. Both birds stand and stretch their bills skywards and give a call. Their bill will be open if they are not carrying a fish. This greeting will sometimes elicit the same behaviour in neighbouring pairs.

Table 1: Number and length of observing sessions per year

	Length of observing session							
Year	31m	60m	53m+60m	2×60m	8×15m	4×29m59s	3×60m	4×60m
2008				**34**				**14**
2010		**7**		**34**				
2011	**13**		**13**	**20**				
Early 2012 (<23 Jun)				47				
Late 2012 (>23 Jun)				52			7	
Total 2012				**99**			**7**	
Early 2013 (<29 Jun)				57				
Late 2013 (>29 Jun)				67				
Total 2013				**124**				
Early 2014 (<1 Jul)				51				
Late 2014 (>30 Jun)				65				
Total 2014				**116**				
Early 2015 (<24 Jun)				60				
Late 2015 (>24 Jun)				50				
Total 2015				**110**				
Early 2016 (<25 Jun)				43				
Late 2016 (>25 Jun)				63				
Total 2016				**106**				
Early 2018 (<27 Jun)					42			
Late 2018 (>27 Jun)					52			
Total 2018					**94**			
Early 2019 (<15 Jun)						52		
Late 2019 (>15 Jun)						84		
Total 2019						**136**		
Totals	**13**	**7**	**13**	**643**	**94**	**136**	**7**	**14**
Grand total of all observing sessions 2008-2019=927								

Plate 2: Positions of all the focal sites within the survey ledge. Most focal sites were occupied ever year from 2008 to 2019. The site H was vacant in 2014 after the storms of the previous winter. The pair at site J tried to push in between pairs E and F in 2015 and 2016 but did not manage to produce a chick. By 2018, the pairs at F and G had moved right to fill the gap left at site H. Site U was only occupied in 2013 and 2015

Recording sessions

Data for each session was collected in two, one-hour tapes in the morning. Three types of data were transcribed from the tapes: arrival time, departure time, and whether an arriving adult was carrying a fish. Data was only recorded for adults known to have chicks. Provisioning Rate was recorded using the method outlined by Wanless & Lewis (2006). Productivity was recorded using the method outlined by Walsh *et al.* (1995). The most difficult observation was the presence or absence of young chicks. Small signs of their presence became easier to detect as the study progressed. Chicks are brooded underneath or against the side of the adult's body. The chick's head is sometimes underneath the adult's wing. The chick's bill can sometimes be seen directly, or sometimes be assumed by the movement of the adult's secondary feathers. Video from earlier years was re-transcribed to check for young chicks. A small number of chicks were not detected on occasional days but were present in the observing sessions before and after. Longer observing sessions would make it easier to detect all of the chicks that are present on any one day.

Parental Attendance

Parental attendance has been measured in different ways at different colonies. The Isle of May records percentage of non-brooding parents present at noon. Cook Inlet, Alaska, recorded total time in minutes that either parent was present over an hour. This was measured either by direct observation or by time-lapse camera.

In this study, parental attendance for each chick was recorded as the percentage of time to the nearest second that its non-brooding adult was present at the ledge during each 2h (2008-2018) or 1h59m56s (2019) session. Attendance could vary between 0% if only one parent was present to 100% if both parents were present for the whole session. On some occasions in 2012, both parents of the chicks on sites F and N were away from the ledge at the same time. Chick F 'Foxtrot' was allobrooded by the chickless pair from site G. Chick N 'November' was left alone on the ledge without protection. This lack of attendance could have been recorded as a negative percentage. The abandonment of 'Foxtrot' and 'November' represent two different decisions for their parents, so any attendance less than 0% was treated as 0% on these occasions (Tony Taylor, pers. comm.).

Analysis

Each measurement (parental attendance, provisioning rate and productivity) had a distribution of values for each year. Parental attendance and provisioning rates did not have normal distribution and were skewed towards zero. Means of each year were calculated and trends were found using the linear model function in R. Each year's distribution is a sample of the whole distribution for each year as not every day is recorded and only 2 hours are recorded. The variation between the distributions for each year was analysed in two ways. In the first method, the Kolmogorov-Smirnov test was used to compare distributions pairwise year-against-year. This method assumes that the recorded distribution for each year is representative of the whole season. In the second method, the yearly distributions were combined to produce an all year distribution. This all year distribution was then compared against each year using the Kolmogorov-Smirnov test. This second method assumes that every year is part of the same distribution and therefore any tested year has to be more extreme to show a significant difference.

RESULTS

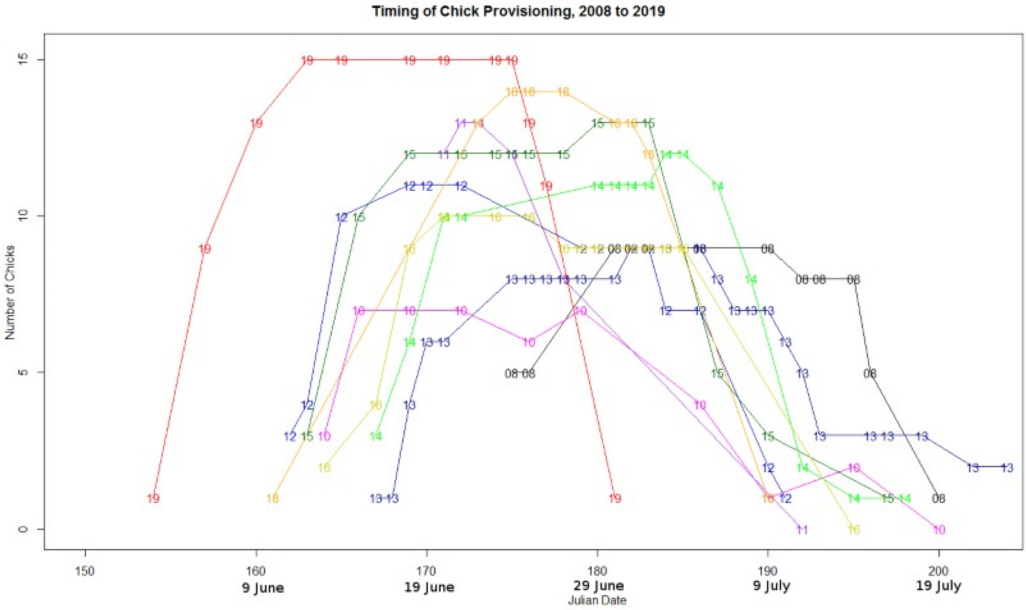

Figure 1: Numbers of chicks observed on the survey ledge during the ten seasons of observation. Each year is colour-coded and labelled as a two-digit year (e.g. the 2008 season is labelled 08). The Julian date is the day of the year taking 1 January as 1. Calendar dates are for non-leap years

Timing of Chick Provisioning

The number of chicks present each year peaked within a three-week window. The timing of that window varied from year to year. 2008 was the latest date that chicks were present (peak 23 June-14 July). 2019 was the earliest date that chicks were present (peak 6 June-26 June). Hatching was early in 2011; observations were not started until most chicks had hatched. The date at which half the chicks had left the ledge in 2011 was similar to 2019 (27 June).

Parental Attendance

Parental Attendance showed a slight decrease over the study period (-0.44% per year, t-statistic p=0.06). Mean parental attendance for the whole study period was 14.6%

Taking each breeding season as a whole, parental attendance was significantly lower in 2012 (9.5%) and 2018 (9.3%) (Komogorov-Smirnoff test, year vs all years, p=0.0712 and p=0.0189 respectively) and significantly higher in 2014 (20.3%, p=0.0094).

The seven observed breeding seasons between 2012 to 2019 were split into early and late observations. For the early part of each season, parental attendance was lowest in 2018 but this was not very significant (K-S test, early year vs all early years, p=0.149). For the late part of each season, parental attendance was significantly lower in 2012 (5.8%, p=0.0055, K-S test late year vs all late years) and significantly higher in 2014 (20.1%, p=0.0257).

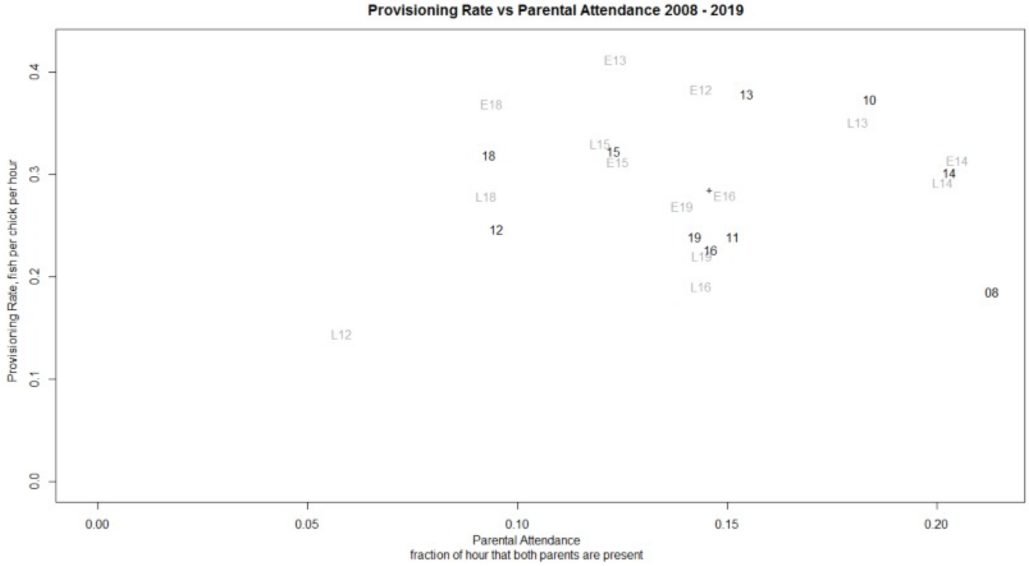

Figure 2: Provisioning rates plotted against parental attendance for the ten seasons. Bold labels as Figure 1. Grey labels for the seven seasons that were also split into early and late sections (e.g. L12 is the late part of the 2012 season

Provisioning Rates

Mean provisioning rate for the study period was 0.285 feeds/chick/hour. There was no significant trend over the ten seasons. Provisioning rates varied from 0.185 feeds/chick/hour in 2008 to 0.379 feeds/chick/hour in 2013. Rates were significantly higher in 2013 compared to 2011, 2012 and 2016 (p=0.0259, p=0.0872 and p=0.0604 respectively, K-S test, pair-wise year vs year). Rates were also significantly higher in 2018 compared to 2011 (p=0.0827).

When split into early and late observations, provisioning rates in late 2013 were significantly higher than in late 2012 (p=0.0407, K-S test, pair-wise late year vs late year).

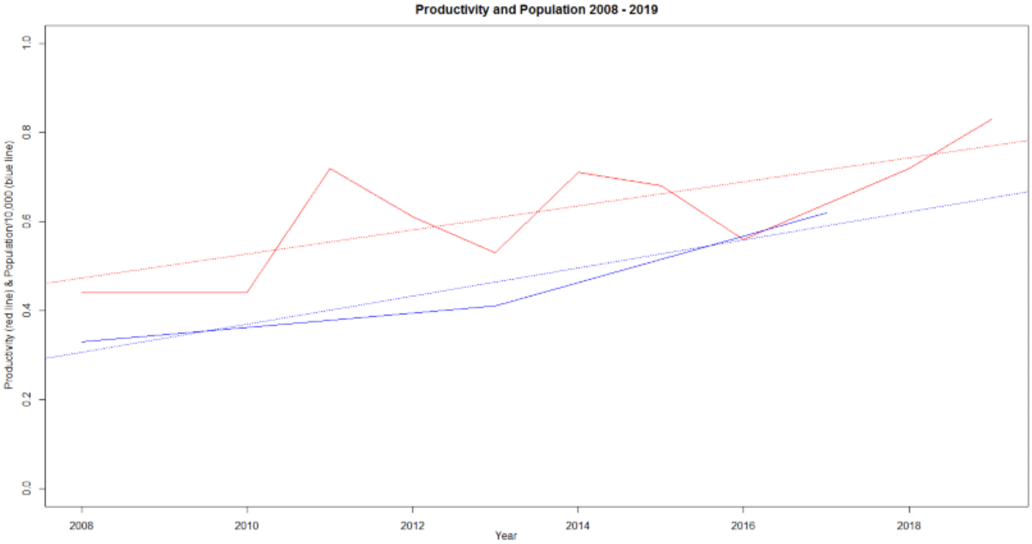

Figure 3: Productivity (red line using maximum value in 2011) from this study and population (blue line, in 10,000s) from Booker (2018) plotted over the survey. Dotted lines are linear models using R

Productivity

There were 181 active or regular sites over the ten breeding seasons of the study. These sites hatched 121 chicks of which 107 chicks were observed until at least 15 days old. This gives a mean productivity of 0.59 chicks per site. Productivity increased over the study. 2011 was difficult to assess due to early hatching and might range from 0.39 to 0.72 chicks fledged per site. Assuming an average productivity in 2011 of 0.55 then productivity increased significantly over the study period (3.1% per year, p=0.0037). Assuming the highest productivity in 2011 showed a reduced but still significant increase (2.7% per year, p=0.012). More eggs hatched in 2011 (15 eggs hatched) than in 2010 (9) and 2012 (11). More eggs failed to hatch in 2016 (5 eggs failed) than in 2015 (3) and 2018 (none).

DISCUSSION

Comparisons of data between Guillemots at different colonies should be made with care. Birds from relatively close colonies can feed in different areas (Birkhead *et al.*, 1986, Hatchwell *et al.*, 1992). The physical characteristics of a particular ledge limit the number of birds present, and departing and returning birds can knock neighbours from the ledge. Comparisons of a particular sub-colony over a number of breeding seasons allow us to put unusual events into context. The late 2012 event on Lundy showed lower than average parental attendance and provisioning rates as well as the only cases of intentional chick abandonment during the survey period.

Parental Attendance

Parental attendance declined slightly over the study period. A top-down explanation could be that there is Storer-Ashmole Halo (cf. Elliot *et al.*, 2009) effect taking place: that the increased population of seabirds on Lundy is reducing the populations of sprats and sandeels around Lundy. The reduced populations of prey species would increase the amount of time that adult Guillemots spend away from the ledge. The largest historical count of Guillemots on Lundy was approximately 19,000 pairs in 1939. We have no quantitative information on parental attendance in Perry's survey. If we make the conservative assumption that these 19,000 pairs are the most that the seas around Lundy can support, then the current population of 6,198 birds is still far from, but heading towards, that total. Parental attendance returned to 20% in 2014; a top-down interpretation could relate this to the large number of seabird deaths in the storms of 2013-14 (Lock, 2014).

A bottom-up explanation for the slight decline in parental attendance could be changes in the Celtic Sea food-web have decreased stocks of Sprats and Sandeels around Lundy. These changes are difficult to apply to Lundy because we have no long-term data set on parental attendance to compare with changes in sea temperature or indices such as the North Atlantic Oscillation. Instead, we must use variations in our ten breeding-season data set and compare these to annual or seasonal variations in local sea conditions.

Parental attendance in late 2012 was significantly lower, suggesting low food availability. Henderson & Henderson (2017) showed that adult sprats caught in the water intake at Hinkley Point were underweight in December 2011 but had recovered in December 2014. Sprats and Sandeels were shown to be the main forage fish on Lundy in 1985-6 (Hatchwell *et al.*, 1992). Underweight sprats in December 2011 could have the same cause as low Guillemot attendance in late June and early July of 2012. By 2014, Guillemot attendance had risen to 20% and sprat condition was back to normal. Riordan & Birkhead (2018) showed that there was a shift in prey availability for foraging Guillemots at Skomer after 2010.

Sprats and Sandeels feed on zooplankton, primarily copepods. The dominant copepod in the Celtic Sea is *Calanus helgolandicus* which is omnivorous and feeds on smaller zooplankton and phytoplankton. Primary production in the Celtic Sea is seasonal. In April, primary production is concentrated on the surface. The Celtic Sea becomes stratified during the peak of seabird breeding activity in June and July and primary production is concentrated below the surface. The Celtic Sea Front is formed where the stratified Celtic Sea meets the tidally mixed waters of the Bristol and St George's Channels. The Celtic Sea Front is another area of high primary production.

Surface concentrations of phytoplankton can be seen in Continuous Plankton Recorder surveys and by satellites that are sensitive to chlorophyll such as the MODIS instrument on the AQUA satellite. April concentrations of phytoplankton near the surface show well in these instruments (Figure 4.A). Low surface chlorophyll in June and July suggests that there is a sub-surface chlorophyll maximum (Figure 4.B). Dedicated ship-based surveys are needed to show concentrations of phytoplankton below 20m (e.g. Hickman, 2012).

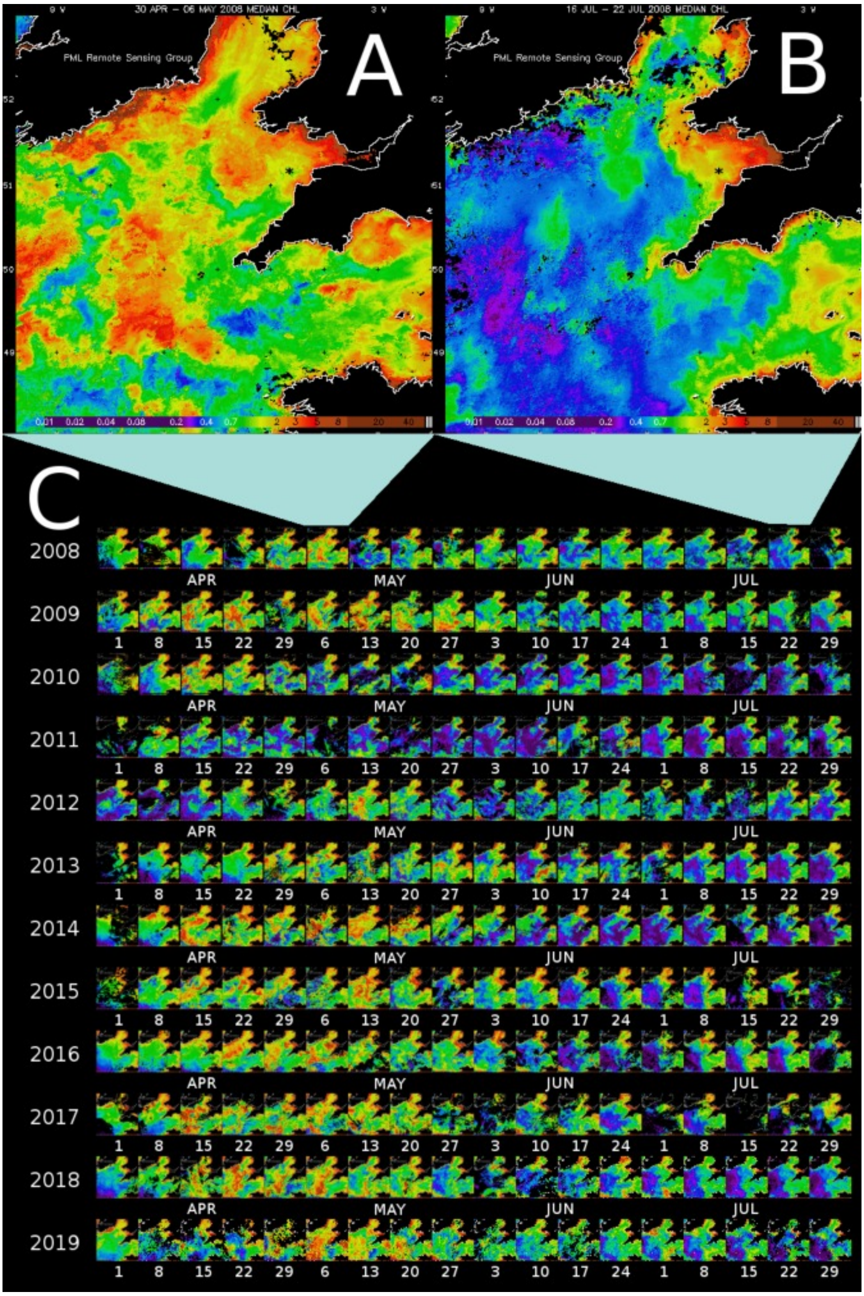

Figure 4: Composite images of surface chlorophyll (OC3M) for the Plymouth area from the MODIS instrument on the AQUA satellite. Composite images of median value of OC3M over seven days. (A) Composite of 30 April to 6 May. Red areas over the Celtic Sea show high surface chlorophyll and therefore high surface phytoplankton abundance during the spring bloom. Position of Lundy shown by black asterisk. (B) Composite of 16 to 22 July. Purple areas other than the Celtic Sea show low surface chlorophyll and therefore imply the presence of a sub-surface chlorophyll maximum. (C) Weekly composite images covering April to July for the survey period. Blue areas in April of 2011 and 2012 imply a weaker spring phytoplankton bloom in these years

Satellite images from the MODIS AQUA instrument suggest that April surface chlorophyll in the Celtic Sea was lower in 2011 and 2012 than other years (Figure 4.C). Low phytoplankton numbers could have led to low or malnourished copepods which in turn could have led to the underweight Sprats observed by Henderson in December 2011 and low parental attendance on Lundy in late 2012.

Satellite images are now used to identify the strength of the Celtic Sea Front and identify smaller short-lived fronts. Relating these fronts to fish and seabird concentrations is an active area of research. Preliminary steps have been made to compare data from this study to front strength and location.

Studies of food availability in the Cook Inlet, Alaska, showed that parental attendance was a better indictor of food availability than provisioning rates or productivity (Harding *et al.*, 2007a, 2007b, Piatt *et al.*, 2007). They looked at three separate colonies: Chisik Island, Gull Island and the Barren Islands. Chisik Island always had the lowest food availability and parental attendance. The Gull Island and Barren Island colonies were always better than Chisik Island and showed greater variation. The Cook Inlet study showed that there was a non-linear dependence of parental attendance on food availability: ‘colony attendance by [Guillemots] at colonies in lower Cook Inlet, Alaska, increased rapidly over a limited range of poor-to-moderate prey densities, and then levelled off to become independent of food at high prey densities.’ (Harding *et al.*, 2007b).

If we assume that large colonies of Guillemots occur near areas of greater food availability (ignoring the effects of predation or the availability of potential breeding islands near oceanic hot-spots) then parental attendance at the highly-studied colonies such as Skomer and the Isle of May could be less sensitive to small variations in sea conditions. It could be beneficial to start long-term studies at smaller, less optimal, colonies. Studies of parental attendance can be less time consuming than the full-scale studies at Skomer but would compliment them by giving wider geographic scope and may be more sensitive to variations in food availability.

Provisioning Rates and Chick Diet

Provisioning rates are difficult to assess without also knowing the species, size and condition of the forage fish. High provisioning rates in 1986 were associated with smaller fish than in 1985 when provisioning rates were lower (Hatchwell *et al.* 1992). It is hoped that video from this study will yield species and size identification. Video from early seasons was used for species identification in Anderson *et al.*, (2014).

Condition of the fish is also difficult to assess. Researchers at Skomer regularly collect stomach samples from adult Guillemots and collect discarded fish to measure the condition of prey species. This work is invaluable but does not need to be replicated on Lundy. Stomach sample collection is invasive, time-consuming, and requires a high level of training. Collecting discarded fish is easier to achieve, especially as we have large numbers of rock-climbers that visit Lundy immediately after the seabird breeding-season. Many of these climbers have visited Lundy for many years and have contributed to conservation efforts by reporting sites where breeding is late, taking photographs of predated seabird carcases, and returning leg rings from otherwise inaccessible cliffs. Climbers could be asked to collect any discarded fish for identification (but see Barrett *et al.*, 2007 for limitations of this method).

Productivity

The productivity of the study ledge increased as the whole island Guillemot population increased. There are signs of decline in numbers of gulls on Lundy. A stable or declining gull population would reduce the predation pressure on an increased Guillemot population. Wide flat ledges are known to be more susceptible to predation than the narrow ledges, observed for this study. Comparisons between individual sites on this ledge and between other study ledges on Lundy may show specific reasons for the increased productivity on this ledge. Sutton (2016) showed that Lundy's Peregrine Falcons were taking an unexpectedly large number of immature larids. A study of the feeding ecology of corvids and *Larus* gulls throughout the year might show reasons why predation pressure on this ledge has decreased (e.g. decrease in rat and rabbit numbers reduce the numbers of predators that could be supported outside of the breeding-season).

CONCLUSIONS

This study only recorded two-hour sessions so it was not able to produce detailed information about feeding-trip duration or the variation of provisioning rates over a whole day that are obtained by studies at Skomer and the Isle of May. The strengths of this study were that it produced useful data on parental attendance with less effort. It also produced video that can be used for other studies of behaviour. Monitoring the health of our highly-productive shelf seas is increasing important in times of climate change. Studies at smaller colonies such as Lundy increase our ability to see the effects of climate change on marine food webs.

ACKNOWLEDGEMENTS

My thanks to the Wardens on Lundy for allowing me to study this ledge and to Helen Booker for suggesting Guillemot diet and provisioning studies on Lundy. The help of many other people who helped in the survey is gratefully acknowledged. The author also thanks the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS) for supplying data for this study.

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GOLDCRESTS ON LUNDY: ANALYSIS OF RINGING DATA, 1990 TO 2018

by

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ABSTRACT

The ringing and biometrics of Goldcrests (*Regulus regulus*) on Lundy between 1990 and 2018 are analysed. The Goldcrests visiting the island in spring and autumn mainly originate in the southwestern quarter of the British Isles. More males than females visit in autumn, perhaps because the females are more reluctant to make sea crossings. Males move earlier in spring and later in autumn, compared with females. Most Goldcrests do not stay on the island for more than one or two days, but their weights suggest that they generally feed well while on the island.

Keywords: *Goldcrest, ringing, biometrics, Lundy, migration*

INTRODUCTION

The Goldcrest (*Regulus regulus*) is Britain's smallest bird, with individuals normally weighing between five and six grams – roughly the weight of a credit card. Their preferred habitat is coniferous woodland, where they feed on small insects and other invertebrates. They reproduce prolifically, with 7-10 eggs per clutch and two broods per year, but most of these die young. Only about 15% of breeding adults survive to breed the following year, and the oldest known bird was ringed in its first autumn and recaptured five years later (Robinson 2005).

Plate 1: Goldcrest on Lundy © Richard Campey

Goldcrests are found in northern Europe including the whole of Britain, and in much of northern Asia, wherever there is suitable habitat. There are outlying populations further south in Eurasia, in areas where mountain ranges hold suitable woodland. There are estimated to be about 520,000 breeding territories in Great Britain (Musgrove *et al.*, 2013), but Goldcrests' small size makes them very vulnerable in severe weather, so numbers fluctuate considerably from year to year according to winter temperatures. Fine weather in the breeding season can lead to very large numbers of birds dispersing away from breeding areas in autumn.

Goldcrests from some northern populations migrate south, west or southwest, to winter in milder conditions. Over a hundred birds ringed in Britain outside the breeding season have been found abroad, in areas ranging from northern France and Germany, north into Scandinavia, and east to Finland and western Russia. The great majority of these were ringed on the east coast of England or Scotland. (Wernham *et al.*, 2002).

On Lundy, since 1947, Goldcrests have been confirmed as breeding in four years, with records in two other years suggesting possible breeding. Most Lundy records are of birds arriving on the island in autumn. These are individuals that are either dispersing away from their natal areas or on migration. Very small numbers then overwinter in some years, before a few migrants pass through in spring (Davis & Jones, 2007).

As throughout the UK, bird ringing on Lundy is carried out by trained individuals who are licensed by the British Trust for Ornithology (BTO) under the Wildlife and Countryside Act 1981. Between 1947 and 2018, a total of 11,017 Goldcrests has been ringed on Lundy. All records of newly ringed and recaptured birds from 1990 onwards have been digitised, and analysis of these 6590 records forms the basis of this paper.

DATA ANALYSED

The standard information recorded for each individual bird captured consists of the following:

- **Whether newly ringed or recaptured**: birds may be newly ringed (N), recaptured at the original ringing location (R), or controlled, i.e. recaptured after being ringed elsewhere (C).
- **Ring number**: Goldcrests are ringed using the smallest available size (AA). Each ring is engraved with a different alphanumeric code, and the address of the BTO, so that birds can be identified individually and reported if re-found.
- **Date and time of capture**.
- **Sex**: male and female Goldcrests can be distinguished by looking at the colour of the central crown feathers: yellow in females, and yellow, with orange showing in the centre when raised, in males.
- **Age**: examination of a bird's plumage can give clues about its age, distinguishing autumn birds hatched in the same calendar year (EURING age code 3) from those that have bred (code 4). The same criteria can be used in spring, separating birds that are nearly one year old (code 5) from older ones (code 6).
- **Wing length**: the standard measurement is from the leading edge of the carpal joint to the tip of the longest primary feather, with the wing in its resting position against the body and the primaries straightened and flattened to their full extent.
- **Weight**: measured in grams, to the nearest 0.1g.
- **Capture location and method**: almost all birds were caught in Millcombe or St John's Valleys, using mist-nets. Four were caught in the Terrace Heligoland trap.
- **Whether a playback lure has been used**: recordings of Goldcrest songs are sometimes played in autumn, to attract birds to the netting area and increase the number caught. The use of recordings is limited in time, so dispersing or migrating birds are not held in the area for too long. Recordings are not used in spring, to avoid disrupting any natural territorial behaviour.
- **Initials of ringer**: the person responsible for the record is noted.

Not all of these data were recorded in every case, for a variety of reasons: results might be unclear to the observer, as in the case of some birds' ages when tail feather shape was intermediate; birds may be deliberately released without measuring and/or weighing, if unexpectedly large numbers are caught and the ringers' priority is to minimise the time for which birds are kept; and occasionally birds are released or escape during the ringing process before the completion of data recording. So each analysis has been carried out using only those records with relevant data, and this explains the variation in size of the samples analysed.

RESULTS AND DISCUSSION

Annual catch size

The number of Goldcrests ringed each year varies greatly. Annual spring and autumn totals are shown in Table 1. The mean number is 210, with extremes of 623 in 1990 and 4 in 2007. Ringers have visited Lundy at a variety of times within the migration periods and their catches have been influenced by weather conditions, which can affect whether mist-nets can be set and also whether birds choose to move to or from the island. So the correlation between catch sizes and UK Goldcrest population size is low; a constant level of catching effort throughout every year's migration seasons would be needed in order to provide a consistent numerical indicator. So the analyses below have been carried out on combined data from all years of this study.

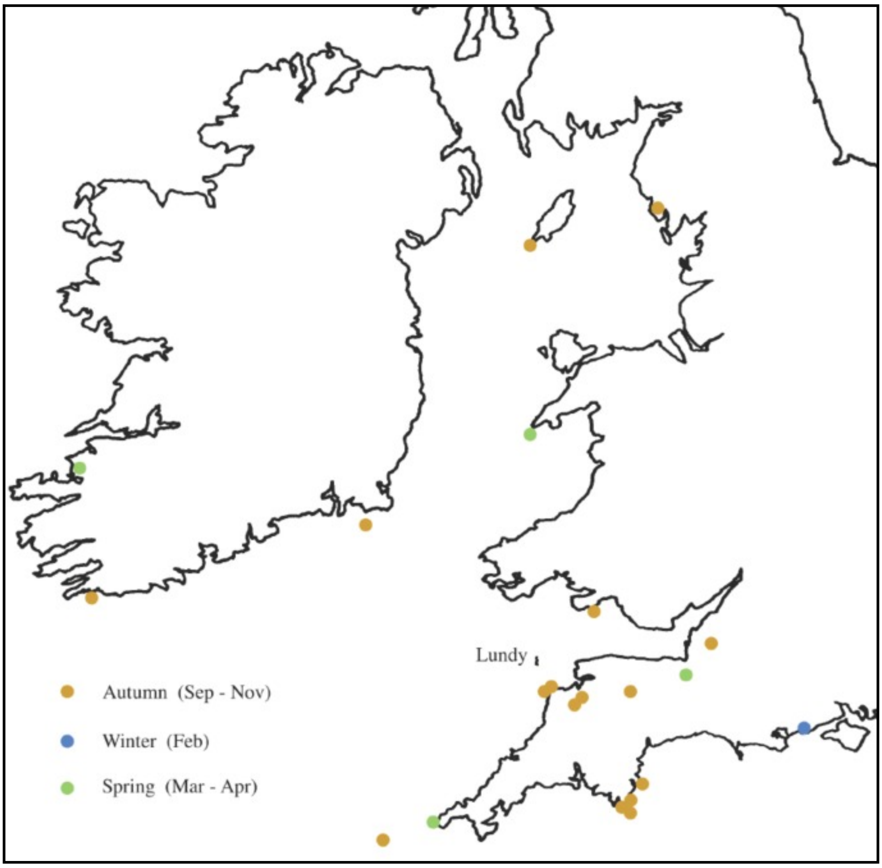
Year	Spring	Autumn	Total
1990	20	603	623
1991	2	26	28
1992	0	100	100
1993	1	305	306
1994	8	44	52
1995	3	520	523
1996	22	115	137
1997	2	335	337
1998	8	32	40
1999	7	266	273
2000	21	131	152
2001	1	51	52
2002	0	136	136
2003	0	179	179
2004	1	93	94
2005	1	306	307
2006	9	75	84
2007	1	3	4
2008	8	520	528
2009	4	7	11
2010	0	51	51
2011	1	175	176
2012	7	296	303
2013	48	409	457
2014	2	59	61
2015	10	223	233
2016	24	241	265
2017	5	474	479
2018	28	68	96
Total	244	5843	6087
Mean	8.4	201.5	209.9

Table 1: Annual catches of Goldcrests on Lundy, 1990-2018

Movements to and from Lundy

Figure 1 shows the ringing or finding locations of the 21 ringed Goldcrests that have moved to or from Lundy. The seasons when they were located away from Lundy are also indicated. All relevant captures on Lundy were in September or October. The locations suggest that birds reaching Lundy originate from a limited area involving southern Ireland (three records), the Isle of Man (one record), Wales (two records) and the western half of England. The general trend has been for birds to move north in spring and south in autumn, the exceptions being one that went to South Wales in October 1988 and one from the Isles of Scilly that was on Lundy the next day, in October 1989.

Figure 1: Recoveries and controls of Goldcrests caught on Lundy



As the map shows, most of the birds involved, when caught by other ringers away from Lundy, were at coastal sites rather than in breeding habitat inland. This comes about because Goldcrests are much easier to catch in mist-nets when they are in low scrub on coasts and islands; in their typical breeding habitat they tend to be high in trees. So the data are biased in favour of migration stop-off points, and of dispersing or migrating individuals rather than the unknown proportion of birds that remain sedentary.

It is possible that birds which moved to the south Devon coast went further south into France, that birds moving east reached the continent and that those from the Isle of Man and Cumbria originated in Scotland. However, it is interesting to note that Lundy

Goldcrest movements contrast strongly with those of the closely related Firecrest *Regulus ignicapillus*. Four ringed Firecrests have moved to or from Lundy. One was found at Penzance, Cornwall, but the other three are beyond the furthest spread of Goldcrest records: one arrived from Beachy Head on the Sussex coast and two went to the Netherlands. This suggests that the Firecrests reaching Lundy move over much larger distances than the Goldcrests. If significant numbers of Goldcrests reached Lundy from the continent, for instance, one would expect even stronger evidence than there is for Firecrests, since the number of Goldcrests caught on the island is twenty times higher, yet there has been none.

Sex ratio

Of the birds for which sex was recorded, 2641 (43.6%) were female and 3412 (56.4%) were male. The percentages varied greatly according to the time of year, with 75.4% females among spring-caught birds and 42.3% females in autumn. A more detailed breakdown of these figures is given in Table 2, which shows that males tended to be caught earlier in spring than females. The difference between catches up to 21 April and those from 22 April onwards is statistically significant (Chi squared test: $p<0.01$).

Table 2: Sex ratios in Goldcrests caught on Lundy

Dates	Female	Male	% Female
Spring:			
25 Mar-21 Apr	73	36	67
22 Apr-17 May	93	20	82
Autumn:			
15-Aug	11	1	92
01-Sep	38	34	53
15-Sep	741	933	44
01-Oct	897	1269	41
15-Oct	693	1032	40
31 Oct-17 Nov	47	68	41

In autumn, females predominated until mid-September, after which males made up 56 to 60% of the catches. Comparison of data obtained between 15 August and 15 September with 16-30 September shows a decrease in females that is statistically significant (Chi squared test: $p<0.001$).

Wernham *et al.* (2002) looked at movements of ringed Goldcrests to, from and within Britain and Ireland. They found that about 60% of the birds involved were males, which is similar to the figure for the overall numbers ringed on Lundy. In mainland Europe, males predominate at migration and wintering sites in the Baltic, Belgium and France (Hildén, 1982, Cramp, 1992, Vercauteren, 1991). Grenmyr (1997, 2000) suggested that such a bias at Swedish bird observatories in autumn came about because the two sexes followed different routes. The males may be more prepared to cross open water while females tend to follow coastlines.

Davis and Jones (2007) state that spring migration of Goldcrests through Lundy is mainly from mid-March to late April. Ringing is rarely carried out on the island before early April, and only nine birds in this study were caught before 3 April. Of those, seven were males. That sample is too small to provide firm evidence, but it is possible that the apparently anomalous Lundy data, with a high percentage of birds caught in spring being female, comes about because males tend to move through Lundy in March, before ringing has started there. In most species of birds, males migrate earlier than females in spring.

Dates of ringing

As indicated in the paragraph above, and as with comparisons between years, ringing on Lundy does not provide a very good indication of the timing of migration, since ringers are not present throughout each season. The earliest and latest capture dates in spring and autumn are included in Table 2, which also shows that the main autumn catching period for Goldcrests is from mid-September to the end of October. Given the limitations of the data, further discussion of migration timing would be of little value.

Recaptures on Lundy

Records from the study period include 484 that involve birds previously ringed on Lundy being recaptured there. Almost all are relatively short-term, with birds recaptured within the same spring or autumn migration season. Two birds were exceptions to this: a male ringed on 6 May 1994 was recaptured on 13 July 1994, and a female ringed on 28 April 2000 was recaptured on 6 and 24 October 2000. It is likely that both birds spent the breeding season on Lundy, with the male having little time to leave, attempt breeding elsewhere and return, and the female being ringed in a year when breeding was proved to have occurred on the island (Davis & Jones, 2007).

All other recaptures are summarised in Table 3. The figures suggest that the majority of Goldcrests arriving on Lundy in spring and autumn move on again quickly. In both seasons the median time between ringing and recapture was two days, with means of 3.6 days in spring and 4.3 days in autumn.

Age

A summary of the ages of all Goldcrests in this study is given in Table 4. Most birds in autumn are aged as being in their first year (96% of those for which a definite age is given), and those aged in spring as in their second calendar year (94% of birds with age given). Goldcrest reproductive rates are high and survival rates low, so a high proportion of young birds is to be expected. In addition, young birds are more likely to disperse away from breeding areas than territory-holding adults, some of which remain sedentary all year (Wernham *et al.*, 2002). This would further increase the proportion of young reaching Lundy.

In the clearest cases, determining a Goldcrest's age by the shape of its tail feathers is straightforward: Plate 2 shows the tail of a first-autumn bird, with pointed juvenile feathers originally grown when the bird was a nestling, and one rounded, adult-type feather. This has not yet reached full length, and is growing to replace one that must have been lost accidentally. However, there can be uncertainty over some individuals with intermediate feather shapes: 2% of Lundy autumn records and 36% in spring are

Table 3: Summary of recaptures of Goldcrests on Lundy

Days after initial capture	Spring retraps	Autumn retraps
1	8	159
2	8	85
3	2	48
4	2	37
5	2	31
6	2	11
7	1	14
8	1	18
9	2	5
10	1	4
11-20		22
21-30		12
31-40		2
41-50		1
51-60		1
Total	29	450

Table 4: Ages of Goldcrests on Lundy

	Age code	Number of birds			% of total	% of known-age birds
		Female	Male	Total		
Spring						
	4	67	21	88	36	
	5	109	37	146	60	94
	6	28	2	10	4	6
Autumn						
	2	47	68	115	2	
	3	2301	3162	5463	94	96
	4	105	122	227	4	4

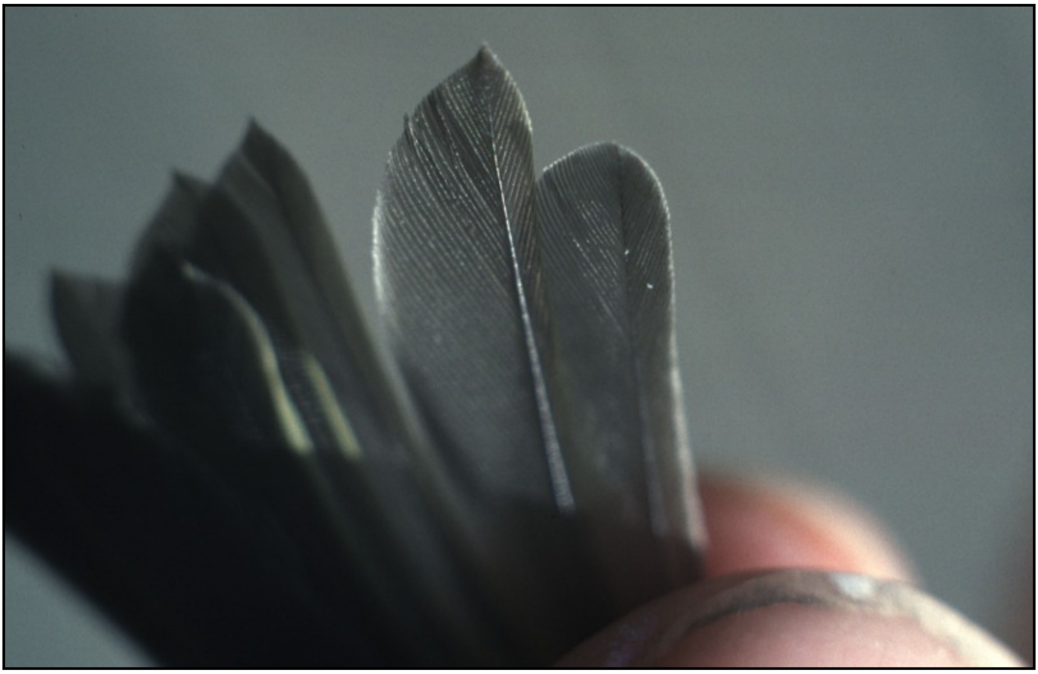


Plate 2: Goldcrest tail with one adult feather growing. © Tony Taylor

recorded as indeterminate. Grenmyr (2000) found that in Sweden up to a third of all Goldcrests were wrongly aged using tail shape, so ringers have become more cautious about using this feature in recent years.

Wing length

The wing lengths of Goldcrests caught on Lundy in spring and autumn are shown in Table 5. Mean wing lengths for females are 51.6mm in autumn and 51.1mm in spring. For males they are 53.7mm in autumn and 53.4mm in spring. As in most Passerine species, males are slightly larger than females. All feathers become worn over time and so the marginal loss in length between autumn and spring is to be expected. Adult birds carry out a full moult at the end of the breeding season, so they have new feathers in autumn (Svensson, 1999).

As discussed above, movements of ringed Goldcrests provide no evidence of birds from continental Europe reaching Lundy. Those from the northern parts of the species' European range tend to be a little larger than British birds, with wing lengths around 2mm longer on average. During autumn of 2005, Rob Duncan ringed Goldcrests on Lundy, and also on the Suffolk coast at a time when easterly winds were bringing continental birds across the North Sea. His data gave a direct comparison between the two locations and is shown in Table 6 (R.A. Duncan, pers. comm.). There is a clear difference in wing lengths, with the Suffolk values about 2mm longer. His Lundy data are very close to the overall Lundy figures for autumn, given in Table 5, with differences in mean lengths of just 0.3mm for females and 0.1mm for males. If significant numbers of continental Goldcrests reached Lundy, wing lengths in Table 5 would be expected to show a greater spread into the higher fifties.

Table 5: Wing lengths of Goldcrests on Lundy

	Number of birds			
Wing length (mm)	Spring		Autumn	
	Female	Male	Female	Male
45			1	
46				
47			1	
48			7	1
49	12		34	4
50	33		320	19
51	63	5	738	84
52	41	8	792	344
53	14	9	333	891
54		25	73	1032
55		7	27	598
56		1	2	171
57	1		1	21
58				5
59				1
Total	164	55	2329	3171
Mean wing length (mm)	51.1	53.4	51.6	53.7
Standard deviation	1.14	1.21	1.14	1.23

Table 6: Comparison of Goldcrest wing lengths on Lundy and the Suffolk coast, autumn 2005

	Number of birds			
Wing length (mm)	Females		Males	
	Lundy	Suffolk	Lundy	Suffolk
48	1			
49	3			
50	20		2	
51	37	2	7	
52	30	11	19	
53	12	17	61	1
54	1	10	50	3
55		7	33	34
56			6	19
57			1	11
58				2
Sample size	104	47	179	70
Mean wing length (mm)	51.3	53.2	53.6	55.6
Standard deviation	1.08	1.10	1.21	0.95

Weight

Mean weights for all Goldcrests captured on Lundy for the first time are 5.26g for females and 5.44g for males. Table 7 shows the wide range of weights recorded, and compares the weights of birds captured in spring and autumn. Females are 0.15g lighter in spring than autumn, but this difference is small compared with the range of values, and the small sample size in spring should be considered.

Body weight can be influenced by a range of factors in addition to the size and sex of the individual. Birds need to build up enough energy stores to support their needs through the night, when they cannot feed, so weight may vary with time of day. They may also accumulate extra fat stores to provide energy during migration or dispersal flights. Weather conditions influence birds' rates of feeding and heat loss, and hence their weight, particularly in a small, insect-eating species such as the Goldcrest. Time of year can be relevant, with a wide range of species accumulating extra fat stores in late autumn, as insurance against the challenges of difficult conditions in winter.

Analysis of Lundy data suggests that date is not a significant factor influencing Goldcrest weights in autumn. The mean weight for females is 5.26g up to 30 September, and identical at 5.26g from 1 October onwards. The equivalent values for males are 5.42g and 5.45g. This rise in mean weight of males is minimal, at less than 1%.

Some passerines are known to adjust their weights according to the level of threat from predators: fat storage, as insurance against poor weather conditions, needs to be balanced against the resulting loss of acceleration and manoeuvrability in flight. On Lundy the threat from raptors is usually high. Merlins (*Falco columbarius*), Kestrels (*Falco tinnunculus*) and Sparrowhawks (*Accipiter nisus*) are regular visitors in autumn and often more than one of each is present. Though Merlins and Kestrels typically hunt in open habitats, both hunt among the trees in Millcombe when migrant Passerines are concentrated there. Even the local Peregrines (*Falco peregrinus*) will do this, despite their large size, and male Peregrines will intercept very small migrants such as *Phylloscopus* warblers approaching the island over the sea and consume them in flight (pers. obs.).

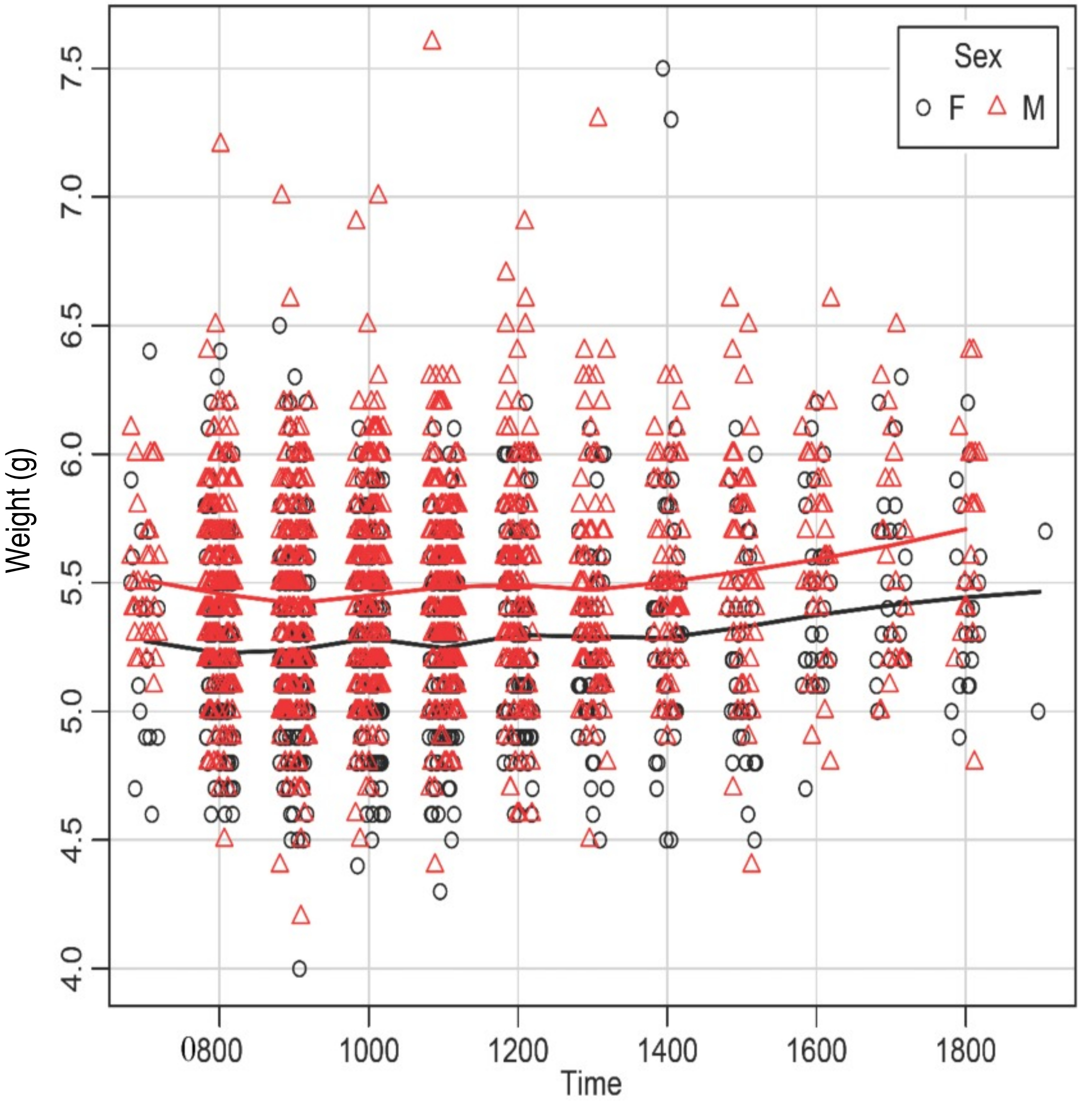
With so many factors influencing birds' weights, conditions are not sufficiently well controlled in the Lundy Goldcrest dataset to allow each factor to be analysed reliably. In the case of time of day, data from a limited range of dates, 1-15 October, were selected, in an attempt to minimise seasonal variations while still giving a reasonable sample size. The results are shown in Figure 2. While the data suggest an increase of about 0.25g through the day for both females and males, the average sample sizes between 08:00 and 12:00 are more than three times greater per hour than outside that period. So the reliability of the data decreases as the afternoon progresses.

A further note of caution is needed because about three quarters of the records before 08:00 and two thirds of those after 17:00 were obtained on dates up to 7th October. Those at other times of day were split more evenly between the first and second quarters of the month. At a season when day length shortens rapidly, this probably reflects the changing times at which Goldcrests are active. It could be that longer days allow the birds to maintain weight more easily, and this would bias the average weights near dawn and dusk.

Table 7: Weights of Goldcrests on Lundy in spring and autumn

	Spring		**Autumn**	
Weight (g)	Females	Males	Females	Males
4.0			2	
4.1	1		2	1
4.2				1
4.3	2		3	
4.4	3		8	4
4.5	7		19	9
4.6	9	2	52	19
4.7	13		69	41
4.8	15	3	138	83
4.9	14	1	139	111
5.0	14	4	261	206
5.1	19	3	212	185
5.2	16	6	266	333
5.3	9	4	225	270
5.4	12	5	201	340
5.5	11	7	216	372
5.6	4	2	113	273
5.7	2	1	99	246
5.8	3	6	80	162
5.9	2	4	49	143
6.0	1	2	50	117
6.1	1		22	50
6.2	1	2	14	41
6.3		1	7	28
6.4			2	12
6.5	1	1	1	13
6.6				5
6.7		1		2
6.8			1	3
6.9				3
7.0				2
7.1	1			
7.2				2
7.3				1
7.4				
7.5	1		1	
7.8				1
Sample size	162	55	2252	3079
Mean weight (g)	5.099	5.471	5.258	5.440

Figure 2: Effect of time of day on Goldcrest weights, 1-15 October



Another line of enquiry involves the weights of birds recaptured a day or more after their original ringing date. Weight comparisons are available for 357 birds. Their mean weight when ringed was 5.34g and on recapture was 5.31g. The mean capture and recapture times were similar, and the sex ratio of the birds involved was the same as for the complete dataset. So these birds appear to be able to maintain weight on Lundy, even though the sample may be biased against the fittest birds: the sooner a bird continues its migration, the smaller its chances of recapture.

The overall impression given by these results is that weight changes through the day and on longer time-scales are slight. Most of the Goldcrests visiting Lundy appear to be able to regulate their weight very effectively, and are not subjected to major stresses in their energy budgets as a result of the local conditions, even though there is very little of their preferred habitat available on the island.

Playback lures

The use of playback lures can increase catching rates greatly. Some ringing groups operating on Lundy have played recordings of Goldcrest songs in autumn and birds respond strongly to them. Several questions arise from this. To what extent does the use of recordings increase catching rates? Do they influence the sex ratio of the catch by attracting females more than males, or vice versa? Do they have different effects on first-year birds and adults?

A total of 1235 birds are recorded as having been playback-lured, all in autumn. Among these, 39% are female, compared with a value of 43% for non-lured autumn records. Interestingly, the value for the 67 lured birds aged as adults is 51% female. This might suggest that while lures are attractive to most Goldcrests in autumn, when the majority are first-year birds, they reduce the catch of adult males.

The uncertainties involved in this last analysis are considerable. The sample size is small; as discussed above, the aging method normally used for Goldcrests is not considered to be entirely reliable; and it is also known that some visiting ringers have not kept records of when lures have been used. It seems plausible that adult males might stay away from lures, if they perceive them as territory-holding birds, but more rigorous experimental procedures, and consistent recording, would be needed to establish this point.

CONCLUSIONS

The ringing and recording of biometrics of Goldcrests on Lundy has shown that the birds visiting the island in spring and autumn mainly originate in the southwestern quarter of the British Isles. More males than females visit in autumn, perhaps because the females are more reluctant to make sea crossings. Males move earlier in spring and later in autumn, compared with females. Most Goldcrests do not stay on the island for more than a day or two, but they generally appear to find ample supplies of food while they are present. Given their very small size, they have a remarkable ability to thrive in habitat that is atypical for the species.

While the data give valuable insights into the lives of the Goldcrests visiting Lundy, the analytical work carried out for this study also highlights the data's limitations. These are an inevitable result of reliance on visiting ringers to carry out the work. Ideally, data would be gathered throughout the migration seasons every year, using a standard number of mist-nets over standard times of day, as happens at officially designated Bird Observatories. Some of the uncontrolled variables could then be eliminated, larger samples gathered and further conclusions drawn. The need for consistent high standards of data recording is also clear.

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This work could not have been done without the dedication of the many bird ringers who have visited Lundy, devoting countless hours to catching, ringing, measuring and recording birds there. Special thanks to Rob Duncan for providing data on migrating Goldcrests in Suffolk. The Lundy Field Society has provided vital financial and other support for all bird ringing on Lundy throughout the Society's existence. I am also greatly indebted to the Wardens and other islanders who have facilitated and supported the ringing.

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MIGRATION STRATEGY IN THE CHAFFINCH, *FRINGILLA COELEBS*

by

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ABSTRACT

Birds have developed morphological and behavioural adaptations as migratory strategies. A comparative study of morphology and demography between the Chaffinches' (*Fringilla coelebs*) sedentary *gengleri* and migratory *coelebs* races was conducted using a ringing dataset collected on Lundy between 1972 and 2017. Migratory individuals were significantly and proportionately longer winged and had greater body weight. The migrant sex and age ratios were skewed towards females and first-year birds and were responsive to annual climatic variations. The results support the species' status as a differential migrant and present the potential of Lundy's extensive ringing efforts in contributing to studies on avian migration.

Keywords: *Chaffinch, differential migration, migration phenology, Lundy, North Atlantic Oscillation*

INTRODUCTION

Avian migration is the result of birds' adaptation to seasonal variations in resource availability and environmental conditions (Alerstam, Hedenström & Åkesson, 2003). The typical pattern of avian autumnal migration in the Northern Hemisphere is from North to South, as birds travel to spend winter in warmer regions; in spring, the birds fly in the reverse direction, returning to their breeding grounds in preparation for the mating season (Jenni & Kéry, 2003).

Morphological adaptations for migration

Migration is energetically demanding and therefore places great metabolic stress on migrating birds (McWilliams *et al.*, 2004). In response, migratory birds gained behavioural and morphological strategies to enhance their capacity for migration. Species that migrate longer distances tend to have longer wing lengths in proportion to body mass to reduce wing-loading (defined as body mass divided by wing area), hence allowing for more powerful and energy-efficient flight (Nowakowski, Szulc & Remisiewicz, 2014). Also, within species, migratory individuals are known to have greater wing lengths and lower wing-loading than sedentary conspecifics, such as in Blackcaps (*Sylvia atricapilla*) (Pérez-Tris & Tellería, 2001) and Yellow-rumped Warblers (*Dendroica coronata*) (Milá *et al.*, 2008).

Additionally, migratory birds that travel southwards from their northern breeding ranges for winter are usually of greater body size and mass than their sedentary conspecifics of southern populations, as an adaptation to reduce heat loss through minimising surface area to body mass ratio (Ashton, 2002). This biogeographical trend in body size and mass is known as Bergmann's rule (Bergmann, 1847) and has been evidenced in avian studies on the intraspecific and interspecific level (Ashton, 2002).

Behavioural adaptations for migration

Classes within migratory bird species have evolved intraspecific variation of migratory behaviour. These classes are defined by categories such as age and sex (Cristol, Baker & Carbone, 1999). Partial migration occurs when only some individuals of a species migrate; in differential migration all individuals in a population migrate, but with differences in timing, duration and distance according to age and sex classes (Ketterson & Nolan, 1983).

Several hypotheses have been developed to explain partial and differential migration:

1) The 'body size' hypothesis predicts that winter conditions force smaller-sized individuals, which face greater relative heat loss and are thus less resilient to the colder and resource-scarce environment, to migrate to more hospitable areas (Ketterson & Nolan, 1976).

2) The 'dominance' hypothesis states that competition for non-breeding resources causes the displacement and redistribution of less dominant individuals (Gauthreaux, 1982).

3) In the 'arrival time' hypothesis, competition for breeding territories and resources mean that individuals of the sex that secures and protects territories for the breeding season will benefit from wintering closer to breeding grounds, so they migrate over shorter distances or depart wintering areas earlier (Myers, 1981).

In most passerines, males and older birds are physically larger, heavier, dominant and territorial (Piper, 1997). Hence, the general trend of differential migration in passerines is that females and younger birds tend to winter further away from breeding grounds than males and older birds. This pattern has been well-evidenced in many species and is especially pronounced in sexually dimorphic species with significant intersexual morphological differences (Ketterson & Nolan, 1976; Cristol, Baker & Carbone, 1999; Catry *et al.*, 2005).

Climate effects on differential migration

Differential migration patterns can also be determined by environmental conditions (Ketterson & Nolan, 1976; Ketterson & Nolan, 1983). Environmental variables such as temperature and precipitation affect habitat quality and food availability in wintering sites, migration stopover points and breeding regions (Barros, Álvarez & Velando, 2013). Due to intraspecific variation such as biological differences caused by sexual dimorphism, individuals of different age and sex classes may respond differently to such environmental stresses (Ketterson & Nolan, 1976; Barros, Álvarez & Velando, 2013). Consequently, winter climates in breeding grounds affect individuals to varying degrees, selecting for stronger individuals while displacing weaker or ill-adapted individuals, ultimately causing intraspecific geographical segregation (Ketterson & Nolan, 1976). As such, in winter, the proportion of individuals in poorer condition increases with decreasing latitude, since only the more resilient ones can afford to remain relatively sedentary at higher latitudes (Ketterson & Nolan, 1976; Catry *et al.*, 2005).

Although studies have established that differential migration is driven by environmental selection, whether these patterns are augmented by climate changes has not been discussed. Current evidence suggests that environmental conditions may amplify intraspecific competition and hence differential migration by limiting the quantity and quality of resources, forcing larger numbers of weaker subordinate individuals to migrate (Ketterson & Nolan, 1976).

In Europe, the large-scale climatic phenomenon known as the North Atlantic Oscillation (NAO) is a major influence on avian migratory behaviour (Hüppop & Hüppop, 2003). Studies have proven the NAO as the most influential factor in yearly variability in European winter temperatures, with a particularly strong effect on northwest Europe (Hurrell, 1995). The NAO index is measured as the sea-level pressure differences between the subpolar and subtropical regions of the North Atlantic, centred on Iceland and Azores respectively. A positive NAO index is indicative of stronger westerly winds blowing across the Atlantic, bringing warmer weather and increased precipitation to northwest Europe; negative NAO indices correspond to colder and drier weather due to weaker warm winds from the west. Therefore, NAO indices from December to March (henceforth 'winter indices') are positively correlated with the corresponding winter temperatures in the North Atlantic region (Hurrell, 1995).

Mean spring passage is advanced in springs following positive winter indices, due to warmer conditions that accelerate plant development and hence food availability (Hüppop & Hüppop, 2003). Existing literature suggests that lower winter indices precede colder winters and springs, which delay the following breeding season and thus the start of autumn migration in the next calendar year (Anthes, 2004). However, NAO effects on autumn migration have not garnered much scientific attention.

Plate 1: Male Chaffinch, ringed on Lundy ©Richard Campey

Avian migration strategy is a complicated phenomenon that is far from being well-studied, especially because such studies demand substantial long-term datasets collected from study sites along migration pathways; these datasets are rarely available and challenging to collect (Hüppop & Hüppop, 2003; Jenni & Kéry, 2003; Payevsky, 2010). The prohibitive cost of precise tracking technology means that many studies still rely heavily on recapture data which are exceedingly rare: recapture rate of the birds ringed in the United Kingdom between 1909 and 2003 stands at a mere 1.90% (Clark *et al.*, 2004).

Given the data collection challenges inherent to avian migration studies, a widespread species with sizeable population and recognised migration pathways is an ideal study target. For these reasons, the Chaffinch (*Fringilla coelebs*) is a highly appropriate model species. It is one of Europe's most abundant bird species (Wernham *et al.*, 2002; Payevsky, 2010). The nominate continental race *coelebs* breeds in north and northeast Europe, migrates in huge numbers to Britain and Ireland in autumn, joining the non-migratory *gengleri* residents for winter (Newton, 1972; Wernham *et al.*, 2002). Within the migratory populations, differential migration where females disperse further from their breeding territories has been observed (Cramp & Perrins, 1994). Linnaeus named the Chaffinch '*Fringilla coelebs*', literally translated as 'bachelor finch', based on his account of highly male-biased wintering populations in Sweden (Wernham *et al.*, 2002).

Yet, there are major knowledge gaps regarding the species' migration tactics. Surprisingly, despite its nomenclature, there are no conclusive studies to ascertain the species' differential migratory patterns (Wernham *et al.*, 2002). Much of the existing literature is focussed on migration speed and timing against climate (Hüppop & Hüppop, 2003; Payevsky, 2010), but none discuss differential migration or the effects of climate on differential migration patterns.

Aims, hypotheses and predictions

This study aims to contribute to the existing knowledge base on avian migration systems, focussing on the effects of environmental conditions on differential migration. Specifically, the primary objectives of this study were to elucidate the migration strategy in Chaffinches and its responses to climatic variations. These were achieved by assessing the species' status as a differential migrant, investigating the morphological differences between sedentary and migratory individuals, and the responses of the species' migratory strategy associated with climate indices in terms of the winter NAO indices and corresponding winter temperatures.

The following hypotheses were investigated:

1) Differential migration exists in Chaffinches where females and younger birds have a higher propensity to migrate, a pattern driven by and reflected in sexual dimorphism and age-related morphological differences.

2) Migratory individuals have developed morphological adaptations favouring enhanced flight efficiencies for migration and heat conservation for colder weather in their northerly breeding grounds.

3) Differential migration patterns are responsive to environmental conditions. When conditions are harsher, higher numbers of poorly-adapted individuals are displaced from their breeding grounds.

METHODS

Study site

Lundy (51°11'N 4°40'W) is a small island measuring five kilometres long and about one kilometre wide situated 18 kilometres off the northwest coast of Devon. The island is a migration hotspot, serving as important stopover for Chaffinches migrating from mainland Europe. In the autumn migration season spanning late September to early December, *coelebs* individuals arrive in massive flocks from Scandinavia, Finland and Russia (Wernham *et al.*, 2002; Davis & Jones, 2007). Residents on Lundy fall under the British and Irish *gengleri* race and are very sedentary: 90% of *gengleri* individuals do not disperse more than five kilometres from their site of birth (Newton, 1972). Therefore, Lundy's resident Chaffinches rarely venture beyond the island's boundaries (Davis & Jones, 2007). The presence of both resident and migratory subspecies makes Lundy a suitable site to study the species' migration tactics through comparison.

Data collection

For this study, Chaffinch records gathered by bird-ringing efforts on Lundy between 1972 and 2017 were analysed. Relevant information extracted from the records were: each bird's unique ring number, age, sex, date of capture, wing length, weight, brood patch and capture method. A separate dataset comprised individuals controlled on Lundy and abroad between 1958 and 2017 was assessed as supplementary data (see Appendix A).

Bird morphometrics, age and sex

Wing length (maximum chord) and body weight measurements of each capture bird was taken via standard procedures, as per recommendations by the British Trust for Ornithology scheme (A. Taylor, 2018, pers. comm.). Wing area data were not available, so for the purposes of this study, a proxy for wing-loading in grams per centimetre was defined as body weight divided by wing length measurement (henceforth 'wing-load estimate').

Birds were aged and sexed according to definitions outlined in Svensson's Identification Guide to European Passerines (Svensson, 1992). The Chaffinch is a distinctly sexually dimorphic species: males are distinguished by bluish-grey crown and nape, rusty-red cheeks and breast and a reddish-brown mantle (Svensson, 1992). A wing length of at least 86 millimetres is strongly suggestive of a male, especially for a bird exhibiting the above plumage characteristics (Demongin, 2016). However, sexing was based primarily on plumage due to overlaps between male and female wing length, further confounded by the averagely shorter wing lengths of the *gengleri* race. Only occasionally was it supplemented by wing length measurement. For the same reasons, it was not reliable to correct outlier measurements as misidentifications may occur.

Age codes were assigned following the European Union for Bird Ringing (EURING) criteria, judging birds based on plumage and moult characteristics (Demongin, 2016; see Appendix B). Chaffinch hatchlings undergo a partial post-juvenile moult in June-October (Demongin, 2016), moulting their greater coverts and tertials, with an observable moult limit that indicates a bird fledged within the current calendar year (EURING age code 3).

This set of feathers is maintained until the birds undergo post-breeding moult in the following year, when a complete moult occurs (Demongin, 2016). Therefore, between January and May, birds seen in the post-juvenile moult plumage were assigned code 5. Throughout the year, individuals in fully moulted plumage were assigned codes 4 or 6. Uncertainties were recorded as code 2. For statistical analyses, all aged birds were categorised as 'first-year birds' (age codes 3 and 5) or 'adults' (age codes 4 and 6).

Residency criteria

Based on past studies, the following criteria were developed to distinguish between migrant and resident Chaffinches:

1. Individuals captured at least once between April and August were regarded as resident birds for the following reasons:

   i) Breeding occurs from April to June (Newton, 1964). Previous studies have established high natal-site breeding fidelity and highly sedentary behaviour in *gengleri* individuals (Newton, 1972; Wernham *et al.*, 2002), and that *coelebs* migrants use Lundy as an autumn stopover or occasional wintering site but adopt a different spring migration pathway and thus rarely appear on Lundy between February and June (Davis & Jones, 2007). It is highly unlikely that an individual caught on Lundy during the breeding season belongs to the migrant *coelebs* race.

   ii) Chaffinches, like many passerines, moult after breeding and prior to their autumnal migration. The species' pre-migration moult period spans June to end September, followed by its autumnal migratory season from end-September to early December (Wernham *et al.*, 2002). It is thus conservative to consider birds captured at least once on Lundy between June and August resident, because during these months the migratory individuals would be moulting in their breeding grounds.

2. Females with brood patches were positively identified as residents, because brood patches indicate breeding activity on the island.
3. Birds in juvenile (age code 3J) plumage were safely considered residents, having fledged on island and therefore belong to the sedentary *gengleri* race (Wernham *et al.*, 2002).
4. Individuals captured and recaptured across at least two non-breeding seasons (September to March) were considered residents. Resident birds may have breeding territories beyond the mist-netting sites, hence they may be missed by mist-netting efforts during the breeding season but caught at other times of the year as they move around the island. Furthermore, it is very improbable that a migrant is captured twice on passage in separate years (A. Taylor, 2018, pers. comm.).
5. Individuals captured and recaptured within one non-breeding season were considered migrants, because the relatively short recapture timeframe suggests that birds were likely intercepted whilst on passage within the same season.
6. Lundy-ringed individuals recovered beyond the island and foreign-ringed birds controlled on Lundy were classified as migrants.

Annual climatic variation

To study the effects of environmental factors on autumnal Chaffinch migration, yearly winter NAO indices and corresponding winter temperatures in the region concerning Lundy were required. We used mean winter NAO indices from year 1972 to 2016 from

Climatedataguide (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based) and regional mean winter temperatures (December to February) for 1972 to 2016 from the UK Met Office (https://www.metoffice.gov.uk/pub/data/weather/uk/climate/datasets/Tmean/date/England_SW_and_S_Wales.txt). Both the winter NAO and temperature indices were recorded such that each winter mean value was calculated from the mean of December in the year before, and the means from January to February (to March for the NAO indices) of the current year. Thus, to match the autumn ringing data to the climate data, both the winter NAO indices and mean winter temperature measurements were shifted backwards one year, so that the climate data reflected the winter conditions following the autumn in which the migrants were recorded.

Hypotheses testing

All statistical analyses were carried out in RStudio version 1.1.383 (R Core Team, 2017; see Appendix C for packages used).

The first hypothesis was evaluated by testing for evidence of differential migration, using chi-square tests to evaluate if the overall proportions of unique females and first-year birds within the migratory individuals differ from those observed in the resident population. Unsexed and unaged individuals were excluded. Paired t-tests were also conducted between the resident and migrant annual sex and age ratios for greater resolution of analysis by addressing possible temporal fluctuations.

Linear mixed effect models were designed to address the morphological comparisons in the first and second hypotheses. Wing length, weight and wing-load estimate were the response variables, with residency status, age group (first-years and adults) and sex as three-way interaction factors, and ring number as a random effect to address pseudoreplication. Interaction terms were removed when non-significant to ensure proper model specification. Significant interactions were further examined using Tukey's HSD post-hoc tests to evaluate differences between age, sex and residency classes.

To test the third hypothesis, regional winter temperatures were first assessed as the response variable against winter NAO indices in a linear model. This was conducted to evaluate any positive correlation between the two climate indices, which is suggested by existing literature (Hurrell, 1995). A binomial regression model was then built, considering sex as a binomial response variable for each annual cohort of migrants against the winter NAO indices.

RESULTS

Overview of ringing data

A total of 9,589 Chaffinch records were collected between 1972 and 2017, of which 143 records were excluded from analyses due to inconsistencies in age and sex. An overview of the remaining 9,446 records revealed that numbers peaked twice annually in April and October, with the latter month accounting for 90.6% of the total dataset analysed (Figure 1). The annual trend in number of records showed a seemingly exponential increase from the year 1972 to 1992 (Figure 2). Thereafter, most years between 1992 to 2011 registered at least 150 records, interspersed by two years with fewer than 150 entries (1998 and 2004).

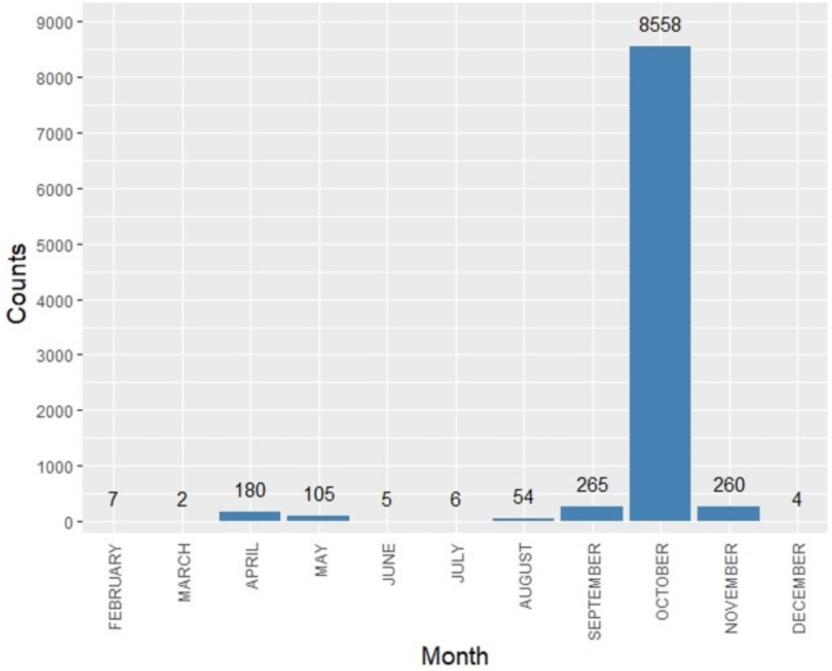

Figure 1: Overall annual trends in number of records by month (*n*=9,446)

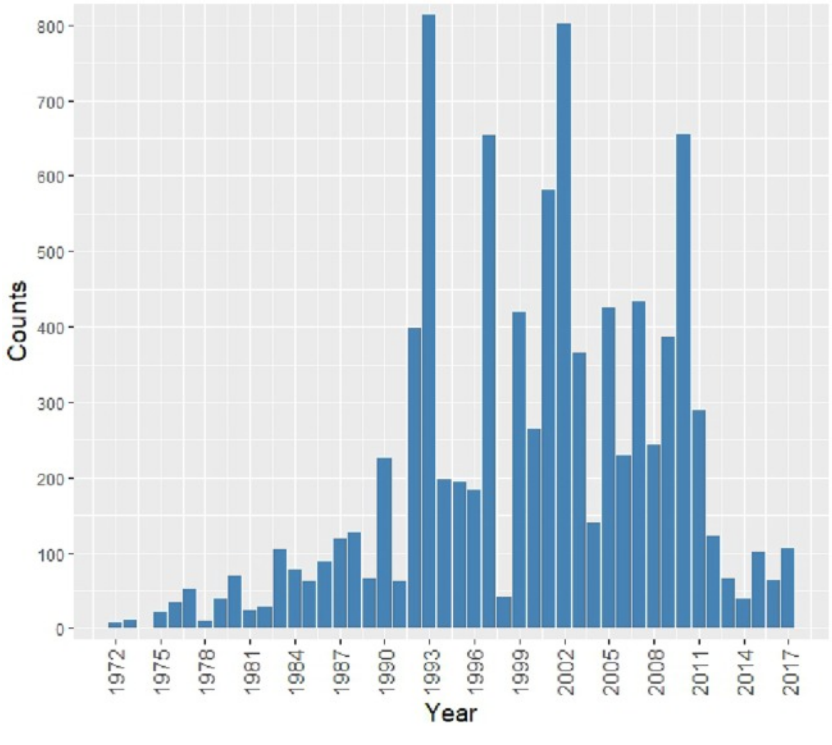

Figure 2: Yearly trends in number of records (*n*=9,446)

Map of recoveries

There were 26 instances of recoveries (Figure 3, see also Appendix A). The geographical pattern in recoveries suggests that migrants to Lundy hailed from Scandinavia or were of north-eastern origin, as shown by recoveries of individuals in Belgium, the Netherlands, Denmark, Norway, Sweden and Russia. Individuals recovered internationally beyond the British mainland were ringed on Lundy during autumn migration season, between September and October. Lundy-ringed individuals recaptured or found on the British mainland were there exclusively between late-November and mid-April, which suggests that they were wintering, or intercepted on spring passage en-route to their breeding grounds. These observations support that *coelebs* individuals use Lundy as an autumn stopover or wintering site as it shows a pattern consistent with the species' known breeding areas, migration season and pathway (Wernham *et al.*, 2002).

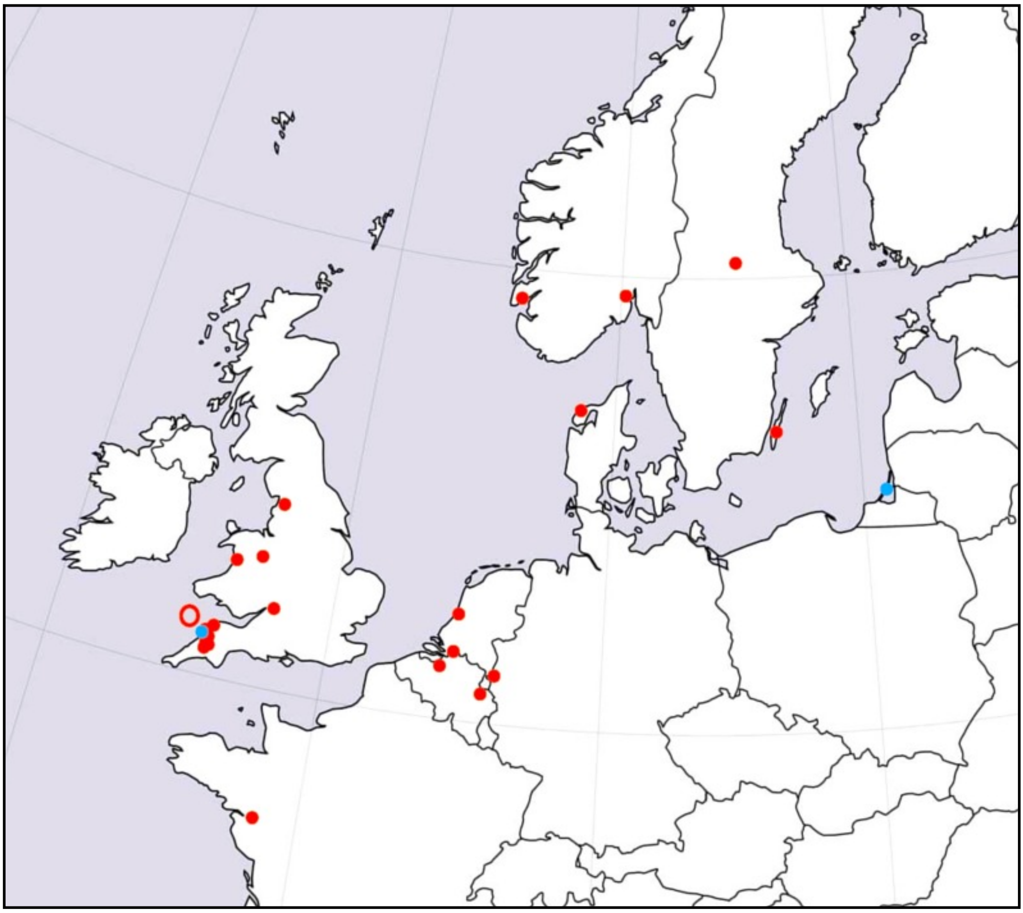

Figure 3: Geographical representation of ringing recovery data (n=26). Lundy is labelled by the hollow red circle. Individuals ringed on Lundy and recaptured elsewhere are given in red (n=23) and individuals ringed elsewhere but captured on Lundy are given in blue (n=3). GPS coordinates were not available, so locations indicated are approximate, based on localities provided in the recovery dataset. Map used adapted from http://www.freeworldmaps.net/europe/europe-blank-map-hd.jpg

Age and sex ratio comparisons in residents and migrants

The 9,446 records were differentiated following the residency criteria into 8,788 records of 8,238 unique migrants and 658 records of 266 unique residents. The observed sex ratios were female-skewed in both residents and migrants. However, there was a significantly greater proportion of females among migrant individuals (0.69) compared to the resident population (0.60) ($\chi^2(1,N=8472)=8.75$, $p=0.0031$, see Figure 4). There was a greater discrepancy in age ratio between the two populations: first-year birds vastly outnumbered adults in migrants (0.73) and this proportion was significantly higher than that observed in the resident population (0.48) ($\chi^2(1,N=8435)=97,1$, $p<0.001$, see Figure 5).

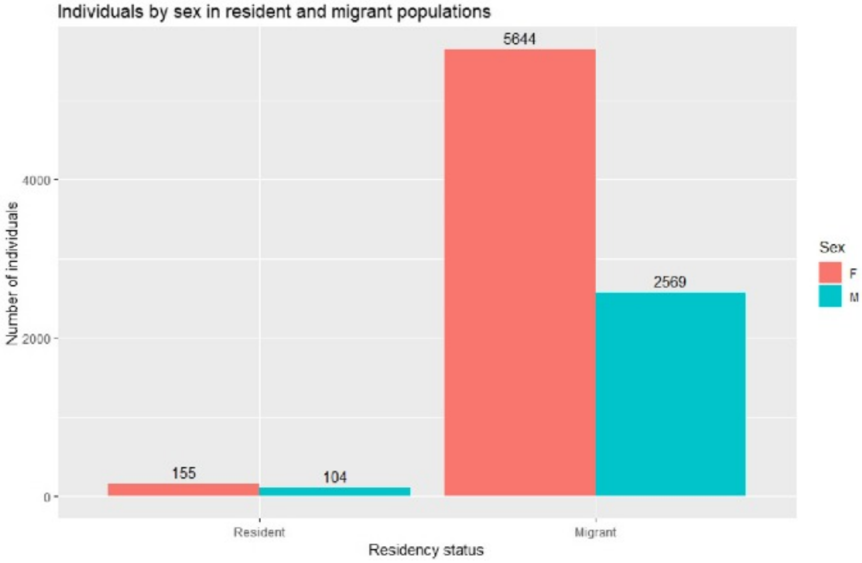

Figure 4: Number of individuals by sex within resident and migrant populations (*n*=8,472)

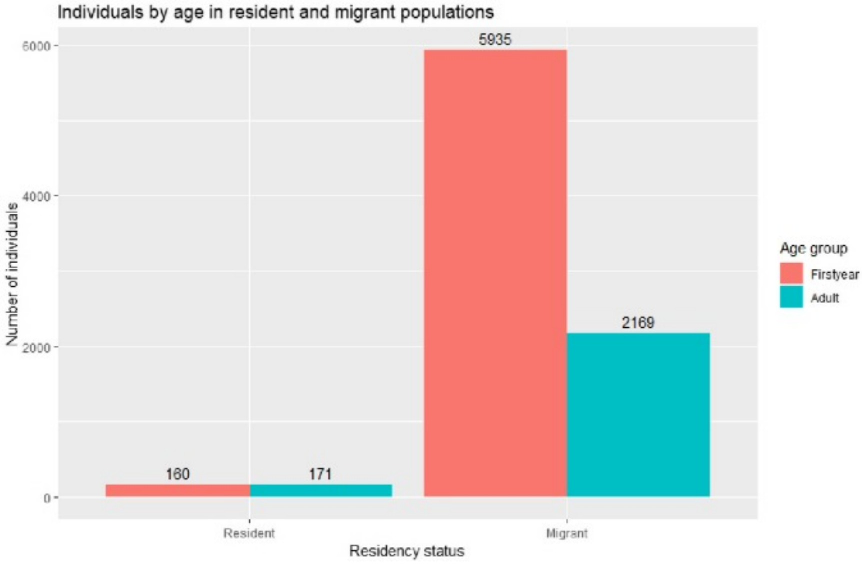

Figure 5: Number of individuals by age within resident and migrant populations (*n*=8,435)

Paired t-tests of annual sex and age ratios supported the chi-squared results. The annual proportion of females within the migrant individuals was on average 0.16 higher than the resident population (paired t-test, t(38)=4.82, P<0.001). Again, the annual age ratio was significantly higher in migrants than residents (paired t-test, mean of difference=0.26, t(37)=7.72, P<0.001).

Sexual dimorphism and age-related morphological differences

There was pronounced sexual dimorphism in terms of wing length, weight and wing-load estimate (Figures 6 to 8 and Table 1). Males had, on average, longer wing length, greater weight and higher wing-load estimate than females.

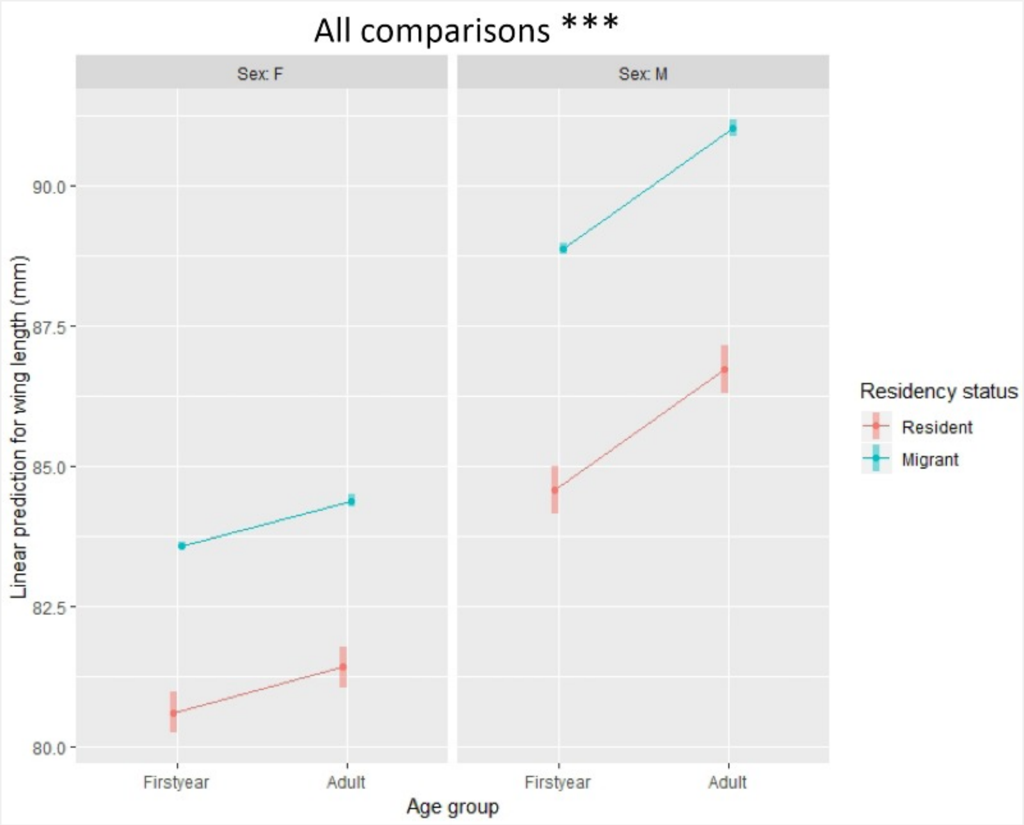

Figure 6: Linear mixed effect model predicted values of wing length in mm for females (left panel) and males (right panel) (*n*=8,863 of 8,024 individuals)

Age group, sex and residency status were tested as fixed effects with two-way interactions between age group and sex, and between residency status and sex. Estimated marginal means are plotted with 95% confidence intervals denoted by shaded vertical bars. Results of Tukey's HSD post-hoc tests comparing across all age, sex and residency classes were significant (P<0.001), showing that migrants, adults and males were longer winged than residents, first-years and females correspondingly.

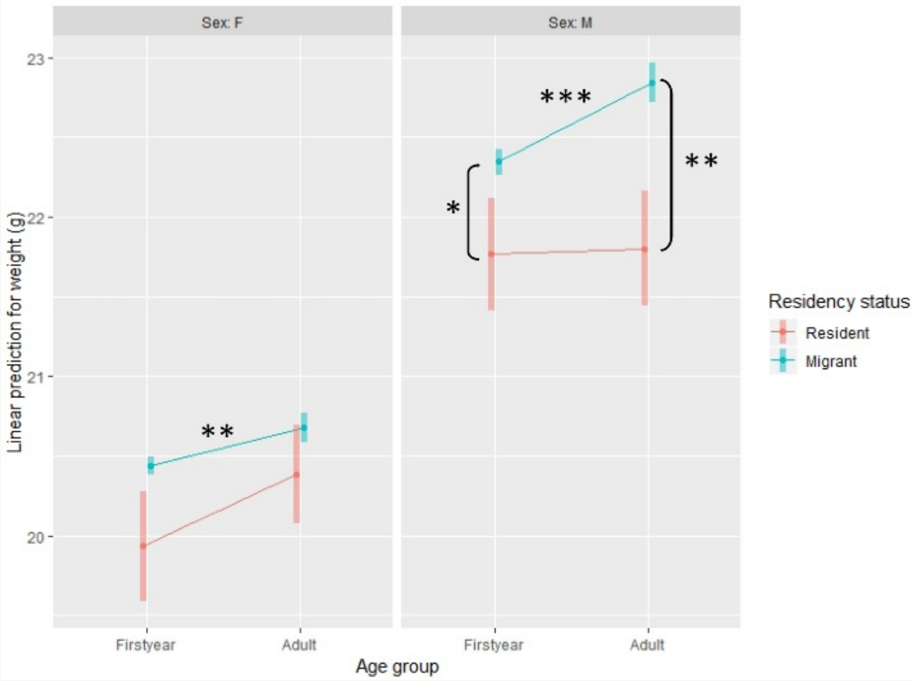

Figure 7: Linear mixed effect model predicted values of weight in g for females (left panel) and males (right panel) (*n*=8,832 of 7,984 individuals)

Age group, sex and residency status were tested as fixed effects with three-way interaction. Estimated marginal means are plotted with 95% confidence intervals denoted by shaded vertical bars. Significant results of Tukey's HSD post-hoc tests are given across age (horizontal comparisons) and residency classes (vertical comparisons) within each sex (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$). Not given in the figure: males were consistently significantly heavier than females when age and residency status were controlled for (all $P<0.001$).

Age-related morphological differences existed: adult individuals had longer wing length and were heavier than first-year birds (Figures 6 to 8). The age-related differences in wing length and wing-load estimates were dependent on sex, denoted by significant two-way interactions (Table 1). Male birds showed a greater increase in wing length with age than female birds (Figure 6). Although there were no overall significant differences in wing-load estimates between the two age groups, male birds exhibited a decrease in wing-load estimate with age, while an increase was seen in females (Figure 8).

Morphological differences between residents and migrants

Migrant birds were significantly longer-winged and heavier but did not differ significantly from resident birds in wing-load estimate (Figures 6 to 8 and Table 1). Additionally, the difference in wing length between migrant and resident birds was significantly greater in males than females, contributing to the significant two-way interaction between residency status and sex (Table 1).

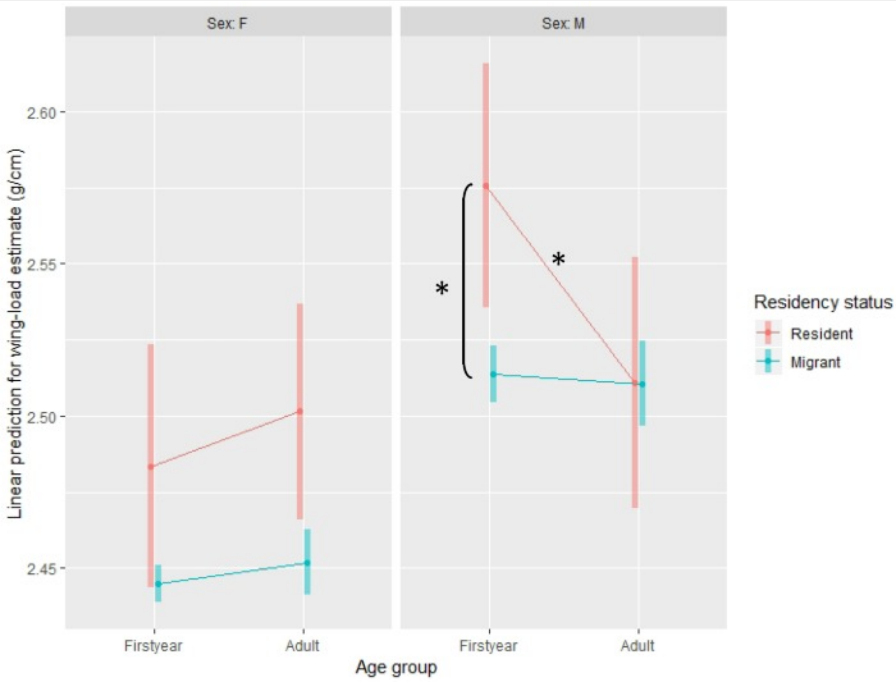

Figure 8: Linear mixed effect model predicted values of wing-load estimate in g per cm for females (left panel) and males (right panel) (*n*=8,776 of 7,956 individuals)

Age group, sex and residency status were tested as fixed effects with three-way interaction. Estimated marginal means are plotted with 95% confidence intervals denoted by shaded vertical bars. Significant results of Tukey's HSD post-hoc tests are given across age (horizontal comparisons) and residency classes (vertical comparisons) within each sex (*: $P<0.05$). Not given in the figure: sexual dimorphism was significant in all age and residency classes except adult residents (migrant adults and first years: $P<0.001$; resident first-years: $P<0.001$; adult residents $P>0.05$).

There was a significant three-way interaction between sex, age and residency status for weight (Table 1). Post-hoc comparisons of estimated means for weight (given in Figure 7) showed that adult birds of both sexes were significantly heavier than first-years amongst migrants but not amongst residents. Furthermore, migrant birds of both age classes were significantly heavier than their resident conspecifics only within males.

The significant three-way interaction between sex, age and residency status for wing-load estimate was further evaluated via post-hoc comparisons (Figure 8 and Table 1). Females showed an increase in wing-load estimate with age, but this effect was insignificant across both residents and migrants. In contrast, wing-load estimate in males decreased with age but only significantly within the resident population. Overall, wing-load estimate was lower in migrants than residents, but only significantly so within first-year males.

Sexual dimorphism was consistently significant for wing length and weight. However post-hoc comparisons of estimated means for wing-load estimates revealed that females had significantly lower wing-load estimates than males across all age and residency classes, except within adult residents where both sexes shared a similar value (Figure 8).

Table 1: Summary of linear mixed effect models

	Wing length			**Weight**			**Wingload estimate**		
Fixed effects	Estimates	SE	*p*	Estimates	SE	*p*	Estimates	SE	*p*
(Intercept)	80.61	0.19	**<0.001**	19.93	0.18	**<0.001**	2.48	0.02	**<0.001**
Age_groupAdult	0.80	0.07	**<0.001**	0.45	0.19	**0.016**	0.02	0.02	0.414
SexM	3.97	0.29	**<0.001**	1.83	0.25	**<0.001**	0.09	0.03	**0.001**
Residency_statusMigrant	2.97	0.19	**<0.001**	0.51	0.18	**0.004**	-0.04	0.02	0.062
Age_groupAdult:SexM	1.34	0.11	**<0.001**	-0.42	0.25	0.102	-0.08	0.03	**0.006**
SexM:Residency_statusMigrant	1.33	0.29	**<0.001**	0.07	0.26	0.774	-0.02	0.03	0.429
Age_groupAdult:Residency_statusMigrant				-0.21	0.20	0.275	-0.01	0.02	0.629
Age_groupAdult:SexM:Residency_statusMigrant				0.67	0.27	**0.013**	0.07	0.03	**0.023**
Random Effects									
σ^2	1.08			1.35			0.02		
τ_{00}	$3.85_{\text{Ring\_number}}$			$1.70_{\text{Ring\_number}}$			$0.02_{\text{Ring\_number}}$		
ICC	$0.78_{\text{Ring\_number}}$			$0.56_{\text{Ring\_number}}$			$0.53_{\text{Ring\_number}}$		
Observations	8863			8832			8776		

Key: Linear mixed effect models with wing length, weight and wing-load estimate as response variables. Age group, sex and residency status were tested as fixed effects; interaction terms are denoted by fixed effects punctuated by colons. Standard errors of the predicted estimates are represented by SE. Ring number was added as a random effect to account for pseudoreplication. Within-group and between-group variances and intraclass correlation coefficient are represented by σ^2, τ_{00} and ICC respectively. Estimated marginal means and pairwise contrasts via Tukey's HSD test for each model are given in Figures 6 to 8.

Table 2: Summary of binomial regression models testing climate data against annual sex and age ratios

	Sex Ratio			**Age Ratio**		
Fixed Effects	Odds Ratios	CI	*p*	Odds Ratios	CI	*p*
(Intercept)	2.25	2.14-2.36	**<0.001**	2.83	2.69-2.98	**<0.001**
NAO	0.97	0.95-1.00	**0.017**	0.96	0.93-0.98	**<0.001**
Observations	42			42		

Key: Binomial regression models with winter NAO indices (NAO) as a fixed effect. The response variables were the proportion of females (Sex Ratio) and first-years (Age Ratio) in the migrant population observed in the preceding autumn.

Climate effects on migrant sex and age proportions

Regional winter temperatures were positively correlated to winter NAO indices ($R^2=0.42$, $F_{(1,40)}=29.1$, $p<0.001$). Winter temperatures increased by 0.33 degrees Celsius per unit increase in winter NAO index. Binomial regressions results showed that winter NAO indices had a significant effect on both annual migrant sex and age ratios (Table 2). With every unit increase in winter NAO indices, the proportion of females and first-years observed fell by 0.97 times and 0.96 times respectively.

DISCUSSION

Evidence of differential migration

This study presents evidence that the Chaffinch is indeed a differential migrant. The comparisons of sex and age ratios between migratory individuals and the resident population suggest a differential migration pattern in which females and younger birds are the more migratory classes. These results are in support of hypothesis 1 and correspond with Linnaeus' notes and more recent observations on the species (Cramp & Perrins, 1994).

Body size hypothesis

The morphological comparisons conducted in this study have established sexual dimorphism and age-related differences followed by a migration pattern that is consistent with the 'body size' hypothesis (Ketterson & Nolan, 1976). Males and adult birds were found to be longer winged and heavier, which are physical traits that can confer more efficient heat conservation and fasting endurance, resulting in enhanced capacity to cope with colder weathers at higher latitudes (Ketterson & Nolan, 1976). The smaller females and younger birds are less adapted in this regard and thus forced to migrate further south where winters are milder.

This study's findings on sexual morphological differences and resulting trend in differential migration are corroborated by studies on sexually dimorphic avian species (Ketterson & Nolan, 1976; Belthoff & Gauthreaux, 1991). Additionally, improved cold resilience in larger individuals has been evidenced by bioenergetic studies conducted on avian species (Kendeigh, 1970). Thus, it is possible that the energetic constraints imposed by body size can explain the differential migration pattern observed.

However, it remains uncertain if the small, yet significant differences found in wing length and weight (the average differences do not exceed 4mm and 2g, Table 1) are influential to the birds' thermal biology. While there is an abundance of literature on the effect of sexual size dimorphism on thermoregulation (Ketterson & Nolan, 1976), there is limited scientific discourse regarding age-dependent variation in thermal ecology. Most of these studies focussed on older birds' enhanced feeding efficiencies, which translate to more effective harvest and storage of energy for improved heat maintenance (Merila & Wiggins, 1997). Furthermore, even though both intersexual and age-related differences in wing length and weight were significant, the latter was much lower (Table 1). Although this observation warrants additional investigation to be conclusive, it suggests that the body size hypothesis might better account for the species' intersexual distinctions in migratory strategies rather than why its young birds are more migratory than adults.

Dominance hypothesis

Longer wings and greater body mass are typical of dominant social classes in birds, as larger birds tend to win physical encounters against smaller conspecifics and are more efficient in procuring and securing resources (Piper, 1997). Younger individuals tend to be subordinate to older conspecifics, as they are physically less developed and possess comparatively limited experience in resource competition (Piper, 1997). Thus, the results of this study suggest that the 'dominance' hypothesis (Gauthreaux, 1982) for differential migration may be applicable to the Chaffinch.

Although the intraspecific discrepancies in physical characteristics point towards males and adults being the socially dominant classes in Chaffinches, it remains debatable if this is true within the migratory population assessed here. Firstly, there is no relevant commentary from the results of this study because it did not aim to evaluate social hierarchy, so any inferences will have to be extrapolated from existing literature. Secondly, studies on social hierarchy in the Chaffinch and related finch species were conducted within captive populations where social ranks were derived from artificially induced conditions and population densities (Marler, 1955). Given that avian hierarchical structures show some degree of plasticity in response to population density and stochastic environmental conditions (Schradin, 2013), the conclusions of said studies must be interpreted and applied with caution to wild populations. That said, the lack of understanding of social structures in wild migratory bird populations presents a challenging yet important opportunity for future research which will be crucial to our understanding of the social mechanisms underlying avian differential migration.

Arrival time hypothesis

Arguably, the ‘arrival time’ hypothesis (Myers, 1981) may also be relevant to the results of this study. As aforementioned, the pronounced sexual dimorphism in wing length and weight are suggestive of male-biased social dominance. Past studies have demonstrated Chaffinch males to be the dominant, territorial sex that is responsible for acquiring and defending breeding territories (Marler, 1955). Accordingly, males stand to gain more benefits in terms of reproductive success than females from wintering closer to breeding grounds. Minimising migration distances would mean incurring less cost associated with migration, allowing males to arrive at breeding grounds earlier and channel more resources towards intrasexual territorial competition (Myers, 1981). The resulting advantage in reproductive fitness would select for males to remain as sedentary as possible, which may have contributed to the differential migration trend seen in this study.

However, much like the ‘dominance’ hypothesis, there is insufficient information to confirm this. Besides the lack of behavioural data to ascertain male territoriality and dominance, proper analysis of this hypothesis demands arrival and departure time of migrants, which were not available. This was largely because bird ringing on Lundy is conducted on a voluntary basis, so seasonal coverage relies heavily on the availability of volunteers. Although capture dates were recorded for every bird, it was not possible to reliably determine migration timings as ringing efforts were non-standardised and intermittent, resulting in irregular coverage of years in their entirety. This issue highlights the value of consistent and standardised ringing in migration studies, and the intensive efforts required in data collection where bird ringing is concerned.

Additional considerations

It is prudent to note that the sex and age ratios calculated in this study are not necessarily representative of the species’ migration strategy.

To determine differential migration patterns by analysing sex and age ratios, it was important to first consider the population structures in both migrants and residents.

This step was imperative to establishing a valid baseline for comparison by eliminating inherent bias in analyses. Unfortunately, literature surrounding the Chaffinch's population demographics is largely missing, save for a single study conducted in Norfolk, United Kingdom, which substantiated the slightly female-skewed sex ratio found in Lundy's resident population (Browne, 2004).

Age and sex ratios are known to vary across intraspecific populations, mostly due to environmental factors that fluctuate with geography (Ketterson & Nolan, 1976). For instance, given the strong sexual size dimorphism demonstrated in this study, it is likely that offspring sexual size dimorphism exists in Chaffinches. Male chicks are likely energetically costlier to produce, thus colder temperatures in the northern latitudes might select for female-biased offspring sex ratio in the migrants (Trivers & Willard, 1973). Sex or age-based differential mortality due to predation pressures and intraspecific resource competition are sensitive to environmental or ecological factors such as predator abundance, habitat quality and ambient temperature (Székely *et al.*, 2004). Thus, without knowledge on population demographics, the observed differences in migrant and resident age and sex ratios may be merely artefacts of variations in age and/or sex ratio determinants and less due to differential migration.

Moreover, it was neither possible nor relevant to associate Lundy's migrant Chaffinches with their breeding populations. Recaptures were a rarity: only 24 out of 8,504 unique individuals were controlled throughout 46 years' worth of data, giving a recapture rate of 0.28%. Of the 26 records, only 12 were controlled beyond the British Isles and were spread around continental Europe and Fennoscandia. There was an obvious lack of information to pinpoint the breeding populations that Lundy's migrants belong to. However, combining the geographical distribution of Lundy's foreign controlled birds with those from previous studies (Wernham *et al.*, 2002), it is highly likely that Lundy's migrants originate from populations spread throughout northeastern Europe. At best, the migrant sex and age ratios measured in this study were average structures from an assemblage of populations.

A viable solution to the above issues is to evaluate temporal variations in sex and age ratio along latitude (*sensu* Ketterson & Nolan, 1976 and Catry *et al.*, 2005). Although such methodologies typically require large-scale efforts with close international collaboration to execute, they would be more reliable ways to assess differential migration patterns because they control for confounding effects of latitude on demographic parameters.

Morphological adaptations in migratory individuals

The morphological differences revealed between migratory and sedentary individuals were in support of hypothesis 2. Migrants had longer wing lengths, greater body mass and lower wing-load estimates than residents, which suggest that migrant individuals are physically larger and have disproportionately longer wings. These findings are consistent with the predictions of aerodynamic theory and studies that compared the ecomorphology of sedentary and migratory intraspecific populations (Pérez-Tris & Tellería, 2001).

Conflicting selective pressures influencing morphological variations

Wing length and body mass have contrasting relationships with avian locomotive efficiency. Shorter and rounded wings give manoeuvrability and are better suited for short-distance flights with frequent take-offs (Pérez-Tris & Tellería, 2001). On the other hand, longer and pointed wings are more energetically costly to develop but are associated with improved flight velocity and efficiency (Nowakowski, Szulc & Remisiewicz, 2014). Body mass is positively related to wing-loading: the heavier the bird, the more weight to be distributed per unit of wing area and thus the more effort expended for flight. Yet, greater body mass is advantageous for heat conservation and improved fasting endurance, which are life-saving traits for cold climates and long-distance travel (Ketterson & Nolan, 1976; Ashton, 2002). Considering the opposing aerodynamic consequences imposed by wing length and body mass, the morphology of migratory individuals would be optimised to reflect a delicate trade-off between the selective pressures of migratory cost and colder climates. Likewise, the discrepancies in age or sex-related variation in morphology between sedentary and migratory individuals may be due to selective forces acting in concert within each population.

Age-related variation of weight

Unlike Lundy's resident birds, migrants showed a significant increase in weight with age. A greater body mass is preferable from a migratory performance standpoint as it suggests a bird in prime physical condition to withstand the caloric and muscular demands of the journey (Guy Morrison, Davison & Wilson, 2007). Yet, increases in body mass can be deleterious as it can impede predator avoidance (Lind *et al.*, 1999), which is an essential survival trait for juvenile birds given their greater susceptibility to predation (Solonen, 1997). Thus, first-year migratory birds might be facing an upper limit constraint on body mass due to predatory pressure. The significant gain in weight with age in migrants is then a consequence of the alleviation of predation risk in adulthood as the birds gain more experience in escaping attacks (Solonen, 1997) and the augmented influence of migratory pressures. There was little biological incentive for the sedentary residents to carry the burden of additional body mass, which may explain why the significant increase in body weight with age was only seen in migrants.

Intrasexual variation in morphological trends

Assuming females were the more migratory sex, it was surprising that differences in morphology between migrant and resident birds were larger in males than females. This finding was in contradiction to hypothesis 2, as it was expected that the more migratory sex would express a greater difference in morphology between residents and migrants. This suggests that selective pressures excluding that exerted by migratory flight were in force. One possibility would be heightened intrasexual competition between migrant males. Colder weather in northern latitudes may limit resource quality and quantity, thus harsher climate could have intensified male-male territorial disputes and hence selected for physically larger, stronger and dominant males (Marler, 1955). The comparatively lower degree of territoriality expressed by females suggests a reduced selective influence by intrasexual competition in migrant females, which may be reflected by the smaller gap in wing length and weight between female residents and migrants.

The opposite age-related trends in male and female wing-load estimates were also against predictions, since lower wing-loading is typically associated with more migratory classes. Again, additional selective forces were likely responsible for this observation. The species is visually dimorphic in adulthood: juveniles from both sexes share similar appearances, but males develop a distinctly more vivid plumage in their second year (Svensson, 1992). Studies have shown that this predisposes male adults to a higher risk of predation, as their brighter colouration renders them more conspicuous (Götmark & Hohlfält, 1995). Hence, predatory pressures would select for the survival of male adults which are better equipped to avoid predatory attacks, such as those with lower wing-loading. The absence of increased predation threat for female adults may account for the lack of significant age-related variation in wing-load estimate. Furthermore, the steeper gradient of decrease in wing-load estimate with age in resident males may be symptomatic of higher predation pressures on Lundy. Raptors which feed on the Chaffinch are plentiful on the island (pers. obs., November 2017; Davis & Jones, 2007).

Limitations to interpretation

Evidently, it is tricky to disentangle the conflicts and reinforcements to age, sex or residency-related trends in morphology by various forces of natural selection. Thus, the possibility that there were other factors confounding this study's findings cannot be discounted and necessitates additional investigation. Specifically, further studies will greatly enrich our understanding of selective pressures responsible for age and sex-related morphological trends within the sedentary population.

It is important to note that the wing-load estimate used in this study is not a perfect index for wing-load. Wing area data were missing, which limited this study's conclusiveness where wing-load is concerned. The lack of reliable allometric formulas to calculate wing area from wing length meant that the wing-load estimate was the closest approximation to wing-load afforded by available data. Wing length measured via the maximum chord method is far from the standard of deriving wing area from photographs or wing tracings (Yalden, 2012). This presents a future direction for additional research to elucidate the aerodynamic adaptations for migration in Chaffinches.

NAO effects on differential migration

The proportion of females and first-year birds was inversely related to the NAO index, which was congruent to the predictions of hypothesis 3. The results suggest that milder winter climates displaced fewer individuals of the more migratory sex and age classes, likely because less harsh weather conditions meant that more individuals could afford to stay sedentary to avoid incurring costs associated with migration.

An important implication of this observation is sex and age spatial segregation of Chaffinches in winter. If, in colder winters, females and younger birds are more inclined to migrate and overwinter southwards, then in these circumstances they would be more susceptible to environmental threats such as habitat loss in their wintering grounds. This would have profound consequences for the migratory *gengleri* subspecies as this can skew sex and age ratios in affected populations. Where anthropogenic threats are concerned, heterogeneous levels of man-made risks across geographical locations will result in unequal exposure to such threats depending on the birds' seasonal distribution. Although there is no information in this study to comment on this, the pattern of differential migration and its responses to climate suggested in the results can serve as a foundation for further research and hypotheses.

Limitations to interpretation

Data collection was limited to Lundy; thus information was inadequate for constructing a complete representation of differential migration in the Chaffinch and its sensitivities to climate. The current dataset relied on intercepting migrants en route. Since the migrants are known to use Lundy as a stopover, the birds could have bypassed the island in weather conditions favourable for onward migration and were thus not captured and reflected in subsequent analyses. This could have resulted in an underestimation of sex and age ratio variation in response to winter NAO indices. To overcome this limitation, it is pertinent to expand the geographical coverage of data, preferably in a latitudinal way parallel to studies by Ketterson & Nolan (1976) and Catry *et al.* (2005).

Another major assumption in the interpretation of winter NAO effects on annual migrant demography was that the indices were representative of relevant winter conditions that affected differential migration. Differential migration is known to be affected by the phenology and resource quality of breeding and wintering sites plus areas along the associated flyway (Anthes, 2004). The NAO is a large-scale climatic phenomenon; thus, its indices do not necessarily reflect local weather conditions that were influential to the extent of differential migration. Consequently, even though regional winter temperatures did show the expected positive relationship with winter NAO indices, this was only indicative of winter temperatures at a stopover site and was not fully representative of the weather conditions of interest.

Unfortunately, due to data deficiency, it was not possible to ascertain the breeding and wintering areas utilised by Lundy's migrant Chaffinches. This hindered the derivation of appropriate local weather indices for sufficient geographical coverage in this study. The inclusion of regional climate indices across continental Europe and other weather indices with recognised impact on site phenology (e.g. rainfall: Gordo, 2007 and references therein) in further analyses is a plausible solution to this challenge. Another consideration is to employ remote sensing technology to identify and monitor environmental conditions at sites of interest, to directly establish the relationship between climatic variations and migratory patterns (Gordo, 2007).

CONCLUSION

This study presents morphological and population demographical evidence supporting the notion that the Chaffinch *Fringilla coelebs* is a differential migrant, and that its females and younger individuals are the more migratory classes. While there are many hypotheses for differential migration, the ‘body size’ hypothesis may be the closest in explaining the phenomenon in this species. However, because these hypotheses share similar predictions, and data inadequacies in this study impaired conclusive judgement, further research is required to disentangle the underlying mechanisms.

In general, migratory individuals showed morphological traits that agree with aerodynamic theory, but discrepancies exist across age and sex classes. A bird’s morphological characteristics are the reflection of selective pressures acting simultaneously and are optimised for individual fitness and survival. Due to the multifaceted and interconnected character of natural selection, teasing apart the cause and effects of each force of selection is no trivial task, and should be a challenge tackled in future studies.

The value of understanding climatic effects on differential migration should not be underestimated. Given impending climate change, seasonal segregation and distribution of intraspecific classes in migratory avian species are likely to shift spatially and temporally in the future. Improving our comprehension of the climatic mechanisms behind differential migration can be key to predicting seasonal population distribution when individuals are highly vulnerable. This will better inform conservation policies, especially those concerned with the protection of sites of migratory importance.

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APPENDIX A: Chaffinch recovery data *(continued on next page)*

Scheme	Ring	Age	Sex	Date	Place	Date	Place	Circumstances	Notes
GBT		4	F	30/10/1958	Lundy	15/10/1961	Kohlscheid, nr Aachen, Germany		
GBT		3	F	13/10/1959	Lundy	14/10/1960	Liege, Belgium		
GBT		3	M	26/10/1969	Lundy	24/3/1973	Googstraten, Antwerp, Belgium		
GBT	B580928	3	M	16/9/1984	Lundy	15/3/1985	Bideford, Devon	Hit window. Flew off unharmed	Later retrapped twice on Lundy
GBT	D184049	3	F	20/10/2012	Lundy	4/4/2014	Mulvika, Re, Vestfold, Norway	Controlled by ringer	
GBT	D184209	5	M	26/4/2013	Lundy	1/5/2016	Ynys Hir, Ceredigion	Freshly dead (Trichomonosis)	
GBT	E186791	4	F	4/4/1988	Hartland Point, Devon	8/10/1989	Lundy	Controlled by ringer	
GBT	F969110	4	M	23/4/1991	Hartland Point, Devon	28/10/1991	Lundy	Controlled by ringer	
GBT	J477793	3	M	26/10/1993	Lundy	15/1/1995	Alston Hall, Lancashire	Controlled by ringer	
GBT	J477809	3	F	26/10/1993	Lundy	8/4/1998	Ottenby, Oland, Sweden	Controlled by ringer	
GBT	J509136	3	M	29/10/1993	Lundy	16/5/1997	Vester Vandet So Thisted, Jylland, Denmark	Controlled by ringer	
GBT	J509136	3	M	29/10/1993	Lundy	9/5/1998	Vester Vandet So Thisted, Jylland, Denmark	Controlled by ringer	
GBT	K923322	4	F	30/10/1997	Lundy	6/11/1998	Zele Heikant, Oost-Vlanderen, Belgium	Controlled by ringer	

APPENDIX A: Chaffinch recovery data *(continued from previous*

Scheme	Ring	Age	Sex	Date	Place	Date	Place	Circumstances	Notes
GBT	L026586	3	F	14/10/2009	Lundy	23/4/2012	Bomyra,Randaberg, Rogaland, Norway	Controlled by ringer	
GBT	L026586	3	F	14/10/2009	Lundy	6/4/2015	Bomyra,Randaberg, Rogaland, Norway	Controlled by ringer	
GBT	N407155	3	M	26/10/1997	Lundy	19/10/2004	Wassenaar Meijendel Sparregat, Zuid-Holland, Netherlands	Controlled by ringer	
GBT	N879249	3	F	24/10/1999	Lundy	22/12/2001	Uley Bury, Gloucestershire	Controlled by ringer	
GBT	P660612	4	F	29/10/2001	Lundy	16/12/2001	Nr Venusbank, Cound, Shropshire	Controlled by ringer	
GBT	P660754	3	F	1/11/2001	Lundy	4/1/2002	Muddiford, Barnstaple, Devon	Killed by cat	
GBT	R009392	3	M	21/10/2002	Lundy	13/3/2004	Tavistock, Devon	Found freshly dead	
GBT	R009559	3	F	22/10/2002	Lundy	7/8/2003	Borlange, Kopparberg, Sweden	Found dead; hit window	
GBT	R009700	3	M	22/10/2002	Lundy	15/3/2003	West Town, Bideford, Devon	Found dead	
GBT	T949551	3	F	7/9/2007	Lundy	20/4/2008	Okehampton, Devon	Killed by cat	Retrapped on Lundy x3 in Oct '07
GBT	V935134	3	F	26/10/2007	Lundy	17/2/2008	Le Chene, Saint-Colomban, Loire-Atlantique, France	Found dead; hit window	
RUM	XY20913	3	F	26/9/2005	Rybachiy, Kaliningrad, Russia	27/10/2005	Lundy	Controlled by ringer	
GBT	Z981660	3	F	25/10/2017	Lundy	12/11/2017	Lifton, Devon	Found dead; hit window	

APPENDIX B: EURING age classification

EURING age code	Age of bird
2	Non-juvenile, exact year uncertain
3J	Hatched in current calendar year, still in juvenile plumage
3	Hatched in current calendar year
4	Hatched before current calendar year, exact year unknown
5	Hatched in previous calendar year
6	Hatched at least two calendar years prior, exact year unknown

APPENDIX C: Statistical analyses

Packages used were lme4 for linear mixed effect models (Bates *et al.*, 2015), lmerTest for processing p-values for fixed effects in linear mixed effect models, using Satterthwaite approximation to degrees of freedom (Kuznetsova, Brockhoff & Christensen, 2017), emmeans to obtain estimated marginal means and conduct Tukey's Honest Significant Difference (HSD) post-hoc tests (Lenth, 2018), and car for verifying homoscedasticity assumptions (Fox & Weisberg, 2011). Data were visualised with ggplot2 (Wickham, 2016), sjPlot (Lüdecke, 2018) and native packages.

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AVIAN COMMUNITIES OF LUNDY 2008-2016

by
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ABSTRACT

Nine years of citizen science data about avian abundance on Lundy are analysed for diversity and similarity. Diversity is relatively stable across the nine-year period, as is similarity in year-to-year comparisons, but there is approximately 30% dissimilarity between years. This appears to be caused by migrant and vagrant birds, and passerines predominate. We make comment on the nature of the data collected, its limitations and also suggest how to improve data collection. We see this as a first step, and it is our hope that this article will stimulate further analyses of existing data, and encourage current and future researchers to further develop data collection and analytic techniques to better understand Lundy's ecology. Such activity will be of direct use to management and conservation efforts on the island but also of intrinsic scientific interest.

Keywords: *Lundy, avian community, diversity, dominance, citizen science*

INTRODUCTION

The Lundy Field Society (LFS) has reported annual bird lists since 1948, compiled from the logged observations of visitors and residents including the wardens. Various individuals have compiled these lists across the decades and the level of detail and manner of recording have differed accordingly. The bird lists are published in the Annual Report and are available online as PDF documents (http://tinyurl.com/yxv5xmov). This kind of citizen science is far from new, as the timeline attests, and it represents a venerable part of the history of ecology (Silvertown, 2009).

From 2008 Tim Davis and Tim Jones have compiled the LFS bird lists in a systematic fashion, making these citizen science data more readily processed. This came after their excellent overview of prior Lundy bird reports, published in book form (Davis & Jones, 2007). Their reports give maximum monthly counts of birds across the year, but also detailed notes of rarities, migrants and vagrants. Commentary is also made where systematic survey work has been conducted in a given year, such as the Royal Society for the Protection of Birds (RSPB) and Joint Nature Conservancy Council (JNCC) seabird monitoring work. Nonetheless, all counts recorded come from informal observational work.

Whilst count data collected by volunteers are of considerable use, it does have weaknesses. Notably, the LFS observations have not been systematically derived using standard techniques, such as set transects, point surveys or territory mapping (Bibby *et al.*, 2000). The data are also compiled by multiple observers, a majority of whom are most likely regular visitors and others who are not. Within this group of observers, abilities to observe and identify will be varied. Furthermore, it is likely that survey effort will be unequal across all observation bouts. This is in part because of the highly seasonal nature of the observations on Lundy. More expert observers tend to visit in spring and autumn, leaving the rest of the year to less expert visitors and the warden. The current warden is an extremely experienced observer, but this has not always been the case, and in the early years when the LFS employed a warden, that person was more often not present between October and March (we are indebted to Tim Davis and Tim Jones for this detail). Gaps in data have necessarily emerged as a consequence.

All of these factors will introduce considerable inconsistency and an unknown degree of error into the data, leading to wide confidence intervals about any point estimate (Snäll *et al.*, 2011). As a consequence any weak population trends will go unnoticed. As Snäll *et al.* point out, the solution to this is to focus on common species where detection is more assured, leaving scarcer birds to formally designed and executed studies. This then makes detailed monitoring an issue of resources, as formal studies are time intensive and rely on a specific level of expertise.

It is possible to design citizen science monitoring programmes that reduce some of the problems listed above (Conrad & Hilchey, 2011) and both the British Trust for Ornithology (BTO) and the RSPB rely on such well considered schemes, and we shall make some recommendations for Lundy in the Discussion. For now, however, we would note that the activity of watching and counting any species on Lundy is useful for reasons beyond formal monitoring. As Conrad and Hilchey make clear, such activities help to educate the visiting population about conservation issues but also help to cement relevant social bonds among those who are well placed to care for the site, with hope such sentiment and action will generalise beyond the island.

Davis and Jones have made a remarkable contribution through their work, one that has made bird reporting on the island more accessible and, as a consequence, opens the data to systematic scientific enquiry, with due caution around data distribution and error. Tracking avian biodiversity and abundance can help to understand the community ecology of these species. As avian species largely consist of mesotrophic predators, with many seed eaters relying upon insects during the breeding season, the community ecology of birds is indicative of the general biodiversity and ecological health of a site (Bibby *et al.*, 2000). In this article we present a series of basic analyses of bird community structure on Lundy drawn from data reported between 2008 and 2016. The principal analyses we present are basic diversity, dominance and similarity indices for breeding and non-breeding birds on Lundy across nine years of data. These indices are effectively tracking alpha diversity of the whole site. In order to drill into beta diversity we would require observations to be tied to habitat and related data, which are not currently available. We then go on to make some comments about the avian community structure of the island before moving onto concluding comments and recommendations.

The aim of our work is to indicate what can be done with such data and to encourage further, and more sophisticated, analyses, by current and future researchers. We note that the Annual Reports also include data on many other aspects of the flora and fauna of Lundy, which presents not only the possibility of similar analyses for other taxonomic groups, but also for integrated data set creation. Our choice of birds, to illustrate the potential of all LFS data, is perhaps born of our other interests, but in no sense should be read as an exclusive recommendation. Thus, we hope that the analyses we present are of intrinsic interest, but more importantly, that they present a starting point for analysing specific scientific questions around, for example, the impact of island management and conservation schemes. Moreover, such data could be usefully related to secondary data on weather and climate, as well as data from other neighbouring sites, such as the island of Skomer. To this end, we hope to initiate a concerted scientific effort. We believe collecting data is only one half of the custodial responsibility we have for sites such as Lundy. The other half is the use of it.

METHODS

Raw data preparation

Our first task was to record the data reported in the LFS Annual Report bird lists using Microsoft Excel 2011™. We used this format as Excel files and comma separated variable (CSV) files could be readily shared between the two authors, but also because Excel enabled the construction of key formulae for later calculations. All analyses reported were conducted on MS Excel 2011™, R (R Development Core Team, 2009) and IBM SPSS v24 on an iMac OS10.13.

The basic data we recorded for all 214 species observed between 2008 and 2016 were: maximum count per month within each year; their British status (from the British List 2017 found at: https://www.bou.org.uk/); and their Lundy status following Davis and Jones. This last amounted to whether or not they were resident breeders, Lundy vagrants, British vagrants, Devon rarities, migrants, etc. We then added Latin nomenclature for each species, as well as information about Order, Family and Genus. Additionally we recorded basic foraging data following descriptions from *The Birds of the Western Palearctic* (BWP) (Snow & Perrins, 1997). The non-exclusive categories for food or dietary choice can be seen in Table 1.

Table 1: Foraging sub-category of food choice: each option was recorded in terms of presence or absence for each species

Category	Options
Food choice	Vertebrates
	Invertebrates
	Plants

RESULTS

Highest count data and species richness

Table 2: Species and bird counts with mean bird count and lower (LCI) and upper 95% confidence intervals (UCI), and Menhinick's Index (MI) of species richness across nine years of citizen science data collection on Lundy

Year	Total Species	Total Count	Mean Count	LCI	UCI	MI
2008	143	47577	332.71	124.06	541.36	0.66
2009	132	71926	544.89	120.15	969.63	0.49
2010	147	61919	421.22	162.00	680.44	0.59
2011	140	42998	307.13	148.39	465.87	0.68
2012	150	78623	524.15	167.74	880.57	0.53
2013	128	38085	383.87	176.01	591.72	0.58
2014	143	35492	248.20	115.12	381.27	0.76
2015	136	60534	445.10	83.38	806.82	0.55
2016	139	48490	348.85	110.25	587.45	0.63

As can be seen from Table 2 the confidence intervals around the count means are large, which introduces a great deal of uncertainty when attempting to derive point estimates of abundance across the nine years of data collected. This is in keeping with the observations made in the introduction (Snäll *et al.*, 2011) but a portion of that may well be driven by fluctuations in migrant numbers. We shall return to this point.

Whilst the total number of species recorded gives basic species richness data, this does not account for sampling effort. Put simply, the more sampling done, the greater the number of species one would expect to record. Given this, Menhinick's Index was calculated (Gardner, 2014), as a form of standardisation, by dividing the total number of species in each annual sample by the square root of the total number of individual birds in each annual sample. The mean for Menhinick's Index=0.61, with a lower 95% confidence interval of 0.56 and an upper 95% confidence interval of 0.66. The coefficient of variation for Menhinick's Index is 0.14. The coefficient of variation should be read as a percentage, thus this represents 14% variation for this index. Whilst this is a descriptive statistic, with no inferential test for significance, at this point we have no reason to reject the hypothesis that richness has been stable across the sampled nine years.

Diversity

Diversity indices use the proportion of each species' contribution to the overall total count in order to produce an unbounded measure of species diversity. We calculated two forms of Shannon diversity (H-index), using a natural log and log base 2 standardisation of proportionality of representation. The natural log method is the most common, and we provide it for the purposes of comparison between studies. However, the log base 2 version is more readily interpretable as the number of yes-no questions one would have to ask to ascertain the identity of a species drawn at random from that sample (Gardner, 2014). We further calculated the exponential of the natural log index (ExpH) in order to give a measure of effective species, which is the number of equally common species within a sample and gives a more intuitive sense of true diversity (Jost, 2006) (Table 3). The mean for the log base 2 H-Index=4.04, with a lower 95% confidence interval of 3.82 and an upper 95% confidence interval of 4.25. The coefficient of variation is 0.08. This gives no reason to reject the hypothesis that diversity has been stable across the nine years. The mean for ExpH=16.78, with a lower 95% confidence interval of 14.39 and an upper 95% confidence interval of 19.17. The coefficient of variation is 0.22. This indicates relatively more variance in the effective species across nine years, and thus diversity, compared with those estimates derived from Shannon calculations. Nonetheless, we consider this indicative of core stability.

Table 3: Two measures of Shannon diversity (natural log (H-LN) and log base 2 (H-Log 2)) and effective species number (ExpH) across nine years of citizen science data collected on Lundy

Year	H-LN	H-Log 2	ExpH
2008	2.86	4.13	17.49
2009	2.46	3.55	11.74
2010	2.82	4.06	16.69
2011	3.09	4.45	21.91
2012	2.76	3.97	15.72
2013	2.99	4.28	19.48
2014	3.05	4.39	21.02
2015	2.45	3.54	11.61
2016	2.73	3.94	15.36

Similarity/Dissimilarity

We converted count data to presence-absence data for all species in all years. This allowed calculation of the similarity between annual samples in terms of species composition but also attenuated issues relating to large confidence intervals as a result of observer and observational effort differences and migration. We used both the Jaccard and Sorensen indices for this purpose, as two of the most commonly used (Gardner, 2014), and ran similarity comparisons across year pairs in a temporal sequence in order to give a sense of change in composition over the total sampling effort. These trends are displayed in Table 4. The indices are bounded as a 0-1 scale and should be read as the amount of similarity at species level across comparisons.

Table 4: Two indices of similarity across eight pairs of years derived from nine years of citizen science data collected on Lundy. A value can be read as a percentage similarity, thus using Jaccard, there was an approximately 70% similarity in species composition between 2008 and 2009; leaving an approximate 30% dissimilarity. The coefficient of variation (CV) is given for each index

	2008-2009	2009-2010	2010-2011	2011-2012	2012-2013	2013-2014	2014-2015	2015-2016	CV
Jaccard	0.70	0.74	0.74	0.73	0.70	0.69	0.78	0.76	0.04
Sorensen	0.82	0.85	0.85	0.84	0.82	0.82	0.87	0.87	0.03

Whilst similarity indices yield slightly different absolute values, they consistently track patterns in fluctuation and are suitably standardised to allow comparison to be made between communities, in this case annual populations of birds on Lundy. Given this, we focused on Jaccard's index. The mean for Jaccard's Index=0.73, with a lower 95% confidence interval of 0.71 and an upper 95% confidence interval of 0.75. The coefficient of variation for Jaccard (0.04) gives no reason to reject the hypothesis that similarity of species composition was similar across the year-on-year comparisons.

We wanted to track certain aspects of similarity across the nine years of data, and in particular we were interested in the kinds of birds that were present for all nine years, or proportions of that overall time. In other words, we wished to better understand aspects of the core community structure on Lundy. To do this we analysed the data at the Order, breeding status (yes-no) and dietary choice levels, as this packaged species into phylogenetically related groupings (to make visual analysis more tractable), those using the island for continuation, and those with some functional commonality at the dietary guild level.

Table 5: The number of species within each Order across years present. Thus Nine indicates each contributing species was present for all nine years, whilst One indicates presence for only one of the survey years. This is a heat map, such that red indicates extreme absence, and green high presence

	Number of years present								
ORDER	Nine	Eight	Seven	Six	Five	Four	Three	Two	One
Anseriformes	2	2	0	0	1	1	1	5	4
Galliformes	0	0	0	0	0	0	0	1	0
Gaviiformes	1	0	0	0	0	1	0	0	1
Procellariiformes	4	0	0	0	0	0	0	2	1
Suliformes	3	0	0	0	0	0	0	0	0
Pelecaniformes	1	1	0	0	0	0	0	0	0
Podicipediformes	0	0	0	0	0	0	0	0	2
Accipitriformes	2	0	2	0	1	0	0	4	2
Falconiformes	3	1	0	0	0	0	0	0	0
Gruiformes	1	0	0	0	0	0	0	0	2
Charadriiformes	15	9	0	2	3	1	5	7	4
Columbiformes	3	1	1	0	0	0	0	0	0
Cuculiformes	1	0	0	0	0	0	0	0	0
Strigiformes	1	0	0	0	0	1	0	0	0
Caprimulgiformes	0	0	0	0	0	0	1	0	0
Apodiformes	0	1	0	0	0	0	0	0	1
Coraciiformes	0	0	0	0	0	0	1	0	1
Bucerotiformes	0	0	0	0	0	1	0	0	0
Piciformes	0	1	1	0	0	0	0	0	0
Passeriformes	52	4	4	3	5	3	6	8	15

Table 6: The number of species within each dietary choice category across years present. Thus Nine indicates each contributing species was present for all nine years, whilst One indicates presence for only one of the survey years. Note that there were data missing for four species for dietary choice as this was not recorded in BWP. This is a heat map, such that red indicates extreme absence, and green high presence

	Number of years present								
DIET	Nine	Eight	Seven	Six	Five	Four	Three	Two	One
All foods	11	2	0	0	2	0	1	0	4
Vertebrates and Invertebrates	12	6	2	0	1	1	5	5	8
Invertebrates and Plants	38	5	4	3	4	3	4	11	5
Vertebrates and Plants	0	0	0	0	0	0	0	1	0
Vertebrates	8	0	1	0	2	2	0	0	4
Invertebrates	19	5	1	2	0	1	3	5	8
Plants	1	2	0	0	1	1	0	4	2

Tables 5 and 6 give a sense of how the bird communities on Lundy have differed across the nine-year period analysed in this paper. Breeding birds are present in all years, with one exception: an eight-year presence for one species (Chaffinch *Fringilla coelebs*). As a result we have not tabulated breeding data. More sporadic attendance is left to non-breeding birds that are migrants or vagrants. To look into Order and dietary choice more systematically, two separate hierarchical cluster dendrograms were produced based on Euclidean distance measures of dissimilarity, which use abundance data rather than mere presence-absence (Figure 1). These were created using the hclust function and the complete method in R. These diagrams show how species within particular presence categories (from one year only to all nine years) cluster in terms of similarity on Order composition and dietary choice. A visual inspection shows that the clustering patterns are very similar for categories 1,3,4 and 6 in both diagrams, but most notably that whilst 1 is a clear outlier in both analyses, the remaining categories are relatively similar to one another. This is in keeping with the presence-absence similarity analyses above.

An independent samples Kruskal-Wallis test was conducted to test the hypothesis that Order was unevenly distributed across each category of the number of years present. No significant results were returned and so we should retain the null hypothesis of even distribution. A visual inspection of Table 5 suggests that passerines dominate generally across the sample. This was tested with a series of Wilcoxon paired sample tests and found to be statistically significant (Table 7). A further independent samples Kruskal-Wallis test was conducted to test the hypothesis that dietary choice was unevenly distributed across each category of the number of years present. No significant results were returned (as above). No further analyses were conducted on dietary choice.

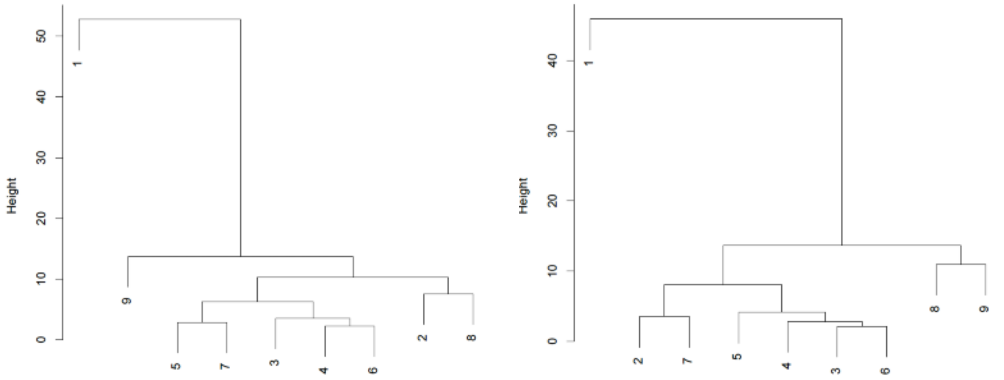


Figure 1: Hierarchical cluster dendrograms displaying dissimilarity between Order structure (left panel) and dietary choice structure (right panel) across the number of years present. The y-axis represents Euclidean distance between clusters, such that the cluster labelled 1 in each panel is in fact the most dissimilar. These clusters represent years of occurrence such that 1 means one year of occurrence for the particular species that contributed data to Order or dietary choice categories, whereas 9 means nine years of occurrence from contributing species

Table 7: Wilcoxon paired sample tests (z) comparing Passeriformes with all other Orders within the whole sample of data. Passerines clearly dominate as an Order on Lundy

	Passeriformes compared with:				
Order	Picif.	Bucerotif.	Coraciif.	Apodif.	Caprimulgif.
Z	-2.689	-2.668	-2.673	-2.675	-2.673
Asymp. Sig. (2-tailed)	0.007	0.008	0.008	0.007	0.008
Order	Strigif.	Cuculif.	Columbif.	Charadriif.	Gruif.
Z	-2.668	-2.670	-2.689	-1.844	-2.670
Asymp. Sig. (2-tailed)	0.008	0.008	0.007	0.065	0.008
Order	Falconif.	Accipitrif.	Podicipedif.	Pelecanif.	Sulif.
Z	-2.675	-2.677	-2.670	-2.675	-2.670
Asymp. Sig. (2-tailed)	0.007	0.007	0.008	0.007	0.008
Order	Procellariif.	Gaviif.	Gallif.	Anserif.	
Z	-2.673	-2.668	-2.670	-2.673	
Asymp. Sig. (2-tailed)	0.008	0.008	0.008	0.008	

Seasonal analyses

A number of the species that breed on Lundy, such as Linnet (*Linaria cannabina*), Meadow Pipit (*Anthus pratensis*), Skylark (*Alauda arvensis*) and Wheatear (*Oenanthe oenanthe*) also occur in large numbers during migratory periods. This means that the overall highest count numbers are far greater than estimates of breeding populations on the island, not least because of limited breeding habitat for these species. Whilst our focus was on the basic nature of which species are present on the island across the nine years, and therefore within each year, we also conducted a series of seasonal analyses. To do this we took highest count data reported on a monthly basis and created totals for spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January and February) across all nine years. Thus each seasonal data package consisted of 9 years × 3 months of data. Table 8 presents the basic richness and diversity analyses.

Table 8: Seasonal data calculated as total highest counts for each season across all nine years (see main text for details). The number of species registered in each season for the entire sample is given, along with the mean of the total highest counts, the 95% confidence intervals (CI) and the coefficients of variation (CV) for each compound season. Menhinick's Index (MI) of species richness and two measures of Shannon diversity (natural log (H-LN) and log base 2 (H-Log 2)) and an effective species number (ExpH) are also given for each compound season

	Species descriptives				**Richness and diversity metrics**			
	No. of species	Mean count	95% CI	CV	MI	Effective Species	H-LN	H-Log 2
Spring	165	1037.70	800.73	5.06	0.40	12.47	2.52	3.64
Summer	133	909.51	1001.60	6.48	0.38	7.47	2.01	2.90
Autumn	180	792.02	470.90	4.07	0.48	19.79	2.99	4.31
Winter	86	720.40	638.71	4.20	0.35	8.05	2.09	3.01

Table 8 shows that there is a large amount of variation (CV) in abundance within the compound seasonal data, but these data are not normally distributed within each season (all tests for deviation from normality returned a significant result). A non-parametric Friedman's test recommended rejecting the null hypothesis that distributions were similar across all seasons (*184.187, df=3, p=0.0001*). Multiple pair-wise comparisons, with a Bonferroni correction, revealed that only spring and autumn were not significantly different in their distribution *(-2.303, p=0.128*). Species richness was relatively stable across compound seasons, the highest values were to be found during spring and autumn. Effective species also differed between the seasons, with spring and autumn having the highest effective species numbers. This pattern is most likely a consequence of migration. The log-2 diversity indices relate to this pattern, showing that more yes-no questions would be required to identify an individual species when drawn at random from the spring and autumn samples, compared to those of the summer and winter.

Table 9: The rank abundance (RA) for the top 13 species in each season (denoted by British Ornithologists' Union Common Names (BOU)) and cumulative percentage (Cum.%) contribution to the overall count across compound seasons (see text for details)

	Spring		**Summer**		**Autumn**		**Winter**	
RA	**BOU**	**Cum. %**	**BOU**	**Cum. %**	**BOU**	**Cum. %**	**BOU**	**Cum. %**
1	Swallow	30.61	Manx Shearwater	54.53	Swallow	22.56	Guillemot	34.46
2	Guillemot	53.17	Guillemot	67.86	Chaffinch	37.04	Kittiwake	60.98
3	Razorbill	60.70	Razorbill	71.67	Starling	47.23	Herring Gull	75.12
4	Manx Shearwater	66.79	Kittiwake	74.57	Redwing	52.99	Starling	78.75
5	Herring Gull	70.05	Herring Gull	77.37	Meadow Pipit	58.36	Fulmar	82.30
6	Kittiwake	73.33	Linnet	79.76	Kittiwake	63.36	Razorbill	85.08
7	House Martin	76.37	Lesser Black-backed Gull	81.65	Guillemot	67.99	Great Black-backed Gull	86.85
8	Willow Warbler	79.19	Shag	83.44	Manx Shearwater	70.50	Lesser Black-backed Gull	88.58
9	Blackcap	81.63	Puffin	85.17	Linnet	72.71	Carrion Crow	90.13
10	Lesser Black-backed Gull	83.52	Gannet	86.52	Goldcrest	74.76	House Sparrow	91.47
11	Meadow Pipit	85.17	Swallow	87.72	House Martin	76.75	Redwing	92.59
12	Wheatear	86.61	Starling	88.90	Herring Gull	78.73	Skylark	93.28
13	Sand Martin	87.86	House Sparrow	90.03	Gannet	80.33	Shag	93.90

We further inspected the seasonal data by calculating rank abundance for recorded species. Table 9 displays the ranking results for species in the top 13 most numerous species during each season, where each season is a compound of 9 years × 3 months, as above. Table 9 clearly shows the summer months as dominated by breeding seabird species.

Rank abundance can obscure issues of detectability (Bibby *et al.*, 2000) meaning that those birds that are harder to detect are also registered less frequently. To inspect this, Pareto charts were constructed for each compound season (Figures 2a-d). The Pareto Principle, with reference to ornithological surveys, assumes that 80% of the birds seen belong to 20% of the species registered (Rispoli, Zeng, Green & Higbie, 2014). Looking at the number of species contributing to the 80% is another way of looking at species dominance, with due caution around detectability. Thus the top 13 ranked species are displayed in Table 9, as this number incorporates the 80% threshold for all seasons. It is worth noting that the 80% threshold varies considerably across seasons in terms of ranking, with autumn meeting it after only 13 species. The x-axis on the Pareto charts give an abridged list of birds by BOU common name in rank order to give a sense of the less abundant species.

Figure 2a: A Pareto chart for all spring bird data collected on Lundy from 2008-2016 (see main text for details). The steep decline of the blue bars (count data in rank order; left y-axis) and the sharp rise of the cumulative percentage data (red line; right y-axis) indicate relatively low diversity (see Table 8 for comparison with Shannon H indices). The list of BOU common names on the x-axis is not a complete list of all birds observed but a reduced list, in rank order, due to space constraints

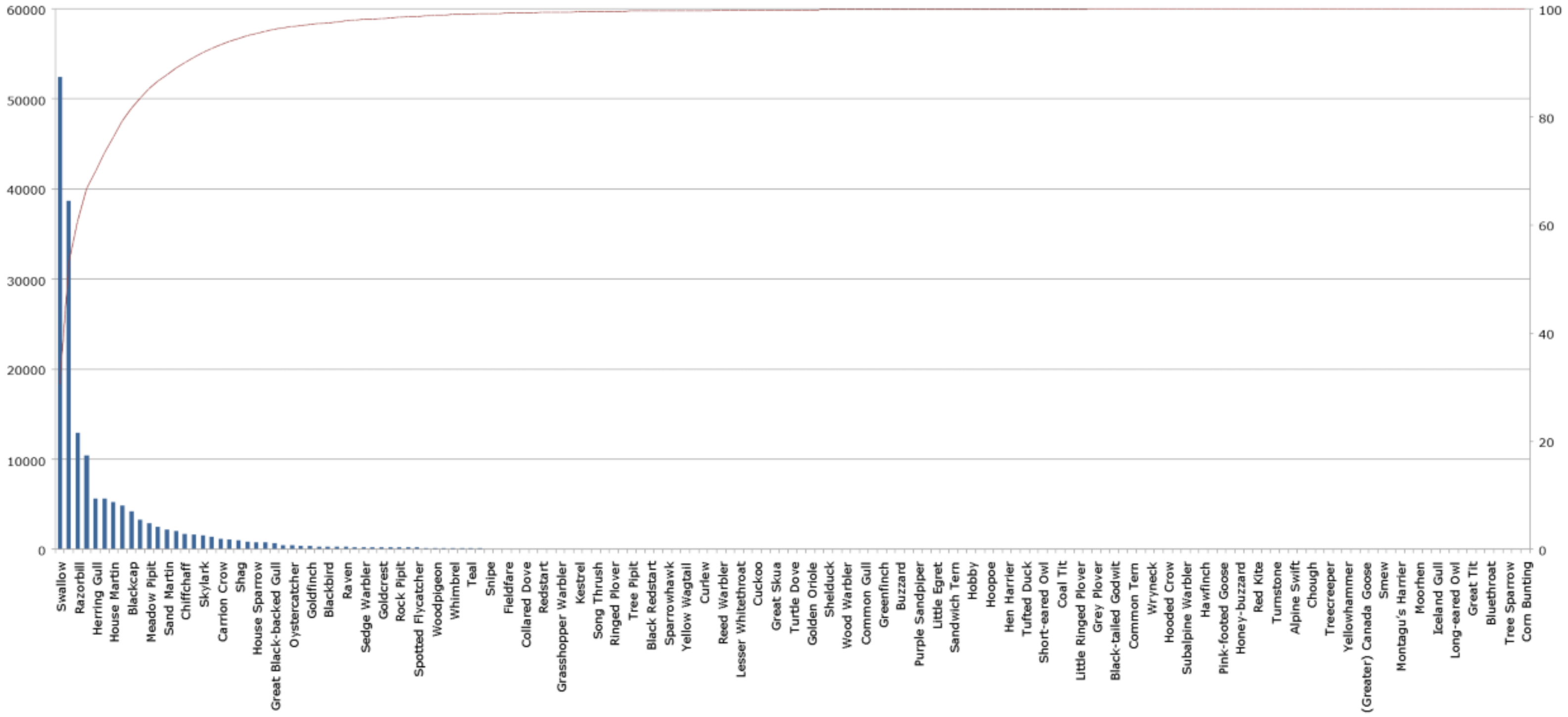
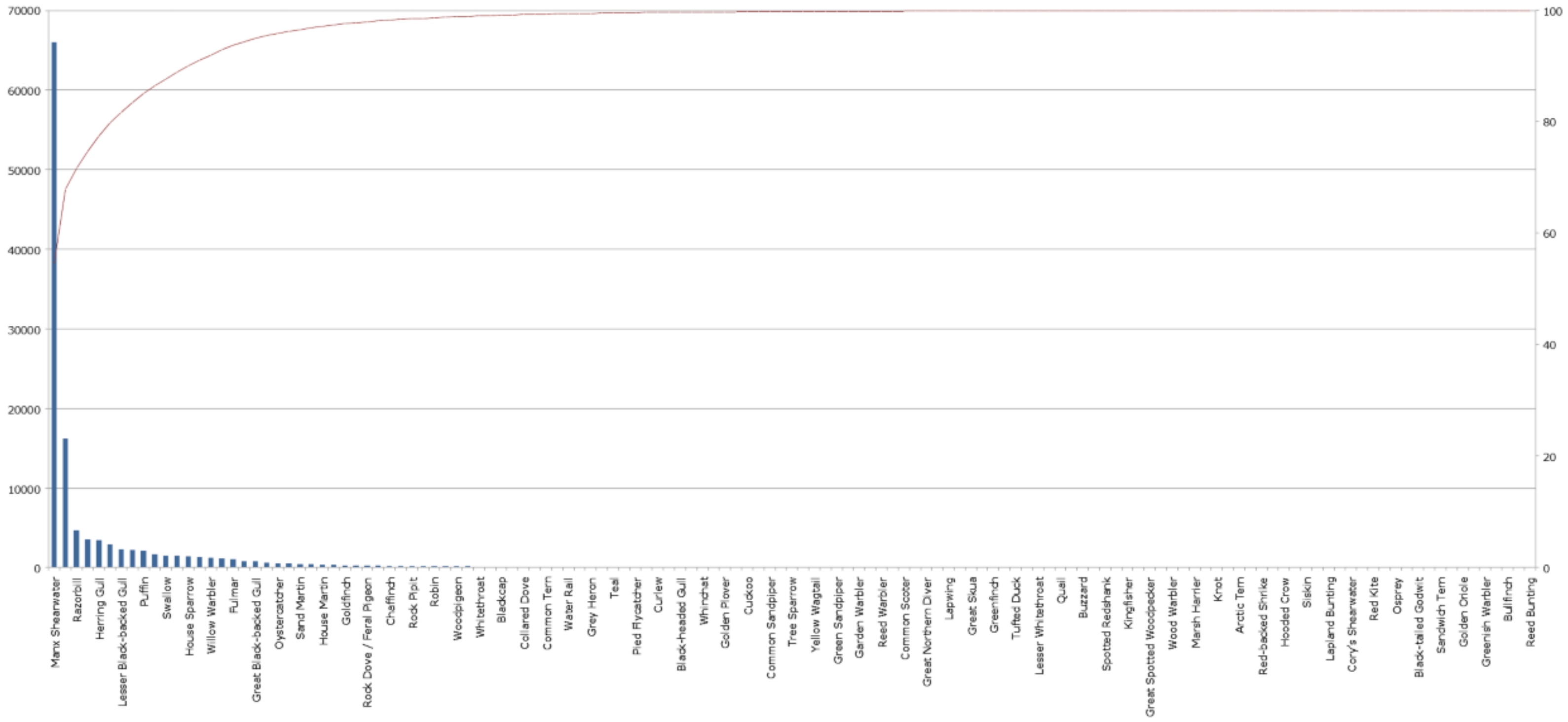


Figure 2b: A Pareto chart for all summer bird data collected on Lundy from 2008-2016 (see main text for details). The steep decline of the blue bars (count data in rank order; left y-axis) and the sharp rise of the cumulative percentage data (red line; right y-axis) indicate relatively low diversity (see Table 8 for comparison with Shannon H indices). The list of BOU common names on the x-axis is not a complete list of all birds observed but a reduced list, in rank order, due to space constraints



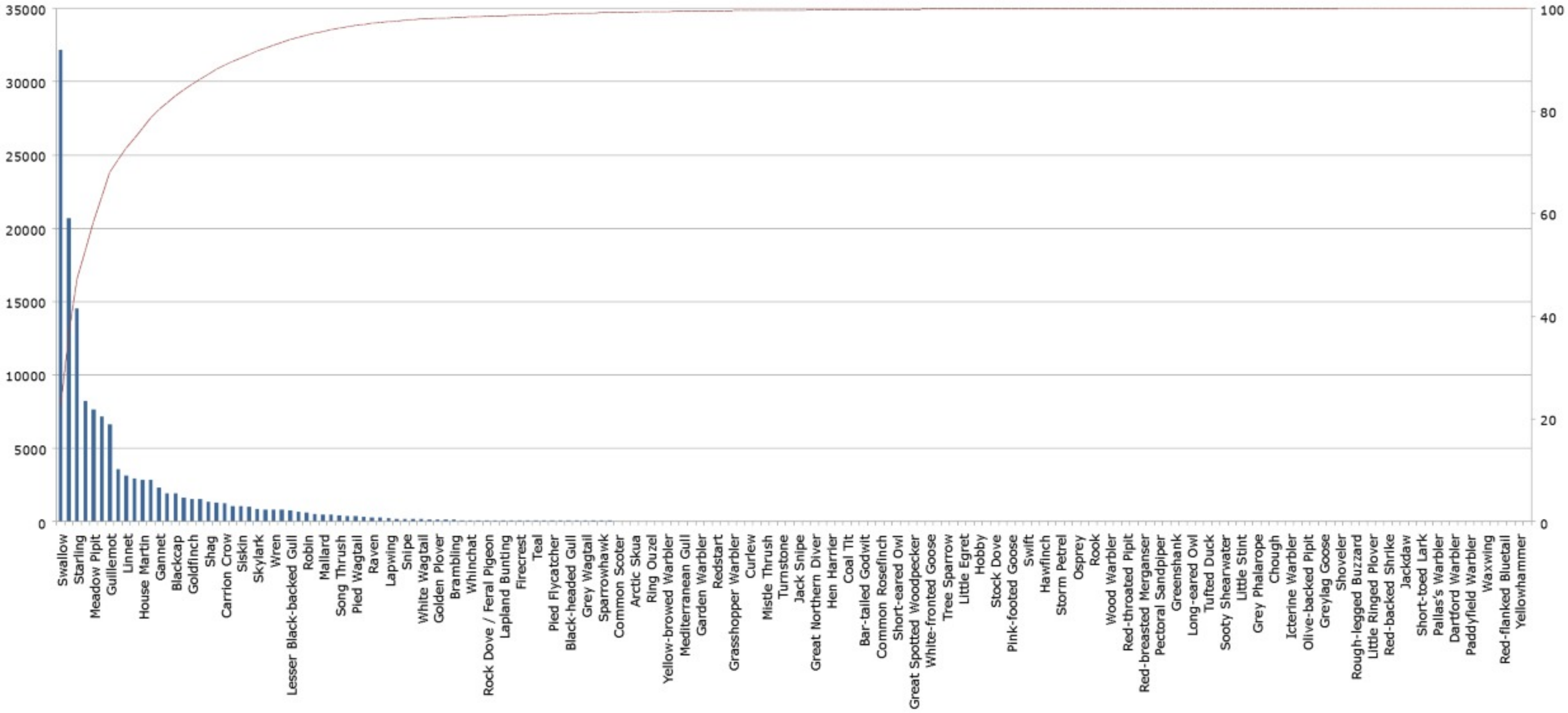


Figure 2c: A Pareto chart for all autumn bird data collected on Lundy from 2008-2016 (see main text for details). The steep decline of the blue bars (count data in rank order; left y-axis) and the sharp rise of the cumulative percentage data (red line; right y-axis) indicate relatively low diversity (see Table 8 for comparison with Shannon H indices). The list of BOU common names on the x-axis is not a complete list of all birds observed but a reduced list, in rank order, due to space constraints

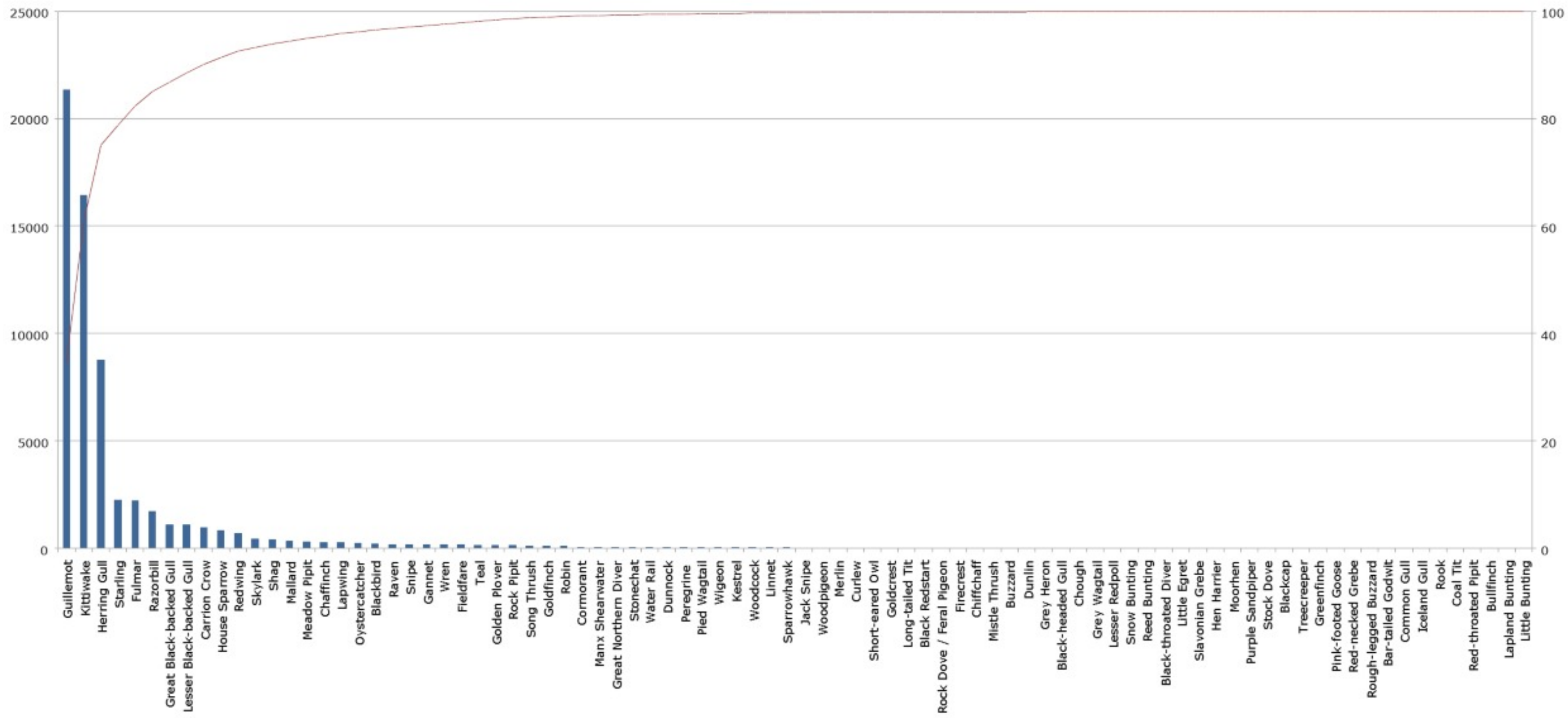


Figure 2d: A Pareto chart for all winter bird data collected on Lundy from 2008-2016 (see main text for details). The steep decline of the blue bars (count data in rank order; left y-axis) and the sharp rise of the cumulative percentage data (red line; right y-axis) indicate relatively low diversity (see Table 8 for comparison with Shannon H indices). The list of BOU common names on the x-axis is not a complete list of all birds observed but a reduced list, in rank order, due to space constraints

DISCUSSION

From our simple analyses of nine years of citizen science data about avian abundance on Lundy, we are confident that the diversity and year-to-year similarity of the population has remained fairly stable for this period. Across all nine years, 41.6% of the 214 total observed species were present at some point in time on the island. This means that more irregular avian visitors to Lundy have introduced variance into the similarity data over time. Nonetheless, a similarity comparison between 2008 and 2016 revealed a Jaccard's Index of 0.699, which is similar to the 2008-2009 comparison, but marginally lower than the lower 95% confidence interval reported in the Results section; this leaves approximately 30% dissimilarity between the species composition at the start of the sample and at the end.

In an attempt to interrogate this variance in similarity, we looked at Order and dietary choice composition across categories of the number of years a species had been present on the island. Whilst some clustering was revealed, using hierarchical dendrograms based on Euclidean distance measure of similarity, the basic distribution of Order and diet was even across all categories. If we had seen an uneven distribution, this would have been indicative of possible challenges to specific kinds of birds that might have driven dissimilarity at certain times.

At present our best hypothesis is that much of the dissimilarity across years is caused by non-breeding migrant and vagrant birds, especially as all breeding birds were present for either all nine or eight years in this sample. Our seasonal analyses support this view. Thus variance will be caused by multiple distal factors. These birds appear to be sustained in terms of diet when on the island. However, Lundy has seen a number of changes over the period of the sample. The sample began at the point that rats had been eliminated from the island, and breeding bird populations have been able to exist without the threat of that predator for the entire period. It is also the case that management practices have changed over this period, including the introduction of large herbivores that will potentially impact on invertebrate communities. Rabbit populations have risen and fallen dramatically, which could have multiple impacts on vegetation, invertebrates and possible predator-prey dynamics (Dickins *et al.*, 2018). The removal of Rhododendron on the east coast and bracken control will also have effects in terms of invertebrate communities, but also on cover and nesting habitats. Whilst all of these factors are duly noted in passing in Annual Reports and similar publications, clear data are not recorded and critically not married to the citizen science data collected in the logbooks. Efforts in this direction would yield potential reward.

Recommendations for future data collection

Re-ordering old data in order to better understand patterns in avian and other communities on Lundy is an important approach, but it does not detract from the problems of citizen science data discussed in the Introduction. We looked at all data from 1948 to 2016 before embarking on this project, and realised that the best one could do with pre-2008 data was really to note presence-absence. We decided to focus on the 2008-2016 data, as abundance data were systematically recorded (but see Tovo *et al.*, n.d., forthcoming, for ways of deriving abundance from presence-absence data).

A key problem for this project was the absence of a digital record. The ideal would be the production of data sets as comma separated variable (CSV) files for use in a number of different applications. This would allow subsequent organisation and analysis by researchers and other parties. There are many ways to do this. As an example, the BTO collate digital information through a dedicated smartphone application called BirdTrack. This enables data to be recorded at various levels of resolution, starting with just basic species identification with no count data, and this is coordinated with location data and uploaded to a central database. This is a very good system for day-to-day birdwatcher data, and becomes more useful when recruited by those who have regular patches, thus generating data both about the patch and observer learning and consistency. The BTO assiduously scan this data and will contact users when something unusual is recorded for verification. Users can look through their own data at any time.

The other system that the BTO use is online uploading of data collected in regular organised surveys at particular sites with set transects, during the breeding and winter seasons, as well as for more focused efforts, for example specific species surveys. Observers may collect data using pen and paper but this eventually finds its way to an online data set, and observers can interrogate their own findings. These surveys are supported by a large amount of online material that explains methods. This enables a certain amount of control over survey effort and also the way in which observations are collected and logged. Clearly individual differences in skill and experience can still have an influence, but the methods make each individual effort more consistent and comparable to others. The BTO is an organisation that recruits its members from dedicated bird enthusiasts who either have much experience or are prepared to gain it. This too helps to reduce variance.

Direct, digital recording of the sort used by the BTO via BirdTrack is difficult on Lundy due to inadequate mobile device coverage. This will most likely improve as 5G rolls out across the United Kingdom, but any solution relying upon mobile applications runs the risk of data loss at upload, when signal is patchy; and data loss due to observers forgetting to upload when returning to the mainland. Given this, we would not recommend developing Lundy-specific applications as a first initiative. Instead, we would recommend looking to investment in computers on the island that enable logbook entries to be made directly in digital format. Files created in this way could be stored on dedicated drives and/or uploaded to cloud storage solutions via the island management team's private internet service. Cloud storage would enable mainland researchers to access data, with due permissions, continuously. Our recommendation would be to make this data open access in keeping with current open science initiatives (see for example: https://openscience.com/ and https://cos.io/).

Computer entry logbook solutions could operate at a number of levels, as indeed the current paper logbooks do. Those visiting the island for vacations collect many observations, and whilst they may have a general interest in nature, they will not be as dedicated as those BTO surveyors tramping through fields on cold, winter days, working established transects. It is therefore important not to make logging observations effortful for these contributors. Thus the opening 'page' should simply ask the contributor to opt for the kind of observation they should like to make and those choices could include all the existing options, which are species specific count data, and more narrative based descriptions of interesting sightings and counts. Whilst this article has processed highest count data, having digitally recorded narrative accounts provides a rich source of data for other kinds of more interpretive and qualitative analyses that would greatly inform those trying to develop user friendly conservation initiatives, for example. Software packages exist in order to do this (e.g. NVIVO).

When creating a digital version of the current logbook solution, a number of modifications might be considered. First, it would be useful to ask observers to rate their own expertise and skill levels on a Likert scale from 0=novice to 3=expert. This would create a useful categorical variable for sifting data in future analyses. For example, it could be used to look at only expert collected portions of data or as a controlling variable in various forms of generalised linear modelling.

Additional levels of entry could be listed as front-page options and these could be tied to more systematic attempts at surveying the island for particular purposes. There will be many ways to do this, but any solution would need to incorporate detailed mapping of the island into portions, akin to the BTO site and transect approach, and should be accompanied by some advice on methods. Further details of systematic methods would depend upon the desired outcome of such work and this in turn would be best linked to the conservation and management interests on the island. It is perhaps at this point that more focused work pulling together observations across taxa could be implemented enabling linkage between, say, vegetative and floristic surveys, invertebrate observations and bird work. In effect a number of available projects could be offered to visitors wishing to make this level of contribution. This might also dovetail with the interests of visiting university parties looking for student projects. This leads to a final suggestion: the creation of a computer based logbook system could be done in such a manner as to coordinate with systems designed to record the professional interventions and data collection of the conservation and management teams working on the island. This would not necessarily have to be publicly available at the point of logbook entry, but data from such work could be made open access after appropriate periods of embargo.

The preceding recommendations require much fully project-managed work to design and implement, and our reviewers feel this may sit best within a formal Bird Observatory set-up as Lundy once was, and could be again. However it is managed, such a project requires a dedicated team and funding to cover both their costs, and costs associated with exploring and trialling different solutions. The manner in which we have described our recommendations reads most like a web page based, or a more formal database solution. The latter is perhaps more useful on an island with poor internet connectivity, the former is better for close to continuous updating. Hidden costs include the development of appropriate metadata for the dataset, error management procedures etc. and decisions would need to be made about just how much investment is worthwhile. It is also likely that the overall project would need to be managed in stages, with clear performance indicators and a decision process around transition between stages. We have not done this work, but we believe it is possible. We also believe it will represent a challenge to extant cultures of recording. But current practices, relying purely on pen and paper logbooks, run the risk of actively creating a non-modern archive and losing much of the richness of the amassed experiences of many dedicated visitors to Lundy.

Data note

Raw data are available at: https://figshare.com/authors/Tom_Dickins/3116847.

ACKNOWLEDGEMENT

We thank Ben Dickins for critical comments on an earlier draft of this paper, and for useful discussions about the analyses. We are also extremely grateful for the detailed commentary of Tim Davis and Tim Jones. All errors are our own.

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A PARTICULER OF LUNDY ISLAND: THE CLAYTON MANUSCRIPT

by

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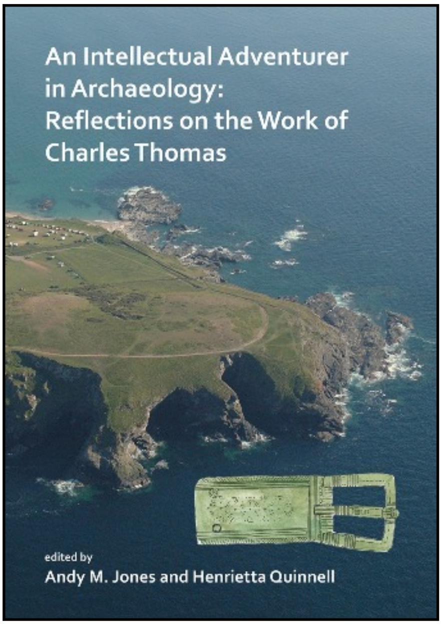
Further information on the modern scientific name of the fish 'Plowers' mentioned in the above paper in LFS Journal, Volume 6, 2018

An omission from the transcription of the seventeenth century Clayton Manuscript was the identification of the fish 'Plowers'. As noted in the table listing fish, no modern synonym could be found. However publication of the paper has prompted one reader to recall his local knowledge. Chris Blackmore recalled that as a child fishing off the Ilfracombe pier, they were 'plagued by the big-biting but small-sized Pouting'. He supplied the local name for them as Glowers.

The transcription of the original document was difficult in that there were few capital letters and the leading capital of Plowers did indeed look like a P in Secretary Hand, but on reflection it could have been a capital G.

So Glowers is the transcription with the modern name of Pouting, *Trisopterus luscus*. This fish which is also known as Pout or Bib is an edible member of the Cod family and therefore is an asset to an island's economy.



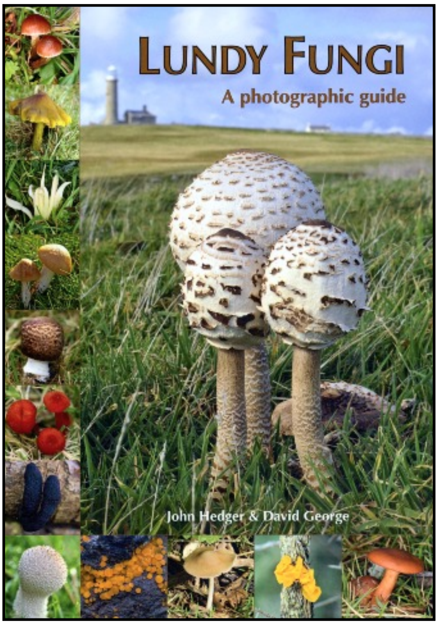
An Intellectual Adventurer in Archaeology: Reflections on the work of Charles Thomas edited by **Andy M. Jones** and **Henrietta Quinnell**. Archaeopress. 2018. 285 pages. ISBN 978-1-78491-861-3

Charles Thomas (1928-2016) is best known, perhaps, for his work in Cornwall but his career stretched much more widely than that. He studied law at Oxford but was already more interested in archaeology following army service in Egypt, and started excavating on his family's land at Gwithian in the vacations. This continued while he took a diploma in archaeology at London and then while working as a tutor for the Workers Educational Association. In the 1960s he obtained a university post at Edinburgh where his interests shifted from prehistory to the centuries following the end of the Roman empire and in particular the spread of Christianity in western Britain and Ireland. He was then invited to set up the department of archaeology at Leicester University in 1967. He returned to Cornwall in 1971 as head of the Institute of Cornish Studies and worked in Scilly and at Tintagel as well as with other organisations promoting the creation of a national archaeology service. He retired in 1991 but continued research in the early Christian period before turning once more to Gwithian.

This book, written by former colleagues and friends from across the country, covers Thomas's long career and very wide range of interests, but it will be the chapter on his excavations on Lundy that will be of most interest to readers of this Journal. Written by Henrietta Quinnell who worked with him on the island, it tells how a chance discovery of a possible sherd of post-Roman pottery led Keith Gardner, an amateur archaeologist working on the island, to contact Charles, eventually leading to the excavations at Beacon Hill cemetery in 1969 under the auspices of the LFS. Initial reports were published in *Current Archaeology* and the LFS *Annual Report* but, in a similar way to much archaeological work at the time, no detailed, definitive publication was produced. Charles continued his membership of the LFS and interest in the island, contributing a chapter on Lundy's pre-Norse name to the volume, *Island Studies*, published to celebrate the Society's fiftieth anniversary. He also worked the evidence from Lundy into an interpretation of the history of Brychan, a king with Irish family origins who ruled a kingdom in South Wales named after him which became Breconshire. Many early Cornish 'saints' are said to have been children of Brychan, and Charles suggested that the king abdicated to pursue a religious life on Lundy where he was buried.

Charles Thomas was a man of hugely ranging interests, from military history to Methodism as well as archaeology, as can be seen from the twenty-page list of his publications at the end of this volume. This book, produced with a great deal of affection, will be of interest to all who met him or whose work intersected with his.

Chris Webster



Lundy Fungi: A Photographic Guide
by **John Hedger & David George**
Lundy Field Society. 2018. 200 pages.
ISBN 978-0-9530-5327-8 hardback
ISBN 978-0-9530-5326-1 softback.
Available from the LFS website at *www.lundy.org.uk*

Lundy Fungi: A photographic guide is the product of some 15 years work by the authors with the support of many others suitably credited in the acknowledgements. The volume lives up to its name with an excellent range of photographs complementing the text for the 250 or so species covered, which in turn represents almost half of the total ever recorded on the island.

The introduction provides a very helpful entry into the world of mycology with explanations of the terms used in the book and a section on fungal taxonomy with reference to the different groups of fungi found on the island. This section is well illustrated by Sharon Read's line drawings which provide a wealth of information in a very clear manner. Throughout the chapter the discussion is always framed in terms of the fungi on Lundy, or the island's habitat, but holds the reader's interest (even for someone not familiar with the island). The widespread use of popular as well as Latin names reinforces the user-friendly style of the publication.

The succeeding chapters are organised on the basis of habitat type with the first, and most substantial, covering grasslands. The stars of this section are the (usually) colourful waxcaps, many of which lend themselves to identification in the field. The waxcap pages are ordered by colour group making it straightforward for the user to home in on the most likely candidates. Fungal taxonomy is something of a moving target these days and here the authors have wisely stuck with the waxcap names used in the standard work for this assemblage (Boertmann, 2010) which will be the ones most people will be familiar with.

The next chapter covers fungi found in grassland with bracken – a vegetation zone which is shown on the vegetation map as extending along much of the eastern flank of the island. The inclusion of bracken allows for a number of very interesting species including Bracken Plums and Custard: a relative of the widely distributed Plums and Custard fungus which is associated with conifers. This bracken associate was only described as a distinct species in 2015 thanks to DNA analysis.

Dung fungi are covered in the next chapter, followed by a chapter on fungi of wet places, a particularly useful section as few books cover this as a distinct fungal habitat. The next section (heathland) will be familiar to grassland enthusiasts and is followed by the woodland chapter which provides an extensive list given that the island supports a relatively limited area of trees and scrub compared with the other vegetation zones. An interesting woodland species is *Perenniporia ochroleuca* which was first recorded in the British Isles in 1999 and turned up on Lundy in 2011.

The habitat chapters conclude with fungi on living plants which provides the reader with examples of rusts, smuts and mildews found on Lundy together with a selection of other fungi affecting leaves and stems.

The volume rounds off with a glossary of terms (invaluable, and helpfully cross-referenced to line drawings where applicable), a comprehensive reading list, and a checklist of all fungi recorded on the island. The list includes common names, habitat and an indication of frequency.

Who will benefit from this publication? Certainly visitors to Lundy will find it a very useful handbook: comprehensive yet portable enough to carry to the field in a pocket or rucksack. It will help them identify many of the fungal species they encounter and thus add to collective knowledge of fungal distribution on the island.

A wider audience will also appreciate this volume. Anyone with an interest in the fungal assemblages on islands or coastal habitat will find the book particularly useful – I know that I will be carrying my copy on coastal walks in Pembrokeshire.

David Harries
British Mycological Society Recording Network coordinator