Reconstructing long-term ecological data from annual census returns: the role of observer bias in counts of bird populations on Skokholm 1928-2002

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Abstract

Long-term ecological data are essential for conservation and to monitor and evaluate the effects of environmental change. Bird populations have been routinely assessed on islands off the British coast for many years and here I take one island, Skokholm, and evaluate the data for robustness in the light of some 20 changes in observers (wardens) on the island over nearly eight decades. It was found that the dataset was robust when compared to bootstrap data with only one species showing significant changes in abundance in years when wardens changed. It is concluded that the breeding bird populations on Skokholm and other British offshore islands are an important scientific resource and that protocols should be enacted to ensure the archiving of records, the continuance of data collection using standardised protocols into the future, and the recognition of such long-term data for science in terms of an appropriate conservation designation.

Highlights

- Here I reconstruct the breeding bird data for Skokholm island, Wales from 1928-2002
- The archival data was evaluated with regard to potential issues of observer bias that might arise in reconstructing a breeding bird dataset
- Tests for robustness of the data showed that potential observer bias was minimal
- Action is recommended for a site designation to recognise the broad ecological value of long-term data of common species

Key words: birds, island biogeography, long-term, population, community, assemblage

1. Introduction

There is an increasing recognition of the value of long-term data for the analysis of the effects of climate change and other long-term ecological and environmental phenomena (Newton, 1974; Fuller & Moreton, 1987; Sparks & Carey, 1995; McCollin et al. 2000; Roy & Sparks, 2000; Roy et al., 2001; Green, & Scharlemann, 2003; Rackham, 2003). As a scientific discipline, ecology is perhaps only a little over a century old, yet processes such as succession or habitat fragmentation may take longer than this to reach any sort of stable end-point (if such could be identified, Begon et al., 1986) making it difficult for ecologists to study such processes without recourse to space-for-time substitution (chronosequences) or proxy data (McIntosh, 1985; Clark, 1986; Niering, 1987). Further, population phenomena such as population growth, synchrony (Ranta et al., 1995), and regular cycles (Elton and Nicholson, 1942) require long-term data for empirical analyses.

It is important to recognise the potential for bias and error when reconstructing long-term data sets. For example, the recolonisation of the Krakatau islands since the eruption of 1883 has been recorded by various people with differing interests over a period that exceeds the life span of any individual recorder. Nonetheless, such data can provide a valuable record when attempts are made later to assemble data in order to understand long-term processes such as succession (e.g., Whittaker et al., 1993; Whitaker, 1998). Long-term breeding records for birds on the island of Skokholm, Wales, have been collected since 1928 and records for landbirds up to 1979 have been used to test hypotheses concerning the theory of island biogeography and extinctions of populations on small islands (see Section 3.2).

Skokholm, together with the neighbouring island of Skomer, have internationally important populations of seabirds and both islands have together been designated as a Special Protection Area under the European Community Directive on the conservation of wild birds (79/409/EEC) (also known as the Birds Directive). These two sites combined are particularly noteworthy for the high proportion (over half) of the world breeding population of Manx Shearwater *Puffinus puffinus* (JNCC, no date).

The aims of this paper are, first, to reconstruct the Skokholm breeding bird dataset to check and re-evaluate the original data with respect to sampling methods, and second, to perform an analysis with respect to potential observer bias. In terms of producing a definitive dataset there are several difficulties, probably the most important of which is in establishing whether breeding has taken place. This issue, along with others related to the accuracy and precision of the data provide the basis for the following evaluation of the data and the subsequent discussion.

2. Materials and Methods

2.1 Study Site

Skokholm is a *c*. 96 ha island lying 3.2 km off the Pembrokeshire coast, Wales, and consists of a rocky plateau, with the highest point being *c.* 50 m above sea level (Goodman and Gillham, 1954; Lack, 1969a). The island is largely treeless with open communities of maritime grassland, bracken, heath and bog. Since being first described in detail (Conder and Keighley, 1947; Goodman and Gillham 1954) there have been changes in the cover and distribution of vegetation types. Ninnes (1998) stated that possibly the most important changes in conservation terms, have been shifts in the area dominated by *Silene maritima*, which had increased from 1% to 15% of the land area over the period 1948-1997, and over half of the *Armeria maritima* dominated turf which had been lost to grassland (although it had also spread into new areas). (*Armeria* forms a burrowing medium for internationally important populations of Manx Shearwaters and Puffins *Fratercula arctica* – see later). Other changes include loss of *Calluna* heath and eutrophication of wetlands. Ninnes (1998) suggested the main underlying factors in these changes were related to grazing, past landuse, and changes in the abundance and distribution of seabirds. Sheep grazing ceased in 1935 although Soay continued to be maintained and Lockley and Buxton (1946) reported a population of 25 rising to 35 in the Autumn of 1946. Thompson (2007) states that Soay sheep were on the island until shortly after 1964. Rabbit *Oryctolagus cuniculus* grazing continued even after concerted, yet ultimately unsuccessful, attempts to exterminate them from the island by introducing myxomatosis in the late 1930s and by using using cyanogas in 1939 and 1940 (Lockley 1935; Lockley and Buxton, 1946; Lockley, 1947 Lockley, 1964). Goodman and Gillham (1954) reported that the rabbit population was around 10,000 and that a few goats and a pony also lived on Skokholm at that time. The last pony died in 1957 and the goats were removed from the island in 1981 (Thompson, 2007).

2.2 Population Estimates

Although records of birds on Skokholm exist for the late 19th Century (Barrett, 1959) systematic bird recording on Skokholm began when Ronald M. Lockley became the tenant farmer in 1927 and started reporting on the presence of birds in summer (Lockley, 1935, 1938a; see also successive annual reports, Table 1), and occasionally winter (e.g., 1927-1932: Lockley 1935), eventually establishing the bird observatory on the island in 1933 (Lockley 1938b, 1947). Lockley became the *de facto* first warden of the observatory (Lockley, 1935) and since that time some 20 wardens (or couples) have been present over the summer season with a median term of 2 year (range 1 – 13 years)(Figure 1). The largest gap in the records was due to World War II (WWII); Lockley left the island in July 1940 and was unable to return until 1946.

A population may be defined as the number of individuals of a given species at particular time and location (Krebs, 2001). In practice, assessing population size is more easily achieved for some species than for others. For large, charismatic bird species that nest in open locations (e.g., peregrine with open nests on cliff ledges) estimates of population size are likely to be fairly accurate. However, for species with hidden nests (e.g., in vegetation (e.g., Skylark *Alauda arvensis*) or in burrows (e.g., Puffin)) indirect methods may have to be used and which may be subject to greater error (Bibby et al., 1992).

Lockley (1935) reported that much of the island was walked each day from late March until the end of June in the performance of other duties so that most of the locations of breeding birds were known. Evidence of breeding was also established through nest searches and nest locations were recorded on large-scale maps together with the whereabouts of suspected nests. Locations were readily plotted since the island was still divided by stone and earth field boundaries. Lockley's method in effect was much the same as what later became the standard in territory mapping

(Marchant, 1983; Bibby et al., 1992) - a technique which had been highlighted in the literature prior to this time, see for example Alexander & Alexander (1909), Palmgren (1930), Williams (1936) plus a major review published a little later by Kendeigh (1944). It is not known whether Lockley was aware of these papers.

Each year wardens have continued to maintain a record of bird ringing, estimates of breeding population sizes, and records of birds on passage or vagrants (Table 1). Thompson (2007) reported that wardens have maintained a daily log of migrant and resident birds and all the logs dating from 1946 were on the island when he was the warden. These data are summarised annually in the warden's reports (Table 1). In addition, breeding records from 1928 to 1934 and up to 1947 were summarised by Lockley (1935, 1947, respectively); up to 1959 by Barham (1960), and for land birds: up to 1967 by Lack (1969a) and up to 1979 by Williamson (1981, 1983).

2.3 Statistical Approach

The approach taken here is a review and analysis of the likely issues that affect estimates of bird population numbers for both land- and seabird species. Before being able to do any analysis it is first necessary to reconstruct the data. For that reason there follows a consideration of issues related to the data before a dataset can be reconstructed and analysed for observer bias. In order to analyse for potential observer bias, the observed differences in bird population estimates between years when wardens were changed were compared to differences between pairs of random draws of population estimates from all years (bootstrap analysis). Data were checked for normality and homogeneity of variances. Although most were normally distributed there were significant differences in homogeneity of variance.

Accordingly, tests of differences were done using Mann-Whitney U-tests in SPSS-17. Numbers of species, overall abundance, and population numbers of species were compared for both landbirds and seabirds.

3. Results and Discussion

3.1 Estimated Population Numbers and Missing Data

Whilst most of the records of population size are single integers wardens have sometimes provided estimates of populations. For example, approximately 10 breeding skylarks were recorded each year from 1951-1953 but when the warden changed in 1954 this changed to 12-15. Williamson (1983) noted how some records appear to be rounded, for example, of the 22 records for Meadow Pipit *Anthus pratensis* between 1946 to 1979, 17 (77%) appear to be rounded to the nearest five and most are approximated (see also Lapwing *Vanellus vanellus*). In total, there were 96 records for landbirds with approximated abundances (i.e., 10.3% of a possible 932 numeric estimates). It is assumed that most landbirds have been assessed by either direct counts of territory mapping. However, there may have been occasional changes in methods, e.g., Rock Pipit *A. petrosus* numbers jumped from 20 in 1987 to 36 in 1988 the difference due to “more accurate counts”. Williamson (1981) noted that it was the most abundant landbirds (Meadow Pipit, Rock Pipit and Wheatear *Oenanthe oenanthe*) that caused the most problems with censusing and hence had the most missing records or estimated populations.

Ten seabird species have bred on Skokholm (Fulmar *Fulmarus glacialis*, Guillemot *Uria aalge*, Great Black-backed Gull *Larus marinus*, Herring Gull *L. argentatus*, Lesser Black-backed Gull *L. fuscus*, Manx Shearwater, Puffin, Razorbill *Alca torda*, Shag *Phalacrocorax aristotelis*, Storm Petrel *Hydrobates pelagicus*). These have been estimated by nest counts, maximum Spring counts (equivalent to the minimum number breeding) (e.g., Guillemot) and more recently by providing both estimates of numbers of apparently occupied nests and maximum counts (Thompson, 2007). Estimates have often been to the nearest 500 or 1000 (e.g., Puffin).

Problems in estimating seabird numbers arise due to issues related to estimating populations of species which nest in inaccessible locations (e.g., on cliff ledges or in burrows), and whose visible numbers at any one time do not necessarily reflect actual populations unless with females sitting tight on a nest. The method for assessing seabirds changed in the 1990s. The recording method for Razorbill changed c. 1978 nationally but was not changed on Skokholm until c. 1993 or 1994 - from ‘apparently occupied nest sites’ to ‘individuals’ (Steve Sutcliffe, pers. comm.). Further, according to the Spring 1995 *The Island Naturalist* (see Table 1) 'the previous estimate for Storm Petrel of 5000 to 7000 pairs in 1969, was based on mist-netting and ringing, which no longer takes place on Skokholm'. The 1994 population was based on counts of calling birds in the Quarry, coupled with “recent surveys of all colonies” to indicate an island population of between 4000 and 7000 pairs.

3.2 Actual or Potential Breeding?

Territory mapping does not require evidence of nests or young since the method implicitly assumes a pair has bred if a male defends a territory during the breeding season (the Common Bird Census (CBC) methodology: Marchant, 1983; Bibby et al., 1992). However, according to Marchant (1983) a single record of a nest containing eggs or young can be accepted as the basis of a cluster. Whilst guidance is not provided in the case where broods fail the implication is that attempted breeding is recorded rather than successful breeding (e.g., in terms of successful fledging). For those cases where recorders have managed to record nesting, if a species nests but is unsuccessful in producing young (e.g., due to the nest being destroyed or abandoned, the eggs failing to hatch, or the young failing to survive) then would this be classified as successful breeding? For example, Peregrine *Falco peregrinus* nested but failed to successfully raise young several times during the 1990s. Similarly, eight pairs of Lapwing attempted to breed in 1994 but no young successfully fledged, and before becoming established on the island, Jackdaw *Corvus monedula* had several pairs nest from 1964-1968 but failed to produce offspring (perhaps due to deliberate attempts to deter nesting), and it was reported in 1994 that the presence of linnet in area suggested breeding had taken place. Following the same line of reasoning, if there are several pairs nesting and only a subset are successful (e.g., Dunnock *Prunella modularis* in 1965), which count should be used?

These are important question since such information might be required to test ecological theory. Since his work focussed on immigration and extinction, Williamson (1983) argued that it was important to record attempts to breed rather than successful breeding. This argument also applies to other work testing the theory of island biogeography (MacArthur and Wilson, 1967) using data from Skokholm and other British offshore islands (see Lack, 1969b; Johnson & Simberloff, 1974; Abbot & Grant, 1976; Reed, 1980, 1981; Williamson, 1981, 1983, 1987; Simberloff, 1983; Tracy & George, 1992; Rosenzweig & Clark, 1994; Manne et al., 1998; Pimm et al., 1988; Russell et al., 1995; 2006; Stracey & Pimm, 2009). For a plant, there are various different life stages that could be construed as colonisation: the presence of a mature plant implies that successful colonisation has taken place (unless planted) – especially if the plant subsequently reproduces. However, would a simple propagule by itself (e.g., a seed), or the successful germination and survival of a seedling, similarly be counted as successful colonisation? By analogy, for birds, the simple presence of an adult (or an adult pair, notwithstanding the difficulty of distinguishing the sexes of many species) does not in the same way as a plant imply colonisation has taken place. As with many British offshore islands, Skokholm has had many bird species recorded which would not normally be expected to breed (e.g., Bee-eater *Merops apiaster*, Osprey *Pandion haliaetus*)(Stracey & Pimm, 2009). Hence, is evidence of attempting to reproduce (e.g., singing, mating, nest-building, sitting), or producing young (eggs, nestlings) sufficient evidence, or should it be taken as the overall successful completion of the process to fledging and perhaps even survival to breed again?

To complicate matters further, Lockley and Buxton (1946, p.7) reported that over 3000 eggs of Herring, Greater and Lesser Black-backed gulls were collected for food in June 1940. If we were to follow the approach of Williamson (1983) for consistency we should include such attempts in population estimates for these species (although we are not told how many nests and of which species these were taken from). Although it was obviously Williamson's intention to record immigrations and extinctions of landbirds – which tend to involve species with breeding pairs (up to and) in the 10s rather than 1000s like some seabird species (Williamson, 1981; 1983) – undoubtedly, there would have been other attempts to nest which went unrecorded either by species with abundant established populations (e.g., Lapwing, Skylark) or perhaps by other rare species which were not as charismatic (and noticeable) as say Buzzards *Buteo buteo*, or else have been subject to population control measures (e.g., Jackdaw, Little Owl *Athene noctua*).

Accordingly, there is a degree of uncertainty in terms of which numbers should be used but it should be recognised that in the past wardens have collected data without regard to these subtleties. Here, I am interested in establishing consistent population estimates of breeding birds hence for landbirds I follow the CBC methodology and therefore focus on suspected or actual breeding. In 1965 it was reported that “as anticipated, Jackdaws have joined the list of breeding species. Three pairs laid two in Calf Bay and one in Little Bay. No young were raised, due partly to control measures”. Following this line of reasoning Jackdaw is accepted as having a population of three breeding pairs in 1965.

3.3 Controlling Bird Abundance via Population and Habitat Management

In order to protect internationally important Manx Shearwater and Puffin populations, control measures have been reported on at various times. It is likely that these would primarily involve gulls, corvids and Little Owl although it is not known whether controls have been reported each year. For example, in 1946 a Little Owl was shot because ‘they preyed heavily on Storm Petrels’ and in 1954 it was reported a 1951 ring of a Storm Petrel was found in a Little Owl pellet (Annual Reports, op. cit.). Williamson (1983) took the view that as Lockley shot or deported Little Owls it should be excluded from the dataset for the purposes of assessing immigrations and extinctions. The problem with this argument is that other species (particularly corvids and Great, Lesser Black-backed and Herring Gulls) have also been subject to control with eggs having been collected or destroyed at various times (e.g., GBBG control measures noted in 1962, 1964). One notable occurrence was in 1940 during WWII – when over 3000 gulls' eggs were collected – providing a valuable human food supplement with 2500 of these reportedly being pickled. (Note, in Williamson's analyses, Great, Lesser Black-backed and Herring Gulls were classified as seabirds and thus excluded from the landbird data.)

For landbirds, if we are to follow the same line of reasoning as Williamson (1983), then species which have been induced to nest by proactive habitat management should also be excluded. Occasional attempts have been noted to encourage nesting by providing suitable habitat. Thompson and Purcell (1997) reported on Linnets *Carduelis cannabina* which nested in a gorse *Ulex europaeas* bush, and an unsuccessful attempt to encourage overwintering Blue Tits *Cyanus caeruleus* to nest by erecting a box. The gorse had been planted deliberately to increase bird diversity and many shrubs and trees were planted around the observatory buildings in the 1980s and 1990s providing cover that was previously lacking. Blackbird *Turdus merula* and Sedge Warbler *Acrocephalus schoenobaenus* have benefitted from this. Further, elder (*Sambucus nigra*) and bramble (*Rubus fruticosus*) has been planted in the east of the island which may also provide a food resource, song-posts and potential nest sites (Graham Thompson, pers. comm.).

A nest box was provided for Chough *Pyrrhocorax pyrrhocorax* in 2005. Other localised artificial habitats include the pond and its associated wetland vegetation, used intermittently for nesting by Mallard *Anas platyrhynchos*, Moorhen *Gallinula* *chloropus* and Water Rail *Rallus aquaticus*, and the buildings, used by Swallows *Hirundo rustica*.

4. Reconstructing the Breeding Bird Data

The data set described here extends over eight decades - from 1928 to 2002 with a hiatus from 1940-1945 due to WWII. Summarising records of landbirds from 1928-1967, Lack (1969a) used a half when the figure was estimated as being between consecutive integers (e.g., 17-18 pairs would be 17½). For larger intervals, Williamson (1983) took the median figure, a figure just above the mid-point.

In terms of the accuracy of the records Williamson (1983) noted that there were discrepancies between pre-WWII records given by Lockley (1947) and Lack (1969a). Singletons were noted for Moorhen *Gallinula chloropus* and Mallard *Anas platyrhynchos* in 1938-39 in Lockley (1947) and for Pied Wagtail *Motacilla alba* in 1931-32, but these were not recorded in the annual reports. Lockley (1935) recorded Oystercatcher numbers to be between 30-35 pairs between 1928-1934, whereas he later recorded each of these figures having an additional 10 pairs for the same years (Lockley, 1938a) and Lockley and Buxton (1946, p. 16) reported the number of nests of Oystercatchers *Haematopus ostralegus* located in 1946 was 43, "…about the average for previous years (1928-1940)". I therefore conclude that Lockley (1935) was in error.

There were 98 records of species being present over the season but presumably not breeding. The species with the highest count of these records was Robin *Erithacus rubecula* which was present in 20 seasons without breeding. Williamson (1983) did not include Rock Pipit in his summary since he stated Lack (1969a) did not regard them as landbirds and their numbers were “even rougher than those for Meadow Pipit”. However, Reed (1980) stated they favoured rocky shores and hence should be considered a landbird. Rock Pipit is reinstated as a landbird here.

Interpolation may be used to estimate abundance for missing years and is most useful for species which had reasonable populations such that they would have been unlikely to have crashed during the missing years. Nine species had values interpolated of which the longest sequence was six years (Rock Pipit 1952-1957). In this case, it can be justified to interpolate these values since it is highly likely that Rock Pipit was present during these years; for 1956 and 1957 specific comments suggest this was so (“apparently another very successful breeding season” and “exceptionally numerous this year”, respectively), plus with an estimated 40 and 38 breeding pairs in 1951 and 1958 respectively it is highly unlikely that this population would have crashed and recovered to almost the same level over such a short time-scale. This is supported by the fact that the mean population over 36 years in which populations were estimated was 35.7 and the minimum was 14 pairs.

Thirty-seven landbird species have been recorded as breeding on Skokholm with a mean of 16.5 species per year; eight other species have been assessed as being present during the breeding season but not breeding (Chaffinch *Fringilla coelebs*, Chiffchaff *Phylloscopus collybita*, Curlew *Numenius arquata*, Kestrel *Falco tinnunculus,* Pintail *Anas acuta*, Snipe *Gallinago gallinago*, Teal *A. crecca*, Whinchat *Saxicola rubetra*) plus one other species suspected but not confirmed (Shelduck *Tadorna tadorna*).

4.1 Robustness of the Data: tests for Observer Bias

The numbers of years species were present when wardens were changed was a limiting factor in being able to analyse for differences. Six of the most frequently occurring landbird and four seabird species were subject to analyses. A statistical significant difference was detected only for only one species: Wheatear. No statistically significant differences were detected for numbers of species, overall abundance (Table 2). This suggests that the dataset is largely robust to the potential effects of observer bias and that abundance data can be used in further analyses.

5. Conclusions and Recommendations

The long-term breeding bird data from Skokholm and from other British offshore islands represent remarkable data that hopefully will continue to be invaluable for testing hypotheses concerning fundamental ideas in ecology and biogeography. Funding bodies are often reluctant to fund long-term studies hence these data represent an extraordinary resource whose future needs to be maintained. Unfortunately, due to changes in wardens and changes in data archiving practices species records for 2003 and 2004 are missing – the first hiatus in records since WWII. This suggests that data management is an issue that need to be addressed – perhaps in part because the value of the landbirds records have not been fully recognised but also with the digital age there are issues concerning how data is to be archived. In the past, records were summarised in published reports and these still exist in hard copy (although can be difficult to find). As seen in Table 1, there has been a remarkable continuity of published annual reporting for Skokholm – albeit via various differing publications - yet as we are now firmly in the digital age there needs to be a method of archiving reports (and a yearly updated breeding bird dataset) to be available to all via the internet. Such data is likely to continue to be of value - at the very least in terms of monitoring year-to-year fluctuations (Bibby et al., 1996) - all else being equal. Similarly, data from other offshore islands also needs to be evaluated and subjected to equally rigorous archiving.

One way greater recognition might be given to these data is to recognise their value for conservation in terms of a conservation designation. The original meaning of the UK designation Site of Special Scientific Interest (SSSI) was recognition of the ecological (or geological) interest of a site (Moore, 1987). British offshore islands with bird observatories are outstanding examples where long-term records have been maintained and which have great potential for the science. One way to recognise this status and to ensure consistency in breeding survey methods is to establish a network of breeding bird survey sites on islands around the British coast and for them to be given a similar status as British Trust for Ornithology/Joint Nature Conservation Committee /Royal Society for the Protection of Birds Breeding Bird Survey sites. Many offshore islands already have long-term datasets and have observatories with resident summer wardens hence it would not be a costly undertaking. Further, because the landbirds themselves are not a conservation priority on such islands, there is a need to recognise that the datasets they comprise are of great significance in terms of the science of ecology and in biodiversity conservation. This value is potentially much broader than the national status given to SSSIs.

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References

Abbott, I. & Grant, P.R. (1976) Nonequilibrial bird faunas on islands. *The American Naturalist* 110(974): 507-528

Alexander, C.J. & Alexander, H.E. (1909) On a plan of mapping migratory birds in their nesting areas. *British Birds* 2: 322-326

Barham, K. (1960) A census of Skokholm breeding birds 1938-59. *Rep Skokholm Bird Obs*. 1959, p. 20

Barrett, J.H. (1959) The Birds of the Parish of Dale, including Skokholm. Field Studies 1: 1-16

Begon, M., Harper, J.L. & Townsend, C.R. (1986) *Ecology*. Blackwell, Oxford, UK.

Bibby, C.J., Burgess, N.D. & Hill, D.A. (1992) *Bird Census Techniques*. Academic Press, UK. 2nd ed.

Boecklen, W.J. & Nocedal, J. (1991) Are species trajectories bounded or not? *Journal of Biogeography* 18: 647-652

Clark, J.S. (1986). Late-Holocene vegetation and coastal processes at a Long Island tidal marsh. *Journal of Ecology* 74: 561-578

Conder, P.J. and Keighley, J. (1947) The distribution of the vegetation of Skokholm. In: *Skokholm Bird Observatory Report for 1947*. West Wales Field Society, pp. 2–5

Elton, C. & Nicholson, M. (1942) The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology* 11: 215-244

Fuller, R.J. & Moreton, B.D. (1987) Breeding bird populations of Kentish Sweet chestnut (*Castanea sativa*) coppice in relation to age and structure of the coppice. *Journal of Applied Ecology* 24: 13-27

Goodman, G.T. and Gillham, M.E. (1954) Ecology of the Pembrokeshire islands: II. Skokholm, environment and vegetation. *Journal of Ecology* 42: 296-327

Green, R.E. & Scharlemann, J. P.W. (2003) Egg and skin collections as a resource for long-term ecological studies B.O.C. Bull.123A: 165-176 http://www.boc-online.org/PDF/124GreenEggAndSkin.pdf

Holloway, S. (2002) *The Historical Atlas of Breeding Birds in Britain and Ireland: 1875-1900*. Poyser, UK.

JNCC (no date) *Special Protection Areas (SPAs)*. JNCC, Peterborough, UK. http://www.jncc.gov.uk/page-162 (Accessed 15/3/06)

Johnson, M. P. & Simberloff, D.S. (1974) Environmental determinants of island species numbers in the British Isles. *Journal of Biogeography* 1: 149-154

Kendeigh, S.C. (1944) Measurement of bird populations. *Ecological Monographs* 14: 67-106

Krebs, C.J. (2001) *Ecology*. Benjamin Cummings, USA. 5th ed.

Lack, D. (1969a) Population changes in the land birds of a small island. *Journal of Animal Ecology* 38: 211-218

Lack, D. (1969b) The numbers of bird species on islands. *Bird Study* 16: 193-209

Lockley, R.M. (1935) Appendix. A census over seven years, on Skokholm, Pembrokeshire. *Journal of Animal Ecology* 4: 52-57

Lockley, R.M. (1938a) A census of pairs of breeding birds, Skokholm, over ten years. In: Lockley, R.M. (1938) *Skokholm Bird Observatory Report for 1937*. West Wales Field Society, p. 11.

Lockley, R.M. (1938b) *I Know an Island*. Harrap, London.

Lockley, R.M. (1947) *Letters from Skokholm*. Dent, London

Lockley, R.M. (1964) *The Private Life of the Rabbit*. Andre Deutsch, London.

Lockley and Buxton (1946) *Skokholm Bird Observatory Report for 1940-1946*. West Wales Field Society.

Manne, L.L., Pimm, S.L., Diamond, J.M. & Reed, T.M. (1998) The form of the curves: a direct evaluation of MacArthur & Wilson's classic theory. *Journal of Animal Ecology* 67: 784-794.

Marchant, J.H. (1983) *BTO Common Birds Census Intructions*. BTO, Tring, UK.

McIntosh, R.P. (1985) *The Background of Ecology*. Cambridge University Press, Cambridge, UK.

Moore, N.W. (1987) *The Bird of Time*. Cambridge University Press, UK.

Newton, I. (1974) Changes attributed to pesticides in the nesting success of the Sparrowhawk in Britain. *Journal of Applied Ecology* 11: 95-102

Niering, W.A. (1987). Vegetation dynamics (succession and climax) in relation to plant community management. *Conservation Biology* 4, 287-295.

Ninnes, R.B. (1998) *Vegetation Changes on Skokholm 1948 to 1997*. Report to the West Wales Wildlife Trust and CCW.

Palmgren, P. (1930) Quantitaive Untersuchungen uber die Vogelfauna in den Walden Sudfinnlands, mit besonderer Berucksichtigung Alands. *Acta Zool. Fenn.*. 7: 1-218

Philippi, T.E., Dixon, P.M. & Taylor, B.E. (1998) Detecting trends in species composition. *Ecological Applications* 8: 300-308

Pimm, S.L., Jones H.L. & Diamond, J. (1988) On the risk of extinction. *The American Naturalist* 132: 757-785

Ranta, E., Kaitala, V., Lindstrom, J. & Linden, H. (1995) Synchrony in population-dynamics. *Proc. Roy. Soc. Lond. B* 262(1364): 113-118

Rackham, O, (2003) *Ancient Woodland*. Castlepoint Press, UK. 2nd ed.

Reed, T.M. (1980) Turnover frequency in island birds. *Journal of Biogeography* 7: 329-335

Reed, T.M. (1981) The number of breeding landbird species on British islands *Journal of Animal Ecology* 50(2): 613-624

Roy, D.B. & Sparks, T.H. (2000) Phenology of British butterflies and climate change. *Global Change Biology* 6: 407-416

Roy, D.B., Rothery, P., Moss, D., Pollard, E. & Thomas, J.A. (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology* 70: 201-217

Rosenzweig, M.L. & Clark, C.W. (1994) Island extinction rates from regular censuses. *Conservation Biology* 8: 491-494

Russell, G.J., Diamond, J.M., Pimm, S.L. & Reed, T.M. (1995) A century of turnover: community dynamics at three timescales. *Journal of Animal Ecology* 64: 628-641

Russell, G.J., Diamond, J.M., Reed, T.M. & Pimm, S.L. (2006) Breeding birds on small islands: island biogeography or optimal foraging? *Journal of Animal Ecology* 75: 324-339

Simberloff, D. 1983 When is an island community in equilibrium? *Science* 220: 1275–1277

Sparks, T.H. (1999) Phenology and the changing pattern of bird migration in Britain *International Journal of Biometeorology* 42: 134-138

Sparks, T.H. and Carey, P.D. (1995) The responses of species to climate over two centuries - an analysis of the Marsham phenological record, 1736-1947. *Journal of Ecology* 83: 321-329

Stracey, C.M. & Pimm, S.L. (2009) Testing island biogeography theory with visitation rates of birds to British islands. *Journal of Biogeography* 36: 1532-1539

Thompson, G. and Purcell, T. (1997) News from Skokholm. Skokholm – the year so far. Skokholm website. http://members.aol.com/skokholm/holm.htm [Accessed 9/11/05]

Thompson, G.V.F. (2007) *The Natural History of Skokholm Island*. Trafford, UK.

Tracy, C.R. & Luke, G.T. (1992) On the determinants of extinction. *The American Naturalist* 139(1): 102-122

Whittaker, R.J. (1998) *Island Biogeography*. Oxford University Press, Oxford, UK.

Whittaker, R.J., Bush, M.B & Richards, K. (1993) Plant recolonisation and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs* 59: 59-123

Williams, A.B. (1936) The composition of a beech-maple climax community. *Ecological Monographs* 6: 317-408

Williamson, M. (1981) *Island Populations*. Oxford University Press, Oxford, UK.

Williamson, M.H. (1983) The land-bird community of Skokholm: ordination and turnover. *Oikos* 41: 378-384

Williamson, M. (1987) Are communities ever stable? In: A.J. Gray, M.J. Crawley & P.J. Edwards (eds) *Colonization, Succession and Stability*. British Ecological

Table and Figure legends

Table 1. Long-term published reporting from Skokholm despite instability in publication title and publishers.

Table 2. Results of Mann-Whitney U-tests between the observed differences between numbers in named groups/species when wardens changed and differences between random years.

Figure 1. The number of species of landbirds each year with shading to indicate periods with different wardens on Skokholm.

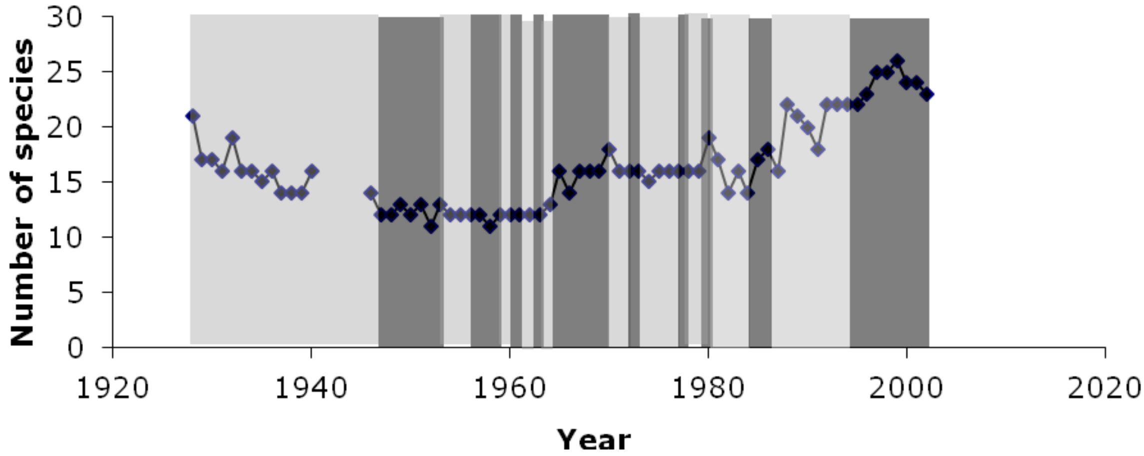
Table 1.

Title	Publisher	Year(s)
Skokholm Bird Observatory Report for 1936.	West Wales Field Society	1936
Skokholm Bird Observatory Report	West Wales Field Society in scientific cooperation with the Council for the Promotion of Field Studies	From 1948
Skokholm Bird Observatory Report	The West Wales Naturalists' Trust	From 1961
Skokholm Bird Observatory and Skomer NNR Report	West Wales Naturalists' Trust	From 1973
Skomer and Skokholm Bulletin	The Friends of Skomer and Skokholm	From 1981
The Island Naturalist - the Journal of the Friends of Skokholm and Skomer	The Dyfed Wildlife Trust	From 1995
The Island Naturalist - the Journal of the Friends of Skokholm and Skomer	The Wildlife Trust West Wales	From 1998
The Island Naturalist - the Journal of the Friends of Skokholm and Skomer	The Wildlife Trust of South and West Wales	2002
Electronic copies	N/A	From 2003

Table 2.

Variable	*N of years*	*Median of differences (observed)*	*Median of differences (random)*	*U*	*p-value*
Landbirds					
Number of species	17	0	-1	118.5	0.36
Overall abundance	17	4	6	125.0	0.50
Lapwing	17	0	0	141.0	0.90
Meadow Pipit	17	-2	5	131.5	0.65
Rock Pipit	17	0	1	130.0	0.62
Oystercatcher	17	0	3	133.0	0.69
Skylark	17	0	-2.5	13.9.5	0.86
Wheatear	17	0	9.5	69.0	**0.009**
Seabirds					
Fulmar	8	5	19.5	28.5	0.71
Guillemot	12	4.5	64.0	45.5	0.13
Great Black-backed Gull	15	0.5	5.0	75.5	0.12
Razorbill	11	-5	-96.0	56.0	0.77

Figure 1.



Number of species
30
25
20
15
10
5
0
1920
1940
1960
1980
2000
2020
Year