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Developing and assessing methods to census and
monitor burrow-nesting seabirds in Ireland

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National University of Ireland, Cork

School of Biological, Earth and Environmental Sciences

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Declaration

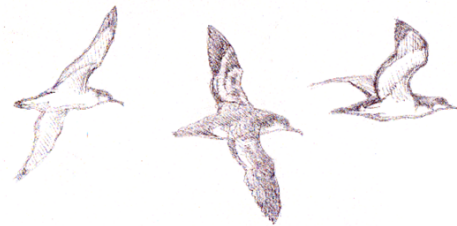
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Gavin Arneill

*I dedicate this PhD thesis to my father, Brian Lucas Arneill.
Without whom I would not have got through the first two
years of the PhD. It breaks my heart that he's not here to see
the end of it.*

Rest in peace Dad.

(26th of February 1953 – 17th of March 2017)



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Abstract

Censusing and monitoring populations are key priorities in conservation. This is particularly challenging for seabirds, where several life history characteristics and the remote nature of breeding colonies of many species make them difficult to study. Burrow-nesting species are the most difficult of all seabird groups to census due to their cryptic breeding habits, nocturnal behaviours within breeding colonies, and coexistence with other burrowing species. Historically estimates of population size in these species were obtained subjectively from the activity within colonies on a given day/night, though the relatively recent development of methodologies such as tape-playbacks have made it possible to generate population estimates using quantitative data. Nevertheless, gaps remain in our knowledge, such as the appropriate sampling approaches to take, the efficacy of some recently established automated methods, and the use of predictive species distribution modelling that could guide these time consuming efforts.

In my thesis, we address some of these issues for three key burrow-nesting species in the northern hemisphere: the Manx shearwater (*Puffinus puffinus*), the European storm petrel (*Hydrobates pelagicus*) and the Atlantic puffin (*Fratercula arctica*). In the first paper, we explore a range of sampling approaches to estimate and detect changes in population size, using data from Manx shearwater censuses as a case study. This demonstrated that *a priori* knowledge of the density and distribution in a colony allows multi-stage stratification that dramatically improves the accuracy of population estimates at low levels of sampling. Power analyses found that many existing monitoring efforts are likely to fail to detect population trends due to the enormous effect of high variation of densities between randomly selected plots. However, subjectively sampling within areas of highest density significantly increases the power to detect declines. My thesis also shows that these breeding distributions can be predicted *a priori* using ensemble species distribution models built on density data from censuses, habitat assessments, and digital elevation models. Another paper in my thesis examines the efficacy of emerging automated techniques, which is far from clear. Results here show, for the first time, that soundscapes obtained from passive acoustic monitoring in the Manx shearwater are driven by in-colony flight paths rather than local nest density, although a decline in density within the colony over two years coincided with a

decline in acoustic activity. The final empirical paper reports new population size estimates for several colonies and uses matrix population models to retrodict populations to explicate discrepancies between our estimates and those of the only previous census, Seabird 2000 (1998-2002). The findings here suggest that existing estimates for burrow-nesting Procellariiformes in Ireland are likely vast underestimates, however, the extent to which this is true for the national estimates cannot be quantified as factors that determine population size vary across a species range. Atlantic puffin populations appear to be in decline across the sites considered in this study. My thesis as a whole highlights the need for the revision and standardisation of the methods used to census and monitor burrow-nesting seabirds. For these breeding populations in the geographic region studied here, the Seabird Monitoring Handbook should be updated. Finally, the findings of this PhD research are synthesised in the form of an Irish Wildlife Manual, providing the National Parks and Wildlife service feasible options to fulfil their international obligations to report the conservation status of these populations.

Chapter 1

General Introduction

The chapters in this thesis are written as individual, stand-alone research papers, aiming to improve censusing and monitoring practices of burrow-nesting seabirds, with a focus on three species that breed in Ireland. The conclusions of each chapter, with the exception of Chapter 5, are not just applicable to the species studied and the breeding range in the Britain/Ireland but can inform census efforts and sampling strategies across a wide range of species and locations. For ease of reading the thesis as a whole, I have cross-referenced chapters where appropriate, though the chapters are written so they can also be read in isolation.

1. General Background

A fundamental goal in ecology is to define the conservation status of any species population. This is of particular importance for species that are indicative of the health of an ecosystem (Grémillet and Charmantier, 2010; Coates *et al.*, 2016; McKenzie *et al.*, 2018). At the global scale, the International Union for the Conservation of Nature (IUCN) define the conservation status of species based on their abundance in relation to their risk of extinction. In the European Union, the Habitats Directive (Council Directive 92/43/EEC) requires each of the member states to maintain a species population at a ‘favourable conservation status’. Specifically, populations must remain at a viable level within natural habitat and a sufficient amount of suitable breeding habitat should exist to maintain its populations on a long-term basis. Wild bird populations are managed under the framework outlined in the Birds Directive (Directive 2009/147/EC) whereby member states are required to report on the conservation status of populations within their boundaries every six years. However, as these are directives and not regulations, the member states decide on how they adhere to these requirements. These approaches of defining a species conservation status have been criticised as the results are biased due to the lack of a common set of monitoring methods used across many species distributions (Lonergan, 2011; Maes *et al.*, 2015),

highlighting the need for further research into standardised approaches in censusing and monitoring populations.

Seabirds are key qualitative indicators of the world's largest biome (Grémillet and Charmantier, 2010) and are subject to multiple threats including by-catch, habitat destruction, overfishing, marine litter and introduced mammalian predators (Jones *et al.*, 2008; Croxall *et al.*, 2012). Yet for many seabirds, their life-history traits, widespread distribution, migratory behaviours and remote breeding colonies mean that data on population size, reproductive parameters and health are limited both spatially and temporally. Major reviews of the available datasets such as Croxall *et al.* (2012) and Paleczny *et al.* (2015) have been produced and report a general declining trend in seabird populations. However, these conclusions are biased towards the seabird populations that have been subject to long-term study (Mitchell *et al.*, 2004; Mavor *et al.*, 2008; Horswill and Robinson, 2015), primarily cliff and ground nesting species that are relatively straightforward to census through observational counts from land and boat (Cotter and Rail, 2007).

Burrow-nesting seabirds are particularly difficult to census due to their cryptic breeding habits, such as nesting in burrows, rock crevices and many species only return to breeding colonies at night. As a result, little demographic and monitoring data are available for their inclusion in meta-analyses (e.g. Paleczny *et al.* 2015). Advances in technology have furthered our understanding of these species' at-sea distribution (Guilford *et al.*, 2008; Grecian *et al.*, 2012; Jessopp *et al.*, 2013; Fayet *et al.*, 2017; Critchley *et al.*, 2018) and breeding distributions (Rayner *et al.*, 2007; Krüger *et al.*, 2017), yet for many species in this group accurate population size estimates are not available. This puts us in a difficult place to report on this group within the context of wider seabird declines, and more urgently it means that EU member states are not fulfilling their obligations to monitor populations of particular importance. Standardised approaches for monitoring burrow-nesting species are limited to the production of national seabird monitoring programmes developed by conservation bodies such as the Joint Nature Conservation Committee (Walsh *et al.*, 1995), New Zealand's Department of Conservation's Conservation Services Programme (Parker and Rexer-Huber, 2016), the Norwegian SeaPOP programme (Anker-Nilssen *et al.*, 2017) and seabird monitoring programs led by the U.S Fish and Wildlife services (Byrd, 2006).

However, the methods in obtaining population estimates to date have varied substantially both across sites (Silcocks, 1999; Smith *et al.*, 2001; Murray *et al.*, 2003) and across censuses (Smith *et al.*, 2001; Perrins *et al.*, 2012).

Across the British Isles (including Great Britain, the Isle of Man, Ireland and their surrounding smaller islands), three previous large-scale censuses on all seabird species have been carried out. Burrow-nesting Procellariiformes were omitted from Operation Seafarer (1969 – 1970; Cramp *et al.*, 1974) and the Seabird Colony Register (1985 – 1988; Lloyd *et al.*, 1991) censuses, which aimed to provide estimates of abundance and distribution of all seabirds that were visually conspicuous in the colony during daylight. The first attempt to census all burrow-nesters at the national scale in Britain/Ireland was Seabird 2000 (1998 - 2002; Mitchell *et al.*, 2004), though it is apparent that methods were not refined and many locations thought to hold breeding populations were omitted due to logistical constraints. Thus, baseline population estimates for these species are incomplete and the details on the methods used at the site level are vague, impeding our ability to carry out repeat surveys to determine changes abundance. Opportunity exists for standardised methods to be used in Seabird 4 (Seabirds count) which has begun with a census of cliff-nesting species in 2015-2017 (unpublished).

The British Isles host internationally important numbers of three burrow-nesting species: the Manx shearwater (*Puffinus puffinus*), the European storm petrel (*Hydrobates pelagicus*) and the Atlantic puffin (*Fratercula arctica*). The Seabird 2000 census estimated that approximately 90%, 3-11% and 10% of the global population of these species respectively breed across Britain and Ireland. The British Isles host a small portion of the global breeding population of Leach's storm petrel (*Hydrobates leucorhous*) and over 80% of these are found to breed on four islands in St Kilda (Newson *et al.*, 2008). Here I briefly outline census techniques that are currently used for burrow-nesting seabirds. I then introduce each of the three study species considered in this PhD and review the methods that have been used to estimate the size and monitor these populations across the British Isles. Specifically, for each species I review: (i) previous estimates of population sizes, (ii) the methods used to obtain these estimates and (iii) the existing monitoring techniques. Finally, I introduce the aim of each chapter within this thesis.

Census techniques for burrow-nesting species

Historically, subjective population estimates were obtained from brief visits to colonies to estimate the activity on a given day, or in the case of many Procellariiformes, activity on a given night (Cramp *et al.*, 1974; Taylor, 1988). These subjective approaches have since been replaced with more quantitative approaches (James and Robertson, 1985; Walsh *et al.*, 1995; Ratcliffe *et al.*, 1998; Smith *et al.*, 2001). Early estimates of population size for most burrowing species were derived from counts of the number burrows present on an island or an extrapolated estimate from a sample of burrows (Gibbons and Vaughan, 1998; Mitchell *et al.*, 2004). This method is still employed to estimate population size across some colonies whereby burrow surveys are conducted to determine the number of burrows that show signs of occupancy such as fresh digging or guano (Brun, 1966; Harris, 1984; Ankler-Nilson and Røstad, 1993; Rodway and Lemon, 2011). The current use of the signs of occupancy method however is largely restricted to burrowing Auks (puffins, auklets) and burrowing penguins due to the development of the tape-playback method that has to date proved to be the most effective method of censusing many Procellariiformes species (James and Robertson, 1985; Walsh *et al.*, 1995; Ratcliffe *et al.*, 1998; Perrins *et al.*, 2012). Tape-playbacks are now widely accepted as the standard method for censusing many burrow-nesting Procellariiformes and much of the literature surrounding this method aims to explain the variation in response rates by changing the origin (Ratcliffe *et al.*, 1998), the quality (Brown *et al.*, 2006) and the sex (Perkins *et al.*, 2017^a) of the calls used.

The application of these methods across numerous colonies to derive national population estimates can present a number of issues dependent on the (i) transferability of the method across colonies and (ii) the sampling effort that is logistically possible across colonies. To date, the sampling strategies and efforts used to obtain baseline estimates have differed across colonies, though the extent to which is unclear due to insufficient reporting of methods used and sampling effort (Mitchell *et al.*, 2004). Generally, whole-island surveys are limited to well-studied sites (Harris, 1984; Mitchell *et al.*, 2004) and for most colonies population sizes are estimated using a sampling approach. Simple random sampling

approaches have been used across many colonies, where counts are carried out in sampling plots that are randomly placed across an island or colony (Smith *et al.*, 2001; Mitchell *et al.*, 2004). Further complexity can be added to a study design when stratified approaches are used, though in censuses of burrow-nesting species to date in Britain and Ireland, these have not been reported (Mitchell *et al.*, 2004). This is a major gap in our knowledge as stratified approaches have been successfully used in censusing other taxa to yield more accurate population size estimates (Wimmer *et al.*, 2013; Metzger *et al.*, 2013). In these censuses, strata are generally defined across geographical space in relation to habitat types, reducing the variation around density estimates, thus increasing our confidence in attained population estimates (Madders *et al.*, 2003; Rosenberg *et al.*, 2016). Further work to refine census efforts in a stratified approach for burrow-nesting species could potentially reduce the amount of sampling required to obtain accurate estimates.

Tape-playback and signs of occupancy surveys are the most established methods used in censusing burrow-nesting species to date. Considerable research has gone into developing automated techniques aiming to reduce the time and cost associated with censusing these species. One such method is passive acoustic monitoring that has been used to estimate the size (Opper *et al.*, 2014), the recovery (Buxton and Jones, 2012) and trends (Borker *et al.*, 2014) of seabird populations. A more recently established method involves the use of infrared cameras to survey Procellariiformes at night (Perkins *et al.*, 2017^b). The efficacy of these methods remains unclear and further testing is required to understand their applicability across species and across colonies.

2. Manx shearwater (*Puffinus puffinus*)



Figure 1. The Manx shearwater *Puffinus puffinus*. © Gavin Arneill

The Manx shearwater is a member of the family Procellariidae within the order Procellariiformes, also known as the ‘tube-noses’ and includes the albatrosses, storm petrels, petrels and fulmars (Brooke, 1990). Their breeding distribution is widespread across the North Atlantic, though an estimated 90% of the global population breed across the British Isles (Mitchell *et al.*, 2004; Brooke, 2013). Manx shearwaters are predominantly site faithful, natal dispersal is low and breeding pairs show high burrow fidelity (Harris, 1972; Brooke, 1978^a). As migratory species, breeding birds return to their breeding colonies in February or March after wintering in the South Atlantic off the coasts of South America and South Africa (Guilford *et al.*, 2008). On return to their breeding colonies, breeding birds carry out burrow maintenance and build fat reserves before laying a single egg in May, and if successful, fledge a single chick in late August or early September (Harris, 1966; Brooke, 1978^a). Due to their susceptibility to predation on land, Manx shearwaters only return to their breeding burrows at night and as a result have an increased dependence on vocalisations, and possibly olfactory cues, for navigation within the colony (James, 1985; Brooke *et al.*, 2013).

2.1. Previous estimates of Manx shearwaters in the British Isles.

Population size estimates across most breeding colonies of Manx shearwaters are limited to the Seabird 2000 efforts reported in Mitchell *et al.* (2004). Seabird 2000 incorporated most of the known breeding colonies across Britain, while in Ireland, many of the sites believed to host a breeding colony of this species were not

counted due to logistical constraints (Mitchell *et al.* 2004). Europe hosts >95% of the species breeding population (342,000-393,000 pairs) of which approximately 320,000 breeding pairs are found across the British Isles (Mitchell *et al.*, 2004; BirdLife International, 2015). Several colonies across Britain are thought to contain the majority of these breeding pairs, specifically the Pembrokeshire islands off the coast of Wales (approximately 168,000 breeding pairs) and Rum (approximately 120,000 breeding pairs) off the west coast of Scotland (Mitchell *et al.*, 2004, see Figure 2). Prior to Seabird 2000, several sites had been subject to limited census effort that produced vague estimates of population size prior to the development of standardised tape-playback methods that now govern the census work of Manx shearwaters and many other Procellariiformes (Walsh *et al.*, 1995; Ratcliffe *et al.*, 1998; Silcocks, 1999; Perrins *et al.*, 2012).

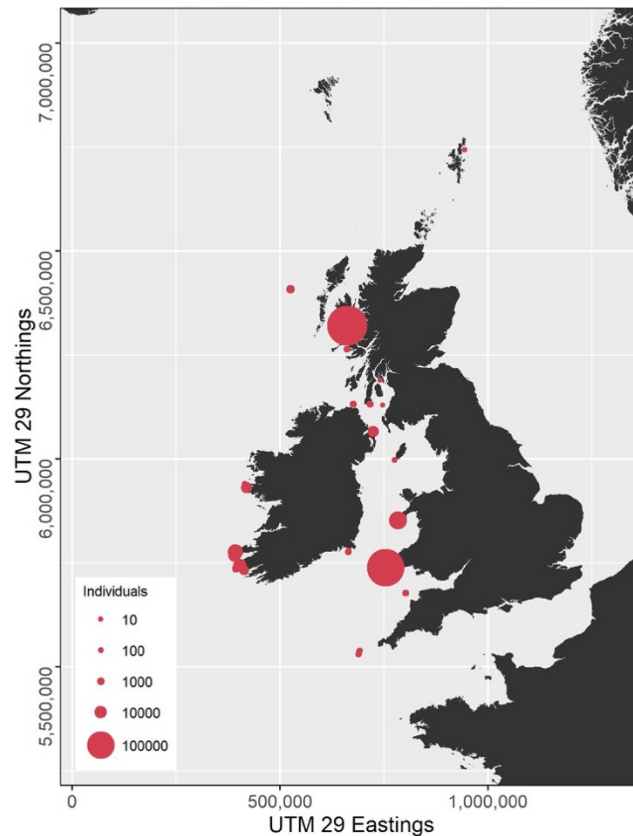


Figure 2. The distribution and density of the most recent population estimates available for Manx shearwaters (*Puffinus puffinus*) breeding across the British Isles (Critchley *et al.*, 2018).

2.2. Census methods for Manx shearwaters

Before the development of tape-playbacks, population size estimates were based subjectively on the amount of vocal activity within an area on a given night (Cramp *et al.*, 1974). The methodology progressed to surveys on signs of occupancy around burrows to estimate the number of apparently occupied burrows within a colony (Walsh *et al.*, 1995; Silcocks, 1999). The first reported use of the now ‘standard method’, tape-playbacks, is outlined in James and Robertson (1985). Several studies in the 90’s continued to use signs of occupancy, as the playback method James and Robertson (1985) put forward was thought to be flawed as females also responded to the playbacks (Gibbons and Vaughan, 1998; Silcocks, 1999). This is now corrected for by measuring response rates on a sample of burrows that are known to be occupied and more recently female calls are also being used (see Perrins *et al.*, 2012; Perkins *et al.*, 2017^a). The method has since been adapted and tested across multiple breeding populations (Smith *et al.*, 2001; Perrins *et al.*, 2012; Perkins *et al.*, 2017^a). Recent studies largely focus on refining the method by increasing the response rate (Brooke, 1978; Perkins *et al.*, 2017^a) aiming to reduce the large confidence intervals that surround population estimates (Perrins *et al.*, 2012; Perkins *et al.*, 2017^a). These large confidence intervals highlight a major limitation of this method, which is that an extensive amount of field time is required to carry out tape-playbacks on often thousands of burrows (Perrins *et al.*, 2012). Furthermore, tape-playbacks are only effective during a narrow time frame within the incubation and chick-guarding period when the response rate is high (Brooke, 2013).

Little has been reported on the use of automated methods for censusing Manx shearwaters when compared to other Procellariiformes (Oppel *et al.*, 2014, Perkins *et al.*, 2017^b). This is likely due to the effectiveness of the tape-playback method that is widely accepted as the standard approach and used across the species’ largest breeding colonies (Smith *et al.*, 2001; Murray *et al.*, 2003; Perrins *et al.*, 2012). The vocal activity of Manx shearwaters suggests that passive acoustic monitoring could be advantageous, yet the efficacy of this method for obtaining population size estimates and the use of acoustic indices in monitoring population trends remains unclear.

2.3. Monitoring Manx shearwaters

Globally, long-term monitoring of Manx shearwaters (studies spanning more than a decade) is restricted to four colonies in Britain, namely the Pembrokeshire islands (Skomer and Skokholm), Rum and Copeland (Mavor *et al.*, 2008). The methods used to monitor this species includes repeated tape-playbacks to establish density within permanent fixed plots, directly recording occupancy in accessible artificial burrows and inspection through burrow access tunnels (Perrins *et al.*, 2012; Stubbings *et al.*, 2015). These permanent plots are used with the aim of detecting temporal trends in breeding populations and to measure demographic parameters such as breeding productivity and survival (Horswill and Robinson, 2015; Stubbings *et al.*, 2015). Yet, for approximately 95% of the known breeding colonies no permanent monitoring plots are established and conclusions on population change are drawn from national census efforts that occur every 10-15 years (Mitchell *et al.*, 2004; Mavor *et al.*, 2008). To date, no regular monitoring programme has been established in the Republic of Ireland for Manx shearwaters.

3. European storm petrel (*Hydrobates pelagicus*)



Figure 3. The European storm petrel *Hydrobates pelagicus*. © Paul Whitelaw

The European storm petrel is a member of the northern storm petrel family Hydrobatidae within the order Procellariiformes. This species is Europe's smallest seabird, weighing on average approximately 23-28 grams (Flood, 2013). Their breeding distribution is widespread across the North East Atlantic, with the largest breeding populations found on the Faroe islands, the British Isles and across the Mediterranean (Snow and Perrins, 1998). European storm petrels migrate to the

South Atlantic to winter predominantly off the west coast of Africa, returning to their breeding colonies in March or April (BirdLife International, 2018). The breeding season for European storm petrels extends to late September or early October when they fledge a single chick. European storm petrels nest in excavated burrows, rock crevices, scree, stone walls and boulder beaches and only return to the nest under the cover of darkness due to their high susceptibility to predation on land (Bolton *et al.*, 2010).

3.1. Previous estimates of European storm petrels in the British Isles.

European storm petrels were omitted from Operation Seafarer (Cramp *et al.*, 1974) and the Seabird Colony register (Lloyd *et al.*, 1991). Population estimates at the national level across the British Isles were first reported in Mitchell *et al.* (2004) from the Seabird 2000 census. An estimated 124,775 breeding pairs of European storm petrels were thought to be breeding in the British Isles, with approximately 80% of these breeding in the Republic of Ireland (Mitchell *et al.*, 2004; see Figure 4). Tape-playback surveys were carried out across a total of 180 islands across the British Isles, of which 125 were found to have breeding European storm petrels (Mitchell *et al.*, 2004). Detailed efforts have been carried out on several sites across Britain such as Mousa off the north east coast of Scotland, on which several studies that refine the tape-playback methodology have been carried out (Ratcliffe *et al.*, 1998; Bolton *et al.*, 2010).

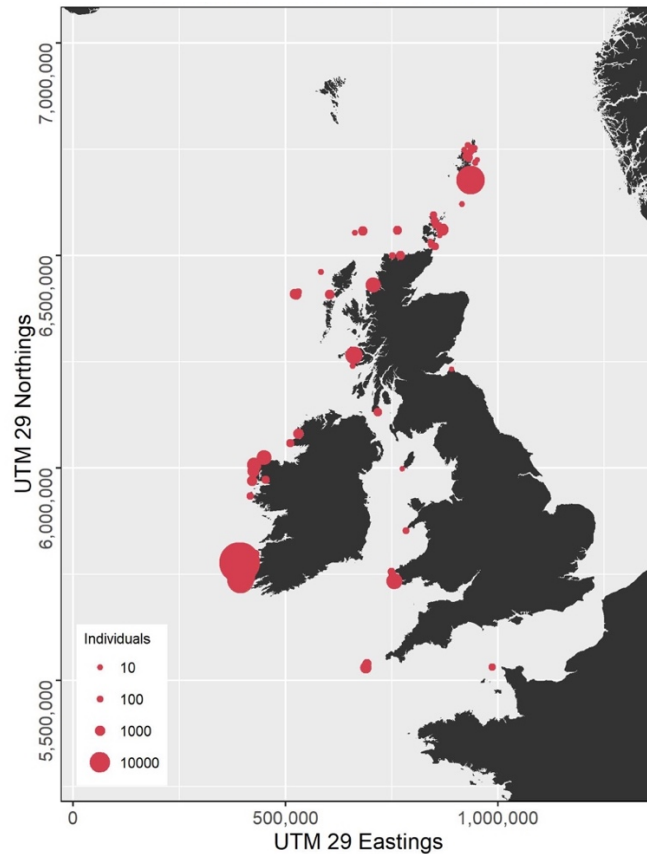


Figure 4. The distribution and density of the most recent population estimates available for European storm petrels (*Hydrobates pelagicus*) breeding across the British Isles (Critchley *et al.*, 2018).

3.2. Methods currently used to census European storm petrels.

Early studies of European storm petrels involved nocturnal work to estimate population size through mark-recapture methods. Mark-recapture methods have been discussed in detail on two islands off the coast of Scotland (Hounscome *et al.*, 2002, 2003, 2006; Insley *et al.*, 2004), outlining the challenges associated with this method including the difficulty in discriminating between breeding and non-breeding birds that are captured. European storm petrels respond to tape-playbacks though response rates are lower than those of other Procellariiformes (Ratcliffe *et al.*, 1998; Bolton *et al.*, 2010). The first published study utilising tape-playback methods for this species was Ratcliffe *et al.* (1998), and remains the most utilised method of censusing European storm petrels (Fowler, 2001; Mitchell *et al.*, 2004, Bolton *et al.*, 2010).

Subsequent publications on census methods for this species largely report refinements to improve the response rate to tape-playbacks including the use of calls from other colonies (Ratcliffe *et al.*, 1998), variation in the quality of recordings (Brown *et al.*, 2006) and digitally manipulated calls (Soanes *et al.*, 2012). European storm petrels are known to have a higher response rate at night (Ratcliffe *et al.*, 1998), however nocturnal fieldwork on remote islands with steep cliffs is often too hazardous. The low diurnal response rate of European storm petrels to tape-playbacks encourages research into alternative census methods, particularly those that can be automated. For example, developments in infrared camera technology have advocated their use in estimating the abundance of this species (Perkins *et al.*, 2017^b). More research is required to refine these methods, test their ability across multiple colonies, and most importantly develop a computational method of analysing the huge amount of data these devices generate.

3.3 Monitoring European storm petrels.

Monitoring efforts are restricted to a few breeding colonies across the British Isles, namely Mousa (Bolton *et al.*, 2010), Skokholm and several small islands across Britain (Hounsoume *et al.*, 2002). Artificial nest boxes were first constructed on Skokholm in 2016 to be used in monitoring this species. Similar nest boxes have since been constructed on several sites across Britain and Ireland. Prior to the establishment of these artificial nest boxes, no systematic effort to attain demographic data such as productivity or survival was in place for this species across the British Isles (Horswill and Robinson, 2015). Despite hosting internationally important numbers of European storm petrels, monitoring efforts are restricted to one colony in Ireland, Skellig Michael (Birdwatch Ireland, 2013). Thus, there is an urgent need to establish monitoring programmes across the British Isles to effectively report, and assess their efficiency in detecting, the demographic trends of this species.

4. Atlantic puffin (*Fratercula arctica*)



Figure 5. The Atlantic puffin (*Fratercula arctica*). © Gavin Arneill

The Atlantic puffin belongs to the order Charadriiformes within the family Alcidae that includes the guillemots, murrelets, puffins and razorbills (Linnaeus, 1758). Their breeding distribution is widespread across the North Atlantic from Newfoundland to Russia, with the largest breeding colonies found in Iceland, Norway and the British Isles (BirdLife International, 2015; IUCN, 2015). Atlantic puffins mainly breed on coastal cliffs on offshore islands, overwinter at sea and only return to breeding colonies in spring (Harris, 1984; Harris *et al.*, 2010; Jessopp *et al.*, 2013). This species shows high site fidelity, returning to the same colony each year (Calvert and Robertson, 2002) and typically breed in the same burrow (Anker-Nilssen and Røstad, 1993; Finney *et al.*, 2003). Breeding birds lay a single-egg clutch and fledge a single chick in July or early August. The productivity rates for this species are particularly low compared to other burrow-nesting seabirds (Harris *et al.*, 2005; Miles *et al.*, 2015; Horswill and Robinson, 2015). Unlike Manx shearwaters and European storm petrels, Atlantic puffins are active in breeding colonies diurnally and consequently the methods in which they are censused and their inclusion in previous census efforts differ considerably.

4.1. Previous estimates of Atlantic puffins in the British Isles.

Atlantic puffins were censused in all national censuses to date, the most recent estimate was 600,751 breeding pairs across the British Isles (Mitchell *et al.*, 2004). Mitchell *et al.* (2004) reported population increases of 33% and 19% since

Operation Seafarer (1969 – 1970) and the Seabird Colony Register (1985 – 1988) respectively. In recent years, Atlantic puffins have experienced rapid declines, and have been given the conservation status ‘Vulnerable’ on the IUCN’s red list of threatened species globally and ‘Endangered’ at the European scale (IUCN, 2015; Miles *et al.*, 2015). The largest known breeding colonies are found off the north coasts of Scotland; where nan Eilean, Shetland and St. Kilda were identified as the most important areas containing the highest proportions of the breeding population in Britain and Ireland (Cramp *et al.*, 1974; Lloyd *et al.*, 1991; Mitchell *et al.*, 2004; see Figure 6).

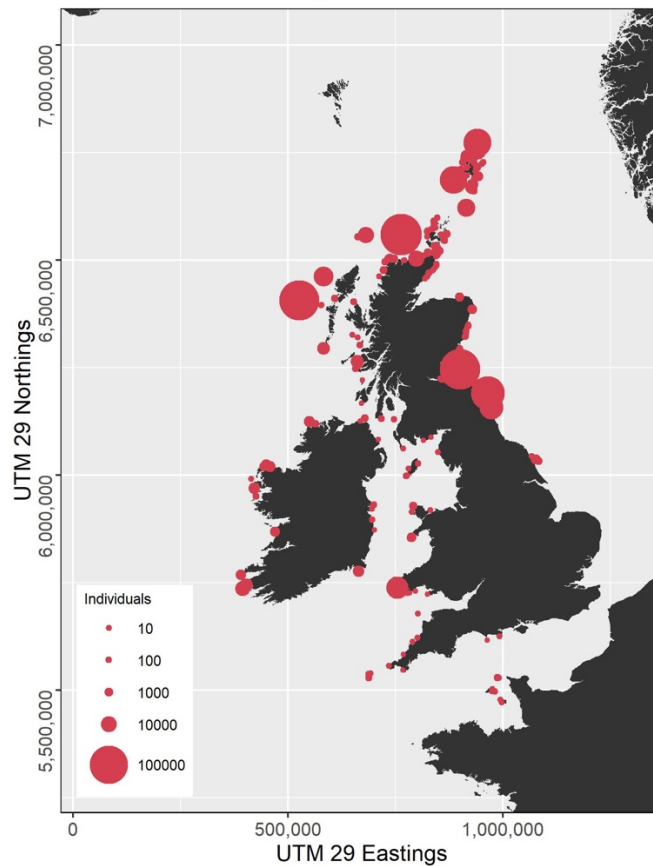


Figure 6. The distribution and density of the most recent population estimates available for Atlantic puffins (*Fratercula arctica*) breeding across the British Isles (Critchley *et al.*, 2018).

4.2. Methods currently used to census Atlantic puffins

Across the three previous national census efforts, the methods reported include a combination of (a) surveys of apparently occupied burrows and (b) observational counts of individuals of birds in flight, on cliffs and rafting in waters adjacent to

colonies (Cramp *et al.*, 1974; Lloyd *et al.*, 1991; Mitchell *et al.*, 2004). These methods are typically carried out as whole-island censuses, however sampling approaches can be used when sub-colonies are discernible across an island (Brooke, 1972; Ashcroft, 1979; Walsh *et al.*, 1995).

The ‘standard method’ of censusing Atlantic puffins involves inspecting individual burrow entrances to determine signs of occupancy such as fresh digging, guano and feathers (Walsh *et al.*, 1995; Anker-Nilsson and Røstad, 1993; Mitchell *et al.* 2004). The first reported use of this method to estimate colony size was in Brun (1966), and it has since been adopted across several sites (Brooke, 1972; Harris, 1980; 1984). The method was refined by Anker-Nilsson and Røstad (1993), constructing the “star method” that permits whole-island sampling to be carried out to determine population size with greater accuracy. However this method is labour intensive and furthermore, in a heterogeneous colony, the burrow may be occupied by other burrow-nesting species (Rayner *et al.*, 2007). Survey accuracy is therefore increased if burrow occupancy is examined by manual inspection or the use of a burrowscope (Rayner *et al.*, 2007; Buxton *et al.*, 2016). Grubbing of burrows (Calvert and Robertson, 2002), which involves reaching into the burrow to search for the presence of a breeding adult, an egg or nest material, is another method used across several breeding colonies in Britain (Walsh *et al.*, 1995; Mitchell *et al.*, 2004). This method is invasive and should be limited to species that are tolerant of disturbance at the nest (Ambagis, 2004; Boland and Phillips, 2005), an issue that is addressed in the literature as Atlantic puffins are known to be sensitive to disturbance in some colonies (Kelly *et al.*, 2015). This method is further restricted by the substrate on the colony as burrows may be too deep to inspect and multiple nest chambers may be found within a single burrow entrance.

A major limitation of the methods discussed above is the necessity to access and inspect individual burrows, a feat that is not possible across many colonies where breeding burrows are located on coastal cliffs and steep inaccessible areas on remote islands. During Seabird 2000, observational counts were only carried out where access to individual burrows was limited (Mitchell *et al.*, 2004). Yet observational counts have been used to estimate population size and trends across some of the largest colonies across the British Isles (Miles *et al.*, 2015). Moreover,

observational counts of burrow-nesting species have previously been reported as the preferred census method as they cause less disturbance compared to other methods (Calvert and Robertson, 2002). The limitations of this method are equivalent to those seen in surveys on cliff and ground nesting species such as Common guillemots (*Uria aalge*), whereby the temporal variation of colony attendance reduces the accuracy of counts (Sims *et al.*, 2006). To overcome this limitation, Miles *et al.*, 2015 suggested the use of repeated counts, reporting the highest total count to reduce the effect of low colony attendance on a given day.

4.3. Monitoring Atlantic puffins

Long-term demographic data for Atlantic puffins is sparse, and the methods used across breeding colonies are inconsistent (Horswill and Robinson, 2015). The breeding population of Atlantic puffins on the Isle of May off the east coast of Scotland is the most intensively studied across the British Isles, and much of the work carried out here resembles that of the work carried out in other well-studied colonies such as Røst, Norway (Harris, 1984; Harris and Wanless, 1991; Anker-Nilsson and Røstad, 1993). The methods used on these sites require individual apparently occupied burrows to be assessed for signs of occupancy. Several other sites across the British Isles, including the Farne Islands, use grubbing methods as discussed previously (Ashcroft, 1979; Walsh *et al.*, 1995; Mitchell *et al.*, 2004). Another approach uses focal samples across an area of apparently occupied burrows to make inference on productivity across years, whereby the number and frequency of prey loading adults returning to burrows is recorded (Breton *et al.*, 2006). The outputs of these monitoring methods have been used to link demographic parameters to variables such as prey availability across years (Harris and Wanless, 1991; Harris *et al.*, 2007) and generally show declining population trends across Britain (Miles *et al.*, 2015). In the Republic of Ireland however there has been no consistent effort to monitor any breeding population of Atlantic puffins.

5. Thesis aims and structure

The overarching aims of this PhD study are:

- (i) To compare the ability and efficiency of a range of census methods and sampling strategies to determine population sizes and detect changes over time for burrow-nesting species.
- (ii) To critically assess the accuracy of historical population size estimates of these species by examining the historical estimates and modelling potential change.
- (iii) To propose standardised census and monitoring strategies for the study species in support of Ireland's commitment to Articles 10 and 12 of the Birds Directive.

In **Chapter 2**, I investigate the ability of different sampling strategies and efforts required to (a) obtain accurate abundance estimates and (b) detect population declines between national population census efforts, that are currently every 10-15 years. This chapter uses census data across four breeding colonies of Manx shearwaters. The study provides insight into the uncertainty surrounding existing national census efforts, with the aim of informing conservation managers of the ability to draw conclusions on population status, and how census efforts can be refined to reduce uncertainty around population size estimates.

One such refinement to census efforts is undertaking stratified sampling approaches, and **Chapter 3** shows how ensemble species distribution models can inform this. I demonstrate the efficacy of ensemble species distribution models that utilise habitat and topographical data, with the aim of accurately predicting the distribution of these three species across breeding colonies. The models are built on distribution data collected for the three species across eight islands in Britain and Ireland. I discuss the scope of these models and how conservation efforts could benefit from their use.

In **Chapter 4**, I investigate the role of passive acoustic monitoring in determining the local nest density of Manx shearwaters. This chapter combines data from tape-playback methods, passive acoustic monitoring and GPS tracking of breeding

birds to determine the drivers of the soundscape within a seabird colony. This chapter is in review for publication in *Ibis*.

In **Chapter 5**, I report revised population size estimates for all three species across several colonies in Ireland. I use Leslie matrix population models to carry out retrospective projections of population size to determine the extent of the discrepancies between recent estimates and those of Seabird 2000. I discuss the potential causal factors of these differences in population sizes and what these findings might suggest for the national estimates.

In **Chapter 6** and **the Appendix**, I synthesise the findings of this PhD research in the form of an Irish Wildlife Manual. This sets out feasible options for ongoing national census efforts to be carried out by the National Parks and Wildlife Service.

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Chapter 2

Sampling strategies for species with high breeding-site fidelity: a case study in burrow-nesting seabirds

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Abstract

Sampling approaches used to census and monitor populations of flora and fauna are diverse. The intricacy of sampling designs typically range from simple random sampling through to complex hierarchal stratified designs, and the efficacy of the approach is determined by the spatial and temporal distribution of the population to be studied. Long-term monitoring programs used to assess seabird population trends are often hampered by large and difficult to access colonies, with spatially variable distribution patterns that require a large amount of time to survey. We aimed to determine the sampling effort required to (a) obtain abundance estimates with a high degree of confidence, and (b) detect population declines under different scenarios of a regionally important species in the Atlantic, the Manx shearwater (*Puffinus puffinus*). Analyses were carried out using data collected from tape-playback surveys on four islands in the North Atlantic. To explore how sampling effort influenced confidence around abundance estimates, we used the heuristic approach of imagining the areas sampled represent the total population, and bootstrapped varying proportions of subsamples. This revealed that abundance estimates from randomly subsampling less than 50% of all plots vary dramatically, leading to unacceptable lack of confidence in population estimates. Confidence is

dramatically improved using a stratified approach. Furthermore, power analyses suggested that the random selection of monitoring plots generally gives little confidence in the statistical power to detect overall population declines of 10%, and density-dependent declines as large as 50%, because variation in density between plots is so large. Thus, current monitoring programs have a high probability of failing to detect population level changes due to maladaptive sampling efforts and the random selection of monitoring plots. However, focusing sampling effort in areas of highest density dramatically increases the power to detect year to year population decline. We discuss what our findings suggest about how these challenging, yet vulnerable seabird populations might be censused and monitored most effectively.

Keywords: Monitoring, Burrow-nesting seabird, Power analysis, Census, Bootstrapping, Population trends

1. Introduction

In recent years, the need for robust methods in which populations can be censused and monitored has become more pressing as anthropogenic impacts intensify (Bender *et al.*, 1998; Oaks *et al.*, 2004; Croxall *et al.*, 2012). Recent publications aim to improve census and monitoring practices by modifying existing methods (Frey *et al.*, 2014; Perkins *et al.*, 2017) and utilising technological advances (Savage *et al.*, 2010; Hodgson *et al.*, 2016) with the aim of reducing the associated costs (Borker *et al.*, 2014; Hartill *et al.*, 2016). Despite ongoing efforts to improve existing methodologies, basic sampling approaches that underpin these efforts remain to be refined and standardised. This challenge is widespread across many species, in particular in avian groups such as seabirds where the accuracy of population size estimates and trends in some species are questionable due to inconsistencies and errors in the methods used.

The methods used to sample populations of fauna and flora vary, both across taxa and often across breeding populations of a given species (Kindberg *et al.*, 2011; Nalwanga *et al.*, 2012; Macnaughton *et al.*, 2015). Simple random sampling is often used in field studies to estimate densities and monitor populations, especially when species are highly mobile (Nalwanga *et al.*, 2012; Carrara *et al.*, 2015). However, these methods may be unsuitable, or indeed unnecessary, when sampling in logistically challenging areas and where individual organisms are static or show site fidelity. Moreover, many species distributions are highly clustered, and random sampling necessitates a uniform distribution for small samples to be truly representative. If spatial patterns of distribution are known *a priori*, this information can be used to obtain more accurate estimates by stratifying sampling approaches. In ecology, stratification is most typically carried out using defined strata across geographical space, predominantly distinctive habitat types to determine species abundance across a mixed landscape (Madders *et al.*, 2003; Rosenberg *et al.*, 2016). Abundance estimates for each strata are then combined to give an overall estimate for the area; this approach has been successful in censuses and monitoring efforts across many taxa (Wimmer *et al.*, 2013; Metzger *et al.*, 2013). Further complexity can be added to stratified sampling in the form of multi-stage stratification, often used in pharmaceutical and educational research. This is a hierarchical design where samples are drawn and

then further subdivided based on another known variable (Thomas and Heck, 2001; Tchoubi *et al.*, 2015). Multi-stage stratification is not commonly used in ecological research, yet is applicable in certain instances such as repeat census efforts where baseline distribution data is available to reduce the effect of variation between strata. The estimate and the surrounding confidence interval attained from any effort will largely be determined by the sampling approach used.

Generating baseline population estimates at a given time is a crucial aim in conservation, but monitoring these populations over time is equally important. In some groups, such as wading bird species or cliff and ground nesting seabirds, whole population counts of individuals are possible (Amano *et al.*, 2010; Chardine *et al.*, 2013). For many species, sampling is more appropriate (Sims *et al.*, 2006; Meyer *et al.*, 2010), which is typically done by regularly sampling population densities in a number of fixed sample plots over time (Corona *et al.*, 2010; Woinarski *et al.*, 2010; Harris *et al.*, 2016; Dolrenry *et al.*, 2016). These sampling approaches are likely to be suitable when distributions do not change rapidly over time (Jackson *et al.*, 2008), and when species are patchily distributed for example within a specific habitat type, precluding the use of random sampling. One group where this is largely thought to be true is in seabirds, which show high site fidelity, are patchy in their distribution, and are migratory, thus only accessible during their breeding season when they return to land.

As apex predators that feed on prey from a range of trophic levels, seabirds are not only key qualitative indicators of the world's largest biome, they are also among the most threatened vertebrates in the world (Diamond and Delvin, 2003; Grémillet and Charmantier, 2010; Croxall *et al.*, 2012). Global monitoring efforts suggest that many seabird populations are in decline (Paleczny *et al.*, 2015). This is primarily because of their sensitivity to invasive mammals, overfishing, by-catch, marine pollution, disturbance, habitat destruction, and climate change (Croxall *et al.*, 2012). However there is considerable uncertainty over the status and trends across all seabird species because most studies are biased towards species that are easy to observe nesting on cliffs or on the ground where whole colony counts are often possible (Cotter and Rail, 2007; Wanless *et al.*, 2007; Collas and Burgun, 2011; Meade *et al.*, 2013). Burrow-nesting seabird species are amongst the most threatened of all seabirds, and yet detailed population

monitoring studies are rare. For example, in Paleczny *et al.*'s (2015) review, approximately 46% ($n = 74$) of the species not considered ($n = 162$) were burrow-nesters. The main reason burrow-nesting species are poorly represented is that they are extremely difficult to census. Many Procellariiformes, for example, are remarkably difficult to census not just because they nest underground, but also because they coexist with other burrowing species and only return to breeding colonies at night (Smith *et al.*, 2001).

The Manx shearwater (*Puffinus puffinus*) breeds across the North Atlantic, with over 90% of the global population on offshore islands around Britain and Ireland (Mitchell *et al.*, 2004). Thorough monitoring efforts for this species commenced with the development of the tape-playback method by James and Robertson (1985), since used in several censuses (Smith *et al.*, 2001; Murray *et al.*, 2003; Perrins *et al.*, 2012). Nevertheless, there remains considerable uncertainty over population size and trends, notably because it remains unclear how to sample individual colonies effectively (Walsh *et al.*, 1995; Mavor *et al.*, 2008). Here, we assess the performance of different sampling strategies across multiple colonies, using data collected from tape-playback surveys, and a bootstrapping approach to determine the levels of variation associated with different subsampling efforts. Subsampling the sampled area allows inference to be made on real data, rather than from simulated or extrapolated abundance estimates. We test the efficiency of a cluster sampling and a multi-stage stratified sampling approach. Cluster sampling groups plots based on the presence or absence of breeding burrows from initial baseline surveys, and sampling is only carried out within areas containing at least one breeding burrow. In multi-stage stratification, the randomly selected plots are stratified by different densities, and sampling occurs within each strata. We then examine the statistical power to detect simulated population changes across two censuses by subsampling variable numbers of plots, which we did for three different simulated declines. In the first instance, our study aimed to inform the design of sampling strategies for obtaining abundance estimates and detecting population declines across national scales. However, it can also inform monitoring trends across any taxa, avian or otherwise, with similar life history and ecological characteristics.

2. Methods

2.1 Tape-playback surveys

Population estimates were obtained from Skomer Island, Wales (2011), and three islands in Ireland; Little Saltee, Co. Wexford (2013), High Island, Co. Galway (2015) and Inishvickillane, Co. Kerry (2016), using tape-playback methods (Figure 1). Surveys were carried out during incubation and early chick-rearing periods (May to June), because the likelihood of a breeding adult being present in the burrow drops sharply once the chick hatches. Playbacks were conducted during the day to minimise the inclusion of non-breeding birds in burrows (Mitchell *et al.*, 2004). Male Manx shearwater calls were played at burrow entrances at a natural volume (ca. 55dB) for three to four call cycles (approximately 15 seconds) or less if an immediate response was received (Smith *et al.*, 2001). Male recordings were used because they are known to elicit a higher number of responses compared to female only calls (Brooke, 1978, Perkins *et al.*, 2017). The recordings used for playback surveys in Ireland were from birds recorded on the Pembrokeshire Islands off Wales, as foreign calls are also known to elicit a higher response rate in other Procellariiformes species (Ratcliffe *et al.*, 1998). This differed on Skomer where the calls used were of birds from the neighbouring island, Skokholm. Response rate corrections were applied at the site level, thus any differences in the calls used during the respective survey efforts have no effect on the analyses here. Across all efforts, sample plots were delineated using ArcGIS (versions 10 - 10.2.2) and visits were randomised in the order in which plots were sampled with tape-playbacks to reduce any temporal bias due to any changes in response rate. When wind conditions were greater than Beaufort force six, tape-playbacks were not carried out to limit the number of potentially missed responses.

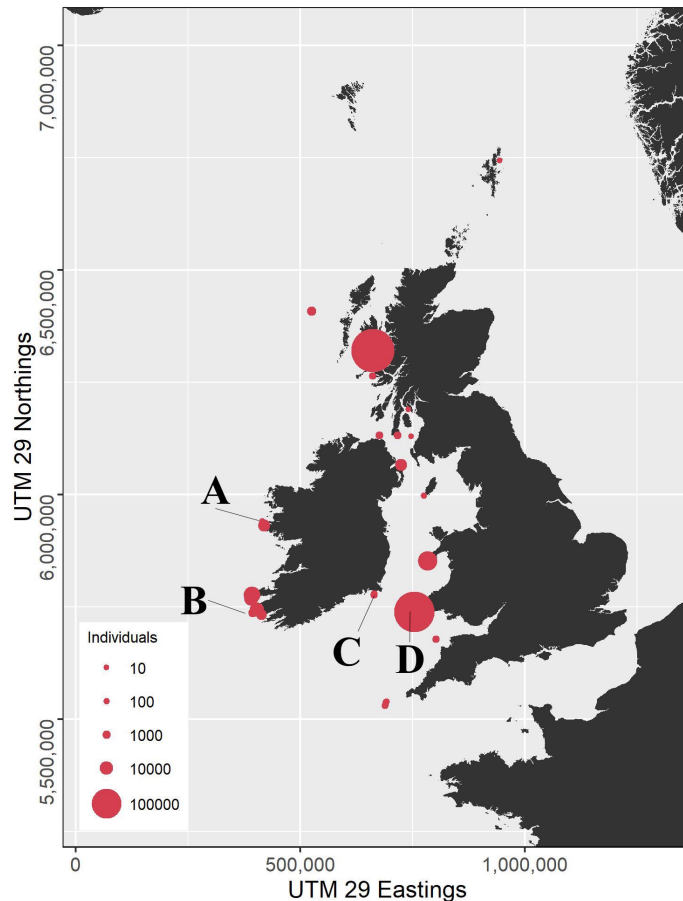


Figure 1. Distribution of Manx shearwater breeding colonies across the British Isles (Critchley *et al.*, 2018). Study sites indicated on the map: (A) High Island, Co. Galway, (B) Inishvickillane, Co. Kerry, (C) Little Saltee, Co. Wexford and (D) Skomer, Pembrokeshire, Wales.

2.2 Abundance Estimates

We used census data available from four study colonies where different sampling strategies had been used, and therefore the posthoc analyses were carried out on each island separately. Abundance estimates were generated using a combination of whole-island counts (Little Saltee; surveyor David Murphy), and sampling using either a random sampling approach (High Island, Skomer (Perrins *et al.*, 2012)), or a clustered approach (Inishvickillane) based on the presence or absence of at least one apparently occupied burrow (AOB). Sampling designs for Skomer and Little Saltee were conceived by the aforementioned surveyors, while the sampling designs for High Island and Skomer were designed throughout the PhD study and driven by the time available to census the islands. Time constraints associated with access to Inishvickillane warranted the clustered design, whereas

on High Island sampling across the entire island was possible. The whole island survey on Little Saltee covered 100% of the workable area, approximately 38%, 16% and 3.5% of the total island workable area was sampled on High Island, Inishvickillane and Skomer respectively. To determine the total number and distribution of burrows across High Island and Inishvickillane, parallel transects 50 metres apart were carried out in a north-south direction across the entire island. Sample plots on High Island were 30m x 30m within each 50m x 50m grid square, while on Inishvickillane sampling used circular plots with a radius of 5.7m within 25m x 25m plots (Figure 2 (A & B)). Sampling across Little Saltee was carried out in rectangular plots of 50m x 10m. Specifically, plots that were inland were sampled using rectangular plots lying parallel to one another spanning the entire grid square. Plots next to the coast used belted transects to follow the coastline. The combination of the two allowed whole-island sampling which we are confident incorporated all of the breeding population (Figure 2 (C)). Methods used to calculate the population size on Skomer Island involved carrying out tape-playbacks in circular sampling plots with a radius of 10m in the centre point, or as near as safely possible, of predefined 100m x 100m grid squares across the island (Figure 2 D; see Perrins *et al.* 2012).

Previous studies that used sampling approaches to estimate population size multiply the total number of responses by a correction factor of 1.98 to correct for the fact that occupied burrows respond approximately 50% of the time (Brooke, 1978). We calculated colony-specific response rates for High Island, Inishvickillane and Skomer by visiting burrows that were known to be occupied multiple times (30 AOBs on High Island, 4 times; 76 AOBs on Inishvickillane, 9 times; 33 AOBs on Skomer, 8 times). No local response rate was calculated for Little Saltee, the average response rate from other Irish colonies recorded during Seabird 2000 were used in its place (Mitchell *et al.*, 2004). Visits were separated by at least 24 hours to reduce playback habituation and we assumed that response rate did not change with time of day (see Perkins *et al.*, 2017).

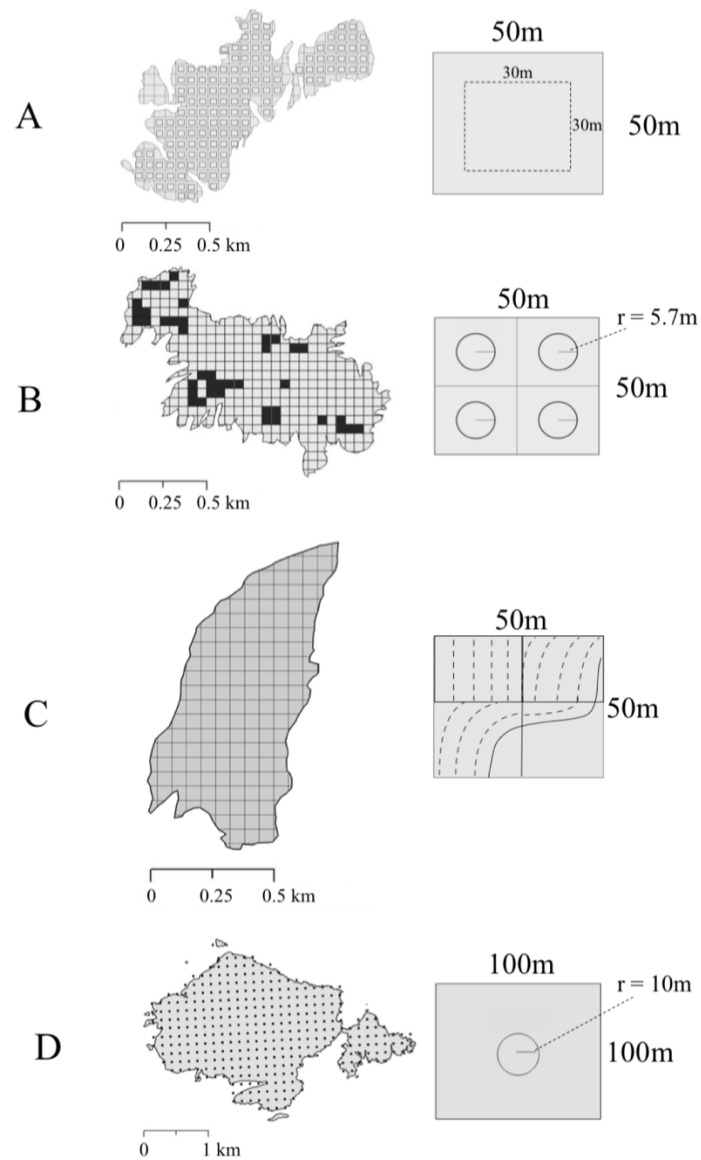


Figure 2. Schematic outlining the sampling strategies used during playback surveys of (A) High Island, Co. Galway, (B) Inishvickillane, Co. Kerry, (C) Little Saltee, Co. Wexford and (D) Skomer Island, Pembrokeshire, Wales. The black squares in B indicate the 50x50m plots that had at least one burrow present.

2.3 Sampling effort and population estimates

We emphasise that, in this heuristic exercise, the total area sampled for each island is treated as a population; thus the abundance estimates reported here are for the area sampled on each island, not extrapolated estimates for the entire island. This is valid as the plots were sampled randomly. To illustrate the variation in subsampling efforts using random, clustered and multi-stage stratified ('stratified') approaches, bootstrap analyses were carried out using the statistical software 'R' version 3.3.2. Random sampling involved subsampling from all plots within a site. In the clustered approach, indicative of sampling when presence or absence is known in an area, subsamples were taken only from sampled plots in which at least one AOB was found. In the stratified approach, which is relevant where repeat census efforts are conducted with a known baseline breeding distribution *a priori*, the plots were stratified for four quantiles (0-25%, 25-50%, 50-75% and 75-100%) of plot density, and proportionately subsampled within each strata. Bootstrap resampling was carried out in 10% increments from 10% to 100% of all plots; thus for these approaches, 10% is 10% of the total sampled plots, not 10% of the entire island's area. Resampling was repeated 10,000 times, the means of all bootstrapped subsamples approximate the actual abundance due to the large number of iterations. Levene's test for equality in variances was used across all bootstrapped samples to compare across sampling approaches. It's important to note that although a clustered design was used on Inishvickillane (discussed in section 2.2), random bootstrap sampling was still possible as not all plots within the larger 50x50m grid squares contained breeding burrows.

2.4 Detecting population change

Power analyses were used to assess how effective subsampling plots would be at detecting different simulated declines in population density across two census efforts. This was carried out using three different simulations of population decline: (1) where there was a decline across the entire colony, plot-specific declines were applied in a normal distribution centred around a 10, 20, 30, 40 and 50% overall population decline and the monitoring plots are selected at random; (2) where there was a decline in high-density areas only and the monitoring plots are selected at random, simulating for example, the destruction of favourable

habitat or the introduction of a disease with density dependent transmission (e.g. Descamps *et al.*, 2012). In simulation 2, the top 25% densest plots were subject to normally distributed simulated declines, producing overall population change in increments of 10% up to 50%. In simulation (3), declines were simulated in a normal distribution across all plots, and the selection of monitoring plots was restricted to the areas of highest density (top 25%) in a clustered approach. Many existing monitoring programmes of burrow-nesting species sample <50 plots (Rodway *et al.*, 1996; Stubbings *et al.*, 2015); thus, we calculated the statistical power associated with sampling 10-50 plots, in increments of 10. To show the statistical power associated with the different simulated declines and subsampling efforts, the packages “effsize” and “pwr” were used in the statistical software ‘R’ (version 3.3.2). The package “pwr” uses Cohen’s *d* effect size (Cohen, 1988) that was calculated for the simulated declines in “effsize”. The 95% confidence intervals of statistical power are reported here to demonstrate the precision of the power associated with each simulation.

3. Results

3.1 Abundance estimates and bootstrapping

A total of 5,183 responses were elicited from playbacks on 21,756 burrows across all study sites over the four censuses. The number of responses and playbacks conducted on High Island, Inishvickillane, Little Saltee and Skomer were: 176/1,599; 224/1,254; 308/5040 and 4,475/13,863 respectively. Local response rates were calculated at $0.55 \pm \text{SE } 0.07$, $0.49 \pm \text{SE } 0.03$ and $0.403 \pm \text{SE } 0.025$ on High Island, Inishvickillane and Skomer respectively. The actual abundance estimates (AOBs) for the area sampled on each island are represented by the broken red line in Figure 3.

Abundance estimates obtained from the bootstrapping analyses across different sampling efforts for the different sampling approaches are shown in Figure 3. As expected, increasing sampling area led to narrower ranges in the bootstrapped abundance estimates for all study sites (Figure 3). Levene’s test for equality in variances showed a clear advantage of clustered and stratified sampling approaches over random sampling; results for each comparison are outlined in

Table 1. Comparing random and clustered sampling approaches, all comparisons for both Little Saltee and High Island produced statistically significant ($p < 0.001$) differences, with less variation in the estimated abundances when using clustered approaches. A similar result was found for Inishvickillane apart from one comparison at 30% sampling. Skomer had fewer significant differences, with two sampling levels showing no statistically significant ($p > 0.05$) difference in variance (see Figure 3 and Table 1(i)). Comparing random and stratified approaches showed that all comparisons across all sites revealed a significant ($p < 0.001$) reduction in variance (see Table 1 (ii)). Thus, the stratified approach proved the most effective at reducing the variance in bootstrapped estimates.

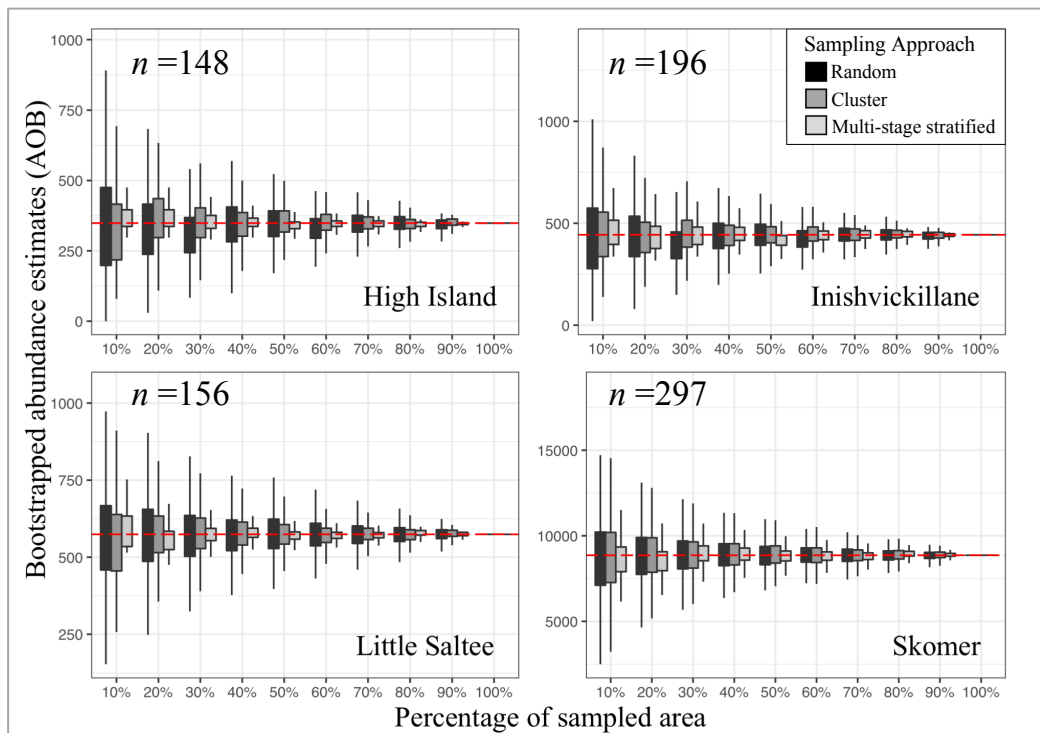


Figure 3. Bootstrapping tape-playback abundance estimates of the sampled area on four Manx shearwater colonies in Ireland and Wales. Boxplots show the range of bootstrapped abundance estimates associated with random sampling, clustered sampling, and multi-stage stratified sampling in plots of different densities defined by the quartiles. The boxes contain the middle 50% of abundance estimates while the whiskers contain the upper and lower 25% of the abundance estimates. The broken red line represents the actual abundance of the entire area sampled (not equating to the entire colony).

Table 1. Levene's test comparing the variance in the range of bootstrapped abundance estimates of Manx shearwaters breeding on four islands off of Ireland and Wales between (i) random and clustered sampling approaches and (ii) random and stratified sampling approaches. Both the F-statistic and p value are reported here, outlining the significance of the differences between the variances in the abundance estimates. The significant difference corresponds to lower variability in clustered and stratified approaches compared to random sampling.

% Area	High Island		Inishvickillane		Little Saltee		Skomer	
Sampled	F	p	F	p	F	p	F	p
<i>(i) Random vs. Clustered</i>								
10%	84.29	<0.001	47.6	<0.001	35.51	<0.001	3.92	0.047
20%	42.86	<0.001	65.11	<0.001	106.67	<0.001	2.99	0.083
30%	17.36	<0.001	7.58	0.001	132.95	<0.001	8.81	0.003
40%	82.82	<0.001	63.73	<0.001	86.91	<0.001	5.99	0.01
50%	65.88	<0.001	74.02	<0.001	157.39	<0.001	4.33	0.038
60%	35.47	<0.001	35.57	<0.001	154.3	<0.001	1.07	0.3
70%	85.9	<0.001	22.61	<0.001	127.23	<0.001	6.34	0.012
80%	88.04	<0.001	63.1	<0.001	131.97	<0.001	5.68	0.017
90%	90.59	<0.001	13.45	<0.001	125.24	<0.001	7.71	0.005
<i>(ii) Random vs. Stratified</i>								
10%	5973.5	<0.001	1126.6	<0.001	3372.9	<0.001	1153.5	<0.001
20%	5461.5	<0.001	1003	<0.001	4446.4	<0.001	1165.2	<0.001
30%	4750.8	<0.001	1173.4	<0.001	4638.9	<0.001	1104.1	<0.001
40%	6351.5	<0.001	1448.6	<0.001	3787.8	<0.001	1063.2	<0.001
50%	5673.9	<0.001	1643.7	<0.001	4917.5	<0.001	1051.1	<0.001
60%	5148.8	<0.001	1359.8	<0.001	4855.2	<0.001	1094	<0.001
70%	6120.6	<0.001	1328.1	<0.001	4410.8	<0.001	968.4	<0.001
80%	5775.6	<0.001	1771.6	<0.001	4977.8	<0.001	1106.4	<0.001
90%	5491.8	<0.001	874.3	<0.001	4711	<0.001	1211	<0.001

3.2 Power to detect population decline

In simulation 1, where the simulated declines were across all plots and monitoring plots were randomly selected, statistical power changed with sampling effort in a similar way across the four study sites (Figure 4). Ability to detect declines in population density was high (above 0.8) only when >20 plots were sampled and the decline was 30-50%. The statistical power to detect a 30% decline, for example, requires at least 30 plots to be sampled to ensure a high degree of confidence in the statistical power to detect the change. The confidence in these power estimates increased substantially with the number of plots sampled when declines of 20% or more were simulated. However, power to detect a 10% decline in the population requires considerably greater sampling effort as confidence intervals remain large at 50 plots, this was true across all sites.

In simulation 2, where the simulated declines occurred in a density dependent manner and where monitoring plots potentially came from all plots, the ability to detect population declines with a high degree of confidence was lower across all sites than in simulation 1 (Figure 5). Similarly, we see a slight increase in statistical power with increased sampling effort, yet the 95% confidence intervals remain large across all sampling efforts.

Simulation 3 shows the statistical power associated with subjectively placing monitoring plots within the most-densely burrowed areas and a simulated decline across all plots identical to that of simulation 1. The ability to detect a population decline was significantly improved compared to simulations 1 and 2, this was true across all sites (Figure 6). Here we demonstrate that fewer plots, located in the top 25% of densely burrowed areas, are needed to attain high statistical power with a high degree of confidence.

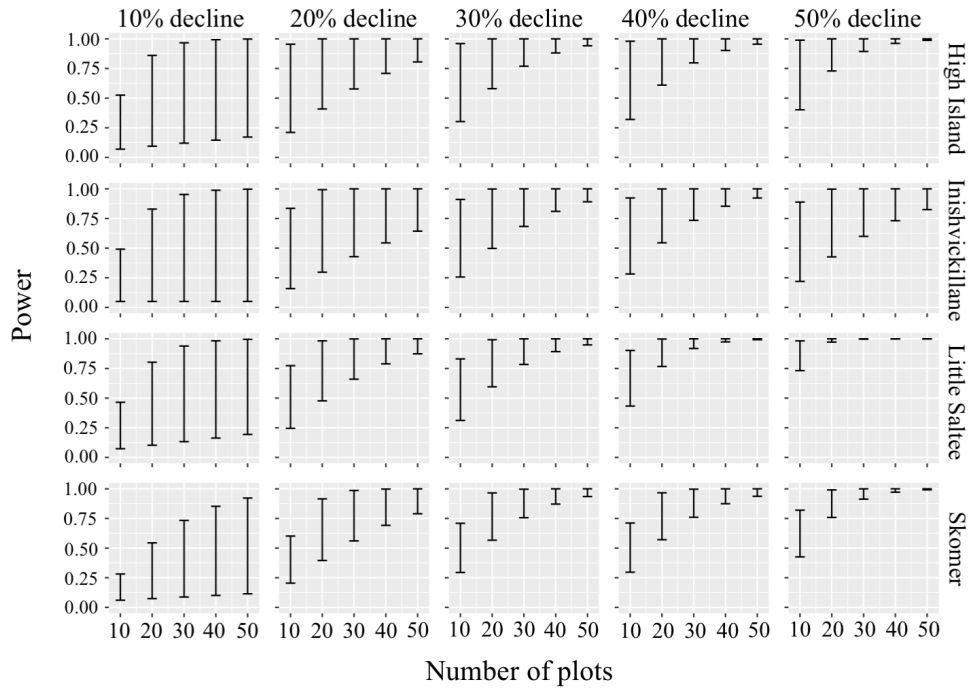


Figure 4. The statistical power (95% confidence intervals) to detect simulated population declines of Manx shearwaters in all plots, not specific to any factor such as density or habitat, across different subsampling efforts on the areas actually sampled at four study sites.

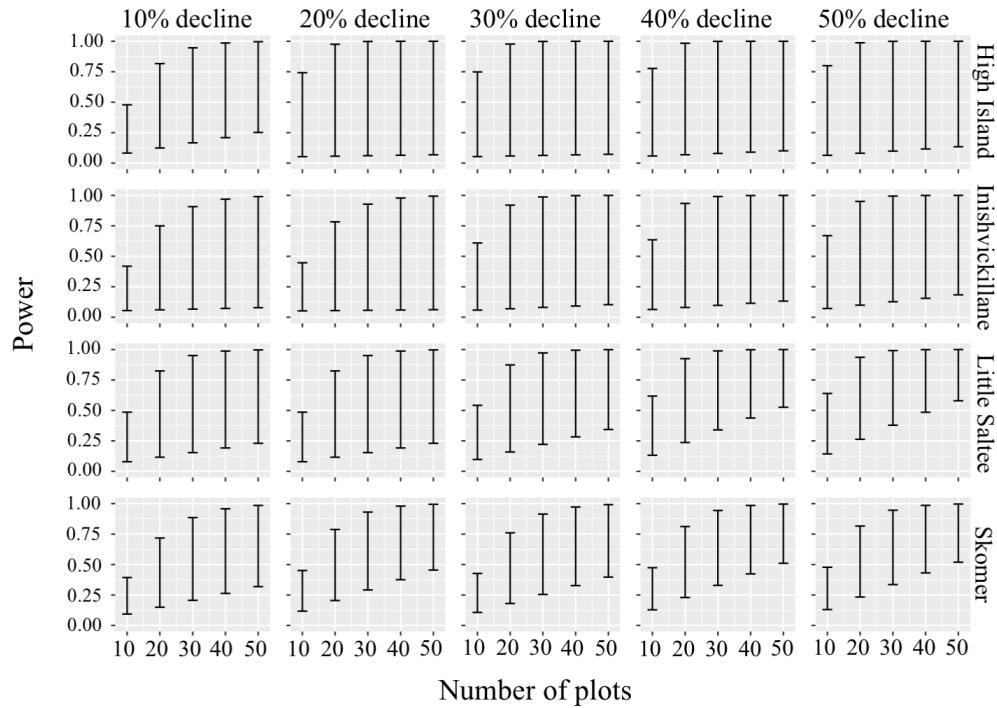


Figure 5. The statistical power (95% confidence intervals) of different subsampling efforts to detect simulated population declines of Manx shearwaters varying from 10-50% of the total population. Declines were simulated in a density dependent manner, simulating for example catastrophic causes of failure within colonies (e.g. disease or habitat loss) across four different study sites.

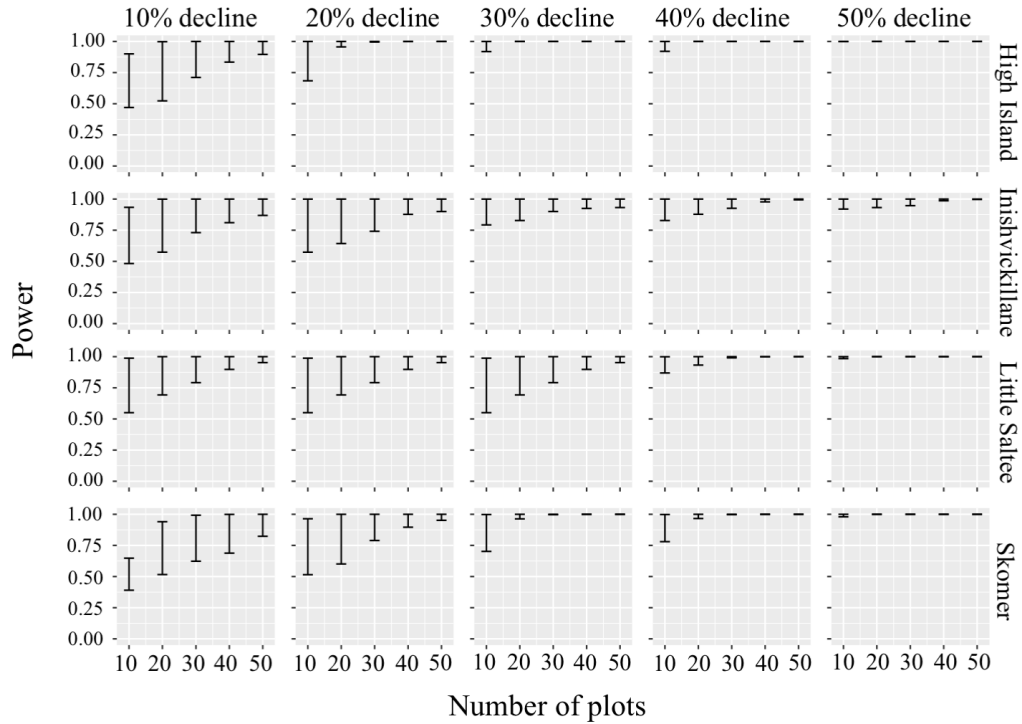


Figure 6. The statistical power (95% confidence intervals) of different sampling efforts to detect simulated population declines of Manx shearwaters varying from 10-50% of the total population. Simulated declines were not specific to any factor such as density or habitat, however monitoring plots were subjectively placed in the most densely-burrowed areas (upper 25%).

4. Discussion

We outline the uncertainty around extrapolated population estimates using three different sampling strategies on empirical data, demonstrating the clear advantage of the use of cluster and stratified sampling over random sampling approaches. Our findings illustrate that many current monitoring efforts are likely failing to detect changes in population densities as the random selection of monitoring plots reduces our ability to definitively detect declines. Finally, our findings suggest that monitoring efforts should be adapted to focus on areas of highest density to detect change.

4.1 *Subsampling for abundance estimates*

We heuristically treated the samples in our analyses as if it were the entire island. Increased subsampling effort across all sampling strategies reduced variation in, and thus increased our confidence in, abundance estimates. This emphasises that relying on low sampling efforts increases uncertainty around population estimates. The clustering approach reduces this uncertainty, and can be applied where preliminary scoping work has been carried out to determine the presence or absence of breeding birds across all potential plots on the island. The effectiveness of this clustering approach, however, is determined by the distribution of the colony. Where many of the plots sampled on High Island contained no AOBs, clustering had a large impact, whereas most plots on Skomer contained at least one AOB and clustering had little effect. Thus, cluster sampling is most effective in colonies where the breeding birds are aggregated and patchily distributed.

On the other hand, stratification dramatically increased confidence in the estimates for all colonies. Two points are relevant with respect to the approach we took and its general applicability. First, typically in ecology, stratified sampling is not multi-stage stratification, and sampling is typically carried out in defined strata across geographical space (e.g. habitat fragments, distance from the coast). However, the approach we took here is likely a reflection of habitat type, as the patchy distribution of burrow-nesting species is largely determined by the quality and availability of suitable breeding habitat (Rayner *et al.* 2007; Krüger *et al.*, 2017). Second, multi-stage stratification based on density is only possible where previous whole island efforts have been carried out to establish the distribution and density of breeding birds. We suggest this approach is valid for repeat census efforts in species, such as the Manx shearwaters, that show high nest site fidelity from year to year, and when habitat changes that could alter the nesting distribution are readily observed through habitat assessments. Although some of the most obvious examples of such species come from birds (seabirds, waterbirds), in principle this should apply across all animal taxa where site fidelity is the norm (Jackson *et al.*, 2008; Cordes and Thompson, 2015), and across all perennial plants (Freckleton and Watkinson, 2002).

Much of the literature on seabird census methods outlines that the increased complexity of the study design required to obtain reliable population estimates is associated with higher costs. Our results show that low sampling efforts carried out in a random manner are unlikely to generate reliable abundance estimates. However, the difference between the random approach and the stratified approach clearly favours a stratified method. Further work is needed to understand the most efficient and realistic way of stratifying sample plots. This has been briefly discussed in Perrins *et al.*, (2012), where they demonstrated that apportioning sampling plots into two groups, coastal and inland areas, was effective on Skomer. However the effectiveness of this simple clustering is likely to vary across sites and further work is required to identify the habitat and topographical features that determine the distribution of burrows. These have been explored in other burrow-nesting seabird species (Scott *et al.*, 2009; Krüger *et al.*, 2017), but to date no study has looked at this for Manx shearwaters (but see Arneill *et al.*, 2018 - Chapter 3).

4.2 Power Analyses

In much of the literature, statistical power is examined over a time series, reporting high power to detect low annual percentage declines (ca. 1% -10%) over periods of typically 5-50 years (e.g. Hatch, 2003; Sims *et al.*, 2006). These studies are largely focused on cliff and ground nesting species, with the aim of estimating the duration of study required to detect specific annual rates of change, when island-wide counts are attainable across years. However, national censuses, and for many burrow-nesting species, even colony censuses, typically occur much less frequently. In Britain and Ireland these occur every 10-15 years and few intensive monitoring programs are in place. Thus, conclusions on the trends breeding populations are drawn from very few data points separated by a long period of time (Mitchell *et al.*, 2004; Mavor *et al.*, 2008). Similarly, monitoring efforts after a specific event such as habitat loss or the introduction of invasive predators may necessitate comparing, and drawing conclusions from, two data points. These attempts to quantify population level change from randomly selected plots have previously failed to produce any meaningful conclusions on population level changes (Thompson and Thompson, 1980; Thompson, 1987). The power analyses reported here indicated, with random sampling, the ability to detect declines in density across two years is hindered by the variation in plot densities. This was

especially true in simulation 2, where the random selection of plots combined with the restriction of declines to areas of higher density, increased the 95% confidence intervals of statistical power. Worryingly, simulation 2 may be a more realistic representation of density declines within colonies (Ryan, 1993; Descamps *et al.*, 2012) and therefore is most illustrative of the problem associated with the random selection of monitoring plots.

Simulation 1 and 2 show that randomly selected plots, that are not representative of the density and variation in the colony as a whole, limit our ability to detect population level change. Thus, when monitoring programs use a sampling design set out to determine the overall magnitude of population change, the program's efficacy is determined by how representative those plots are of the population as a whole (Ankler Nilson and Røstad, 1993). Our analyses show that an enormous proportion of the colony would need to be resurveyed to account for spatial variation in density, a feat that is not logistically and economically feasible for many wildlife monitoring programmes limited in resources. To overcome this issue in burrow-nesting seabirds, we show that subjectively distributing monitoring plots in areas of high density increases statistical power to detect modest changes by removing the enormous, variance-inflating effect of low density plots. Additionally, the densest plots contained the majority of breeding birds due to the patchy distribution of breeding burrows, that is likely driven by favourable breeding habitats. For High island, Inishvickillane, Little Saltee and Skomer; the top 25% of plots contained approximately 58%, 60%, 42% and 46% of the population respectively.

Our findings suggest that intense baseline survey efforts are needed to establish monitoring plots in areas of high density to increase the statistical power to detect population declines. By restricting monitoring to plots of higher density, the monitoring approach will sacrifice the ability to detect population expansion in newly established areas. This is noted in other taxa, such as marine turtles, where static monitoring programs have failed to detect expansion in breeding sites (Jackson *et al.*, 2008). Furthermore, the restriction of sampling to areas of highest density could mean other density dependent processes that effect areas of low density could be missed as sampling is not representative. However, as demonstrated in our analyses, the effort required to detect population level changes

in distribution is beyond the scope of the resources of many conservation programmes. This restriction of sampling efforts to areas of highest density to detect declines is appropriate from a conservation perspective. This prioritisation of detecting decline is outlined in other seabird studies (Sims *et al.*, 2006; Rodway and Lemon, 2011), with the recommendation that whole-island surveys are carried out at least every 5 years to ensure the monitoring plots are objectively placed according to the colony's distribution. These conclusions are not solely pertinent to tape-playback efforts on burrow-nesting seabirds; the same conclusions apply to other species and methods where the variation in density of monitoring plots will largely determine the power to detect population changes. To adhere to the conclusions of the analyses carried out here, considerable effort is required to obtain baseline estimates of the population with a high level of confidence when surveying colonies such as Skomer. Moreover, the amount of effort required to obtain both a reliable abundance estimate and to optimally select monitoring plots of high density is dependent on the size of the colony.

4.3 Conservation implications

It has been suggested that for effective conservation, efforts should aim to conserve approximately 60-80% of a species baseline population, making accurate baseline population estimates of great importance (USFWS, 1992; Hatch, 2003). Furthermore, the variation around abundance estimates must be sufficiently small to detect an acceptable change in population density over time. This study suggests that random selection of monitoring plots, irrespective of colony size and distribution, will likely fail to detect modest population changes due to the enormous influence of plots that vary in density. Additionally, some standardised assumptions and methods should be made to correct for other sources of error involved in tape-playback surveys, such as the type of calls used during playback surveys, spatial variation in phenology, size of sampling plots and temporal variation in response rates. Thus a common set of methods should be established that (a) are simple in execution and (b) use sampling approaches with consideration of the key issues raised in this paper. At the global population level, seabird monitoring programs should have a set goal of creating standardised approaches that allow comparable datasets to assess the impact of future

perturbations, including resource patch use and climate scenarios on seabird populations at large scales.

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Chapter 3

Species distribution models accurately predict the breeding distribution of three burrow-nesting seabird species

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Abstract

Species distribution models (SDMs) can provide valuable insight into species' relationships with environmental gradients, aiding conservation by identifying key habitats for vulnerable populations. Here, we use population distribution and habitat surveys in combination with digital elevation models to produce ensemble SDMs for three burrow-nesting seabirds; Manx shearwater (*Puffinus puffinus*), Atlantic puffin (*Fratercula arctica*) and European storm petrel (*Hydrobates pelagicus*). Ensemble models combined classification tree analysis (CTA), flexible discriminant analysis (FDA), generalised linear models (GLM) and multivariate adaptive regression splines (MARS) to identify important predictor variables for each species. The predictive accuracy of constructed models was determined using cross validation, data-split training, and Area Under Curve (AUC) evaluation metrics. Accuracy was high across all models, but ensemble models performed better than all single-algorithm models for each species. Habitat type was one of the most important predictor variables for all species. Predictive topographical variables varied slightly across species, with elevation, slope, flow drop and distance from the coast in general contributing the most across the ensemble models. The accuracy of the ensemble SDMs provides a robust

methodology for predicting the breeding distribution of difficult to census species, and will aid in the prioritisation of census efforts.

Keywords: Burrow-nesting seabird, Census, Digital Elevation Models, Habitat, Seabirds, Species distribution models

Introduction

Understanding the relationship between an organism and its environment is one of the primary objectives in ecology, and is becoming increasingly important due to climate change, the continued expansion of invasive species, and the intensification of anthropogenic land use (Baxter and Possingham, 2011; Croxall *et al.*, 2012; Russell *et al.*, 2015). Gradients in biotic and abiotic factors that create microclimatic conditions have been shown to act as central driving factors in the spatial distribution of both plants and animals (Chen *et al.*, 1999; Peterman and Semlitsch, 2013). In recent decades, the ability to explore these relationships and predict distributions of species across the environment has advanced significantly (Guisan *et al.*, 2013; Espinoza *et al.*, 2014; Golding and Purse, 2016) leading to the production of powerful species distribution models (SDMs) across a range of spatial scales (Oppel *et al.*, 2012; Torres *et al.*, 2015, Scales *et al.*, 2015).

The principal use of these SDMs is highlighted in studies that inform conservation measures for the protection (Lavers *et al.*, 2014; Warwick-Evans *et al.*, 2016) and monitoring of breeding populations (Peterman and Semlitsch, 2013; Mędrzycki *et al.*, 2017). Such predictive modelling is based upon (a) datasets that contain at least presence data of species (sometimes both presence and absence) and (b) the assessment of the habitat conditions in which the species were most abundant (Phillips *et al.*, 2006). The main aim is to use the relationship between fine-scale environmental gradients, species' abundance, and population dynamics to project predicted abundance patterns across the geographical area to be studied (Grecian *et al.*, 2012; Fithian *et al.*, 2015). Recent work aims to further improve SDM methods, for example, the selection of any single-algorithm modelling approach has been shown to influence the resulting predictions (Oppel *et al.*, 2012; Scales *et al.*, 2015; Quillfeldt *et al.*, 2017). In the last decade, model averaging techniques

have been adapted to create ensemble SDMs that overcome this problem (Thuiller *et al.*, 2009; Grenouillet *et al.*, 2011).

SDMs have a role to play in reducing the amount of time and thus the cost associated with obtaining baseline information about populations, particularly when models can be created with reasonable accuracy for species that are cryptic, wide-ranging or inaccessible (Lavers *et al.*, 2014; Krüger *et al.*, 2017). Seabirds are amongst the highest profile species of conservation concern, are widely accepted to be key indicators of the largest biome, and have shown substantial declines in breeding populations (Grémillet and Charmantier, 2010; Croxall *et al.*, 2012; Paleczny *et al.*, 2015). Many seabird species present a major challenge in census efforts due to their life-history characteristics, the inaccessibility of the breeding colonies and diurnal activity patterns.

One seabird group that has proved to be the most difficult to census are the burrow-nesting species (Walsh *et al.*, 1995; Smith *et al.*, 2001; Mitchell *et al.*, 2004; Opper *et al.*, 2014). Censusing burrow-nesting species is challenging because of the amount of field time required to estimate burrow occupancy (Perrins *et al.*, 2012), their co-existence with other burrowing seabird and mammalian species (Smith *et al.*, 2001), inconsistency in the methods used across censuses due to technological advances (Mitchell *et al.*, 2004), and because many species are nocturnal at the colony. Several factors are known to determine the quality of nesting habitat for some burrow-nesting species including pedological characteristics (Bancroft *et al.*, 2005; Whitehead *et al.*, 2014) and the introduction of mammalian predators (Buxton *et al.* 2015). Thus, the creation of SDM's that can utilise previous knowledge to best predict the distribution of these species in their remote breeding grounds would identify key habitats for these breeding populations. These predictions can aid future sampling efforts using stratified approaches that have been shown to greatly reduce the amount of sampling required to estimate abundance, while increasing the accuracy of results when compared to a random sampling approach (Wimmer *et al.*, 2013; Arneill *et al.*, 2018 – Chapter 2).

Here we assess the efficacy of predictive species distribution modelling for three burrow-nesting seabirds: the Manx shearwater (*Puffinus puffinus*), the Atlantic puffin (*Fratercula arctica*) and the European storm petrel (*Hydrobates pelagicus*)

using data available from population surveys on several offshore islands around the British Isles. The aim of this study was to describe the fine-scale environmental features and gradients that drive the abundance patterns of these species, and to develop a model that can predict their distribution. This study represents the first comprehensive test of ensemble SDMs across multiple sites and species, and intends to highlight the utility of simple habitat assessment when designing sampling effort for difficult to census species.

Methods

Census efforts

Tape-playback census methods (James and Robertson, 1985) were carried out across a total of seven offshore islands around the British Isles (Figure 1). Manx shearwaters were censused on six islands, and European storm petrels on three islands. Density estimates were generated using a combination of whole-island counts (Little Saltee, Beginish), and sampling using either random sampling approaches (High Island, Inishmurray, Great Saltee, Skomer), or a clustered approach (Inishvickillane) based on the presence or absence of at least one apparently occupied burrow (AOB) (see Table 1). Logistical constraints at each site necessitated different intensity and design of sampling efforts, so all resulting densities were standardised to estimates of the number of breeding pairs within 50m x 50m grid squares. For some study sites this represents an extrapolated estimate because areas were subsampled. Where possible, local call response rates were applied to islands in order to increase accuracy. No local response rate was calculated for Little Saltee and Great Saltee, thus the mean response rate from Irish colonies calculated during Seabird 2000 surveys (Mitchell *et al.*, 2004) was used in its place. The absence of breeding burrows on Beginish meant that no playbacks could be conducted to obtain a local response rate at this site.

To obtain population size estimates for Atlantic puffins, observational counts across multiple visits were carried out at six island colonies (High Island, Beginish, Inishvickillane, Great Saltee, Little Saltee and Ireland's Eye) following the protocol outlined in Walsh *et al.* (1995). Counts were carried out as early in the breeding season as logistically possible (April-June) because the number of non-

breeding and prospecting birds is known to increase later in the breeding season (Mitchell *et al.*, 2004). To reduce potential observer error in the density estimates, counts were carried out by two observers, with birds rafting on the water recorded as far as they could be accurately identified using binoculars (ca. 300m). To account for any potential time of day effects, where possible three counts were carried out per day between 06:00 – 09:00, 11:00-14:00 and 18:00-21:00. The density estimates used in the production of SDMs are the highest recorded counts of individuals observed on land during the surveys, as models were constructed using data that does not extend beyond the coastlines and using the highest count minimises the proportion of individuals that were missed during a single count (Walsh *et al.*, 1995; Miles *et al.*, 2015).

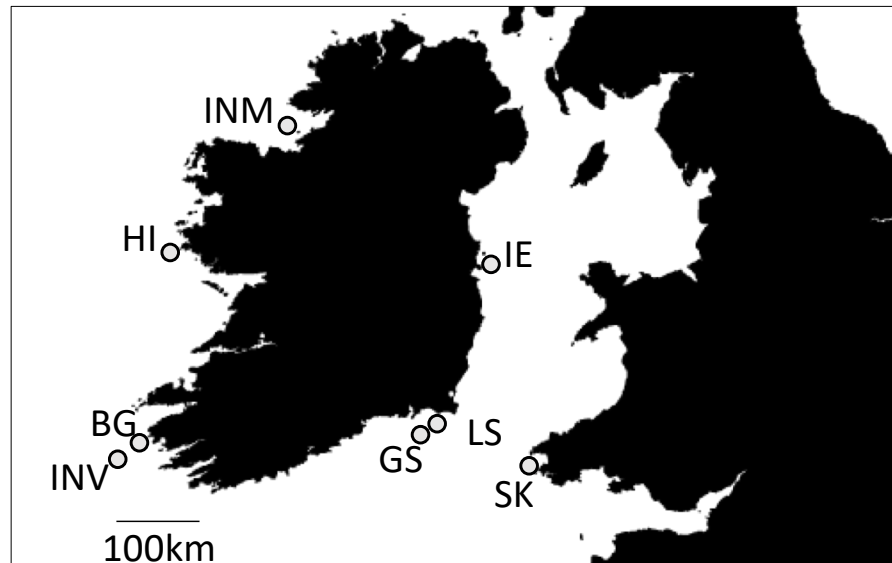


Figure 1. Location of colonies on which survey data was collected for Manx shearwater, Atlantic puffin and European storm petrels across the British Isles. For Manx shearwaters: High Island (HI), Beginish (BG), Inishvickillane (INV), Great Saltee (GS), Little Saltee (LS) and Skomer (SK). For Atlantic puffins: High Island (HI), Beginish (BG), Inishvickillane (INV), Great Saltee (GS), Little Saltee (LS) and Ireland's Eye (IE). For European storm petrels: Inishmurray (INM), High Island (HI) and Beginish (BG).

Table 1. Census efforts used to determine density estimates used in the construction of ensemble species distribution models for Manx shearwaters (*Puffinus puffinus*) and European storm petrels (*Hydrobates pelagicus*) across all sites.

Study Site:	Skomer, Pembrokeshire	Little Saltee, Co. Wexford	Great Saltee, Co. Wexford	High Island, Co. Galway	Beginish, Co. Kerry	Inishvickillane, Co. Kerry	High Island, Co. Galway	Beginish, Co. Kerry	Inishmurray, Co. Sligo
Species:	Manx shearwater	Manx shearwater	Manx shearwater	Manx shearwater	Manx shearwater	Manx shearwater	European storm petrel	European storm petrel	European storm petrel
Study Year	2011	2013	2014	2015	2016	2016	2016	2016	2017
Study Period	4 th June – 15 th June	20 th May – 6 th July	4 th June – 13 th July	25 th May – 11 th June	23 rd July – 27 th July	7 th May – 15 th June	17 th July – 11 th August	27 th July – 30 th July	25 th July – 30 th July
Sampling Approach	Random	Random	Random	Random	Random	Clustered	Random	Random	Clustered
Sampling method	Circular plots (314m ²)	Transects (50m x 10m)	Quadrats (50m x 50m)	Quadrats (30m x 30m)	Burrow survey Transects (50m x 4m)	Circular plots (100m ²)	Transects (50m x 4m)	Transects (50m x 4m)	Transects (50m x 4m)
Response Rate	0.403 (± 0.03)	0.44 (± 0.1)*	0.44 (± 0.09)	0.55 (± 0.068)	N/A ⁺	0.49 (± 0.03)	0.56 (±0.154)	0.56 (±0.035)	0.58 (±0.02)
<i>n</i> of AOB/AOS on which response rate was measured	33	Not calculated	Not calculated	30	Not calculated	76	30	30	92
<i>n</i> of repeated measures of response rate	8	Not calculated	Not calculated	4	Not calculated	9	21	3	3
Area of whole island sampled (%)	3.5%	100%	7%	38%	100%	16%	11%	100%	14%
Total area of island (Hectares)	Approx. 334	Approx. 37	Approx. 89	Approx. 42	Approx. 14	Approx. 83	Approx. 42	Approx. 14	Approx. 90
	*average response rate from Seabird 2000 (Mitchell <i>et al.</i> , 2004) ⁺ no burrows present, included in models as it represents true absence data.								

Habitat and topographical data

The densities and distributions of all Manx shearwater, Atlantic puffin and European storm petrel colonies were collated into a raster grid dataset of 50m x 50m across each study site. Habitat surveys were carried out during census efforts using the DAFOR (Dominant, Abundant, Frequent, Occasional and Rare) scale as outlined in Fossitt (2000) on Great Saltee, Little Saltee, High Island, Inishvickillane, Ireland's Eye, Beginish and Inishmurray. Here this was used to define the habitat within each grid square, allowing habitats with similar DAFOR characteristics to be grouped as categorical variables. Features such as stone walls, ruins and waterbodies within grid squares were noted in the form of binary covariates. Skomer's habitat data was mapped using a combination of field data and aerial photographs on ArcGIS. Habitat data was projected in the form of a raster dataset of 50m x 50m grid squares comparable to that of the density and distribution of each species. Stone walls and rocky outcrops were mapped incorporating observations from aerial photographs, archived Ordnance Survey Ireland (OSI) maps, and field observations. High resolution Digital Elevation Models (DEMs) were produced for each island using elevation data (sampled at 1 arc-second resolution, or approximately every 30 meters) from NASA's freely available Shuttle Radar Topography Mission (SRTM). DEMs were used to calculate topographical parameters including slope, aspect, flow length and flow drop for each grid square using Spatial Analyst in ArcGIS (10.6 ESRI Inc, USA). In addition, the shortest distance from the center of each cell to the island coastline was calculated.

Table 2. Description of the habitat types, one of the highest scoring predictor variables in ensemble models across all species.

Habitat index	Habitat Description
1	Bluebell (<i>Hyacinthoides non-scripta</i>) and red campion (<i>Silene dioica</i>) dominated areas.
2	Bog and waterlogged grassland
3	Boulder Beach
4	Open vegetation dominated (>50%) by bracken (<i>Pteridium aquilinum</i>).
5	Dry heath tussock grassland
6	Heather dominated upland habitat.
7	Areas of exposed rock, no top soil.
8	Dry calcareous and neutral grassland with rocky outcrops
9	Scree
10	Sea campion (<i>Silene uniflora</i>) dominated areas
11	Sea pink (also known as sea thrift, <i>Armeria maritima</i>) dominated area
12	Both sea campion (<i>Silene uniflora</i>) and sea pink (<i>Armeria maritima</i>) present in approximately equal densities
13	Coastal cliff habitat: exposed rock (>50%) with ledges that may support salt-tolerant plants such as sea pink (<i>Armeria maritima</i>).

Modelling methods

Several species distribution models including classification tree analysis (CTA), flexible discriminant analysis (FDA), generalised linear models (GLM) and multivariate adaptive regression splines (MARS) were generated using the ‘biomod2’ package in R (Thuiller *et al.*, 2016). The use of biomod2 allows the construction and comparison of both single-algorithm and ensemble models. Model performance was assessed by the goodness of fit (explanatory power) and model accuracy (predictive power), as a default the package governs model selection by filtering models that have a true skill statistic (TSS) score lower than 0.7. To further interpret the models’ predictive accuracy, data were split into training and test datasets (80:20) multiple times to allow quasi-independent sensitivity tests that assess the models performance to changes in initial conditions (Thuillier *et al.*, 2009). In biomod2 collinearity among covariates was removed by dropping correlated covariates that had the least contribution to both single-algorithm and ensemble models. Spatial autocorrelation was assessed using

Mantel tests in the statistical software R and addressed using the block cross-validation method outlined in Roberts *et al.*, 2017.

Model accuracy was determined by the average Area Under Curve (AUC) of the Receiver Operating Characteristic (ROC) of the cross validated models. The evaluation metrics reported are the mean of ROC scores of the five model runs cross validated five times. Variable importance for single-algorithm models was evaluated using biomod2's randomisation function (Thuiller *et al.*, 2016). The package uses a weighted average technique based on the single-algorithm models AUC values for ensemble forecasting. To calculate variable importance for the ensemble models, this weighting can be applied to the variable importance scores for single-algorithm models, which are summed for each variable and divided by the number of models used in the ensemble model (Fletcher *et al.*, 2016). Model prediction outputs are the probability of presence as continuous values between 0 and 1, ensemble model predictions were created using the weighted average across all single-algorithm models produced in 'biomod2'.

Results

Model performance

The accuracy of both single-algorithm models and ensemble models was high, with ROC scores ranging from 0.64 - 0.93 across all single-algorithm and ensemble models. The highest ROC scoring single-algorithm models were 0.89, 0.85 and 0.88 for Manx shearwater, Atlantic puffin and European storm petrel respectively. Ensemble models built for each species incorporated 20, 7 and 5 models and performed better with ROC scores of 0.92, 0.93 and 0.93 for Manx shearwater, Atlantic puffin and European storm petrel respectively (Table 3). Average sensitivity and specificity scores for all model types for each species are outlined in Table 2. Ensemble models performed particularly well, with sensitivity scores ranging from 82.14 – 95.29 across the three species. Specificity scores for both Manx shearwaters and European storm petrels were lower than sensitivity scores at 80.87 and 79.2 respectively. Conversely, the ensemble model for Atlantic puffins scored higher in specificity (92.58) than sensitivity (82.14). To illustrate the models predictive accuracy, figures 2-4 show examples of (i) the known

distribution from survey efforts and (ii) ensemble model predictions (probability of occurrence from 0 to 1) for two of the study sites for each species. Comparisons across all other study sites are outlined in the Supplementary Figures 1-3.

Table 3. Model performance of single-algorithm and ensemble species distribution models built using the “biomod2” package in the statistical software R. Model performance is measured by the ROC values, the predictive power to determine presence = sensitivity (Sens.) and the predictive power to determine absence = specificity (Spec.) of each model that performed above the TSS threshold of 0.7 as filtered by the R package.

<i>Model</i>	<i>Species</i>								
	<u>Manx shearwater</u>			<u>Atlantic puffin</u>			<u>European storm petrel</u>		
	<u>Sens.</u>	<u>Spec.</u>	<u>ROC</u>	<u>Sens.</u>	<u>Spec.</u>	<u>ROC</u>	<u>Sens.</u>	<u>Spec.</u>	<u>ROC</u>
<i>CTA</i>	78.4	84.83	0.85	30.95	97.03	0.64	66.46	81.48	0.76
<i>FDA</i>	86.88	76.89	0.88	85.72	82.37	0.85	71.88	83.78	0.82
<i>GLM</i>	82.03	82.37	0.89	71.15	93.80	0.82	100	66.92	0.88
<i>MARS</i>	85.47	79.3	0.88	68.18	96.12	0.82	91.73	73.46	0.88
<i>Ensemble</i>	88.76	80.87	0.92	82.14	92.58	0.93	95.29	79.2	0.93

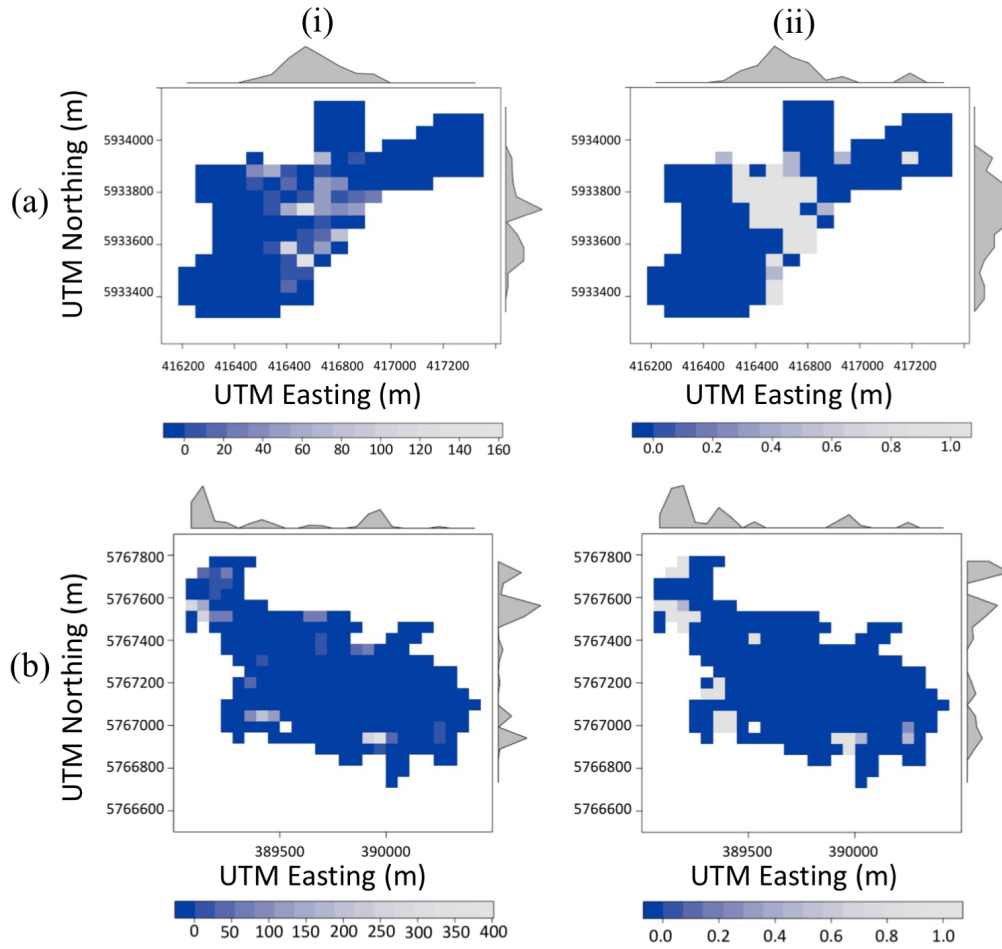


Figure 2. Comparison of (i) actual distributions attained from survey efforts (the number of apparently occupied burrows (50m x 50m)) and (ii) spatial predictions of ensemble models (probability of occurrence between 0 and 1) across two Manx shearwater colonies: (a) High Island, Co. Galway, (b) Inishvickillane, Co. Kerry.

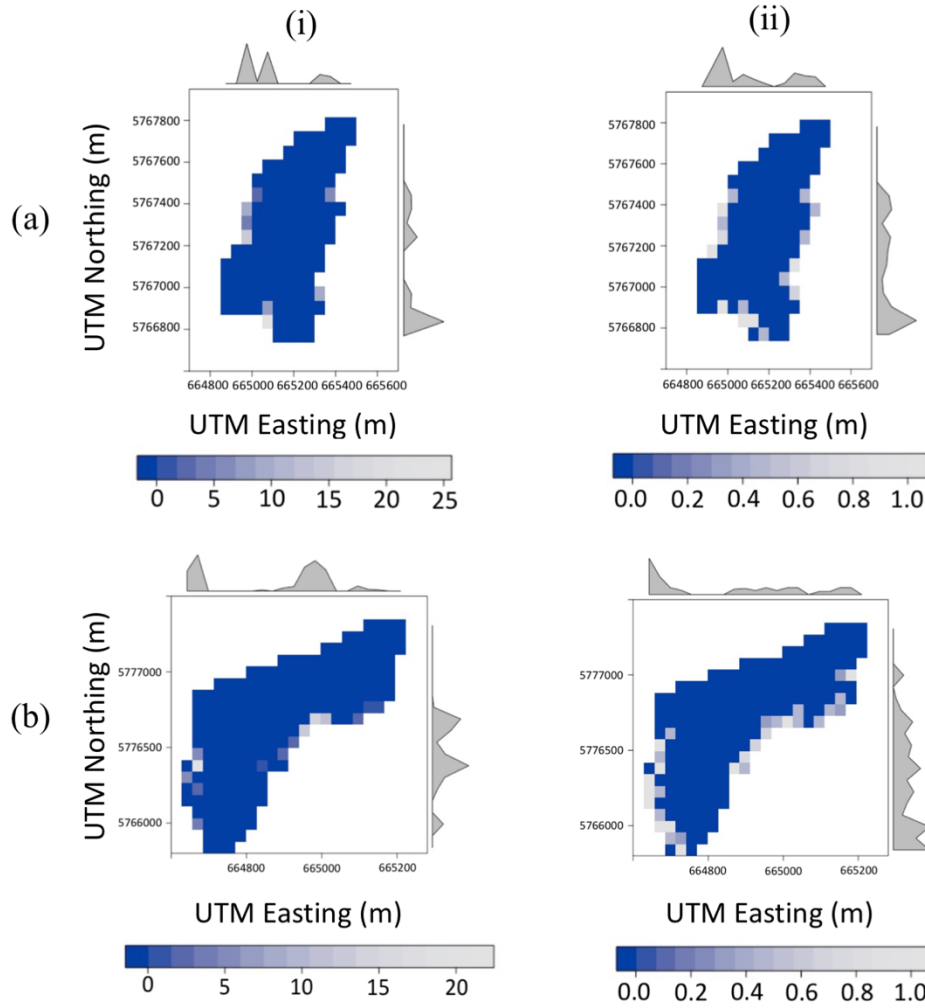


Figure 3. Comparison of (i) actual distributions attained from survey efforts (the number of apparently occupied burrows (50m x 50m)) and (ii) spatial predictions of ensemble models (probability of occurrence between 0 and 1) across two Atlantic puffin colonies: (a) Little Saltee, Co. Wexford, (b) Great Saltee, Co. Wexford.

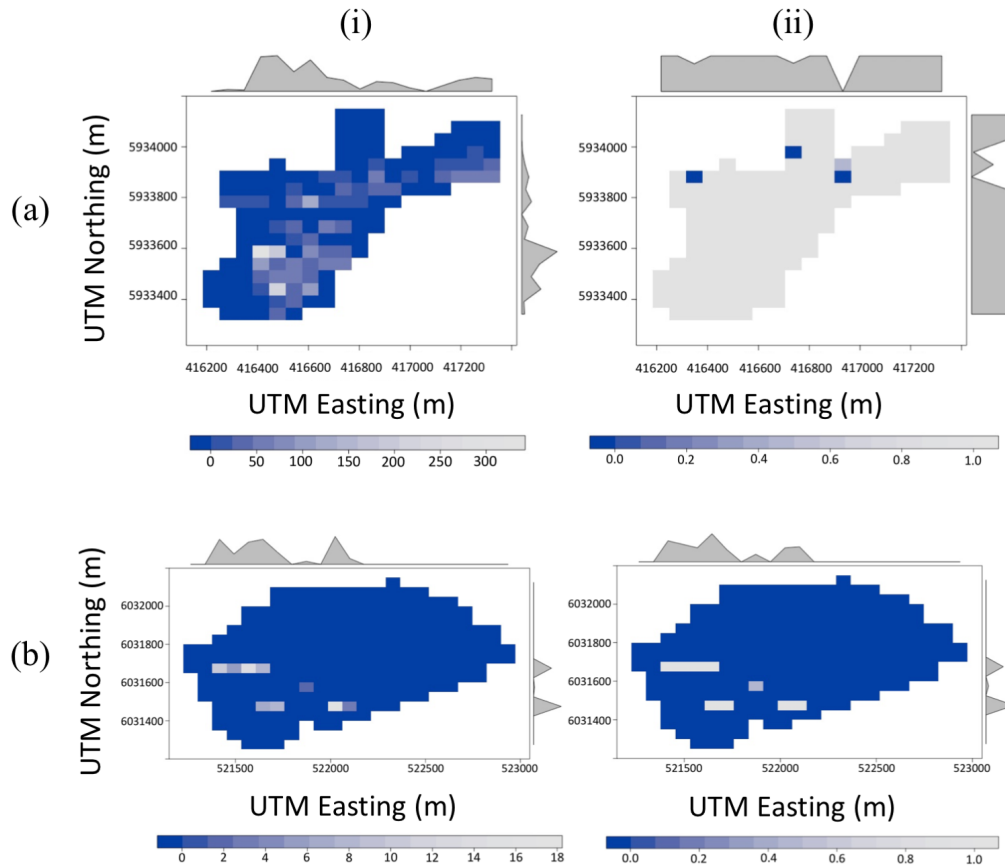


Figure 4. Comparison of (i) actual distributions attained from survey efforts (the number of apparently occupied sites (50m x 50m)) and (ii) spatial predictions of ensemble models (probability of occurrence between 0 and 1) across two European storm petrel colonies: (a) High Island, Co. Galway and (b) Inishmurray, Co. Sligo.

Predictor variable importance

The ranking of variables with the highest contributions across models and species was broadly comparable; the highest contributors to the ensemble models for each species are highlighted in Table 4. Habitat type was one of the highest contributors across all single-algorithm and ensemble models for all three species, accounting for 29.23% – 37.19% of the sum of all importance values for the ensemble models. The boxplots for habitat type (Figure 5; index of habitat types in Table 2) suggest that the preferred habitat type varies across each species. The most important habitat types determined from the Manx shearwater ensemble model show this species preference to areas dominated by bluebell (*Hyacinthoides non-scripta*) and red campion (*Silene dioica*), sea campion (*Silene uniflora*), sea pink (*Armeria maritima*), and a mix of sea campion and sea pink. European storm petrels showed

similar variation to Manx shearwaters with highest predicted occurrence in areas with stone walls and dry-heath tufted grassland. Atlantic puffins showed greater restriction in breeding habitat compared to the Procellariiform species, with model predictions highest in sea campion dominated areas and coastal cliff habitat.

The main topographical predictor variables differed across each species' ensemble model. Elevation and distance from the coast were two of the main predictor variables for Manx shearwater, together accounting for 59.1% of the sum of all importance values (Table 4). The density plot curve suggests that Manx shearwater breeding is favoured in elevations between sea level and 100m, within 200 metres of the coastline (Figure 6 (i) & (ii)). Slope and flow drop were two of the main predictor variables for Atlantic puffin, accounting for 30.2% of the sum of all importance values (Table 4). The density plot curve for slope suggests that Atlantic puffin breeding is highest in areas with slopes between 0 and 20 (degrees), and flow drop of 0 and 35 (%) (Figure 6 (iii) & (iv)). Elevation and slope were two of the main predictor variables for European storm petrels, accounting for 36.88% of the sum of all importance values (Table 4). The density plot curve for elevation suggests that European storm petrels prefer elevations from sea level to 20m and areas with discrete slopes of 0 and 5 (degrees) (Figure 6 (v) & (vi)).

Table 4. Mean variable importance for single-algorithm (CTA, FDA, GLM, MARS) and ensemble (EM) models for each species. Variable importance scores are calculated by 1 minus the correlation score for each model. Scores were converted to % of the sum of all variable importance scores for each model here. The top three most important predictor variables for each species ensemble model are highlighted in bold.

<i>Species</i>	<i>Model</i>	<i>Habitat type</i>	<i>Aspect</i>	<i>Elevation</i>	<i>Flow drop</i>	<i>Flow length</i>	<i>Slope</i>	<i>Distance from coast</i>
<i>Manx shearwater</i>	CTA	34.2	3.26	35.7	3.41	2.93	12.73	7.73
	FDA	46.29	0.30	30.41	0.07	0.87	1.70	20.36
	GLM	24.44	0.74	38.57	4.52	0.63	0.48	30.62
	MARS	18.07	1.21	38.47	0.0	7.37	3.89	31
	EM	29.23	1.45	36.32	2.18	3.15	4.88	22.78
<i>Atlantic puffin</i>	CTA	37.36	2.43	18.48	14.52	3.10	3.58	20.53
	FDA	59.73	1.52	7.70	2.37	5.89	22.80	0.00
	GLM	19.88	6.86	20	12.01	7.52	19.53	14.20
	MARS	34.02	0.0	0.0	35.68	30.30	0.00	0.00
	EM	34.15	3.74	12.21	14.06	11.91	16.16	7.76
<i>European storm petrel</i>	CTA	43.35	6.23	18.24	1.70	18.36	10.62	1.50
	FDA	36.77	3.31	17.57	6.13	8.26	18.04	9.82
	GLM	47.88	4.62	17.86	0.0	0.0	26.47	3.17
	MARS	35.82	5.64	20.58	9.32	10.11	14.24	4.3
	EM	37.19	4.93	19.89	7.06	9.04	16.99	4.89

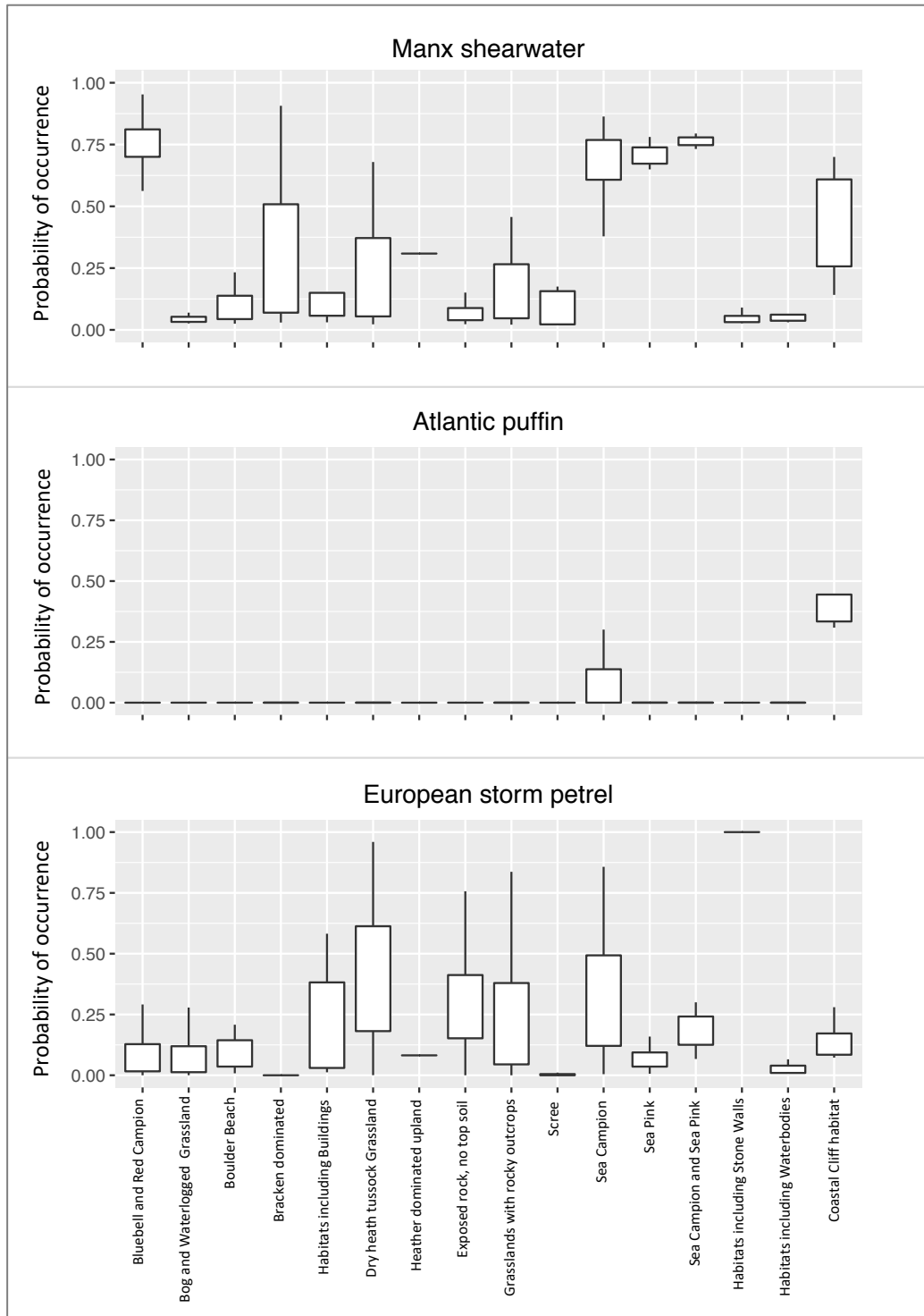


Figure 5. Box-plots displaying the variation in ensemble model predictions of occurrence (probability scale from 0 to 1) across habitat types, one of the most important predictor variables for Manx shearwater, Atlantic puffin and European storm petrel.

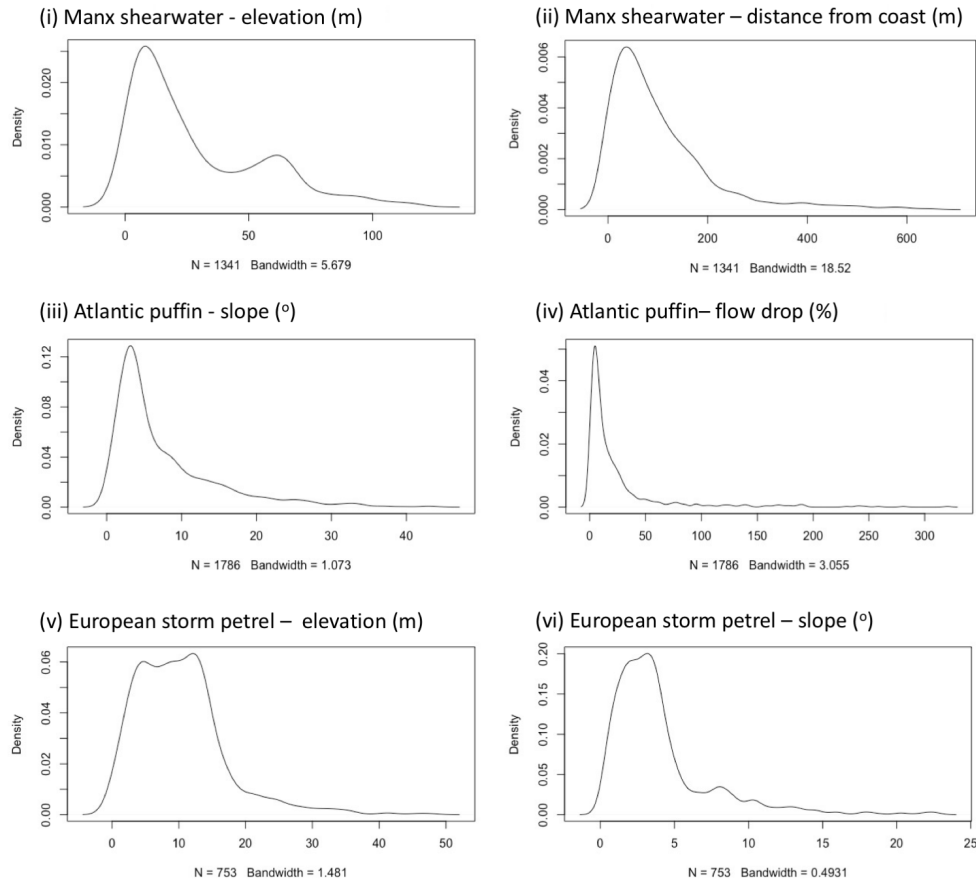


Figure 6. Density plots of the top two non-habitat type predictor variables from final ensemble model (EM), in order of importance for each species.

Discussion

Predictive species distribution models informed by a set of predictor variables obtained from habitat assessments and digital elevation models accurately predict the breeding distribution of three burrow-nesting seabird species across eight islands. Across the species, model performance was high, with ensemble models more accurately predicting the distribution of breeding birds compared to single algorithm models. The model's ability to determine presence (sensitivity), was high across the three species while the ability to determine absence (specificity), showed more variation across species. Habitat type was one of the most important predictor variables across all models, while the most important topographical variables for each species varied between elevation, slope, flow drop and distance from the coast.

The application and translation of model averaging techniques to ensemble SDMs has increased suddenly over the last decade as it is thought to provide better interpretation of predictor variable importance and generate more accurate predictions (Thuiller *et al.*, 2009; Breiner *et al.*, 2015; Fletcher *et al.*, 2016). Our findings are consistent with these studies, where averaged models (ensemble models) performed better than single-algorithm modelling techniques across all species considered. While there is no consensus on which evaluation metric is preferable in ranking model performance, the AUC index has previously been criticised for over estimating the performance of models (Boyce *et al.*, 2002; Lobo *et al.*, 2008). This criticism is directed towards studies that utilise presence only data, a common limitation in SDMs for rare species (Breiner *et al.*, 2015) or movement data (Scales *et al.*, 2015), though here we used both presence and absence data. One key challenge faced when using SDMs is matching the spatial resolution of the response (burrows) and predictor (habitat, topography) variables. Here, the resolution of our models was limited by bird density plot-size as LiDAR data were available at a finer resolution (30m). Thus, potential exists to explore finer-scale relationships with habitat. However, these predictions are more affected by the sample size of the data used in model training, compared to the spatial scale of the plots (Araujo and Guisan, 2006; Hirzel *et al.*, 2006; Guisan *et al.*, 2007).

The use of SDMs as a predictive tool has been questioned as the predictive power of the models is often tested within the same spatial and temporal range as the data on which the model is trained (Torres *et al.*, 2015). Here, we model the distribution of three species that breed primarily in the North Atlantic, where constructed models should have high transferability across sites. This is particularly true for Manx shearwaters, where approximately 90% of the global population is thought to breed across the British Isles (Mitchell *et al.*, 2004). There will be exceptions, however, because the second most important site for Manx shearwater is on the island of Rum where the entire colony is well above the maximum elevation sampled for our sites. Further extrapolative work could use these models to predict distributions across multiple sites that can then be ground-truthed using current census methods such as tape-playback surveys. This is particularly important across the range of both Atlantic puffins and European storm petrels as it would increase our confidence in the accuracy of these models.

Our ensemble models highlight the importance of habitat type as a good predictor of the breeding distributions in these burrow-nesting species. Across all three species, sea campion (*Silene uniflora*) dominated in areas with a high probability of occurrence. The importance of this plant species in predicting the distribution of seabirds is likely due to a shared preference for soil type, where softer soils facilitate burrowing, yet the sea campion's woody root system provides structural support, reducing the risk of burrow collapse. The importance of this habitat type is well known; for example, on the Farne islands the removal of sea campion by Atlantic grey seals (*Halichoerus grypus*) reduced the available breeding ground for the island's Atlantic puffin colony (Hirons and Hirons, 1972). The ensemble model for Manx shearwaters suggests that the probability of occurrence for this species is highest in areas dominated by bluebell and red campion. Bluebell and red campion dominated habitat is widely distributed across Skomer, the largest colony of breeding Manx shearwaters and this likely influences the model predictions. Similar to sea campion, red campion thrives in well-drained soils (Baker *et al.*, 1947; Fossitt, 2000). Ensemble models for Atlantic puffins showed that the probability of occurrence for this species across habitat types is more restricted, where Atlantic puffins are only found in habitat dominated by sea campion and areas of coastal cliff habitat.

The ensemble model for European storm petrels showed considerable variation across different habitat types compared to Manx shearwaters and Atlantic puffins. Highest probabilities of occurrence for this species were associated with areas containing stone walls and dry heath tussock grassland habitat. However, models performed relatively poorly at determining absence of breeding, likely due to the wide range of habitat types this species breeds in. This is highlighted in the poor fit seen in Figure 4(a)(i) where much of the island is predicted to be suitable for breeding European storm petrels. This may suggest that the population has not yet reached its carrying capacity i.e. not all suitable habitat is occupied or another key covariate is restricting the distribution of this breeding population on the island. One exception to this, highlighted in Figure 4(b), is where much of the island was dominated by unsuitable breeding habitat such as waterlogged soils and dense bracken (Inishmurray). Due to this lower accuracy in predicting areas of no

breeding, designing a stratified sampling approach *a priori* for this species is more challenging compared to Manx shearwater and Atlantic puffins.

The importance of topographical variables in the ensemble models differed across the three species. For the two Procellariiform species, elevation was one of the most important predictor variables, with peaks in probability of occurrence at elevations of less than 50m above sea level. These findings suggest that these two species do not show preference towards higher elevations like other Procellariiform species (Rayner *et al.*, 2007; Pinet *et al.*, 2009; Troy *et al.*, 2017). Unlike these studies, the offshore islands we surveyed are largely free of the anthropogenic activities such as agricultural land use and infrastructure that limit the availability of breeding habitat to higher elevations on settled islands. In fact, we see the opposite, particularly with Manx shearwaters where the distance from the coast is an important predictor variable, with highest probabilities of occurrence within 200m of the coastline. This finding was also noted by Perrins *et al.* (2012) and remains true across all islands considered in this study. This may be explained by previous work that suggests the presence of mammalian predators may constrain breeding distributions to areas near cliff faces and crevices where predation risk is lower (Buxton *et al.*, 2016).

Another important topographical predictor variable in the ensemble models for two of the species, Atlantic puffin and European storm petrels, was slope. Peaks in probabilities of occurrence were found in areas where slope was between 0-10 degrees. The values shown in the density plots suggest that gentle slopes are favoured by these species; however the extent of the gradient is likely influenced by two factors: (i) the averaging of DEM values to the grid square, as the ledges above the slopes would be incorporated, and (ii) birds are not breeding on sheer rocky cliffs, rather more gentle slopes where burrowing is still possible. Flow drop was one of the top predictor variables for Atlantic puffins, highlighting the importance of areas where the probability of precipitation movement into the grid square is low, thus indicating areas where the risk of burrow flooding is low.

Our models generated predicted breeding distributions for three burrow-nesting species that accurately reflected the true distribution obtained from intensive surveys. Our modelling was possible because considerable effort was taken to

assess habitat in the field. Improved availability of further predictor variables would allow refinements to models. For example, accurate digital soil depth and soil moisture data (Tromp-van Meerveld and McDonnell, 2006) may be important predictor variables, as burrow-nesting seabirds have been reported to alter the habitat in which they breed, including soil characteristics (Bancroft *et al.*, 2005). However, this data is not currently available for offshore islands around Ireland. We suggest that well-parameterised ensemble models can be used to inform survey efforts on islands with unknown distributions of burrow-nesting species. Much of this modelling approach can be carried out before visiting an island, for example the construction of the DEM and the mapping of distinct habitat types from satellite imagery or aerial photographs. Nonetheless accurate data of the distribution of habitat types across a single island is required from field surveys and dependent on the size of the island being studied, this can take several days to ascertain. Applying our models to poorly surveyed islands (particularly around the British Isles) will identify priority areas for census work and enable more efficient stratified sampling approaches to be used (Arneill *et al.*, 2018 – Chapter 2). In an ideal study system, these predictions would then be ground-truthed to determine the accuracy of the models prediction (Peterman and Semlitsch, 2013; Krüger *et al.*, 2017). Needless to say, the efficacy of models is dependent on good quality habitat data, highlighting the need for further research into methods of remotely mapping offshore island habitats.

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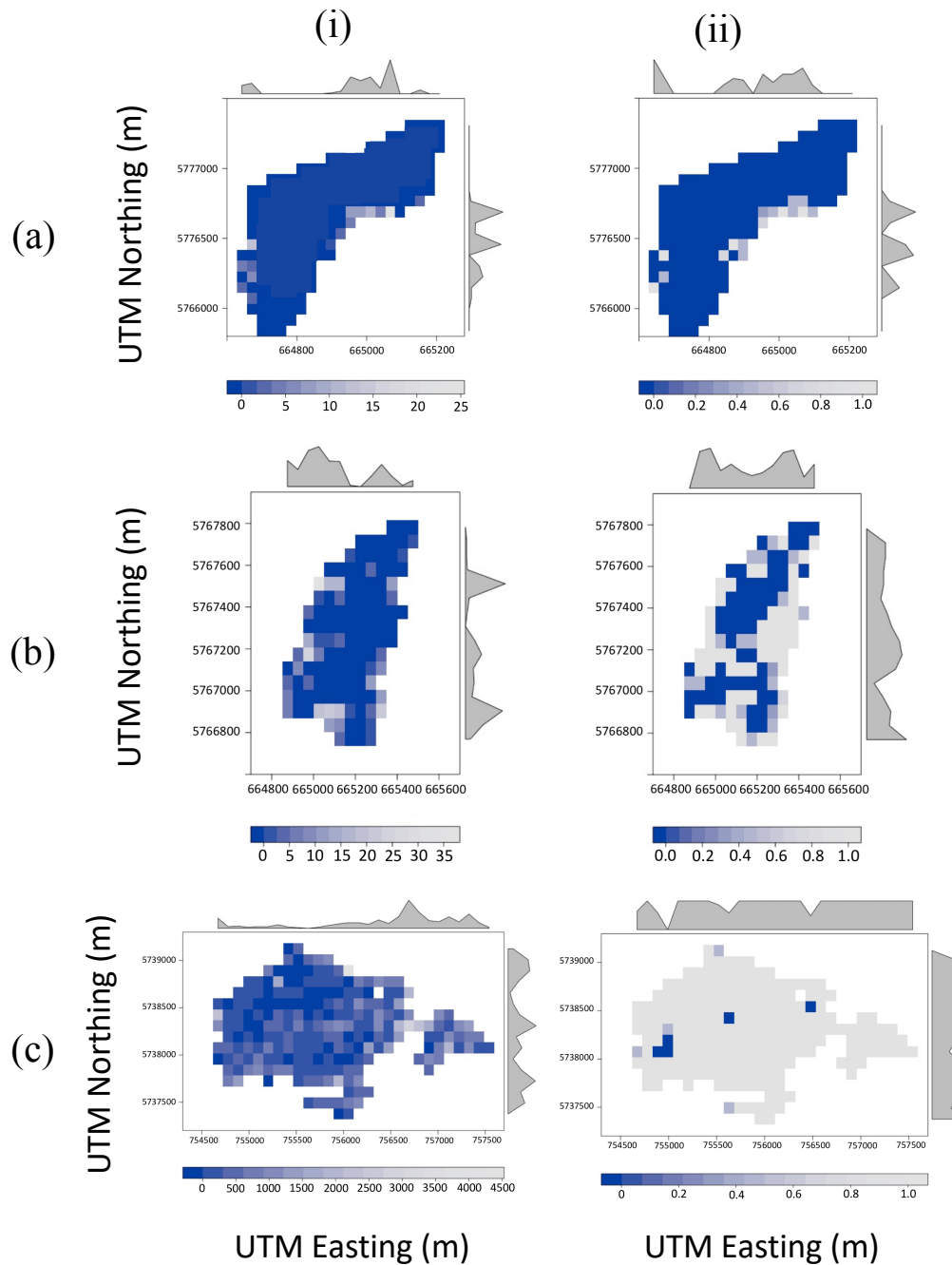
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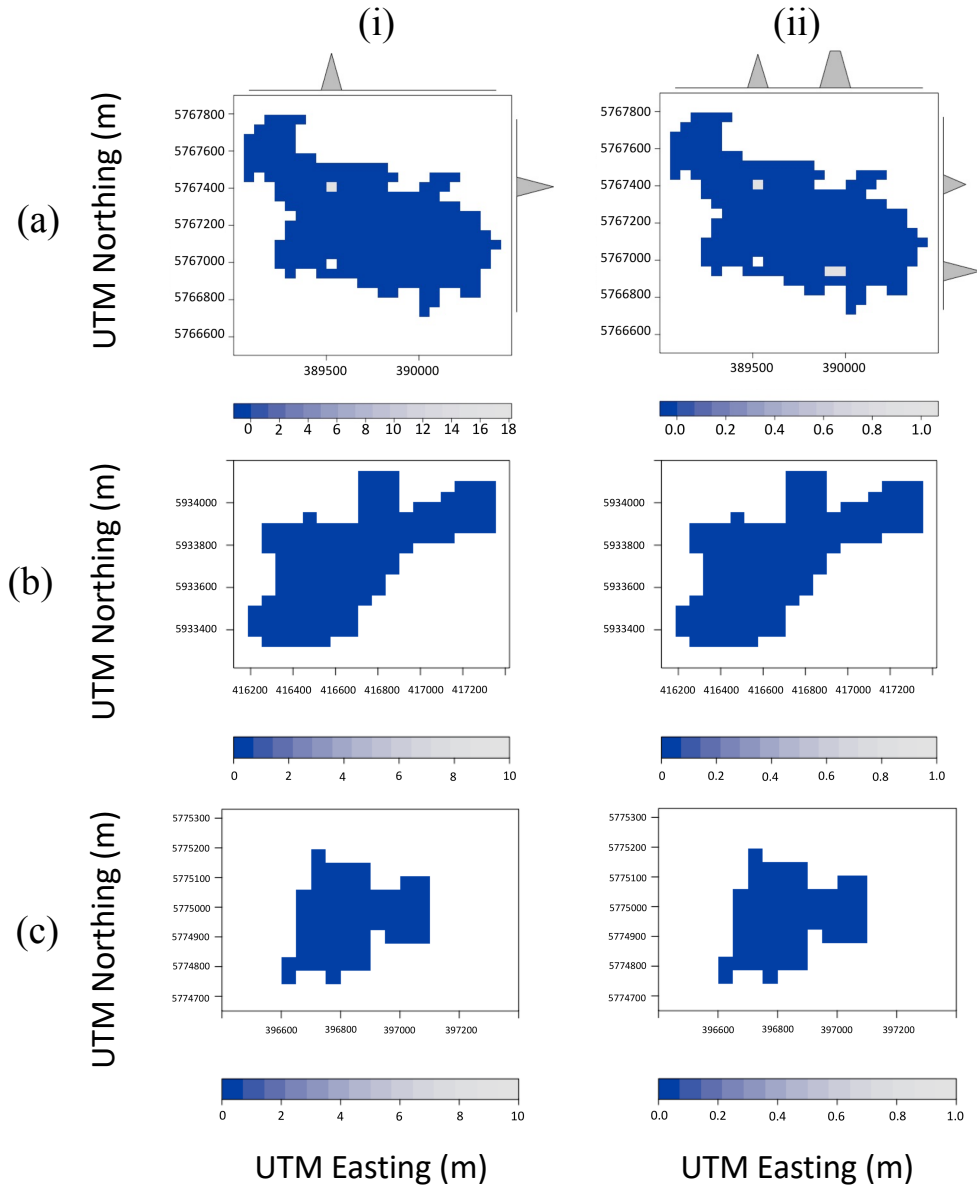
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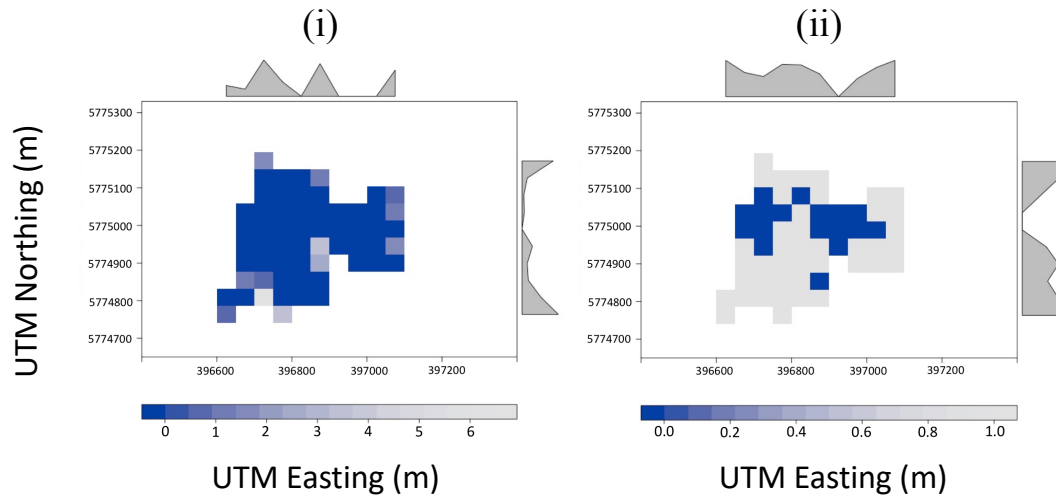
Supplementary Material



Supplementary Figure 1. Comparison of (i) actual distributions attained from survey efforts (the number of apparently occupied burrows (50m x 50m)) and (ii) spatial predictions of ensemble models (probability of occurrence between 0 and 1) across three Manx shearwater colonies: (a) Great Saltee, Co. Wexford, (b) Little Saltee, Co. Wexford and (c) Skomer, Pembrokeshire, Wales.



Supplementary Figure 2. Comparison of (i) actual distributions attained from survey efforts (the number of apparently occupied burrows (50m x 50m)) and (ii) spatial predictions of ensemble models (probability of occurrence between 0 and 1) of Atlantic puffins across three islands: (a) Inishvickillane, Co. Kerry, (b) High Island, Co. Galway and (c) Beginish, Co. Kerry.



Supplementary Figure 3. Comparison of (i) actual distributions attained from survey efforts (the number of apparently occupied sites (50m x 50m)) and (ii) spatial predictions of ensemble models (probability of occurrence between 0 and 1) for the European storm petrel colony on Beginish, Co. Kerry.

Chapter 4

Flight paths rather than nest density shape soundscapes in a colonial seabird

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Abstract

Passive acoustic monitoring is increasingly being viewed as a cost-effective way to monitor wildlife populations, especially those that are difficult to census using conventional means. Burrow-nesting seabirds are amongst the most threatened birds globally but they are also one of the most challenging taxa to census, making them prime candidates for passive acoustic monitoring. Passive acoustic monitoring has the potential to determine presence/absence, or quantify burrow-nesting populations, but its effectiveness remains unclear. We compared passive acoustic monitoring, tape-playbacks, and GPS tracking data to investigate the reliability of passive acoustics as a census method for the Manx shearwater (*Puffinus puffinus*). Variation in acoustic activity across 12 study plots on an island colony was examined in relation to burrow density and environmental factors across two years. As expected fewer calls were recorded when wind speed was high, and on moon-lit nights, but there was no correlation between acoustic activity within a plot and the density of breeding birds as determined by tape playback. However, there was a positive correlation between acoustic activity and the flight paths of breeding individuals around the colony detected by GPS. Contrary to previous studies, this suggests that the acoustic soundscape reflects in-colony flight patterns, not the local density of breeding birds. Nevertheless, these flight paths were consistent across three years, while a decline in acoustic activity across

all plots over two years coincided with a decline in breeding bird density. This suggests that in our population, acoustic monitoring could generate usable indices of population trends.

Keywords: Passive acoustic monitoring, Population size estimation, Seabird, Telemetry, Burrow-nesting seabird, Procellariiformes, Monitoring

Introduction

Time and cost-efficient methods for monitoring population trends are highly sought after in conservation (Wätzold and Schwerdtner, 2005; Nichols and Williams, 2006). Automated monitoring platforms are becoming increasingly important because they lower cost, whilst reducing observer bias and observer disturbance during monitoring (Carey, 2009). Passive acoustic monitoring has been widely used in both terrestrial and marine ecosystems, especially on cetaceans (Mellinger *et al.*, 2007; VanParijs *et al.*, 2009; Borker *et al.*, 2014). The large distances that underwater vocalisations travel advocates the use of passive acoustics in the marine environment, allowing the measurement of patch usage and presumed habitat quality in vocalizing species (Verfuß *et al.*, 2007; Pirota *et al.*, 2014). The general effectiveness of acoustic monitoring remains far from clear, however, for a wide variety of reasons. For example species differ in critically important factors, including call frequency, call volume, and call directionality, all of which influence detectability. Furthermore determining exactly what area is being sampled and how detectability changes with distance from the centre of the sample plot is extremely challenging (Robbins *et al.*, 2015; Dufour *et al.*, 2016). Thus there is a pressing need for further studies in a broader range of taxa before the full potential of passive acoustic monitoring can be realised.

Despite the limited distances over which sound travels in air, many researchers have used passive acoustic methods to study a wide range of questions among avian species in terrestrial systems. These range from behavioural studies on vocal communication (Crane *et al.*, 2016) and sexual selection (Taff *et al.*, 2014), to the identification of new species (McKay *et al.*, 2010). Several studies have reported on the use of passive acoustic monitoring to examine the efficacy of island-population restoration efforts (Buxton and Jones, 2012; Croll *et al.*, 2016), to

determine colony attendance (Mckown, 2008), and to assess breeding bird density (Oppel *et al.*, 2014). The colonial nature of most seabird species potentially makes the use of acoustic monitoring a cost-effective tool, increasing efficiencies in collecting data across multiple colonies over a large geographical scale, determining species assemblages and numbers, and estimating breeding parameters such as phenology (Borker *et al.*, 2015; Frommolt *et al.*, 2017).

Seabirds are amongst the most threatened taxa globally, with declining population trends observed across the majority of monitored species due to various anthropogenic pressures (Croxall *et al.*, 2012; Paleczny *et al.*, 2015). Yet, for many seabird species, primarily burrow-nesters, demographic data is not available to accurately define the conservation status of populations (Paleczny *et al.*, 2015). Many burrow-nesting seabirds are difficult to monitor due to their low detection probability in breeding colonies by not being visually conspicuous while in their burrows, or only returning to the colony at night. Census methods are laborious, often requiring individual burrows to be assessed by visual inspection or tape-playbacks to determine the number of occupied burrows within the narrow window of incubation and chick-guarding when birds respond to playbacks (James and Robertson, 1985; Mitchell *et al.*, 2004). However, an increased use of vocalisations at night-time when many burrow-nesters return to the colony (Brooke, 1986) suggests acoustic monitoring could be effective. Previous work on another burrow-nesting seabird species demonstrated that automated recording devices have the potential to serve as a tool for linking call activity to local density of breeding birds (Oppel *et al.*, 2014). Although the importance of controlling for factors that influence detectability has been well appreciated – for example moon illumination and wind speed (Buxton and Jones, 2012; Oppel *et al.*, 2014) – to date no study has shown conclusively that acoustic recording can provide counts of individuals within a population.

The effectiveness of passive acoustic monitoring to infer the density or occurrence of breeding birds is likely to depend on the behaviour of the birds being recorded. One reason for this is that much of the vocalization recorded may be caused by non-breeders (James *et al.*, 1985). Another is that the acoustic soundscape may be affected by within-colony movement of breeding birds across a site, or by flight paths ('flyways') from breeding colonies to rafts or to foraging grounds at sea.

Although telemetry studies have been widely used to study behaviour and fine-scale distribution of individuals at sea (Nesterova *et al.*, 2015; Burger and Shaffer, 2008; Lascelles *et al.*, 2016), to our knowledge it has never been used to understand the acoustic soundscape within a colony.

In this study we examine the soundscape of the Manx shearwater (*Puffinus puffinus*), a burrow-nesting Procellariiform. This species predominantly breeds in large colonies on remote offshore islands across the North Atlantic, only returns to the colony at night for incubating change-overs or chick provisioning, is highly vocal and rarely censused (Mitchell *et al.*, 2004). We combine passive acoustic monitoring and plot census surveys using tape-playback methods to determine whether passive acoustic monitoring can estimate local seabird density within a breeding population. Furthermore, we predict that the vocalisations from birds flying within the colony may influence the soundscape and test this using data from GPS-tagged Manx shearwaters. We also controlled for the effects of environmental variables on the acoustic soundscape.

Methods

Density and distribution of Manx shearwaters

The study site was High Island, Co. Galway, off the west coast of Ireland (53.54663N, -10.2573W). From the 23rd of May to the 11th of June 2015, tape-playback sampling was carried out in the centre of twelve 50m x 50m grid squares that were randomly selected from plots known to vary in density from initial census work undertaken across the whole island in the same year. Tape-playbacks were carried out as used in previous studies (Smith *et al.*, 2001; Perrins *et al.*, 2012; chapters 2,3,5), following the method devised by James and Robertson (1985). Calls used for tape-playbacks were from a male Manx shearwater recorded on Skokholm; male calls were used because they elicit a higher response rate (but see Perkins *et al.*, 2017), and survey efforts were carried out during this period because response rate drops dramatically post chick-guarding stage (Brooke, 1986). Following methods outlined by Smith *et al.* (2001) and Perrins *et al.* (2012), local response rate was calculated with repeated measures across 33 occupied burrows in 2015 and 48 occupied burrows in 2016. This method measured variation in

which burrows that are known to be occupied would respond to a series of four tape-playbacks trials separated by 24 hours to reduce the risk of habituation.

Acoustic recording

Several previous studies found that Wildlife Acoustic's Song Meter units can record vocalisations up to 50 metres away (Buxton and Jones, 2012; Oppel *et al.*, 2014; Dufour *et al.*, 2016). In 2015 and 2016, acoustic recorders (Wildlife Acoustic SongMeter 3 in 2015 and Wildlife Acoustic SongMeter 4 in 2016) were deployed across the same 12 study plots (Figure 1; Table 1). Recorders were placed on an 80cm wooden stake driven into the centre of the plots. Recorder height was approximately 50cm above the ground to ensure the recorder stood above the vegetation across all study plots. In 2015, two recorders were available and these were moved in a random order across the 12 study plots in cycles of six nights. These cycles were carried out non-consecutively across the breeding season from the 25th of May to the 23rd of August when fledging began. The addition of 10 extra acoustic recorders in 2016 enabled concurrent monitoring across all 12 study plots to collect comparable data between 8th of June and 24th of August non-consecutively. All recorders were programmed on identical cycles, where constant recordings were taken between 23:00 and 04:00 when birds are known to be most active in the colony (Brooke, 1978). The gain and sample rate of each recorder was +42.0 dB and 16kHz respectively as default settings.

Table 1. Density of apparently occupied burrows (AOB) across the 12 study plots determined through tape-playback and application of calculated response rate in 2015 and 2016.

<i>Plot</i>	<i>2015 AOB</i>	<i>2016 AOB</i>	<i>Mean Density</i>
1	10	7	8.5 ± 2.1
2	36	24	30 ± 8.5
3	16	11	12 ± 2.8
4	2	0	1 ± 1.4
5	6	2	4 ± 2.8
6	16	11	13.5 ± 3.5
7	10	6	8 ± 2.8
8	2	2	2
9	0	2	1 ± 1.4
10	28	18	23 ± 7.1
11	2	0	1
12	8	8	8

Telemetry

GPS tags (i-gotU GT-120, Mobile Action Technology, Taiwan) were deployed on 5 breeding Manx shearwaters in 2014, 36 in 2015, and 9 in 2016. Birds were tracked during chick rearing in 2014, 2015 and 2016, and additionally during incubation in 2015. GPS tags were attached using a temporary attachment method (Tesa tape) to the mantle feathers and removed on return of the bird to the colony. All telemetry work was conducted under approval of UCC animal ethics committee and under licence by the BTO and Irish National Parks and Wildlife Service. We analysed GPS data from 2015 and 2016 to explore in-colony flight and its relationship with the measured acoustic soundscape in the same years, and from 2014-2016 to assess consistency in use of flyways and space use in relation to the location of acoustic recorders. Sampling intervals of GPS tracks differed between incubation and chick rearing, incubation trips recorded fixes every 8 or 12 minutes while chick rearing recorded fixes at 4 minute intervals. The number

of times individual tracks intersected the acoustic study plots (circular plot with radius of 50m) was calculated in ArcGIS (10.3.1) (see Figure 1).

Acoustic analyses

Manual segmentation was carried out to provide training vocalisations that were later used in the automated extraction of signals from all data using the Wildlife Acoustics Song Scope software (© 2017 Wildlife Acoustics, Inc.). Manual segmentation of data consisted of the visual inspection of time-frequency spectrograms of twenty randomly selected recordings across various acoustic backgrounds; these segments were inspected using the Audacity 2.1.2 software (© 2018 Audacity Team). Manual segmentation was used to reduce the number of false positive detections and to limit false negatives where detections were missed (Dufour *et al.*, 2016). Measured signals were combined with five high-quality pre-recorded reference calls to enhance the accuracy of the call recognition model; these recordings were obtained from Skokholm (Xeno-Canto), and manually recorded calls from High Island and Great Blasket, Co. Kerry. Song Scope requires several optimal model parameters that were obtained from the various recordings manually segmented as above. These parameters include: frequency range; minimum frequency; maximum syllable duration; maximum song duration and sample rate (Hz); Fast Fourier Transform window size, dynamic range and maximum Hidden Markov Model (HMM) states based on the properties of the Manx shearwater call.

Once created, recognition models ran through all data across both years. To reduce the number of false positives, identified calls were discarded where the quality score of recognized calls was <60. False negative calls, defined as calls that possessed all frequency characteristics but were missed by the recognition model, were identified as outlined by Buxton and Jones (2012), with a randomly selected 15 minutes of recording visually scanned from each recording hour within each plot from each year. Visual scans were restricted to recordings where calls could be distinguished from background noise on spectrograms. The 15 minute samples were extracted from the 850 hours of recording, approximating 23% of data. Environmental conditions that affect the rate of false negatives have been discussed in depth in previous studies (Buxton and Jones, 2012); we report the

false negative rates across three different categories of wind speed (0-10 knots, 10-20 knots, 20-30 knots) to show that the average number of false negatives increased with the wind speed (Supplementary Table 1).

Data Analysis

A total of 850 hours of recordings were obtained from the two years across the 12 study plots, and a total of 24,502 calls were identified using the Song Scope recognizer. The Song Scope recognition model performed with an accuracy of $75.4\% \pm 3.37\%$ of calls across all training data. Detected calls (per hour or per night) is the number of vocalisations detected in the recordings by the recognition model. These scales were selected to correspond to the availability of environmental data on which the analyses could be carried out. The mean number of calls per hour ranged from 9.55 to 87.05 and from 6.3 to 66.93 across the 12 study plots in 2015 and 2016 respectively. Analysis of the relationship of calls per hour with density and environmental data was carried out using a zero-inflated negative binomial mixed model in the R package “glmmADMB” (Bolker, 2006). This model was used to account for over-dispersion in the data due to large numbers of zero values and positive integers, where the dispersion statistic theta (θ) was greater than 15 in all models. Plot, hour and date were included as a random effects to account for repeated measures at each of the plots. Hourly environmental data including wind speed, wind direction and cloud cover were sourced from weather stations within 100km of the study site (Met Éireann), while nightly moon illumination data was sourced from the US Naval website (US Navy). These environmental covariates were included as they are known to affect the quality of recordings (wind) and the attendance within the colony (moon illumination and cloud cover). Recording hour was included as a factor to compare the number of calls to determine any variation throughout the night. To remove zero-inflation, potential variability in the number of calls between hourly recordings, and lack of variability in some environmental factors such as moon illumination, data were also aggregated at the nightly scale and modelled using a negative binomial mixed model in the R package “glmmADMB”. Where environmental data was hourly, the nightly average was used.

To compare the acoustic activity and the telemetry data that were collected at different time periods throughout the season, the number of times individual tracks intersected the acoustic study plots was compared with the average calls per hour and the total calls per night at each plot using a Spearman's Rank correlation test. To ensure the flight paths did not change temporally and allow comparison with the acoustic activity, Dutilleul's modified t-tests that account for spatially auto-correlated data were carried out to test the consistency across the telemetry data (2014, 2015 and 2016).

Results

Temporal and Environmental variation

More calls were recorded during the incubation period compared to the chick-rearing stage ($p = 0.04$, $z = 1.96$, $df = 1$, Table 2), and significantly fewer calls occurred during 23:00-00:00 in both years compared to all other recording hours (00:00 – 04:00) ($p = < 0.001$, $z = -3.42$, $df = 4$). Fewer calls were recorded in 2016 at hourly ($p = < 0.001$, $z = -9.11$, $df = 1$, Table 2) and nightly ($p = < 0.001$, $z = -4.5$, $df = 1$, Table 2) scales. Calls per hour was largely driven by the environmental variables; decreasing with wind speed ($p = < 0.001$, $z = -3.82$, $n = 850$, Table 2), which is reflected in the significant increase in the rate of false negatives with wind speed from manual inspection of spectrograms (see Supplementary Table 1, $p = < 0.001$, $effect = 1.147 (\pm 0.24)$, $n = 840$). Calls also decreased with moon illumination ($p = < 0.001$, $z = -11.59$, $n = 850$). At the nightly scale, the number of calls also decreased with wind speed ($p = 0.005$, $z = -2.793$, $n = 170$) and moon illumination ($p = < 0.001$, $z = -5.13$, $n = 170$). Cloud cover, wind direction and an interaction between cloud cover and moon illumination all had no significant effect on the number of calls either per hour or per night (Table 2).

Density and acoustic soundscapes.

No relationship was found between the density of breeding birds around the recorders at either the hourly number of calls scale ($p = 0.45$, $z = -0.75$, $n=850$, Table 2), or the nightly number of calls scale ($p = 0.52$, $z = 0.65$, $n = 170$, Table 2). A visual representation of the mean density of breeding Manx shearwaters, the

average vocal activity at both temporal scales, and in-colony flight are shown in Figure 1 (a-d). There was a strong but marginally non-significant correlation between telemetry data (the number of tracks intersecting the acoustic monitoring plots) and vocal activity indices (hourly: $\rho = 0.4895$, $p = 0.1098$, $n = 12$; nightly: $\rho = 0.49$, $p = 0.11$, $n = 12$). One data point had high leverage ($D_i = 0.71$) with a particularly low number of intersecting tracks and a relatively high vocalisation rate. This was from a plot close to the tagging location, with an underestimation of intersections likely due to a combination of (i) GPS fixes not being taken when birds are underground in the burrow and resulting track fixes occurring outside of the 50m radius of the plot, and (ii) tracks originating or terminating in the area intersect the plot area only once resulting in very few ‘transitions’ through the area. Removing this plot from the analyses reduced the p value further (hourly: $\rho = 0.6$, $p = 0.056$, $n = 11$; nightly: $\rho = 0.55$, $p = 0.08$, $n = 11$, Figure 1 (e and f)). Dutilleul's modified t-tests showed that the number of track intersections occurring across plots was highly consistent across years, with correlation values varying from 0.9967 to 0.999 ($p = <0.001$).

Table 2. Model summaries of factors effecting acoustic activity at both the hourly scale and nightly scale as discussed above. Effect sizes reported in “log” format as per model output.

	<i>Hourly model</i>			<i>Nightly model</i>		
	<i>Effect</i>	<i>z</i>	<i>p</i>	<i>Effect</i>	<i>z</i>	<i>p</i>
<i>Density</i>	-0.02 (± 0.4)	-0.75	0.45	0.01(± 0.02)	0.65	0.52
<i>Incubation</i>	0.36 (± 0.18)	1.96	0.04	0.007(± 0.45)	0.01	0.9
<i>23:00-00:00</i>	-0.6 (± 0.18)	-3.42	< 0.001	<i>N.A</i>	<i>N.A</i>	<i>N.A</i>
<i>Year: 2016</i>	-2.19 (± 0.2)	-9.11	< 0.001	-2.13(± 0.46)	-4.5	< 0.001
<i>Moon</i>	-2.41 (± 0.2)	-11.59	< 0.001	-2.1 (± 0.4)	-5.13	< 0.001
<i>Wind speed</i>	-0.06(±0.06)	-3.82	< 0.001	-0.08(± 0.02)	-2.793	0.005
<i>Cloud Cover (CC)</i>	0.0336	0.2	0.838	0.473(± 0.3)	1.583	0.114
<i>CC: Moon</i>	0.397	1.94	0.053	-0.553(± 0.4)	-1.48	0.139

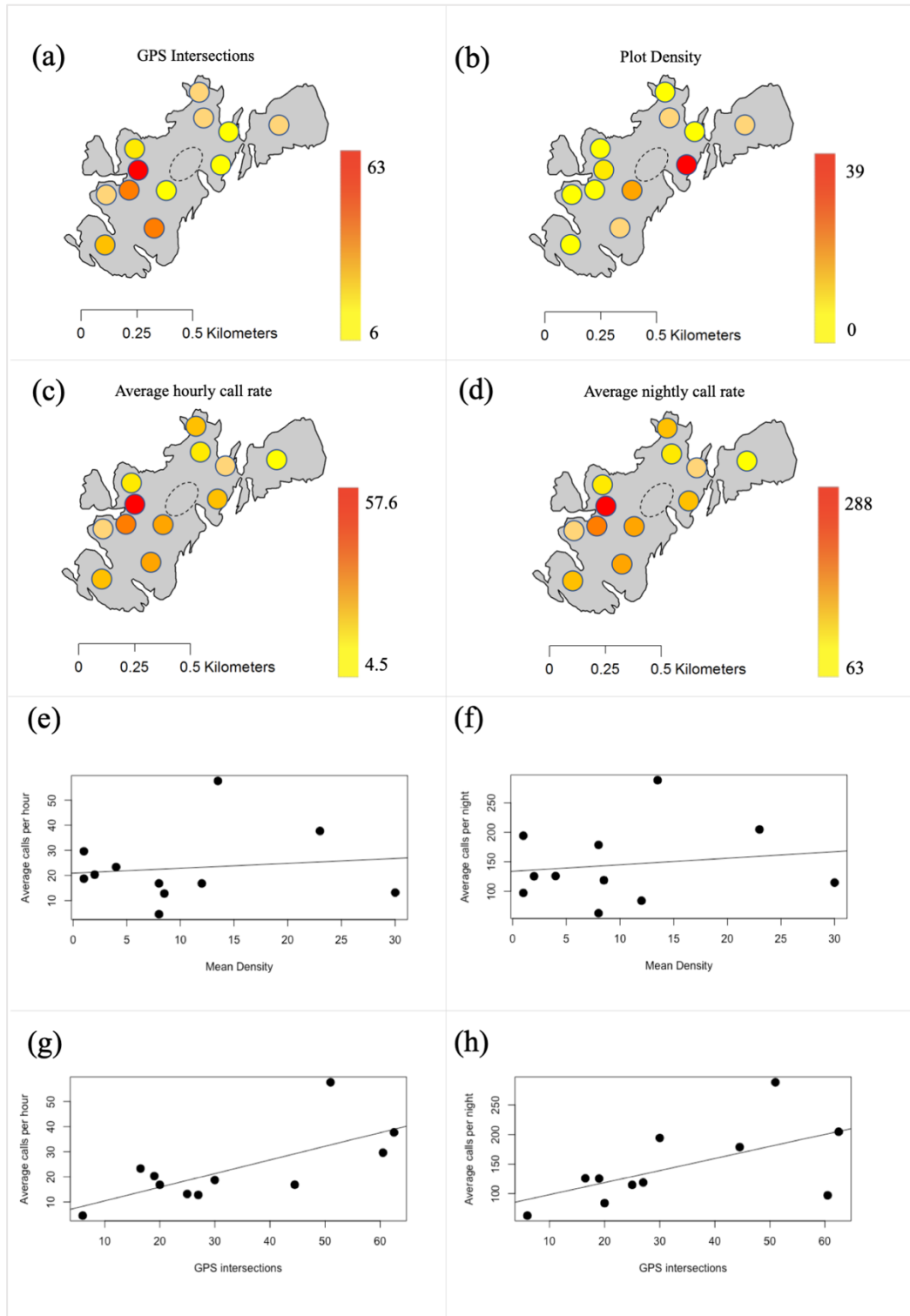


Figure 1. Visualisations of the distribution of (a) the number of intersections by GPS tracked Manx shearwaters, (b) the mean density of apparently occupied burrows, (c) the average calls per hour and (d) the average calls per night as recorded by Wildlife Acoustic recorders. The oval shaped broken line represents the location where breeding adults were GPS-tagged on High Island, Co. Galway, Ireland. Scatter plots show the correlation between the average number of calls at both the hourly and nightly scale to the average number of intersections ((e),(f)) and number of GPS intersections ((g),(h)).

Discussion

Monitoring wildlife populations is extremely labour intensive and considerable effort is being put into identifying efficient, automated methods for doing so inexpensively (Borker *et al.*, 2014; Perkins *et al.*, 2017; Hodgson *et al.*, 2018). Passive acoustic monitoring is one of the most promising of such methods (Borker *et al.*, 2014; Oppel *et al.*, 2014). However, contrary to expectations, we did not find the relationship between acoustic activity and local burrow density reported by Oppel *et al.*, (2014) in a closely related seabird species, the Cory's shearwater (*Calonectris borealis*). This was true for both hourly and nightly temporal scales. Our study had similar densities of breeding birds around recording units (0-36 AOB) to Oppel *et al.*'s study (8-56 AOB), and accounted for the environmental and temporal variation that was removed in Oppel *et al.*, (2014). Thus, the relationship between the acoustic activity and density estimates used in Oppel *et al.*, (2014) to determine colony size is not directly transferable to this colony. All other studies, including ours, report findings that advocate the use of acoustic recording as a tool for monitoring seabird populations using indices (Buxton and Jones 2012; Borker *et al.*, 2014). More generally, the use of passive acoustic monitoring is usually limited to determining species richness (Wimmer *et al.*, 2013) and presence or absence of species in an area (Mellinger *et al.*, 2007; Pirotta *et al.*, 2014).

We suggest that the lack of a correlation between the local soundscape and local breeding density is robust because several typical environmental and biological drivers of acoustic soundscapes were detected in our data. The number of calls were higher during the incubation period, for example, when adults are continuously present before the chicks become thermally independent relatively early in life (Paiva *et al.*, 2010). Additionally, the number of birds in the colony is likely to be highest during incubation before breeding birds fail and leave, and before prospecting males, who are highly vocal on the ground, leave the colony (James, 1985). The relationships between acoustic activity and environmental variables in our study are consistent with those reported previously (Granadeiro *et al.*, 1998; Buxton and Jones, 2012; Borker *et al.*, 2014). An example of this is the significantly reduced number of calls on moonlit nights, a well-known phenomenon thought to be a predator avoidance mechanism (Bretagnolle *et al.*,

2000; Oppel *et al.*, 2014). We found that the number of calls recorded declined with wind speed, which we interpret as a reduction in detectability due to associated background noise rather than reduced presence (Buxton and Jones, 2012; Oppel *et al.*, 2014). Furthermore the quality of acoustic recordings can be affected severely by anthropogenic sound (Barber *et al.*, 2010; Hildebrand, 2009), though this was not a problem on our offshore study site away from human activities. Thus, these well-known patterns give confidence in our conclusion that local soundscapes do not reflect local density in our study site.

Instead of reflecting local burrow density, however, GPS tracks of breeding adults intersecting monitoring plots may explain the soundscape because they were marginally correlated with acoustic activity within the sample plots. To our knowledge, this is the first such demonstration of movement patterns driving the acoustic soundscapes in an avian species. In other taxa such as cetaceans (Mikkelsen *et al.*, 2016), passive acoustic monitoring and telemetry work supports these findings but this is to be expected since cetaceans are not typical central placed foragers. Several behavioural factors are likely to explain the pattern we observed in our study species. First, it has been suggested that breeding Manx shearwaters are vocal in flight and quieter on the ground (Perrins *et al.*, 1973; James, 1985), an effective way of social information transfer without revealing the location of burrows to predators. Immature prospecting birds are thought to be highly vocal in the colony (Perrins *et al.*, 1973; James, 1985), thus many of the vocalisations we recorded at sample points were likely a combination of non-breeding birds and breeding birds commuting from elsewhere in the colony. Similarly, within the burrow, unless responding territorially to a threat or tape-playback, breeding birds remain quiet through the late incubation and chick-rearing periods as the sexual function to calling early in the season is replaced by calls solely for mate recognition (James, 1985).

Our finding that breeding birds do vocalize within the colony, albeit away from their own burrow site, is likely explained by social information exchange. Empirical information for social information exchange in seabirds is evident or has been proposed in many species to occur at the colonies or on rafts nearby (Birkhead, 1985; Burger, 1997; Weimerskirch *et al.*, 2010; Wakefield *et al.*, 2013). While our tracking data was too coarse (4-minute intervals between GPS locations

to preserve battery life) to identify fine-scale flight paths between the colony and these rafts, the highly consistent distribution of tracks across years suggests that persistent flyways occur. Obtaining finer temporal scale GPS data could help to separate the effects of social information exchange and local topographic features driving within-colony movement. The number of GPS intersections are likely to increase approaching breeding areas of central based foragers, therefore future work testing the strength of this relationship on larger islands with similar patchily distributed colonies would allow us to determine whether this relationship is found at greater distance from breeding colonies.

The absence of a relationship between the density of birds breeding in the recording plots and acoustic activity suggests the method cannot be used to estimate population size. However it does not necessarily mean acoustic activity is independent of the number of birds breeding on the whole island for two reasons. First, breeding birds were being detected in flight, even if not breeding within the plots being monitored; furthermore this pattern was consistent across two years. Second, the decline in nest density over two years coincided with a drop in acoustic activity across the corresponding two years. Thus our results support the growing evidence for the idea that passive acoustic monitoring can be used to generate usable indices of population change. Given the difficulty and time consuming nature of monitoring burrow-nesting species, coupled with large time intervals between surveys at many sites (as long as 15 years, Mitchell *et al.*, 2004), this would be of wide benefit to conservation managers. A longer time series, or more realistically, robust correlations between acoustic activity and population density across a representative sample of independent colonies are needed to determine this.

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Supplementary Material

Supplementary Table 1. False negative rate defined as the calls skipped by the recognizer from manual visual inspection of randomly selected 15 minute recordings from each hour recorded across all study plots. False negative rates for 1. Each plot and 2. Different categories of wind speed in knots reported below to demonstrate the effect of increased wind on the recording quality thus detection rate of recognition model.

<i>1. Plot</i>	<i>Mean false negative rate \pm SE</i>
<i>1</i>	0.64 (\pm 0.1)
<i>2</i>	1.41 (\pm 0.28)
<i>3</i>	2.72 (\pm 0.3)
<i>4</i>	1.57 (\pm 0.27)
<i>5</i>	1.33 (\pm 0.28)
<i>6</i>	0.86 (\pm 0.14)
<i>7</i>	0.34 (\pm 0.11)
<i>8</i>	1.63 (\pm 0.36)
<i>9</i>	1.48 (\pm 0.32)
<i>10</i>	2.54 (\pm 0.47)
<i>11</i>	1.50 (\pm 0.41)
<i>12</i>	0.99 (\pm 0.24)
<i>Average</i>	1.42 (\pm 0.2)
<i>2. Wind Speed (knots)</i>	
<i>0-10</i>	1.2 (\pm 0.1)
<i>10-20</i>	1.5 (\pm 0.17)
<i>20-30</i>	3.1 (\pm 0.7)
<i>30+</i>	N/A

Chapter 5

Critical assessment of population size estimates for three burrow-nesting seabirds using matrix population models

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Abstract

Our ability to obtain accurate population size estimates for most species is hampered by the high cost associated with carrying out censuses, particularly when resources are limited. Further difficulty arises when comparisons are to be made across censuses, this is especially true for historical estimates where data storage is generally poor. Population modelling approaches can be useful to interpret realistic level of population change across years using certain demographic parameters. National censuses of seabird populations in Britain and Ireland are generally carried out every 10-15 years. However, estimates of the population size of burrow-nesting species have only been reported in the most recent census, Seabird 2000 (1998-2002), and the accuracy of these are unclear due to known difficulties associated with censusing these species. Here, we report new colony estimates for Manx shearwater (*Puffinus puffinus*), European storm petrel (*Hydrobates pelagicus*) and Atlantic puffin (*Fratercula arctica*) across seven islands in Ireland. We used Leslie matrix population models to (i) retrodict population sizes across 1998-2016 and (ii) discuss the potential changes in demographic parameters that might explain the discrepancies in new estimates and those of Seabird 2000. We show that the population sizes of Manx shearwater and European storm petrels across most colonies were significantly underestimated as retrospective estimates were much higher than those reported in Seabird 2000. Atlantic puffin populations appear to be declining due to low productivity rates,

particularly on Great Saltee where the population appears to be declining at an alarming rate. This study demonstrates how matrix population models can be used to explain the discrepancies between estimates and explore the demographic parameters that drive observed population trends.

Keywords: Census, Matrix population models, Leslie matrix, Burrow-nesting seabirds, Demography, Seabird

Introduction

Seabirds are key qualitative indicators of the marine ecosystem playing important roles as apex predators (Block *et al.*, 2011), scavengers (Votier *et al.*, 2004) and nutrient distributors (Bancroft *et al.*, 2005). Global assessments of their population status are limited to the IUCN Red list of Threatened Species and two major reviews (Croxall *et al.*, 2012; Paleczny *et al.*, 2015). These publications present data since 1950-2010 suggesting that at least one third of seabird populations are threatened with extinction, over half are thought to be in decline, and three species are now extinct. However, for many species, data is either unavailable or limited spatially and/or temporally. The life-history characteristics of many seabirds increases the difficulty in obtaining demographic data as they often breed in large widely distributed colonies, often on remote islands, are migratory, and nest on steep cliff faces, in discrete rock crevices or in burrows.

Seabirds that nest in burrows are the most challenging to census and monitor (Mitchell *et al.*, 2004; Opper *et al.*, 2014; Buxton *et al.*, 2016). Baseline abundance estimates are essential for the conservation of these seabirds as they are amongst the most vulnerable to threats such as habitat destruction and predation from introduced mammalian predators (Major *et al.*, 2006; Jones *et al.*, 2008). In the last decade, the majority of research on monitoring burrow-nesting species has aimed to refine existing census methods to provide more accurate population estimates (Perkins *et al.*, 2017^a), whilst novel methods have been tested to utilise technological advances that reduce the time and cost associated with censusing (Opper *et al.*, 2014; Dufour *et al.*, 2016; Perkins *et al.*, 2017^b). Although the efficacy of novel methods remains unclear, the adoption and development of

methods such as tape-playbacks has dramatically improved our understanding of the population size of these species (Perrins *et al.*, 2012; Perkins *et al.*, 2017^a).

Ireland hosts breeding populations of four burrow-nesting seabirds; Manx shearwater (*Puffinus puffinus*), European storm petrel (*Hydrobates pelagicus*), Atlantic puffin (*Fratercula arctica*) and Leach's storm petrel (*Hydrobates leucorhous*). Despite three national seabird census efforts; Operation Seafarer (1969 – 1970, Cramp *et al.*, 1974), Seabird Colony Register (1985 – 1988, Lloyd *et al.*, 1991) and Seabird 2000 (1998-2002, Mitchell *et al.*, 2004), population estimates for all burrow-nesting species are limited to Seabird 2000. The Seabird 2000 census was the first national census to utilise tape-playback methods (James and Robertson, 1985) for burrow-nesting Procellariiformes in Ireland. Mitchell *et al.* (2004) reported that internationally important numbers of European storm petrels breed on islands off the south west coast of Ireland, representing 3-11% of the global population (ca. 100,000 breeding pairs). Estimates of Manx shearwaters, Atlantic puffins and Leach's storm petrels were approximately 10% (37,178 pairs), <1% (21,000 pairs) and <1% (310 pairs) of the global breeding populations respectively (Mitchell *et al.*, 2004). The accuracy of these national estimates however is far from clear, as many sites were not surveyed due to logistical constraints, and reports of the methods used are vague.

One approach that has been used to explain trends in populations over time is matrix population modelling (Caswell, 2001). These models allow for the simulation of population trajectories over time and have been used to relate trends to increased predator abundance (Cuthbert *et al.*, 2001; Soanes *et al.*, 2010; Miles *et al.*, 2015), by-catch (Cuthbert *et al.*, 2001) and changes in climatic factors such as sea surface temperature (Soldanini *et al.*, 2016). These models are sometimes used to design or determine the efficacy of conservation efforts for vulnerable species (Ezard *et al.*, 2010). Typically, matrix population models are used to project population trends forward in time (Soldanini *et al.*, 2016; Monadjem *et al.*, 2018), however matrix population models can be constructed to determine the historic trajectories of populations. For example, Beissinger and Peery (2007) used these models to identify the causes of decline in the endangered Marbled Murrelet (*Brachyramphus marmoratus*).

The initial aim of this study set out to obtain new, accurate estimates of Manx shearwaters, European storm petrels and Atlantic puffins breeding and assess population trends since the previous censuses on several offshore islands in Ireland. We used Leslie matrix population models to carry out retrospective projections of these recent estimates to retrodict population sizes across 1998-2016. We examine the causal factors that may explain discrepancies between our estimates and those reported in Seabird 2000.

Methods

Population size

The methodologies used to attain the population size estimates reported in Mitchell *et al.* (2004) followed those outlined in the Seabird Monitoring Handbook (Walsh *et al.*, 1995). At the site level, the methods are reported using a numbered system representative of various approaches ranging from “Best Guess” to “Complete count”, yet no details are reported on the exact timing and the spatial extent of any sampling efforts. For Manx shearwaters and European storm petrels, a total of 40 and 125 colonies respectively were ‘sampled’ using tape-playback surveys (James and Robertson, 1985; Mitchell *et al.*, 2004), while no island was subject to a ‘complete count’. Atlantic puffin colonies in Ireland were surveyed using observational counts of individuals on land and on the water adjacent to breeding colonies, though no details are reported on the number of counts that were carried out at each site (Mitchell *et al.*, 2004).

Here, tape-playback surveys (James and Robertson, 1985) were carried out across six islands to census both Manx shearwaters and European storm petrels. Manx shearwaters were censused on Little Saltee, Co. Wexford (2013); High Island, Co. Galway (2015) and Inishvickillane, Co. Kerry (2016). European storm petrels were surveyed on High Island, Co. Galway (2016); Beginish, Co. Kerry (2016) and Inishmurray, Co. Sligo (2017) (Figure 1). Logistical constraints necessitated differing sampling approaches and sampling effort across sites; detailed methods used to derive population size estimates for each species/island are outlined in Table 1. The response rate, defined as the frequency in which an apparently occupied burrow (AOB) or site (AOS) responds to tape-playback was calculated

during each survey with the exception of Little Saltee. To overcome this the average response rate measured during the Seabird 2000 census (Mitchell *et al.*, 2004) was used in its place. The samples sizes, number of repeated measures and calculated response rates for all other sites are reported in Table 1.

Total population sizes of Atlantic puffin were estimated using the standard protocol of repeated island-wide counts across four islands; Great Saltee, Co. Wexford; Little Saltee, Co. Wexford; Inishvickillane, Co. Kerry and Ireland's Eye, Co. Dublin (Figure 1). Population size was estimated on Great Saltee in 2015 and on all other islands in 2016. Observational counts followed the protocol outlined in the Seabird Monitoring Handbook (Walsh *et al.*, 1995). Initial scoping visits were carried out in April of each study year to establish the distribution of the sub-colonies and counts were carried out as early as logistically feasible (April-Early June) to limit the inclusion of prospecting birds (Walsh *et al.*, 1995; Mitchell *et al.*, 2004). The highest recorded total count of Atlantic puffins was used to minimise the proportion of individuals that were missed during any one count (Miles *et al.*, 2015). The alternative method of sampling for signs of occupancy (Walsh *et al.*, 1995) was not used, as the majority of breeding burrows were located on difficult to access coastal cliffs or steep slopes.

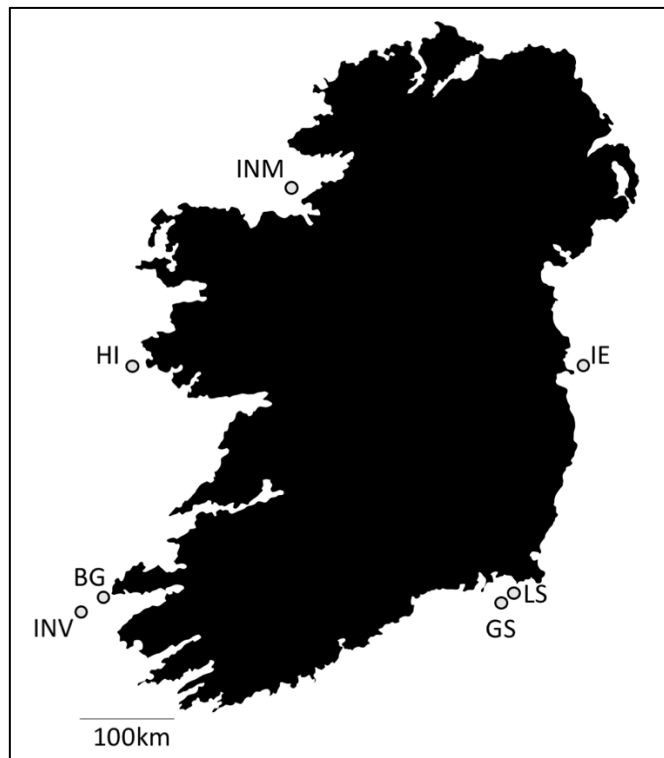


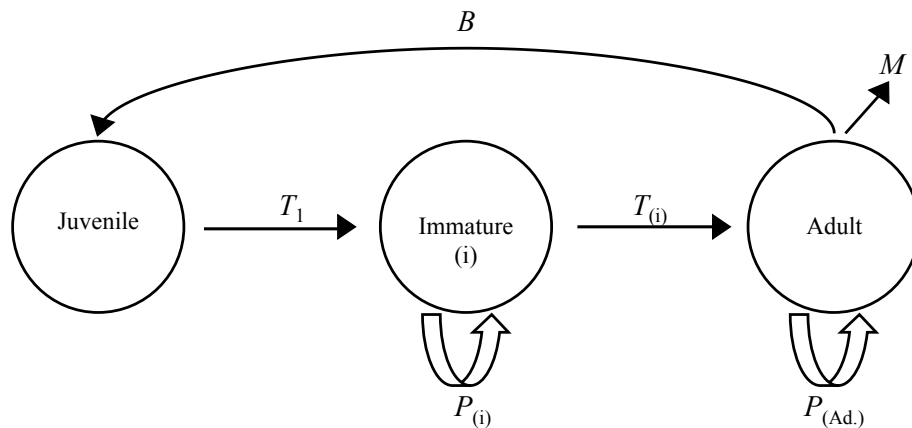
Figure 1. Map of Ireland outlining the location of colonies where censuses were carried out. For Manx shearwaters: High Island (HI), Inishvickillane (INV) and Little Saltee (LS). For European storm petrels: High Island (HI), Beginish (BG) and Inishmurray (INM). For Atlantic puffins: Inishvickillane (INV), Great Saltee (GS), Little Saltee (LS) and Ireland's Eye (IE).

Table 1. Census efforts used to determine population size estimates for Manx shearwaters (*Puffinus puffinus*) and European storm petrels (*Hydrobates pelagicus*) across all sites.

Study Site:	Little Saltee, Co. Wexford	High Island, Co. Galway	Inishvickillane, Co. Kerry	High Island, Co. Galway	Beginish, Co. Kerry	Inishmurray, Co. Sligo
Species:	Manx shearwater	Manx shearwater	Manx shearwater	European storm petrel	European storm petrel	European storm petrel
Study Year	2013	2015	2016	2016	2016	2017
Study Period	20 th May – 6 th July	25 th May – 11 th June	7 th May – 15 th June	17 th July – 11 th August	27 th July – 30 th July	25 th July – 30 th July
Sampling Approach	Random	Random	Clustered	Random	Random	Clustered
Sampling method	Transects (50m x 10m)	Quadrats (30m x 30m)	Circular plots (100m ²)	Transects (50m x 4m)	Transects (50m x 4m)	Transects (50m x 4m)
<i>n</i> burrows subject to playback	5040	1640	1254	-	-	-
<i>n</i> responses received	308	178	224	-	-	-
Response Rate	0.44 (± 0.1)*	0.55 (± 0.068)	0.49 (± 0.03)	0.56 (±0.154)	0.56 (±0.035)	0.58 (±0.02)
<i>n</i> of AOB/AOS on which response rate was measured	Not calculated	30	76	30	30	92
<i>n</i> of repeated measures of response rate	Not calculated	4	9	21	3	3
Area of whole island sampled (%)	100%	38%	16%	11%	100%	14%
Total area of island (Hectares)	Approx. 37	Approx. 42	Approx. 83	Approx. 42	Approx. 14	Approx. 90
*average response rate from Seabird 2000 (Mitchell <i>et al.</i> , 2004)						

Population models

To draw comparisons between the estimates reported here and those reported in Mitchell *et al.* (2004), demographic parameters reported in the literature were used to construct Leslie matrix population models for each species (Leslie, 1945; Caswell, 2001). These models operate by multiplying a vector of population sizes at time t by a matrix of stage-specific demographic parameters, producing a new vector of population sizes at $t+1$. Additionally, matrix models use the number of breeding females in the population which is assumed to be half of the pre-breeding population (Caswell, 2001). Iterations of this process allow the calculation of population growth rates (λ). Because data were not available for our sites, we used weighted averages from other colonies for the following parameters: survival probabilities, productivity, rate of juvenile dispersal, age at first breeding and the rate of skipped breeding events obtained from the literature (Supplementary Tables 1-3). Variation in the demographic parameter estimates across colonies is small, thus the application of these to populations that are distributed in a similar geographical area is thought to be appropriate. Leslie matrices for each species were founded on the life cycle:



where (' T_1 ') is the transition from juvenile to immature₍₁₎ (calculated by: the number of juveniles \times juvenile survival rate \times natal dispersal rate). Across species the number of immature stages differed, thus in some cases 'i' denotes multiple immature years; thus ($P_{(i)}$) is the probability of survival at the immature stage_(i); (' $T_{(i)}$ ') is the transition rate between the final immature stage _(i) to breeding adult (calculated by: number of immatures_(i) \times probability of survival for immatures_(i)). Adult survival probabilities are denoted with ($P_{(Ad.)}$), productivity (B) and the probability of skipped breeding/sabbatical year (M). For many seabird

populations, no data is available for the rate of immigration in these breeding population, thus limiting any inference on the net exchange across these breeding populations and how this effects population growth rates.

In order to estimate the proportions of the population within each age class, we projected the pre-breeding population size estimates across 40 years to determine the stable age structure using matrices built upon the weighted means of all demographic parameters for each species (Table 2). This is necessary as the population estimates obtained from tape-playback surveys/observational counts are those of the breeding adults, not juveniles or immatures. To ensure the life stages had indeed stabilised by 40 years, we visually inspected the graph of proportions as a function of year (Figure 2). These proportions were then used to calculate the number of birds within each age class at time t using the known pre-breeding population size estimates. With these stable age structures, we used an inverse approach to the Leslie matrices to retrodict population size across 1998 – 2016. The inverse approach uses the ‘solve’ in R to run a reverse loop of the constructed Leslie Matrix, thus projecting the known population size backwards in time. The weighted mean of each demographic parameters (Supplementary Tables 1-3) were used to calculate growth rate (λ) values across typical years.

We tested the sensitivity of the population growth rates to stochastic events and anomalies in sea surface temperature (SST) that occur on average every 5 years (Reed *et al.*, 2015; Soldatini *et al.*, 2016). We implemented irregularities in fecundity (productivity (-60%) and incidences of skipped breeding (+7%)) using a Bernoulli distribution (following Soldatini *et al.*, 2016; Monadjem *et al.*, 2018). The changes in these two parameters are representative of the responses observed in other seabird populations (Reed *et al.*, 2015; Soldatini *et al.*, 2016) as long-lived seabirds prioritise adult survival (Miles *et al.*, 2015; Soldatini *et al.*, 2016). λ values were calculated for years where stochastic change was simulated. To further test the sensitivity of the annual growth rates of these populations to the deviations in the demographic parameters, sensitivity coefficients were calculated as outlined in Cuthbert *et al.* (2001). Individually, each parameter was multiplied by 0.95 to simulate a small proportional change of 5%, representing a realistic level of uncertainty (White, 2000). Sensitivity coefficients are reported as the percentage change in population growth rates due to the 5% change.

All models were constructed using the package ‘popbio’ (Stubben *et al.* 2012) in the statistical software ‘R’ (version 3.3.1). Retrospective population estimates and surrounding 95% confidence intervals were estimated using the uncertainties around the initial population estimate at time t and the demographic parameters (Supplementary Tables 1-3). Retrospective projections modelled three incidences of stochastic change/SST anomalies across 1998-2016.

Results

Population size

Breeding population estimates attained from tape-playbacks surveys of Manx shearwaters were 719 (95% CI: 591-847), 818 (95% CI: 660-976) and 2,743 (95% CI: 2296-3190) apparently occupied burrows on Little Saltee, High Island and Inishvickillane respectively. Estimates of the total number of apparently occupied sites of European storm petrels were 3,821 (95% CI: 2980-4663), 75 (95% CI: 70-79) and 280 (95% CI: 88-472) for High Island, Beginish and Inishmurray respectively. The highest whole island total count of individual puffins early in the breeding season were 120, 270, 43 and 6 for Great Saltee, Little Saltee, Inishvickillane and Ireland’s Eye respectively. Estimated population size and the corresponding Seabird 2000 estimates for each colony are outlined in Table 3.

Demographic modelling

Matrix population models were constructed using the weighted averages of demographic parameters reported across several breeding populations of Manx shearwater, European storm petrel and Atlantic puffin. We obtained λ values of 1.016, 1.033 and 1.012 for Manx shearwater, European storm petrel and Atlantic puffin respectively, from the models, indicating an increasing trend in these populations over time. To attain retrodicted population estimates with a high degree of accuracy, we simulated anomalies in fecundity (decreased productivity and increased skipping of breeding) that are thought to occur on average every five years, yielding population growth rates in those years of 0.997, 1.016 and 0.993 for Manx shearwaters, European storm petrels and Atlantic puffins respectively.

These models were used to produce retrospective population estimates for each breeding population (Table 3; Figure 3). Sensitivity analyses indicated that adult survival was the most important parameter in the matrix population models for all species, producing larger declines in population growth rates compared to all other parameters (Table 4).

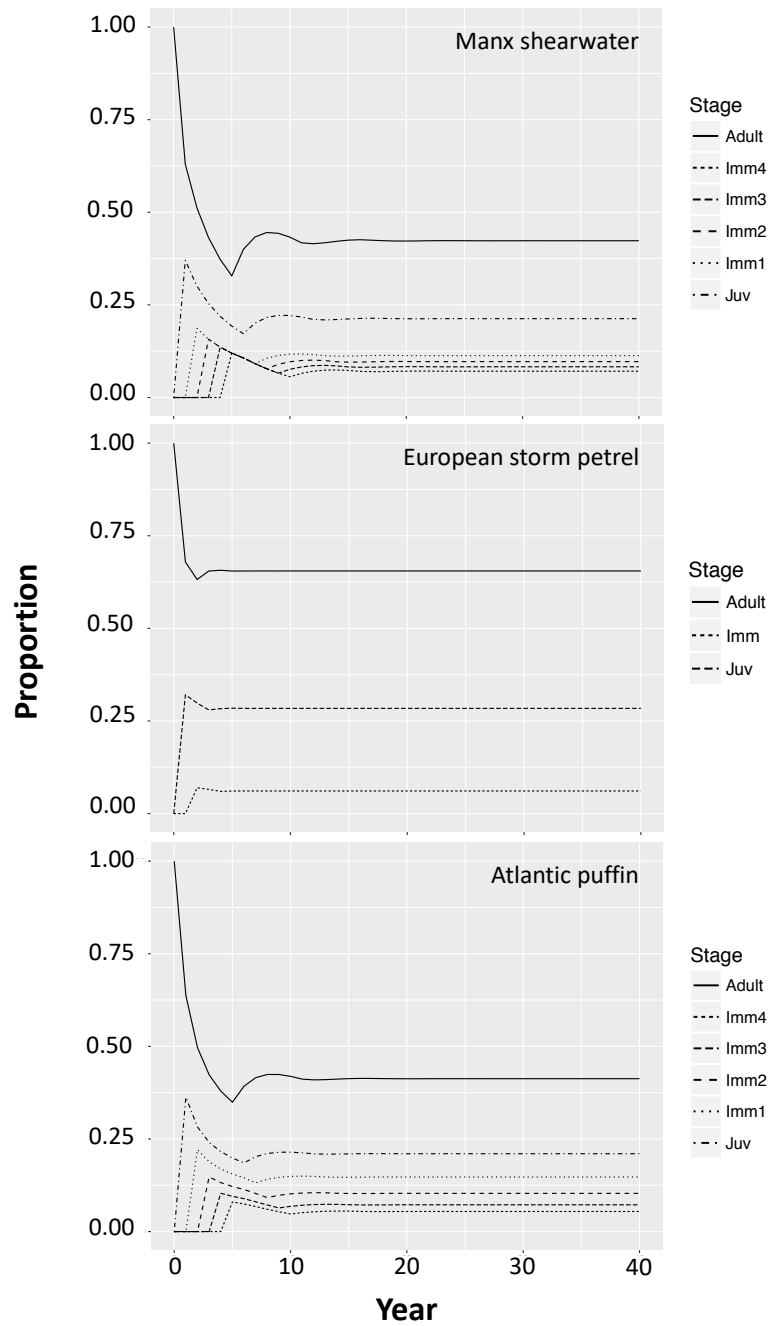


Figure 2. Graph showing the stable age structure of each species determined by the projection of Leslie Matrix population models over 40 years. Models used the pre-breeding estimates of adult population size reported in this study.

Table 2. Proportions used for the stable age distribution as determined by each matrix population model built on demographic parameters in the literature (Supplementary Tables 1-3).

<i>Stage</i>	<i>Manx shearwater</i>	<i>European storm petrel</i>	<i>Atlantic puffin</i>
<i>Juveniles</i>	0.213	0.284	0.210
<i>Immature stage 1</i>	0.113	0.061	0.147
<i>Immature stage 2</i>	0.097	-	0.103
<i>Immature stage 3</i>	0.083	-	0.072
<i>Immature stage 4</i>	0.071	-	0.054
<i>Breeding Adult</i>	0.423	0.655	0.413

Table 3. Seabird 2000 estimates, recent population size estimates and retrospective projection of population estimates of breeding Manx shearwaters, European storm petrels and Atlantic puffins on several offshore islands in Ireland.

<i>Species</i>	<i>Island</i>	<i>Seabird 2000 estimate¹ (1998-2002)</i>	<i>Recent estimate (2015-2017)</i>	<i>Retrospective estimate (1998-2002)</i>
<i>Manx shearwater (AOB (95% C.I.))</i>	Little Saltee	100	719 (591- 847)	557 (406-757)
	High Island	22	818 (660-976)	634 (503- 744)
	Inishvickillane	643	2,743 (2296-3190)	2126 (1477-2670)
<i>European storm petrel (AOS (95% C.I.))</i>	Beginish	450	75 (70-79)	45 (41-49)
	High Island	60	3,821 (2980-4663)	2279 (1403-3156)
	Inishmurray	n.c	280 (88-472)	169 (32-302)
<i>Atlantic puffin (Individuals (95% C.I.))</i>	Great Saltee	1522	120	106 (78-141)
	Little Saltee	300	270	235 (175-319)
	Inishvickillane	56	43	37 (27-51)
	Irelands Eye	n.c	6	5 (3-7)

¹Mitchell *et al.* (2004); n.c = not counted

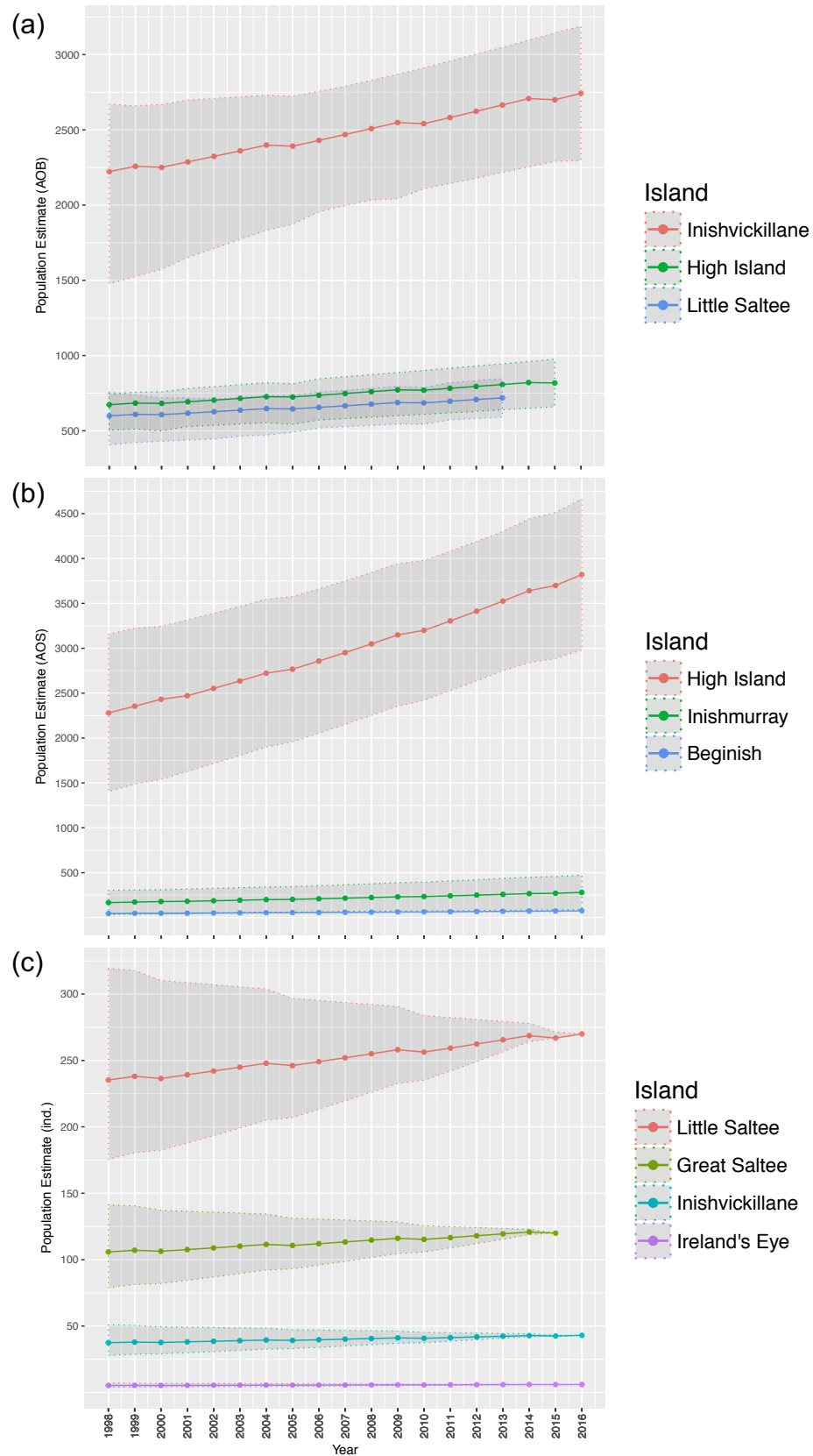


Figure 3. Retrospective population estimates of breeding (a) Manx shearwaters (AOB), (b) European storm petrel (AOS) and (c) Atlantic puffin (individuals) on several Irish colonies determined by population growth rates (λ) from Leslie matrices. Shaded area represents the 95% confidence interval from variation in demographic parameters and initial population estimate.

Table 4. Sensitivity analyses of population growth rates (% change in λ values) when subjected to 5% decline in the weighted mean of demographic parameters used to construct Leslie matrices for three burrow-nesting seabirds in Ireland.

<i>Parameter</i>	<i>Manx shearwater</i>	<i>European storm petrel</i>	<i>Atlantic puffin</i>
<i>Adult survival</i>	-2.9	-4.5	-3.4
<i>Fecundity</i>	-0.4	-0.3	-0.3
<i>Immature survival</i>	-1.6	-1	-1.2
<i>Skipped breeding (M)</i>	-0.4	-0.3	-0.3

Discussion

This study aimed to attain accurate breeding population estimates of several Manx shearwater, European storm petrel and Atlantic puffin colonies in Ireland. These estimates were notably different to previous estimates reported in Mitchell *et al.* (2004) across all colonies. New Manx shearwater estimates were larger than previous surveys, whilst lower numbers of puffins were recorded. A combination of higher and lower estimates between new and previous census efforts was seen across European storm petrel colonies. We discuss the differences in the two censuses considering the retrodicted population size estimates from Leslie matrix models, and the variation in demographic parameters that could explain our findings.

Across all Manx shearwater colonies and one European storm petrel colony censused here, population sizes were previously vastly underestimated in Mitchell *et al.* (2004). Assuming accurate estimates were produced in both censuses, population growth rates of Manx shearwaters would need to range from 1.23 - 2.18, and the European storm petrel colony on High Island would have required an annual growth rate of 3.88. Such population growth rates are unrealistic for seabirds, as they produce few offspring (Brooke, 1990), demonstrate delayed maturation (Harris, 1983) and show little breeding dispersal (Cadiou *et al.*, 2010). Population growth rates in seabirds are not expected to exceed 1.1 (Hatch, 2003; Wanless *et al.*, 2005; Horswill and Robinson, 2015). The discrepancies in population size estimates for colonies with seemingly enormous population

growth are likely a result of differences in census methods, as population size estimates can differ significantly across two censuses when the sampling approaches are inconsistent (Smith *et al.*, 2001; Perrins *et al.*, 2012; Arneill *et al.*, 2018 – Chapter 2). Due to a lack of detail reported in the methods used during Seabird 2000, exact comparison of the sampling approaches is not possible. Though the difference in field effort (< 3 days per island in Seabird 2000 and 11-42 days in those reported here) suggests that more area was sampled during recent surveys, yielding more accurate estimates (Mitchell *et al.*, 2004; Arneill *et al.*, 2018 – Chapter 2).

The difference in population size estimates of European storm petrels on High Island is likely due to a sampling bias during Seabird 2000 where tape-playback efforts were restricted to the island's stone walls and ruins (Mitchell *et al.*, 2004; Steve Newton, pers.comm.). The expansion of the tape-playback sampling across the island showed that European storm petrels predominantly breed in the dense dry-heath grassland that is widespread across the island (Arneill *et al.* 2018 – Chapter 3). The smaller population estimate on Beginish is likely due to one, or a combination, of two factors: (i) the sampling approach and (ii) the recent introduction of grazing livestock to the island. Differences in sampling approaches and efforts between two censuses have been shown to produce large discrepancies in the population estimates attained (Perrins *et al.*, 2012; Arneill *et al.*, 2018 – Chapter 2). However, the latter is more likely the causal factor, as the introduction of livestock to burrow-nesting seabird colonies significantly reduces the availability of suitable breeding habitat (Rayner *et al.*, 2007; Pinet *et al.*, 2009). Furthermore, Beginish is a small island (approximately 14 hectares) and little effort is required to obtain an accurate estimate of population size. Inishmurray was not surveyed during Seabird 2000, therefore no comparisons could be made to any previous census.

The retrospective projection of Atlantic puffin populations suggests there should have been an increasing trend in these populations from 1998-2016. Yet a lower number of Atlantic puffins were recorded on all sites compared to those reported in Mitchell *et al.* (2004). The confidence interval surrounding the retrospective projections on Little Saltee and Inishvickillane show that known variation in demographic parameters may explain the observed population decline in these

colonies. The variation in population growth rates is primarily due to the variable productivity rates in this species that are particularly sensitive to changes in the quantity and quality of available prey to provision young (Wanless *et al.*, 2005; Breton and Diamond, 2014). These changes in population size estimates are consistent with the declining trends observed in other colonies (Harris *et al.*, 1998; Mavor *et al.*, 2008; Miles *et al.*, 2015) and support the species recent classification as “Endangered” at the European scale on the IUCN red list of threatened species (IUCN, 2015).

The decline observed on Great Saltee however is much larger than that of the retrodicted population size estimates and their surrounding 95% confidence intervals. Here both estimates are expected to approximate the true population size as whole-island observational counts are less susceptible to sampling error than other methods (Walsh *et al.*, 1995). This finding is similar to trends reported on Fair Isle across a comparable time frame (1986-2012), whereby observational counts indicated a population decline of approximately 50% while demographic models predicted a growth in the population (Miles *et al.*, 2015). The authors concluded that low recruitment of immatures into the breeding population was the most probable mechanism of change, and demonstrated this by modelling low immature survival and high immature dispersal rates. Modelling the changes outlined by Miles *et al.* (2015) on the Atlantic puffin population on Great Saltee does not explain the change in population size observed here. To simulate the decline on Great Saltee, the changes in these immature parameters need to be accompanied by significantly reduced productivity (approximately -90%) or a reduction in adult survival (approximately -10%) (see Figure 4).

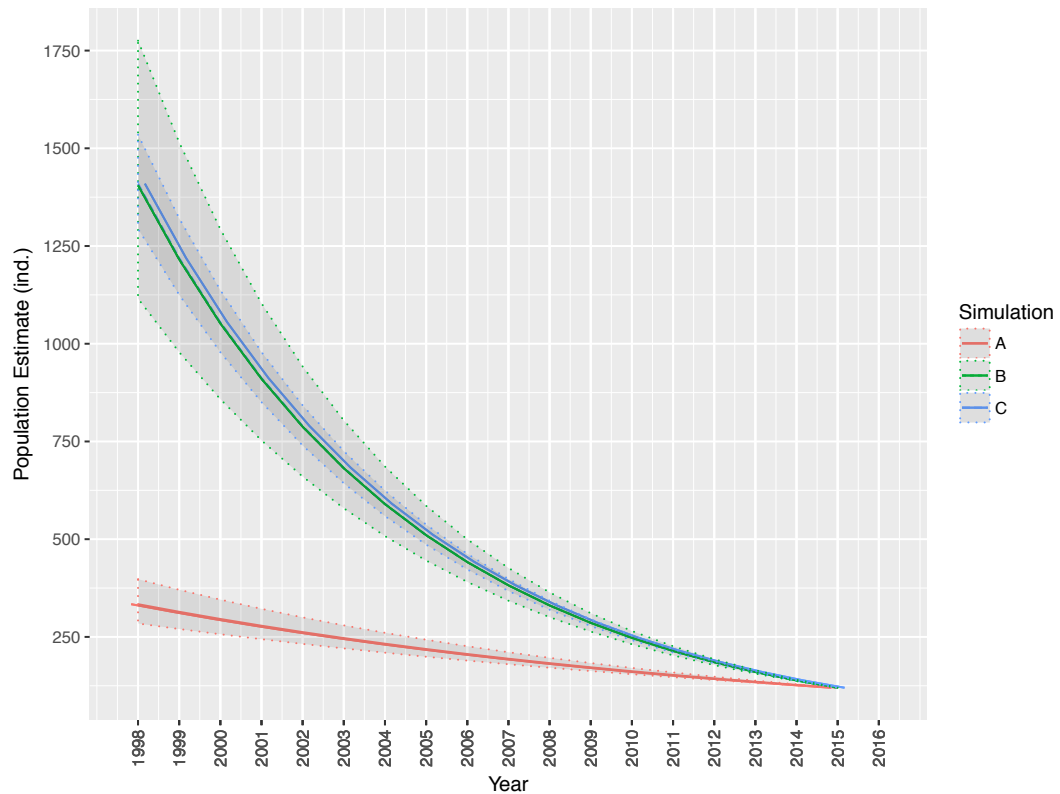


Figure 4. Simulations of the possible changes in demographic parameter driving the decline in the Atlantic puffin population on Great Saltee, Co. Wexford. Simulation A demonstrates reduced immature survival and increased immature dispersal as per Miles *et al.* (2015). Simulation B builds on simulation (A) with a 10% reduction in adult survival and simulation (C) combines simulation (A) and a 90% reduction in productivity rates.

Reduced productivity or adult survival rates within the breeding population on Great Saltee is plausible due to the population of Brown rats (*Rattus norvegicus*) on the island (Kelly *et al.*, 2008). Expanding populations of avian and mammalian predators alter the demographic parameters of these populations, whereby increased predation events result in reduced adult survival, productivity and recruitment rates (Jones *et al.*, 2008; Finney *et al.*, 2003; Miles *et al.*, 2015). For example, in another Auk species (*Aethia pusilla*) the lowest productivity rates ever recorded for this species (0.09–0.16 chicks fledged) were linked to the disruption of adults attempting to brood or provision young chicks by rats (Major *et al.*, 2006). The impact of rats on the breeding populations of seabirds has been widely reported (McChesney and Tershy, 1998; Martin *et al.*, 2000; Fukami *et al.*, 2006; Mulder *et al.*, 2009) and successful eradication programmes have prevented island extinctions (Taylor *et al.*, 2000; Pascal *et al.*, 2008). Further study is required to

determine the exact cause of the decline on Great Saltee and the conservation efforts required to prevent further declines.

This study demonstrates the use of retrospective population modelling to infer the historic population size of these colonies. Our models are thought to be accurate as they produced population growth rates similar to those of other long-lived species and the sensitivity analyses demonstrated that adult survival was the most important demographic parameter (Brault and Caswell, 1993; Gaillard *et al.*, 1998; Monadjem *et al.*, 2012; Soldatini *et al.*, 2016; Monadjem *et al.*, 2018). Several factors limit our ability to draw solid conclusions from these modelling efforts. Firstly, the availability of population size estimates meant that an estimate obtained from a single breeding season had to be used. One might suggest that the year of the original census in Seabird 2000 or more recent censuses may have been conducted in an atypical year, though long-term datasets such as that reported in Miles *et al.* (2015) and the low incidences of skipped breeding (Supplementary Tables 1-3) suggest that the difference in population sizes from year to year are not sufficient to explain the differences in population sizes estimates reported here. Furthermore, the underlying assumption that the colonies in which demographic parameters were available are representative of these breeding populations produces considerable uncertainty, despite the low variation around the values reported in the literature. Further work to adapt these models to site specific parameters would increase the accuracy of these projections, highlighting the importance of constant monitoring plots at key sites.

We present compelling evidence that the population size estimates of burrow-nesting Procellariiformes in Ireland were vastly underestimated in Seabird 2000. The extent to which the national estimates of these populations are underestimated cannot be quantified because factors that determine colony size often vary temporally and spatially across a species range. However, our findings are strengthened by recent national abundance estimates of Manx shearwaters of 88,491 (95% CI: 60,155 - 116,942) individuals reported from offshore aerial surveys (Rogan *et al.*, 2018). These numbers are likely to be even higher as these surveys omitted some coastal areas off the south west coast where huge numbers of Manx shearwaters are known to breed (Mitchell *et al.*, 2004). Estimates of Atlantic puffin population sizes reported here support growing evidence of the

decline in the breeding populations of this species (IUCN, 2015; Miles *et al.*, 2015). This is particularly true for Great Saltee, where we show that the observed population change is likely due to significantly reduced productivity or lowered adult survival. The omission of site level data on the spatial distribution of sampling prevented direct comparison and replication of censusing, highlighting the necessity of the standardisation and reporting of detailed census methods. Thus, it is essential that considerable effort is put into the next census of these species to establish reliable baseline estimates.

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Supplementary Material

Supplementary Table 1. Parameter values used to construct Leslie matrix population models for retrospective projection of populations of breeding Manx shearwater (*Puffinus puffinus*).

Demographic Parameter	Weighted Mean	Standard Dev.	Sources
Age-specific survival:			
<i>Juvenile (0-1 years)</i>	0.61	0.07	1,2
<i>Immature (1-2 years)</i>	0.87	0.08	3
<i>Immature (2-3 years)</i>	0.87	0.08	3
<i>Immature (3-4 years)</i>	0.87	0.08	3
<i>Immature (4-5 years)</i>	0.87	0.08	3
<i>Adult (5 +)</i>	0.87	0.08	3
Productivity (Average across British Isles)	0.697	0.04	3,5
Recruitment age	5		6
Skipped breeding	0.157		7
Dispersal			
<i>Natal</i>	0.25 (females)		4,6
<i>Adult</i>	Low		
1. Cuthbert <i>et al.</i> , 2001; 2. Brooke, 1990; 3. Büche <i>et al.</i> , 2013; 4. Brooke, 1978; 5. Mavor <i>et al.</i> , 2008; 6. Harris, 1966; 7. Perrins <i>et al.</i> , 1973 (Horswill and Robinson, 2015)			
For a list of all individual values and sources see the supplementary material of the JNCC report: Horswill, C. & Robinson, R.A., (2015), Review of Seabird Demographic Rates and Density Dependence, JNCC Report 552, ISSN 0963-8901			

Supplementary Table 2. Parameter values used to construct Leslie matrix population models for retrospective projection of populations of breeding European storm petrel (*Hydrobates pelagicus*).

Demographic Parameter	Weighted Mean	Standard Dev.	Sources
Age-specific survival:			
<i>Juvenile (0-1 years)</i>	0.222		1
<i>Immature (1-2 years)</i>	0.90		1
<i>Adult (3 +)</i>	0.949		1
Productivity	0.448	0.05	2
Recruitment age	3		1
Skipped breeding	0.04		1
Dispersal			
<i>Natal</i>	0.06		3
<i>Adult</i>	Unknown		
1.Soldatini <i>et al.</i> , 2016; 2. de León and Minguéz, 2003; 3. Cadiou <i>et al.</i> , 2010			

Supplementary Table 3. Parameter values used to construct Leslie matrix population models for retrospective projection of populations of breeding Atlantic puffin (*Fratercula arctica*).

Demographic Parameter	Weighted Mean	Standard Dev.	Sources
Age-specific survival:			
<i>Juvenile (0-1 years)</i>	0.709	0.022	1
<i>Immature (1-2 years)</i>	0.709	0.022	1
<i>Immature (2-3 years)</i>	0.709	0.022	1
<i>Immature (3-4 years)</i>	0.76	0.019	1
<i>Immature (4-5 years)</i>	0.805	0.017	1
<i>Adult (5 +)</i>	0.906	0.02	2-4
Productivity (Average across British Isles)	0.61	0.15	4-9
Recruitment age	5		8,10
Skipped breeding	0.078		8
Dispersal			
<i>Natal</i>	0.23		10
<i>Adult</i>	0.04	0.04	1,8,11
1.Breton <i>et al.</i> , 2006; 2.Harris <i>et al.</i> , 2005; 3.Lahoz-Monfort <i>et al.</i> , 2011; 4.Baer <i>et al.</i> , 2010; 5.Shaw <i>et al.</i> , 2010; 6.Mavor <i>et al.</i> , 2008; 7.Newell <i>et al.</i> , 2010; 8.Ashcroft, 1979; 9.Harris, 1980; 10.Harris, 1983; 11.Kress and Nettleship 1988. (Horswill and Robinson, 2015)			
For a list of all individual values and sources see the supplementary material of the JNCC report: Horswill, C. & Robinson, R.A., (2015), Review of Seabird Demographic Rates and Density Dependence, JNCC Report 552, ISSN 0963-8901			

Chapter 6

General Discussion

For many seabird populations, we lack baseline population size estimates as several of their life history characteristics and their widely distributed colonies make them difficult to census (Croxall *et al.*, 2012; Paleczny *et al.*, 2015; IUCN, 2015). This is particularly true for burrow-nesting species that have proved to be the most difficult seabirds to census as they are inconspicuous in their burrows, often coexist with multiple burrowing species, and many are only active within the colony at night (Smith *et al.*, 2001; Perrins *et al.*, 2012; Opper *et al.*, 2014). Our lack of knowledge in the size and status of these populations is a major limitation in their conservation as these species are particularly vulnerable to threats such as introduced mammalian predators and habitat destruction (Major *et al.*, 2006; Rayner *et al.*, 2007; Jones *et al.*, 2008). Accurate data on the size and status of these populations allows us to make links to such threats and therefore allows appropriate conservation action to be taken in a timely manner (Capizzi *et al.*, 2010; Watson *et al.*, 2014).

Ireland is obligated under Articles 10 and 12 of the EU Birds Directive (Directive 2009/147/EC) to protect its seabird populations and yet does not have reliable population estimates, let alone trends, for burrow-nesting seabird species. This is true for many countries whereby the population sizes of many burrow-nesting seabirds remains unknown. To gain a better understanding of Ireland's burrow-nesting seabird populations, this research aimed to further our knowledge of how to accurately census and monitor three burrow-nesting species in Ireland: the Manx shearwater (*Puffinus puffinus*), the Atlantic puffin (*Fratercula arctica*) and the European storm petrel (*Hydrobates pelagicus*). We found that extensive sampling efforts are required to obtain accurate population estimates of these species when sampling is carried out in a random manner, but the accuracy of estimates can be dramatically improved using prior knowledge of the distribution of breeding burrows (**chapter 2**). Furthermore, understanding these species habitat and topographical preferences can accurately predict their breeding distributions

and guide these censuses using species distribution modelling (**chapter 3**). Although the use of traditional methods requires considerable field effort (**chapter 2,3,5**), they are necessary to determine the efficacy and scope of emerging automated approaches (**chapter 4**). The work as a whole improves our understanding of how best to census and monitor burrow-nesting species (**chapters 2,3,4**). Specifically in the Irish context, current knowledge of the size and status of these species populations is unreliable (**chapter 5**), combining the findings of the work carried out here with existing knowledge, aids in the revision and standardisation of the methods to census and monitor these species in the future (**Appendix Section 1**).

In this chapter, I discuss the findings of the previous chapters in the context of (1) censusing and (2) monitoring these three burrow-nesting seabirds. I highlight some of the issues faced while undertaking this research, discuss the broader scope of these findings and present some direction for future work in this field.

6.1 Census methods

In general, this thesis demonstrates that at the site level a considerable amount of fieldwork is required to determine the baseline distribution and population size data of burrow-nesting species with a high degree of accuracy. The approach used to obtain this baseline data is dependent on the species and the site being surveyed. Here I outline how the work presented in my thesis furthers our understanding of various methodologies and the sampling approaches used across these species.

6.1.1 *Manx shearwaters and European storm petrels*

The tape-playback method developed by James and Robertson (1985) has been widely adopted as the standard methodology across many breeding colonies of Manx shearwaters and European storm petrels (Ratcliffe *et al.*, 1998; Smith *et al.*, 2001; Murray *et al.*, 2003; Bolton *et al.*, 2010; Perrins *et al.*, 2012; Perkins *et al.*, 2017^a). The method has since been adapted to increase the response rate by changing the origin, sex, quality and duration of the recorded calls used (Ratcliffe *et al.*, 1998, Brown *et al.*, 2006; Perkins *et al.*, 2017^a). These changes to the method improve our confidence in receiving a response from an occupied burrow and

therefore somewhat reduce the confidence intervals surrounding populations estimates. However, our findings in **chapter 2** suggest that a more immediate priority is the revision of the fundamental sampling strategies that underpin these censuses. Explicitly, the marginal reduction in confidence intervals due to an increased response rate is meaningless if low levels of random sampling are used that produce huge uncertainty around estimates. This is particularly true if it is necessary to spend more time at each burrow to increase the response rate, necessitating more time in the field to sample the same area (Perkins *et al.*, 2017^a). Thus future censuses should focus on the size of area that is logistically feasible to sample on the site before carrying out the survey and refining methodologies for a marginal increase in the response rate.

The work in **chapter 2** built on a discussion point of Perrins *et al.* (2012) who briefly deliberated the potential causes of the large differences in population size estimates across two censuses of Manx shearwaters on Skomer, the largest known breeding colony of this species (Smith *et al.*, 2001). Moreover, the need for this work to be carried out was strengthened by the discrepancies between population size estimates reported here and those of Seabird 2000 (**chapter 5**). We demonstrated that *a priori* knowledge of the distribution and density of breeding birds can be used to design stratified approaches to tape-playback surveys that dramatically improve our confidence in abundance estimates (**chapter 2**). These findings are not solely pertinent to Manx shearwaters, but also applicable across species with similar patchily distributed breeding sites with high site fidelity, including the European storm petrel. To determine what drives these distributions, in **chapter 3**, we explored several environmental gradients using ensemble species distribution models and showed that habitat assessments and digital elevation models can be used to predict the distribution of these species. The accuracy of these model predictions suggest that this method can be used to define priority areas for censusing. Moreover, model predictions highlight areas where breeding is unlikely to occur, further reducing the area to be sampled. The scope and limitations of this research are discussed in detail in **chapter 3**, where we suggest that further training data from different islands would introduce more habitat types and topographical variables, increasing confidence in the transferability of these models across a wider range of islands.

The timing of effective tape-playback surveys has been discussed in the literature and is directly linked to the phenology, whereby response rates are highest during the incubation and chick-guarding stages (James and Robertson, 1985; Ratcliffe *et al.*, 1998). Here, all Manx shearwater surveys were carried out from mid-May until mid-June and the measured response rates were comparable to those of other censuses (Murray *et al.*, 2003; Mitchell *et al.*, 2004; Perrins *et al.*, 2012; **chapters 2,3,5**). Across the European storm petrel surveys, ambiguity around the appropriate timing of tape-playbacks necessitated some exploratory work during the initial census on High Island in 2016. To determine when response rates were highest, tape-playbacks were repeated three times every second day on 30 apparently occupied sites during the survey period (19th of July to the 31st of July) when response rates were thought to be highest (Steve Newton, pers. comm.). We found the response rate peaked in the last week of July (Figure 1), was higher than those reported in previous studies (Ratcliffe *et al.*, 1998; Bolton *et al.*, 2010) and similar across the censuses (**chapter 3,5**). This trial advocates future research in determining the variation in response rates both temporally and across multiple colonies to inform future censuses. For example, a study could be done across this species range to determine if these peaks in response rate vary across latitudes with phenology (Parmesan, 2007).

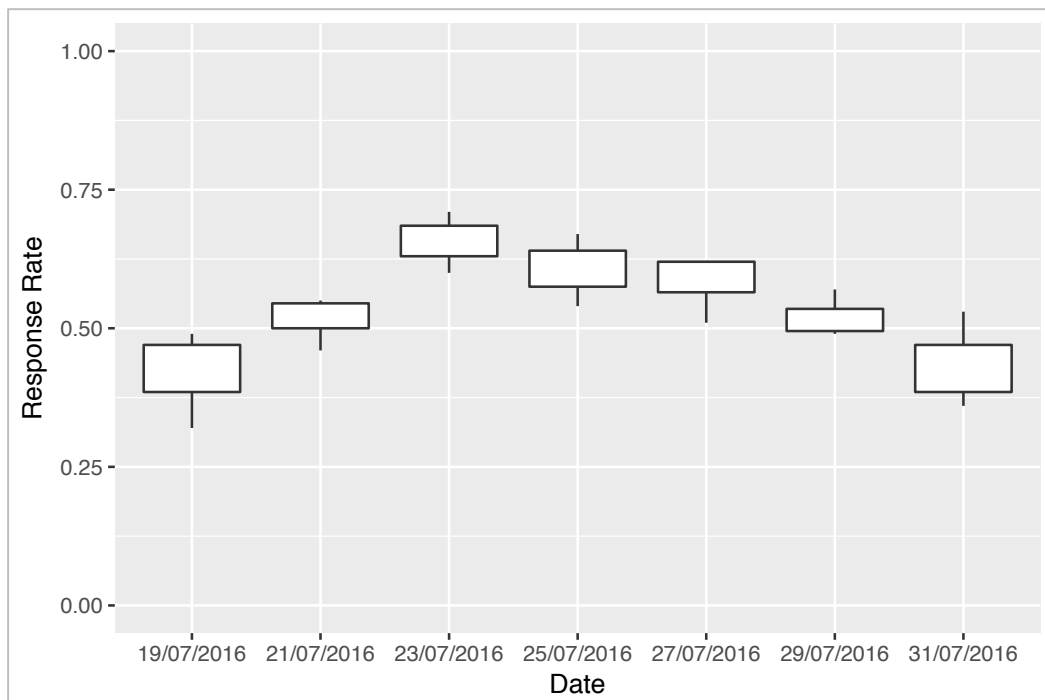


Figure 1. Variation in European storm petrel response rates over on High Island in 2016.

Publications on the use of alternative methods to estimate population size of burrow-nesting Procellariiformes are generally limited since the widespread uptake of the tape-playback method. In **chapter 4** we examined the efficiency of passive acoustic monitoring in determining local breeding density of Manx shearwaters. Our work, based on that of Oppel *et al.*'s (2014) study on Cory's shearwater (*Calonectris borealis*), did not find the expected relationship between acoustic activity and local breeding density across the Manx shearwater colony on High Island, Co. Galway. Our results suggests that consistent flyways across the colony drive the soundscape, rather than the density of birds breeding within areas. Further work should explore the transferability of passive acoustic monitoring as a census method across Procellariiformes. While current restrictions on the battery capacity in GPS technology limits the scope of tracking the fine scale movements of seabirds within colonies, we present a novel application of telemetry data on which further work should be built to examine the movement within colonies.

6.1.2 Atlantic puffins

The Seabird Monitoring Handbook (Walsh *et al.*, 1995) recommends the use of signs of occupancy as the standard methodology for Atlantic puffins, advising that observational counts should only be used when burrows are inaccessible for inspection. These methods reported in Walsh *et al.* (1995) are informed by work on well-studied islands such as the Isle of May, Scotland (Harris, 1980;1984) and Røst, Norway (Ankler-Nilsson and Røstad, 1993). Two points should be considered in respect to carrying out surveys for signs of occupancy, (i) the accessibility of burrows across the island(s) to be censused and (ii) the number of burrow-nesting species breeding on the island(s). For example, on three of the four colonies censused here, breeding burrows were located on inaccessible steep slopes or coastal cliffs. Furthermore, three of the four colonies host breeding populations of Manx shearwaters (**chapter 5**). Therefore to ensure comparable results across sites, the density and distribution data reported in my thesis were obtained from whole-island observational counts (**chapter 3 and chapter 5**).

Access to some of the breeding burrows on Great Saltee, Co. Wexford allowed for some experimental work on the signs of occupancy method, albeit an insufficient amount to include as a stand-alone chapter in my thesis. We used a burrowscope

(Sextant Technology Ltd., New Zealand) to sample 108 and 137 accessible burrows within breeding areas of Atlantic puffins in 2016 and 2017 respectively. We found that the majority of burrows that had signs of occupancy were empty, while those that were occupied contained either Atlantic puffins or Manx shearwaters (Figure 2). Although these data may have been influenced by some unusual factor, for example, especially high failure early in those seasons, these findings suggest that in heterogenous colonies, signs of occupancy may not be an appropriate counting method due to the inability to differentiate species (Rayner *et al.*, 2007). Future work on islands where large numbers of breeding burrows are accessible is required to draw definitive conclusions. Furthermore, burrowscoping should be carried out early in the season to include those birds that potentially fail in their breeding attempt as the season progresses.

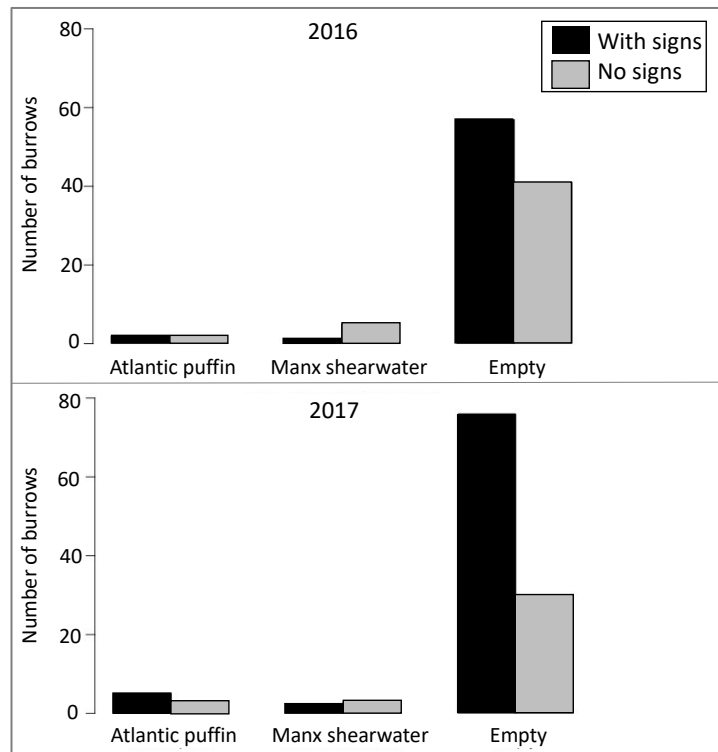


Figure 2. Graph showing the number of burrows (with and without traditional signs of occupancy) examined using a burrowscope (Sextant Technology, Ltd) on Great Saltee, Co. Wexford that were occupied by Atlantic puffins, occupied by Manx shearwaters or empty.

Further work is essential to establish the extent of the issue with the signs of occupancy method highlighted here and should be carried out on sites where this method is regularly employed (e.g the Isle of May). Moreover, counts of

apparently occupied burrows through the signs of occupancy method requires access to colonies early in the breeding season (March) to produce accurate population size estimates (Harris, 1984). Access this early in the year is often restricted on many sites due to weather conditions. Based on the fact that this preliminary work found high rates of unoccupied burrows, and the possibility of erroneously counting different species using the signs of occupancy method, we suggest that it is appropriate that observational counts are used in national census efforts as a transferable and therefore standardised method of obtaining population size estimates for this species (**Appendix Section 1**).

Burrow-nesting seabirds are globally distributed and the findings outlined in my thesis, with the exception of chapter 5, are applicable to the burrow-nesting species that are distributed and studied in many countries including New Zealand, Iceland, Norway and the United States (Ankelr-Nillsen and Røst, 1993; Major *et al.*, 2006; Buxton and Jones, 2012; Croxall *et al.*, 2012; Borker *et al.*, 2014; Paleczny *et al.*, 2015). Specifically, the conclusions drawn on censusing these species from the analyses in **chapter 2**, and the modelling approach in **chapter 3**, are directly transferable to the majority of burrow-nesting species that are patchily distributed and show high site fidelity. The drivers of the distribution of breeding burrows will vary across species (**chapter 3**) and therefore models should be adapted for each species within their respective breeding ranges to ensure accurate predictions can be made. These predictions can inform censuses to establish the baseline distribution and density across breeding colonies, on which repeat censuses can be designed in a multi-stage stratified approach (**chapter 2**). While it is clear from **chapter 4** that passive acoustics cannot quantify the population size of all Procellariiformes, further work should explore this relationship and that of the flight paths first reported here.

6.2 Monitoring methods

Current monitoring programmes for Manx shearwater, European storm petrel and Atlantic puffin across the British Isles are restricted to several colonies in Britain (Mavor *et al.*, 2008). In the Republic of Ireland, reports on population changes are limited to the difference in estimated population sizes across the national censuses of Atlantic puffin (Mitchell *et al.*, 2004). The extent to which conclusions can be

drawn from changes observed between these censuses is dependent on the consistency of sampling used at the site level (**chapter 2,5**). Furthermore, conclusions with regards to the changes in the national population size should not be made, as population trajectories differ at the site level (**chapter 5**). One of the aims in **chapter 2** was to determine what sampling is required to establish an effective monitoring strategy for these species in Ireland. The findings suggest that the placement of monitoring plots within areas of highest density is necessary to detect population declines and ensure conservation action can be taken in a timely manner. Thus, accurate baseline information on the distribution and density of these birds across sites to be monitored is necessary to ensure monitoring plots are appropriately placed.

Existing monitoring practices for these species are likely failing to detect population level changes due to the random selection of monitoring plots. For example, on Skomer, Manx shearwaters are monitored within twenty fixed plots every year. Density of breeding birds varies substantially across these monitoring plots, ranging from 2 AOB to 218 AOBs in 2017 (Büche *et al.*, 2013). The analyses reported in **chapter 2** shows that this approach has less than 50% chance of detecting a population decline of 10% between years. Furthermore, this approach only has sufficient power (> 0.8) when the population level declines are as high as 50%. Similarly, attempts to quantify population level change on Rum showed that the random selection of over 50 plots failed to produce any meaningful conclusions on population level changes (Thompson and Thompson, 1980; Thompson, 1987). The findings in **chapter 2** give direction for the establishment of monitoring plots in Ireland, but also highlight how existing monitoring programmes globally can be revised to ensure effective monitoring of burrow-nesting species with similar breeding characteristics.

In **chapter 4** we show that automated monitoring techniques may provide an alternative strategy of monitoring populations through acoustic indices. These findings supported that of previous work (Buxton and Jones, 2012; Borker *et al.*, 2014; Dufour *et al.*, 2016), though the extent to which this recently established method can accurately describe changes necessitates long-term study. In **chapter 5** we demonstrated how demographic parameters such as productivity and survival rates can be used, highlighting that monitoring programmes should not solely

focus on changes in the density of breeding birds. Measuring these demographic parameters in Ireland would allow more confident inference to be made from future modelling of population trajectories (**chapter 5**). These models can then be built and used to determine how management approaches in Ireland can be adapted to conserve these species. For example, across several threatened species these models have been used to determine the best approach to mitigate population declines due to threats such as by-catch (Meyer *et al.*, 2015), habitat loss (Flockhart *et al.*, 2015) and disease (Rhodes *et al.*, 2011).

6.3 Summary of future work

These findings suggest that a review of the existing methodologies in place for censusing and monitoring species that are patchily distributed with high site fidelity at a global scale is a logical next step. Reviewing these efforts would highlight areas that require revision to ensure standardised, and therefore comparable, approaches are used across these populations (**chapter 2 and chapter 5**). Further work is necessary to acquire habitat data and expand LiDAR data to offshore islands, this would permit the construction of species distribution models at such fine-scales as outlined in **chapter 3**. The expansion and collation of this data across multiple species and multiple colonies could inform a model for predicting the distribution of suitable burrowing areas, not specific to a single species. Such a model could guide future censuses on islands where presence or absence of breeding burrow-nesting seabirds is unknown. Future work in passive acoustic monitoring (**chapter 4**) across multiple colonies and species should explore two factors: (i) the number of acoustic monitoring stations and (ii) the number of recording nights required to understand the variation across years and across sites, the former is likely to vary with the size of the site to be monitored.

More immediately, accurate population size estimates should be obtained across breeding colonies using a standardised framework that considers the findings reported in my thesis (**Appendix Section 1**). The Republic of Ireland is in a position where the priority should be to establish and report more accurate populations size estimates of these species across all known colonies. A logical first step would be to target key breeding sites for these species (**Appendix Section 2 Table 1**) outlined as important colonies in Mitchell *et al.* (2004). In order to

establish accurate estimates, realistic targets should be outlined that fall within the resources available for survey efforts. As an example, Table 2 in Section 2 of the Appendix highlights the cost associated with surveying Manx shearwaters on High Island in 2015 (**chapters 2,3,5**). Estimated costs can be adapted to the number of available observers and the survey duration. At the national scale, multiple teams of multiple observers should be deployed to carry out surveys within the three distinct areas around Ireland; the Irish sea and the east Celtic sea, the south west and the west Celtic sea, and the west coast. Once accurate baseline data on the distribution and density of breeding burrows are obtained, effective regular monitoring plots can be established.

6.4 Conclusions

In conclusion, it is essential that the brief census methods reported in the Seabird Monitoring Handbook (Walsh *et al.*, 1995) for Manx shearwater, European storm petrel and Atlantic puffin, and potentially other burrow-nesting species such as Leach's storm petrel are revised. As highlighted in this thesis, standardisation of the approaches used across breeding populations and across censuses is essential to produce comparative datasets from which conclusions can be drawn. We demonstrated how existing methods such as tape-playbacks can be used in different sampling approaches that significantly reduce the amount of fieldwork required to obtain accurate abundance estimates. Furthermore, strata in relation to the density of breeding birds can be defined by areas of favourable habitat, and predicted distributions can be obtained through species distribution modelling. More research will be required to determine the scope of automated techniques that aim to reduce these labour intensive surveys. Finally, we present a draft Irish Wildlife Manual (**Appendix Section 1**) outlining suggested census methods to obtain accurate estimates of these breeding populations. Ideally the approaches outlined in this manual would be adopted across each species' breeding range to produce comparative data on which definitive conclusions can be drawn on the size and status of their breeding populations.

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7. Appendix

Section 1

The following Irish Wildlife Manual (in prep) was drafted for the National Parks and Wildlife Service to provide logistically feasible options to carry out the national censusing of burrow-nesting seabirds for the Seabird 4 (Seabirds count) census.

This document is formatted as per the guidelines outlined for Irish Wildlife Manuals, thus is not identical to the other chapters presented in this thesis.

DRAFT

Census methods for burrow-nesting seabirds in Ireland



DRAFT
Irish Wildlife Manual



An Roinn Ealaíon, Oidhreachta,
Gnóthaí Réigiúnacha, Tuaithe agus Gaeltachta

Department of Arts, Heritage,
Regional, Rural and Gaeltacht Affairs



Census methods for burrow-nesting seabirds in Ireland

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Cover photo: © Gavin Arneill

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1 Introduction

1.1 Overview of previous seabird censusing in Ireland:

As apex predators in the marine environment, seabirds are likely to respond to changes in lower trophic levels, making their populations suitable as key ecosystem indicators' (Diamond and Delvin, 2003; Parsons *et al.*, 2008; Grémillet and Charmantier, 2010). Understanding and monitoring seabird populations informs their conservation status, aids in the creation of management plans, and identifies the direction of future scientific studies. Monitoring efforts across the globe have shown a significant declining trend in many seabird populations (Paleczny *et al.*, 2015), linking these to various anthropogenic pressures such as habitat destruction and disturbance, the introduction of alien species, overfishing of prey species, fisheries bycatch, and climate change (Croxall *et al.* 2012).

Census methods for seabirds are dependent on the lifestyle and the habitat in which they breed. Consequently, the level of difficulty in censusing different species varies primarily due to these two factors. Inferences on the trends in seabird distribution and population health are largely derived from cliff nesting seabirds, where the number of breeding birds are estimated based on apparently occupied sites (AOS). Difficulty arises when seabird species nest in inaccessible areas such as small remote islands and areas of cliff not visible for land counts. Several studies have used a combination of boat and land-based techniques to overcome this problem (e.g. Cotter and Rail, 2007). Additionally, remote sensing techniques such as aerial photography can be used for species such as the Northern Gannet (*Morus bassanus*) that are easily distinguished from an aerial view (Murray *et al.*, 2015).

Seabird species that nest in burrows, rock crevices and areas of scree are particularly challenging to census. Thus, the size and demographic trends for many breeding populations of this group are not known. The first estimates of seabird populations at the national level in Ireland were the product of Operation Seafarer and the Seabird Colony Register (SCR) Census; two large-scale projects conducted between 1969 – 1970 and 1985 – 1988 respectively. These efforts were designed to provide a comprehensive account of the distribution and abundance of the seabirds breeding along the coasts of Britain and Ireland (Cramp *et al.*, 1974; Lloyd *et al.*, 1991). The third project of this type known as Seabird 2000, conducted largely from 1998 – 2002, aimed to greatly improve on the coverage and survey methods of prior efforts (Mitchell *et al.*, 2004). Seabird 2000 was the first effort to report population estimates for all of Ireland's burrow-nesting species; however, no detailed methodologies were published in the summary of this project and thus detailed replication at the site level cannot be carried out. The aim of this manual is to standardize the methodological techniques, recording procedures and post survey data archiving that will be used in future surveys, taking into account i) the enormous logistical constraints associated with working on islands, and ii) the likelihood that resources will be limited.

2 Censusing burrow-nesting seabirds in Ireland

Ireland hosts large breeding populations of three burrow-nesting seabird species; the Manx shearwater (*Puffinus puffinus*), the European storm petrel (*Hydrobates pelagicus*) and the Atlantic puffin (*Fratercula arctica*). Recently, the Leach's storm petrel (*Hydrobates leucorhous*) is thought to have recently established breeding populations on offshore islands in the north west of the country. The first national census of all seabirds was first undertaken during Seabird 2000; petrel and shearwater species were omitted from earlier surveys for logistical reasons. Based on Seabird 2000, Ireland probably holds at least 10% of the global population of Manx shearwaters, 3-11% of European storm petrels, <1% of Atlantic puffins and <1% of Leach's storm petrels (Mitchell *et al.*, 2004). All three species are currently red- or amber-listed species of conservation concern due to suspected population declines. The accuracy of these population trends and estimates are far from clear, however, and thus there is a need to gain better breeding population estimates and to initiate a carefully planned monitoring programme.

This document outlines two census methodologies for the petrel and shearwater species breeding in Ireland and one method for the Atlantic puffin, designed to account for the fact that resources will likely limit the number of islands that can be censused in detail, whilst nevertheless realizing that important presence/absence and distribution data can also be generated with less intensive visits over a larger number of sites. Valuable data can be collected using the "Distribution and Habitat Mapping" methodology. This approach can be done during relatively brief visits to islands, and can be easily employed by volunteers and staff with limited time. The second "Detailed Survey", which utilizes the map generated by the Distribution and Habitat methodology, is for detailed censusing that is likely to require multiple days, depending on the size of the island, or more specifically, the size of the area over which the target species breeds on the island and the number of response rate measures. These methodologies have been informed by a review of the literature and analyses of data collected by G. Arneill (PhD thesis) carried out from 2015 – 2018, and after a workshop held in Edinburgh and attended by members of University College Cork (UCC), National Parks and Wildlife Service (NPWS), British Trust for Ornithology (BTO), Royal Society for the Protection of Birds (RSPB), Joint Nature Conservation Commission (JNCC), Scottish Natural Heritage (SNH), Centre for Ecology and Hydrology (CEH) and Marine Scotland (MS).

Disclaimer: this manual can be used to aid the design of a census effort that aims to obtain a colony size estimate. It is not possible to give exact details of the level of sampling effort as the amount of sampling that is necessary to obtain colony size estimates with a high degree of confidence is site specific, and largely determined by the resources available to carry out this logistically challenging work. Therefore, the information regarding the amount of tape-playback sampling for the Procellariiform species within this manual should be used as a guide and be tailored to each individual colony.

2.1 Manx shearwater (*Puffinus puffinus*)



Figure 1. The Manx shearwater *Puffinus puffinus* (Procellariiformes: Procellariidae), Blasket Islands, Co Kerry.
Photograph © Gavin Arneill.

2.1.1 Overview of Breeding Ecology:

The Manx shearwater is a pelagic seabird of the tubenose family Procellariidae, which also includes albatrosses, fulmars, petrels, and storm petrels (Brooke, 2013). The species spends most of the time at sea, carrying out large foraging trips (Shoji *et al.*, 2015) and trans-Atlantic migration to winter off the coasts of South America and South Africa, before returning to reproduce on land in the Northern Hemisphere (Harris, 1966; Guilford *et al.*, 2008). Manx shearwaters usually return to breed in their natal colonies concentrated in north-western Europe (Harris, 1972). Seabird 2000 census work suggests that Britain and Ireland together host approximately 90% of the total global population (Mitchell *et al.* 2004). Elsewhere, Manx shearwaters are also known to breed in France, Iceland, the Faroe Islands, Madeira, and the Azores, and more recently established colonies have been found along the eastern coasts of North America and Newfoundland (Lien and Grimmer, 1978; Thompson, 1987; Brooke, 2013).

Manx shearwaters return to breeding sites under the cover of darkness and thus visual detection at the colony throughout the day is not possible. Reports before the development of tape-playback surveys (James and Robertson, 1985) recorded estimates from the activity around the colony on any given night (Cramp *et al.*, 1974; Lloyd *et al.*, 1991; Mitchell *et al.*, 2004). Diurnal tape-playback methods have since been adopted internationally and are the recommended method for surveying this species (Walsh *et al.*, 1995; Smith *et al.*, 2001; Mitchell *et al.*, 2004; Perrins *et al.*, 2012; Perkins *et al.*, 2017^a). This method works by playing a vocal recording of shearwaters down individual burrows in order to elicit a vocal response from the burrow's occupant. This is carried out on a number of sample plots throughout the colony, and after applying a correction factor that takes into account that a predictable proportion of birds present tend to respond, an estimate of the breeding population can be generated.

2.1.2 Census unit:

Apparently Occupied Burrows (AOB): an apparently occupied burrow here is a burrow where a response was evoked when a tape-playback was carried out.

2.1.3 Distribution and Habitat Mapping – accompanying Form 2.1.3

The Distribution and Habitat Mapping approach is recommended when survey effort is limited to a one or two day visit. Although a robust population estimate cannot usually be made from these short visits, very useful data can be collected. **The main aim of this method is to map i) the presence and absence of burrows, occupied or otherwise, over the entire island using a tape playback method, and ii) at the same time, to map the broad habitat categories and other features of note on the island.** These data will not only provide an invaluable “atlas” of the island’s distribution, they will also guide future intensive monitoring efforts.

There are two ways to do the Distribution and Habitat Mapping. We strongly recommend you use the first approach (a), but if there is no capacity to do this, the second approach can be useful if done thoroughly and carefully. You need to prepare a detailed map before visiting the island.

a) Detailed Mapping (preferred; requires some GIS expertise and GPS).

- i) Grid overlay: Create a grid overlay of the entire island so that you can ensure you visit all parts of the island to within a set distance using a GPS device. For smaller islands (< 30-40 ha) or when time is not too restricted the grid is recommended to consist of 50m x 50m squares. For larger sites, such as Great Blasket, grid squares of 100m x 100m are more realistic. Save the GPS coordinates and label centroids of grid squares to inform sampling efforts.

Tutorial on how to create sampling grid:

http://gis.mtu.edu/wp-content/uploads/2012/06/Regular_Sampling_Tutorial.pdf

- ii) It may be useful to use aerial photographs to outline areas on your map that are noticeably different in their broad habitat type, though these areas will be defined in more detail in the field using line transects as described below.

iii) Fieldwork

- For larger islands, walk along a transect line through the centre (or as close as possible to the centre) of every 100m x 100m grid square on the island.
- For smaller islands, do this through the centre points of the 50m x 50m grid squares.
- During these line transects, map very roughly the main habitat types in the square and define the main/dominant habitat type in the recording form for that transect, paying particular attention to identifying habitat that is likely suitable for Manx shearwaters; this is generally penetrable soil that includes short-medium height vegetation, commonly including species such as Sea Pink (*Armeria maritima*) and

Sea Campion (*Silene uniflora*). Also map habitat where you suspect birds are very unlikely to breed, such as waterlogged grassland and areas of dense impenetrable vegetation. Also map areas that you could not walk through (e.g. bramble, steep cliffs, rocky areas without any soil). Note the inaccessible areas such as steep cliffs/slopes that had habitat that is suitable for breeding birds, also give some indication of the steepness of the slope.



Figure 2. Suitable habitats for breeding Manx shearwaters *Puffinus puffinus* (Procellariiformes: Procellariidae), as outlined in section 2.1.3(iii). Photograph © Gavin Arneill.

- Note in the “Additional Notes” column on Form 2.1.3 any signs of suspected predation from species such as rats, peregrine falcon, gulls, cats, mink.
- Estimate very approximately the abundance of burrows in the individual grid square (0, <10, <50, <100, <500, >500) and enter into the “Estimated Number of burrows” column on Form 2.1. If you think there really are no burrows in the square, please wander away from the centre of the transect to ensure you have a reasonable view of the entire square, before continuing on the original route into the next grid square.
- If you do see burrows anywhere in the grid square within sight of these transects, carry out tape-playbacks at the individual burrow entrances of a randomly selected sample of burrows until you get one definite response that confirms the presence of breeding shearwaters in that grid square. Do this for a maximum of 20-40 burrows but stop as soon as you have established the birds are present. These presence/absence efforts should be carried out in May, before any detailed efforts that should commence from mid-May until early June when the response rate is highest.

To undertake the tape playback method to survey breeding shearwaters and petrels one needs a Section 22 9 (D) licence under the Wildlife Acts and an appropriate recording. For more information on both these aspects please consult david.tierney@chg.gov.ie

- Playback is carried out by playing the recorded call for three-four call cycles (approximately 15 seconds) at a single burrow entrance, waiting for 10 seconds for a response, and then moving immediately on to the next burrow. Be consistent in how long you play the calls for (i.e. don't play for longer than 15 seconds). Note the number of burrows played to and whether any responses were received on Form 2.1.3, as well as note the GPS coordinates of the area of burrows played to.
- Note in the “Additional Notes” column on Form 2.1.3 what proportion of burrows had signs of rabbit occupancy (droppings at entrance or nearby).

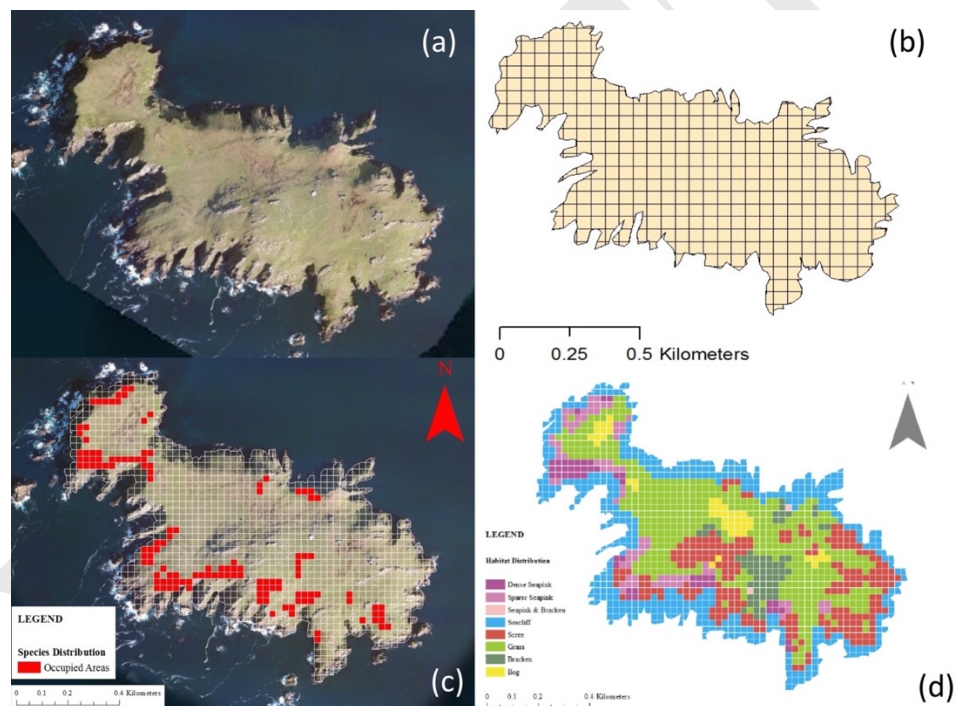


Figure 3 Mapping habitat for surveying breeding Manx shearwaters as outlined in section 2.1.3(a)(iii). Sourcing satellite imagery (a), creating fishnet grid in which to transect (b), defining presence or absence burrows and responses from tape-playbacks (c) and defining habitat types across the island (d).

b) Rough mapping approach (less-preferred, hand drawn mapping approach)

- Print off a map of the island from whatever online source that gives the best satellite imagery of the site.
- Using this map, note areas that obviously differ in habitat type from the satellite imagery, for example stone walls, water bodies, dense vegetation, rocky outcrops. Include a scale bar that will be given on the satellite imagery, the scale will depend on the size of the island.

- iii) In the field, visit within 50-100m all accessible areas on the island and map in further detail habitats that are suitable for breeding birds, ideally using the DAFOR scale (outlined in Fossitt 2000) – on Form 2.1.3.
- iv) Note the presence and absences of burrows in these areas. Where burrows are found, label these areas with a number on the map and give an estimate of the number of burrows in the labelled area (<10, <50, <100, <500, >500) in the “Estimated number of burrows” column of Form 2.1.3.
- v) If you do see burrows on these visits, carry out tape-playbacks at the individual burrow entrances of a randomly selected sample of 20-40 burrows. This is done by playing the call for three-four call cycles (approximately 15 seconds) and waiting 10 seconds for a response. Label on the map where you carried out playbacks, and on the form note the number of burrows played to and of any responded in the labelled area.

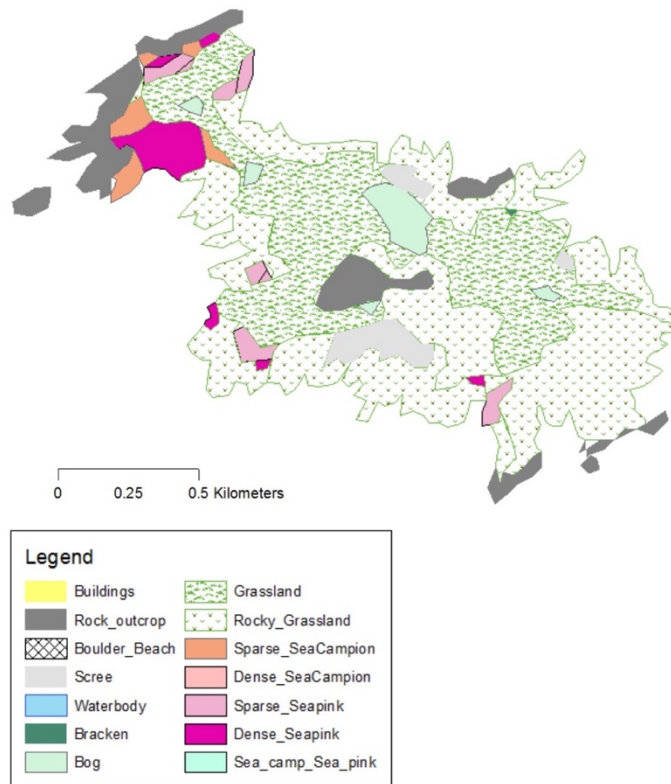


Figure 4 Example of rough mapping approach, noting: habitats, presence of burrows and any playback efforts for breeding Manx shearwaters *Puffinus puffinus* (Procellariiformes: Procellariidae), as outlined in section 2.1.3(b).

For clarity these were drawn digitally to represent what can be hand drawn.

2.1.4 Detailed Survey – accompanying Form 2.1.4.

This method involves a two-step approach: first generate a habitat map and an atlas of the distribution as outlined in 2.1.3, and second estimate the number of occupied burrows (by playing calls of shearwaters down burrows and listening for responses) in a number of circular plots distributed through areas occupied.

2.1.4 (a) Preliminary work

- i) Produce site level GIS map as described in 2.1.3 a above, with either a 50 x 50m grid or a 100m x 100m grid. Save GPS coordinates **and label the centre of the grid squares (centroids)** where sample plots will be located. The tutorial linked in 2.1.3 above demonstrates how to do this.
- ii) Using the map produced from the “Distribution and Habitat mapping” effort described in section 2.1.3, group each of the individual grid squares into strata that differ by estimated density (number of burrows). The number of strata will be determined by the level of detail recorded during the mapping effort and the homogeneity of the distribution of burrows across the island to be censused. A very simplistic approach would be to use three strata (‘low density’, ‘medium density’ and ‘high density’), however the more strata used the more accurate the attained population estimate. By increasing the number of strata the variation in plot density within each strata is reduced, thus reducing the confidence interval surrounding the extrapolated population estimate. There is no need to do sampling plots within grid squares where there are no burrows.

Mapping the sampling effort before going into the field allows you to visualise the approach, to ensure that a broad coverage of the island’s suitable potential breeding areas are sampled.

One circular plot is to be carried out in the centre of each grid square (100 x 100 or 50 x 50 depending on the resolution).

- iii) How many plots to do depends on how much time you have. But as a rule of thumb, it is recommended that at least 10-15 plots are sampled in each of the strata, though the more area sampled the better the population estimate that can be derived. Note that estimates from low sampling effort should be used with caution and confidence intervals should always be reported. For islands that are thought to host a large breeding colony, such as Rum and Skomer, much more effort should be invested into obtaining colony size estimates
- iv) Logistically, it is not feasible to sample plots in a truly random way as transit times between plots can be excessive on large islands, thus we recommend grouping plots to be sampled within close proximity of each other and then randomising the order in which these groups are visited. This can be done in excel by creating a random number beside each group of plots, and then sorting the list of grouped plots using the random number column. See <http://www.excel-easy.com/examples/randomize-list.html> for tutorial on how to randomise lists in excel.
- v) Ensure the following is sourced before field visits: high quality calls (call should remain clear at > 55dB) of duetting male and female Manx shearwaters, battery operated mp3/dictaphones, battery operated waterproof speakers (if mp3/dictaphone speaker not capable of 55dB), handheld GPS units, multiple measuring tapes (50 metres in length, brightly coloured (white) and non-metallic tape), recording sheets.

To undertake the tape playback method to survey breeding shearwaters and petrels one needs a Section 22 9 (D) licence under the Wildlife Acts and an appropriate recording. For more information on both these aspects please consult david.tierney@chg.gov.ie



Figure 5 Some necessary equipment to carry out tape-playback surveys of breeding Manx shearwaters *Puffinus puffinus* (Procellariiformes: Procellariidae), as outlined in section 2.1.4(a)(v).

- vi) Tape playbacks should be carried out during the incubation and chick-guarding stage (approximately mid-May to early June). Seek advice from NPWS.

2.1.4 (b) Fieldwork

- i) Tape-playbacks consist of playing the call of the duetting call of male and female Manx shearwaters for three-four natural cycles or approximately 14-15 seconds in the entrance of a burrow. The call should be played at a natural volume (ca. 55dB) and not be distorted. After the three to four call cycles, or 14-15 seconds, the observer should listen for approximately 10 seconds to detect any response. Tape-playbacks should be carried out in wind conditions of Beaufort 4 or lower to avoid false negatives (observer not hearing a response).
- ii) The radius of the circular sampling plots to be used differs depending on the grid size:
 - The radius should be 10m for 100m x 100m grid squares. Typically one such plot would require approximately 30 – 90 minutes to survey, including transit between plots, varying depending on the density of burrows in the plot.

- The radius should be 5.7m for 50m x 50m grid squares. Typically one such plot would require approximately 15 – 45 minutes per plot, including transit between plots.
- iii) Please go to the exact centre of these squares using the GPS coordinates of centroids from the GIS map. **It is important not to move the position of the plot** (for example if there are no burrows in the centre of the grid square even though you know there are some elsewhere in the square). **This is important because i) this is an essential part of the sampling procedure and ii) these are the precise plots that will be revisited in future years.** This approach greatly improves our ability to detect any population change.
- iv) Use two 5.7m lengths of tape measures to create a manageable slice of the circular plot, and systematically play the calls down every burrow in that slice. Then move one of the tape measures to create a new slice and repeat the calls (see Figure 7).

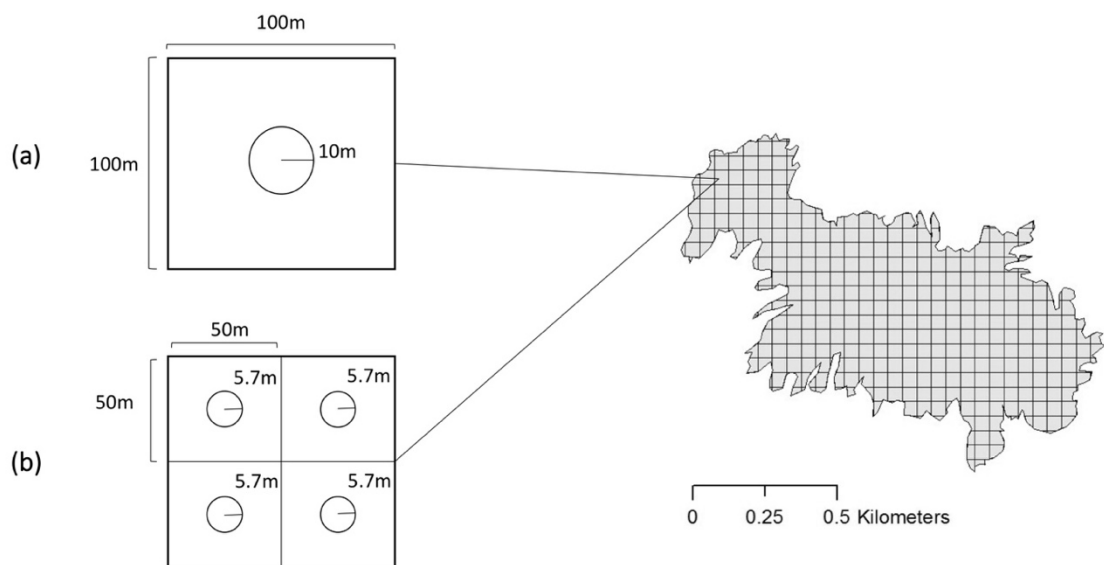


Figure 6 Visual representation of where to position circular plots within grid squares for the Manx shearwater tape-playback sampling methods, as described in detail in section 2.1.4(b) of this text. Note the plot radii differ for 100 x 100m grid squares (10m) and for 50 x 50m grid squares (5.7m).

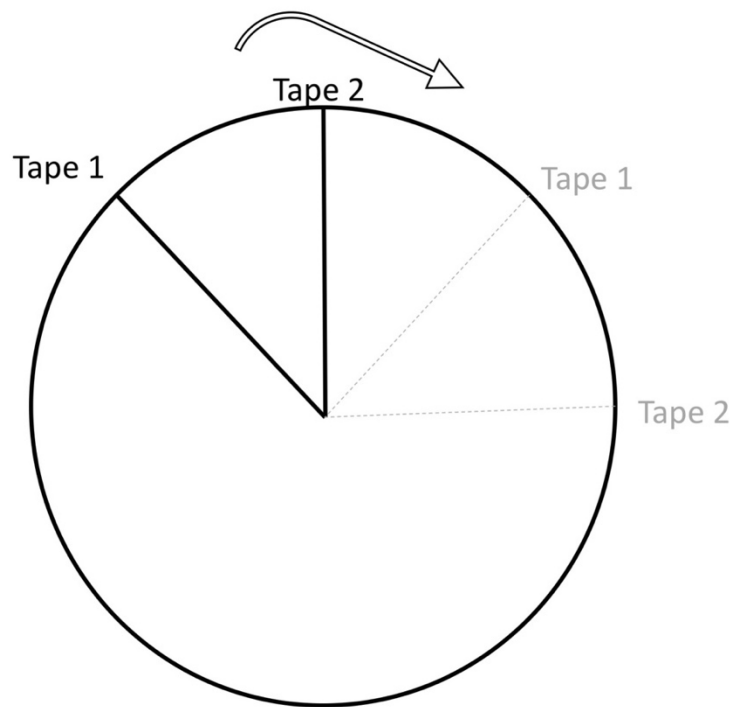


Figure 7 Visual representation of how to sample “slices” of circular plots to be used for the Manx shearwater tape-playback sampling method, described in detail in section 2.1.4(b) of this text. Note that the length of the tape (radius of the circle) is either 10 m in larger 100m x 100m grid squares or 5.7m in smaller 50m x 50m squares.

(c) Non-essential additional effort:

i) Response rates: It is helpful to work out what proportion of birds respond: Establish AOB's (≥ 30 active nests) where repeated measures of response rate can be taken throughout the survey effort. Response rate measures should be taken at least three times with 24 hour rest periods between measures to reduce habituation. Detailed guidelines can be found in the appendices of this report (section 5.1.1), response rates will be measured in detail at several sites and standard corrections can be applied to colonies where measures of response rate are not possible.

ii) Marking permanent plot locations: If counts are going to be repeated in the future to monitor changes in the population, GPS points do not permit sufficient accuracy to visit the exact area in the future. Thus, assuming permission is given from the land owner, permanent stakes should be installed to the centre point of the sample plots to be visited again. We recommend doing this in both areas of high density and in areas where density is low but habitat is suitable for the possible expansion of breeding burrows.

2.2 European storm petrel and Leach's storm petrel

The methods for surveying both European- and Leach's storm petrels are identical with the exception of (a) the tape-playback recording used (a call for each species) and (b) recording the possible apparent burrow entrances from Leach's breeding in excavated burrows.

Additionally, on sites where survey efforts focus on Leach's storm petrel surveys, note that European storm petrels are known to respond to the tape-playback of Leach's storm petrels so observers should be capable of distinguishing the species calls.

2.2.1 Overview of Breeding Ecology:

European storm petrel



Figure 8 The European storm petrel *Hydrobates pelagicus* (Procellariiformes: Hydrobatidae), High Island, Co Galway. Photograph © Paul Whitelaw.

The European storm petrel, *Hydrobates pelagicus*, is Europe's smallest seabird with a population size of an estimated 438,000-514,000 breeding pairs in Europe, of which 10.6% - 43.1% are believed to breed in Ireland (Mitchell *et al.*, 2004). Despite their conservation status of "Least Concern" on the IUCN Red List of Threatened Species, European Storm petrels are listed on Annex 1 of the EC Birds Directive due to the lack of knowledge of the size and trends of the breeding populations. Ireland's only population estimates come from Seabird 2000 (Mitchell *et al.*, 2004), which identified the south west coast of the country, most notably the Blasket Islands and the Skelligs, as hotspots for the species, with other important colonies on islands along the west coast (Mitchell *et al.*, 2004).

Like Manx shearwaters, this species returns to breeding colonies only at night to reduce the risk of predation at the colony, and therefore censusing this species is logistically challenging. The majority of census work carried out to date has used the tape-playback method, first developed by James and Robertson (1985) and later adopted by Ratcliffe *et al.* (1998) for European storm petrels. Although breeding birds respond to tape-playbacks, the response rate of this species has been noted as considerably lower than other burrow-nesting seabird species (Ratcliffe *et al.*, 1998; Mitchell *et al.*, 2004). Alternative methods include the use of mark-recapture studies (mist-netting and ringing) to determine colony size, but these cannot discriminate between breeders and non-breeder, and do not record the distribution of breeding birds

within a colony (Insley *et al.*, 2002). European storm petrels nest in crevices, scree slopes, stone walls, and in areas of dense vegetation where their nests often have no clear nest entrance. Many recent studies aim to utilise advances in remote sensing techniques such as infrared video recording (Perkins *et al.*, 2017^b) to census petrel species as an alternative to tape-playbacks. However to date the only practical way to census them accurately remains the tape playback method.

Leach's storm petrel Breeding Ecology



Figure 9 The Leach's storm petrel *Hydrobates leucorhous* (Procellariiformes: Hydrobatidae), Shetland.

Photograph © Brydon Thomason.

Ireland's population of Leach's storm petrels is limited to only a few small colonies located in the north west of the country, during Seabird 2000 the national population estimate was thought to be 310 breeding pairs (Mitchell *et al.*, 2004). This accounts for roughly <0.005% of the estimated global breeding population, the distribution of breeding colonies ranges across the Atlantic and Pacific basins, with higher numbers recorded in Pacific areas (Brooke, 2004). Akin to European storm petrels and Manx shearwaters, Leach's storm petrels only return to their breeding burrows under the cover of darkness thus are difficult to census. Leach's storm petrels primarily breed in burrows (both excavated and natural holes) and rock crevices. Burrow entrances are not as detectable as Manx shearwaters burrows, often concealed with vegetation and spanning a length of 1-4 foot in depth, thus approaches outlined here are similar to that of European storm petrels with the exception of the call used for tape-playbacks and the additional recording of detail of burrowed areas on mapping efforts.

2.2.2 Census unit:

Apparently Occupied Sites (AOS): where a response was evoked when a tape-playback was carried out during survey effort.

2.2.3 Distribution and Habitat Mapping – Form 2.2.3 (Leach's 2.4.3)

The Distribution and Habitat Mapping approach is recommended when survey effort is limited to a one or two-day visit per site. Although a robust population estimate cannot usually be made from these short visits, extremely useful data can be collected. **The main aim is to map i) the presence and absence of suitable breeding sites, occupied or otherwise, over the entire island using a tape playback method, and**

ii) at the same time, to **map the broad habitat categories** and other features of note on the island. These data will not only provide an invaluable “atlas” of the island’s distribution, they will also guide future intensive monitoring efforts.

(a) Detailed Mapping (preferred; requires GIS and GPS).

- Grid overlay: Create a grid overlay of the entire island so that you can ensure you visit all parts of the island to within a set distance using a GPS device. For smaller islands (< 30-40 ha) or when time is not too restricted the grid is recommended to consist of 50m x 50m squares as per Manx shearwater surveys. For larger sites, such as Great Blasket, grid squares of 100m x 100m may be more realistic. Save the GPS coordinates and label centroids of grid squares to inform sampling efforts.

Tutorial on how to create sampling grid:

http://gis.mtu.edu/wp-content/uploads/2012/06/Regular_Sampling_Tutorial.pdf

- It may be useful to use aerial photographs to outline areas on your map that are noticeably different in their broad habitat type, though these areas will be defined in more detail in the field using line transects as described below.
- For larger islands, carry out line transects/walkovers (100m length per square) through the centre points of the 100m x 100m grid squares.
- For smaller islands, carry out line transects/walkovers (50m length per square) through the centre points of the 50m x 50m grid squares.
- For each transect and thus each grid square, and with the aid of satellite images or aerial photographs of the island, note in the form for each transect the suitable habitats that storm petrels are most commonly found to breed. This includes: (a) *stone walls and buildings* that have suitable walls in which storm petrels can nest, (b) *open ground* primarily dry-humid, tussocky acid grassland (Fossitt’s GS3) and (c) *boulder beach* area that is above the tide line in Form 2.2.3 (Leach’s Form 2.4.3).
- Map waterlogged areas where birds could not breed and areas of dense vegetation that could restrict access for surveys including, for example, dense bramble or steep slopes. Record if the areas that are inaccessible have habitat that is suitable for breeding petrels.
- Note in “Additional Notes” column of Form 2.2.3 (Leach’s Form 2.4.3) any signs indicating the presence of species such as rats or other predators.
- Establish whether storm petrels are present in the square. This can be determined by carrying out tape-playbacks along line transects, stopping every 5 metres along the transect and play the call at >80dB at waist height for approximately 10 seconds. Repeat this 5 times along the transect per grid square, or until you hear a response to confirm presence in the square. Details on the logistics and the method of carrying out tape-playbacks across different habitats (Stone walls/Open ground/Boulder Beach) to determine apparently occupied sites (AOS’s) are outlined in section 2.2.4 of this manual. Note the number of times tape-playbacks were carried out along the transect in the

“Total Number of playbacks” column and whether a response was heard
 “Responses (Yes/No)” columns on Form 2.2.3 (Leach’s Form 2.4.3).

To undertake the tape playback method to survey breeding shearwaters and petrels one needs a Section 22 9 (D) licence under the Wildlife Acts and an appropriate recording. For more information on both these aspects please consult david.tierney@chg.gov.ie

Although this approach will not be sufficient to estimate total numbers of storm petrels in the square, it should be a robust measure of presence/absence and allow us determine where storm petrels breed on the island.

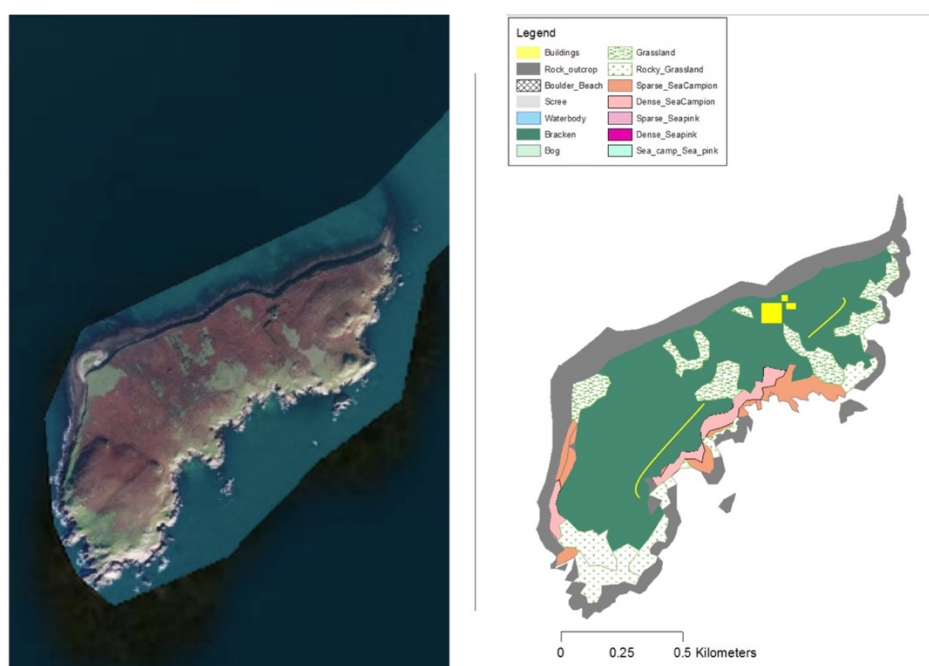


Figure 10 Example of habitat mapped on Great Saltee, Co. Wexford (right). This mapping of habitat allows the definition of potential breeding sites for European- and Leach’s storm petrel as outlined in section 2.2.3. This can be created by: (1) Sourcing satellite imagery; (2) creating a fishnet grid in which to transect; (3) defining presence or absence from tape-playbacks; and then (4) defining habitat types across the island. *Note the detail marking out buildings & stone walls (yellow), separating the open ground habitat into types that are suitable (rocky grasslands) and boulder beach areas should be mapped when present.*

(b) Rough mapping approach (less-preferred, hand drawn mapping approach)

- Print off a map of the island from whatever source gives best imagery of the site
- Draw on the map itself, or on a traced version of the map, the three main habitat types that could be used by storm petrels: stone walls & buildings; open ground; and boulder beach areas. Also note water bodies, dense vegetation, rock outcrops where (a) birds are not likely to breed and (b) access to survey is restricted.
- In the field, visit within 50-100m of all accessible areas on the island and map habitats that are suitable for breeding birds, noting in detail the different

habitats (Stone walls/Open ground/Boulder Beach) and detail the vegetation in 'open ground' habitats using the DAFOR scale (Fossitts 2000) – on Form 2.2.3 or Leach's 2.4.3.

- Use tape-playbacks to determine presence or absence of breeding birds and to get a crude feel for the extent of their distribution in areas of suitable habitat: this can be done by playing the tape-playback call (>80dB) for approximately 10 seconds and listening for responses for 30 seconds. Repeat this throughout the area of suspected suitable habitat; how frequently will be determined by the size of the area and the time available to cover the whole island. Details on the logistics and the method of carrying out tape-playbacks across different habitats (Stone walls/Open ground/Boulder Beach) to determine AOS's are outlined in section 2.2.4 of this manual. If carried out, note the number of playbacks carried out and if any responses were received. Record these on Form 2.2.3 or Leach's 2.4.3 and mark on the map mark those points within areas of suitable habitat where i) playback surveys undertaken and ii) where birds responded with as much accuracy as possible given the time available.

2.2.4 Detailed Survey – accompanying Form 2.2.4 (Leach's 2.4.4)

The detailed map generated in the Distribution and Habitat Mapping approach (section 2.2.3(a)) is required to identify where to use tape playback along **transects**, not the circular plots used for shearwaters. As storm petrels breed in a range of habitats, this next stage utilises three different approaches to be used at the three main habitat types that storm petrels are known to breed in: stone walls & buildings, open ground and boulder beach. The preparation required is outlined in 2.2.4 (a) and each method is outlined in detail below in 2.2.4 (b).

a) Preparation

- i) Produce site level GIS map
- ii) Grid overlay: Use the map generated above in section 2.2.3 to select areas for sampling storm petrels using playback. For smaller islands or when time is not too restricted the grid is recommended to consist of 50m x 50m squares. For larger sites, such as Great Blasket, grid squares of 100m x 100m are more realistic. Save the GPS coordinates and label centroids of grid squares to inform sampling efforts.
- iii) Define areas to be sampled as areas of (A) Stone wall, (B) Open ground and (C) Boulder beach, separate approaches should be taken for each, see 2.2.4(b) for details.
- iv) Logistically, it is not feasible to sample transects in a truly random way as transit times between transects can be excessive on large islands, thus we recommend grouping transects to be sampled within close proximity of each other and then randomising the order in which these groups are visited. This can be done in excel by creating a random number beside each group of plots, and then sorting the list of grouped plots using the random number column. See <http://www.excel-easy.com/examples/randomize-list.html> for tutorial on

how to randomise lists in excel. If more than one of the habitats is present on the island, randomise in a stratified manner.

- v) Map (ideally with GPS coordinates) all areas to be sampled on the island. This should be done before fieldwork, allowing the visualisation of what is going to be sampled and informed by the Distribution and Habitat Map to ensure a broad coverage of the islands breeding areas.
- vi) How many transects to do depends on how much time you have. Ensure transects are carried out in a random manner. Generally, the more area sampled the more accurate the population estimate that can be derived. Detailed report of the number and location of transects (GPS points) is essential to allow repeat counts to be carried out in the future. Confidence intervals should be reported.
- vii) Ensure the following is sourced before field visits: high quality call (call should remain clear at > 80dB) of male European storm petrel (Leach's efforts should use the male call of the Leach's storm petrel), battery operated mp3/dictaphones, battery operated waterproof speakers, handheld GPS units, measuring tapes (50 metres in length), recording sheets.

To undertake the tape playback method to survey breeding shearwaters and petrels one needs a Section 22 9 (D) licence under the Wildlife Acts and an appropriate recording. For more information on both these aspects please consult david.tierney@chg.gov.ie

Tape playbacks should be only carried out during the late incubation and chick-guarding stage when response rates from adults are highest. Work carried out by UCC showed that on High Island in Galway, highest response rates were recorded during the period 20th of July – 8th of August, in both 2016 & 2017. However this is likely to change to some extent from year to year and to differ between colonies. If access to nests is possible, ideally one should check the timing of breeding for your population. If this is not possible, ideally restrict survey visits to the period 20 July – 8 August, or as close as possible to this period.

b) Fieldwork

i) General notes

In the “Habitat type” column of Form 2.2.4, define the type of habitat being surveyed A) Stone wall, (B) Open ground and (C) Boulder beach.

The way tape-playback is used differs slightly between the three main habitat types (stone wall, open ground and boulder beach) in which storm petrels primarily breed, and hence, the following methods section is split into three parts. On some islands, it may be necessary to use all three methods.

Tape-playbacks should be carried out in conditions of Beaufort 4 or lower to avoid false negative results i.e observer not hearing a response when one was elicited.

For safety reasons, these methods should be carried out during the day. Response rates at night have been noted to be considerably higher (Ratcliffe *et al.*, 1998); however surveys at night are dangerous, logistically extremely difficult, and not recommended.

ii) Survey method for Stone walls & buildings

In the “Additional notes” area on recording forms, define the condition of the site’s stone walls, identify areas where maintenance such as cement rendering and mortar has occurred as this is not suitable breeding habitat.

1. Where possible, the surveyor should remain on the sheltered side of the wall to aid detection of responses, in some monastic ruins where the wall’s widths are greater than approximately 2 metres, in this case the method should be repeated on both sides.
2. Playbacks are recorded along areas of known length (with tape measure) along the walls. Ideally transects should be conducted along a part (a sample length) of all individual walls and buildings on the island. If not possible, try do as many as possible and make sure you sample them randomly.
3. If the wall is longer than 50 metres and time is limited, sample a 50m transect along the wall. Make sure you map the start and end points of all sampled walls on your map and GPS coordinates of all areas surveyed.
4. Standing at the starting point along the wall to be sampled, facing and within 1 metre of the wall, play the call at >80dB from the speaker at roughly waist height for approximately 10 seconds, followed by approximately 30 seconds of listening to detect any responses.
5. Repeat step 5 every two metres along the wall, noting the number of responses in the “Total Number of responses” column on Form 2.2.4.
6. When carrying out these playbacks, often birds responding from playback can be heard responding at the next point (2 metres on); ensure not to double count from AOS that are noticeably the same AOS recorded in the previous playback.

iii) Survey Method for Open ground

The term ‘open ground’ is used here to cover European storm petrels and Leach’s storm petrels that are breeding in burrows or short accessible dense vegetation areas such as dry-humid grassland (e.g Fossitt’s GS3).

Within the predefined grid squares (50m x 50m on small islands/100m x 100m on larger islands), a sampling approach using line transects and systematic tape-playbacks can be used to survey for AOSs where no well-defined nest entrances are observable.

1. Transects of 50 metres in length and 4 metres in width (2 metres either side of the line) should be laid out from a randomised starting point within the grid squares, 100m x 100m grid for larger islands and 50m x 50m grids for smaller islands. Map the location of the transect, note the coordinates of the start and end of transects on Form 2.2.4, and the bearing direction in which the transect was walked. It is essential to do this so that surveys can be repeated at the identical site in future years.

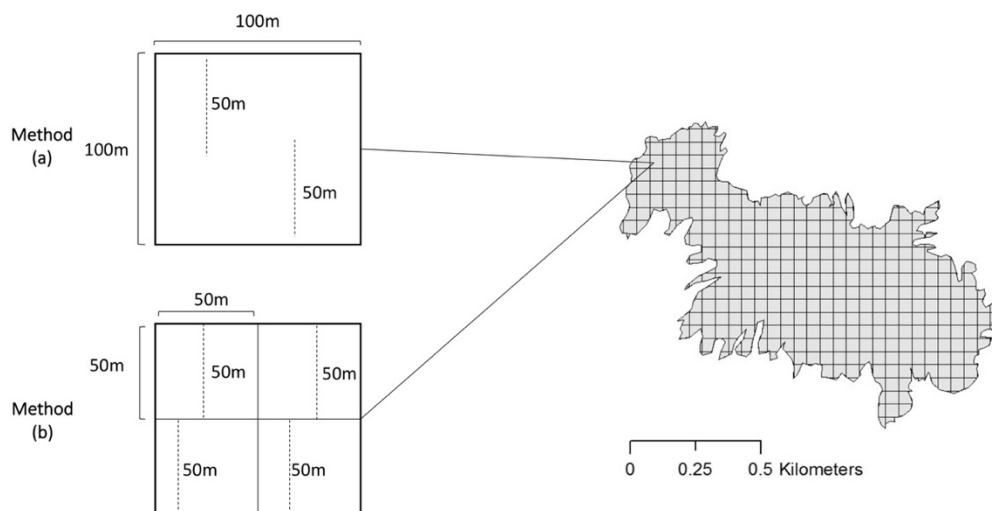


Figure 11 Visual representation of tape-playback sampling methods for European storm petrels and Leach’s storm petrel as described in detail in section 2.2.4(b)(iii) of this text. Transects (dotted lines) starting from a random point within grid cells to be sampled.

2. Every 5 metres along the transect line, the tape-playback call should be played at a high volume (>80dB) but remain clear, and not distorted for approximately 10 seconds, followed by a listening period of approximately 30 seconds. Hold the speaker at approximately waist height to stay constant across transects and note the number of responses heard, also note where no responses were observed. Note the number of responses in the “Total Number of responses” column on Form 2.2.4
3. The number of transects per grid square is determined by the length of the visit and the number of observers. A minimum of two transects should be carried out per grid square, where habitat is favourable for breeding birds to obtain a more accurate estimate of colony size.
4. Along these transects, **do not stand on tufts of vegetation** (as seen in Figure 12 below) within which the storm petrels may be breeding.



Figure 12 Example of dry grassland habitat that European storm petrel (*Procellariiformes: Hydrobatidae*) are found to breed in on High Island, Co Galway. Photograph © Gavin Arneill.

iv) Survey method for Boulder Beach

This method is also applicable to areas of rocky outcrop/scree inland. Caution should be taken with loose substrate for safety reasons and because of the potential for destroying nests just under boulders. Note in Form 2.2.4 the habitat type as boulder beach when this is carried out.

1. Divide the suitable boulder beach habitat outlined on the map produced in the “Distribution and Habitat mapping” effort into workable areas where transects of 50m length and 4 metres width are possible. If no boulder beach habitat on the island spans 50 metres in length, carry out smaller transects in areas and note the length of the transects to ensure some sampling was carried out. Transects should be at least 5 metres apart. Randomise the order in which areas will be sampled around the coast.
2. Note the size of the workable area that was sampled and ideally randomly select starting points for transects both along the coast and also across (different shore heights) to ensure all suitable breeding habitat is sampled and not biased to a certain shore height. Do not carry out transects below the tide line as birds are not likely to be breeding there.
3. Every 5 metres along the transect line, the tape-playback call should be played at a high volume (>80dB) but remain clear, and not distorted for approximately 10 seconds, followed by a listening period of approximately 30 seconds. Hold the speaker at approximately waist height to stay constant across transects and note the number of responses heard, also note where no responses were observed. Note the number of responses in the “Total Number of responses” column on Form 2.2.4.

(c) Non-essential additional effort:

Response rates: It is helpful to work out what proportion of birds respond: Establish AOS (≥ 30 active nests) where repeated measures of response rate can be taken throughout the survey effort. Response rate measures should be taken at least three times with 24 hour rest periods between measures to reduce habituation. Detailed guidelines can be found in the appendices of this report (section 5.1.2), response rates will be measured in detail at several sites and standard corrections can be applied to colonies where measures of response rate are not possible.

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2.3 Atlantic puffin (*Fratercula arctica*)



Figure 13 The Atlantic puffin *Fratercula arctica* (Charadriiformes: Alcidae), Saltee Islands, Co Wexford. Photograph © Gavin Arneill.

2.3.1 Overview of Breeding Ecology:

The Atlantic puffin (*Fratercula arctica*; Charadriiformes; Alcidae), is the only burrow-nesting species breeding in Ireland that are observable around breeding burrows in daylight. Most Atlantic puffins breed annually with the same mate and lay a single-egg clutch (Harris *et al.*, 2005; Miles *et al.*, 2015). Atlantic puffins overwinter at sea, returning in the spring to breed and form colonies on coastal cliffs and offshore islands (Jessopp *et al.*, 2013). Difficulties censusing Atlantic puffins arise due to the large size of the breeding colonies that are often heterogeneous with other auk and burrowing species and have variable numbers of juvenile and prospecting birds present.

The favoured counting unit for Atlantic puffins is the apparently occupied burrow (AOB) (Anker-Nilssen and Røstad, 1993) and this is the method recommended by Walsh *et al.* (1995) in the *Seabird monitoring handbook for Britain and Ireland*. These are characterised by signs of regular use such as feathers, guano or freshly excavated earth at the burrow entrance (Harris and Murray, 1981; Harris and Rothery, 1988). Yet, this method is laborious and requires access to breeding colonies to visually inspect each burrow entrance. As many puffins breed on steep slopes and sea cliff habitat, access is limited for inspection. Furthermore signs of occupancy can be difficult to discriminate when other burrow-nesting species and rabbits are present. Previous estimates of Atlantic puffins in Ireland at the national scale are limited to the Seabird 2000 estimate (Mitchell *et al.*, 2004) and used primarily observer counts of individual adults. In Ireland, counts of apparently occupied burrows were limited to just a few sites (Mitchell *et al.*, 2004).

The use of signs of occupancy at burrow entrances is a standard method that has been used to estimate the size of Atlantic puffin populations in previous census efforts (Walsh *et al.*, 1995; Mitchell *et al.*, 2004). However, recent research carried out found that in Ireland (Arneill, in prep), sites where burrows are accessible for inspection and where Atlantic puffins are the only burrow-nesting species breeding are very limited,

thus the use of observational counts is the only logistically feasible standardised method at the national scale. If a site shows the characteristics of single species burrow-nesting (Atlantic puffin) and accessible burrows in breeding areas, refer to Walsh *et al.* (1995) for this censusing methodology.

Therefore an alternative method of observational counts is outlined in Walsh *et al.* (1995) to count the individuals around breeding colonies. It is essential that observational counts of birds on both rafts and cliffs is carried out early in the breeding season, in order to minimise the inclusion of non-breeding prospecting birds that arrive on breeding colonies later in the season. Counts should be carried out as early as possible, ideally in April, if logistically feasible.

2.3.2 Census unit:

Individuals (INDV)

2.3.3 Distribution and Habitat Mapping – accompanying Form 2.3

Preparation

- i) Produce site level GIS map
- ii) Ensure the following is gathered before fieldwork: 8x42 binoculars, telescopes, tripods, recording forms, handheld GPS unit, surveys should be carried out in no higher than Beaufort 4.

Fieldwork

- Visits should ideally be undertaken during the early breeding season in April. This is to minimise the inclusion of prospecting non-breeding birds that arrive at breeding colonies later in the season.
- On arrival at the study site, a scoping exercise should define breeding areas across the study site. Often multiple distinct breeding areas can be identified around the island by observing puffins loitering near burrows. Map the distribution of these areas with as much accuracy as possible.
- Split the breeding areas into manageable and distinct counting sections. So for example, one breeding area may be best split into two count sections because the entire colony cannot be viewed easily from the one vantage point.
- Note the GPS coordinates of vantage points that permit the best possible field of view over sub-colonies, this can also be mapped. Vantage points should be at a distance (>50m) that does not disturb the loitering birds on the cliff. From this point, count the number of individuals visible on the ‘cliffs’ and the number of puffins rafting on the water adjacent to breeding areas.
- Previous work has shown that colony attendance peaks in the evening (18:00-21:00) – (Arneill, in prep). It is essential to time your counts to take place at this time. If this is not logistically possible, do carry out counts when it is possible but highlight that the survey took place outside of these times.

- To get an estimate of variation in count numbers associated with this approach, two observers should do the counts completely independently of one another, starting at different locations to ensure independence.
- Before doing the official count, try to calibrate your count accuracy. Spend time at one location ensuring your counts on the water and on the land agree when done at identical times. Keep on doing this until they match within 10%.
- Then begin the survey properly, being careful to ensure that each observer starts in different locations and records numbers completely independently. Do not be tempted to adjust numbers to ensure they agree.
- Ideally these counts should be repeated over multiple evenings to improve the accuracy of the counts. Again, do not adjust numbers to ensure they agree with previous evenings numbers.
- Counts of rafting puffins should be carried out with as much accuracy as possible, auks rafting at a distance where they cannot be accurately identified as Atlantic puffin using a telescope and are possibly Razorbill or Guillemots should be noted as ‘Auk sp.’

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DRAFT

5 Appendices

5.1 Measuring response rate for tape-playback surveys

5.1.1 Manx shearwater (*Puffinus puffinus*) response rates

Method

- i) During the Distribution and Habitat Mapping, areas of high burrow density and presence of Manx shearwaters will be located. These areas can then be visited at the start of the Detailed survey effort to establish Apparently Occupied Burrows (AOB) to measure response rate during the survey effort.
- ii) On the first day of fieldwork, mark out 30-50 burrows that respond to tape-playbacks during the day. These AOBs should be marked and numbered, this can be done using bamboo canes with a numbered flag that made from fluorescent tape.
- iii) On the second day of fieldwork, after a 24 hour period of rest to reduce any possible habituation to tape-playbacks, these marked AOBs can be visited and subjected to tape-playbacks as outlined in section 2.1.4 of this manual. On Form 3, note the burrow number and whether a response was received or not. Note the weather conditions, like the playback surveys, this should not be carried out in conditions higher than Beaufort 4 to reduce the risk of not hearing a response.
- iv) This should be repeated at least three times to give at least three measures, leaving a 24 hour rest period between each visit.
- v) Response rates for each day can be calculated by dividing the number of responses by the number of AOB's marked. E.g on the first day you marked 40 AOBs, on the third day 20 of those responded. Response rate for the third day is $20/40 = 0.5$. Do this for each of the days. Report all raw data to NPWS for these daily measures.
- vi) Overall response rate for the survey period is the average of the measured response rates and the variation around the overall response rate is the variation seen in the repeated measures.

5.1.2 Storm petrel (European and Leach's) response rates

Method

- i) During the Distribution and Habitat Mapping, areas of suitable breeding habitat and presence of storm petrels will be located. These areas can then be visited at the start of the Detailed survey effort to establish Apparently Occupied Sites (AOS) to measure response rate during the survey effort.
- ii) On the first **night** of fieldwork, mark out 30-50 AOS that respond to tape-playbacks. This is carried out in areas that are safe to visit at night as the response rate of storm petrels has been shown to be significantly higher

than diurnal measures. These AOS's should be marked and numbered, this can be done using bamboo canes with a numbered flag that made from fluorescent tape.

- iii) On the third **day** of fieldwork, to measure the diurnal response rate and after at least a 24 hour period of rest to reduce any possible habituation to tape-playbacks, these marked AOS's can be visited and subjected to tape-playbacks as outlined in section 2.2.4 of this manual. These measures of diurnal response rate are important to correspond to the survey efforts that are carried out diurnally, the only night-time work is to identify as many AOS as possible and not bias measures to those that respond diurnally. On Form 3, note the number of the marked AOS and whether a response was received or not. Note the weather conditions, like the playback surveys, this should not be carried out in conditions higher than Beaufort 4 to reduce the risk of not hearing a response.
- iv) This should be repeated at least three times to give at least three measures, leaving a 24 hour rest period between each visit.
- v) Response rates for each day can be calculated by dividing the number of responses by the number of AOS's marked. E.g on the first day you marked 40 AOS's, on the third day 20 of those responded. Response rate for the third day is $20/40 = 0.5$. Do this for each of the days and report all raw data to NPWS for these daily measures.
- vi) Overall response rate for the survey period is the average of the measured response rates and the variation around the overall response rate is the variation seen in the repeated measures.

Section 2

Appendix Section 2 Table 1. Priority areas for each species outlining the top 5 most densely populated islands that were surveyed in Seabird 2000 according to Mitchell *et al.* (2004). Table outlines the percentage of both the estimated Irish breeding population and global breeding population of each species on each site.

<i>Species</i>	<i>Island</i>	<i>Area</i>	<i>Seabird 2000 estimate¹ (1998-2002)</i>	<i>Percentage of Irish population</i>	<i>Percentage of global population</i>
<i>Manx shearwater</i>	Inishtooskert	2	9,696	26	2.8
	Puffin Island	2	6,329	17	1.9
	Inishnabro	2	5,611	15	1.6
	Great Blasket	2	3,584	9.6	1.05
	Cruagh	3	3,286	8.8	0.96
<i>European storm petrel</i>	Inishtooskert	2	27,297	27.3	5.7
	Great Skellig	2	9,994	10	2.1
	Inishvickillane	2	6,394	6.4	1.3
	Puffin Island	2	5,117	5.1	1.08
	Stags of Broadhaven	3	1,912	2	0.4
<i>Atlantic puffin</i>	Puffin Island	2	5,125	24.4	0.1
	Great Skellig	2	4,000	19	0.08
	Great Saltee	1	1,522	7.2	0.03
	Tory Island	3	1,402	6.7	0.03
	Illanmaster	3	1,367	6.5	0.03

Area: 1 = Irish sea and east Celtic sea; 2 = South west and West Celtic sea; 3 = West coast

Global populations obtained from IUCN, 2018.

Appendix Section 2 Table 2. Table illustrating the approximate cost of the census of Manx shearwaters on High Island, Co. Galway in 2015. Figures are outlined in a way that the number of observers and the duration of the survey efforts can be adjusted. Figures should be adjusted according to salary scales, cost of fuel, cost of boat hire for the survey year. This example uses the Research Assistant salary (scale 1) and costs of fuel in Ireland in 2015.

Cost item	Additional details	Approximate cost
<u>Staff</u>		
Field staff	For two field staff for one month.	€3410
<u>Travel</u>		
Fuel	2 return trips at €60	€120
Boat to High Island	2 return trips at €150	€300
<u>Equipment</u>		
Tape-playbacks	3 Dictaphones at €38 each	€114
Tape measures	2 x 50m tapes at €41 each	€82
Printing	50 sheets at €0.06 per page	€3
Batteries	20 x AA	€20
<u>Accommodation</u>		
Tents	3 Tents at €220 each	€660
B&B	2 nights at €40 per person	€80
<u>Consumables</u>		
Groceries	2 trips (ca. 8 days) at €100	€200
Gas cooker and canisters	2 x cookers, 20 x canisters	€64
Water	30 x 5L	€53.70
<u>Contingency</u>		
Approximate Total:		€5606.70