Decline of Leach's Storm Petrels *Hydrobates leucorhous* at the largest colonies in the northeast Atlantic

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Abstract

Leach's Storm Petrel *Hydrobates leucorhous* has undergone substantial population declines at North Atlantic colonies over recent decades, but censusing the species is challenging because it nests in burrows and is only active at colonies at night. Acoustic playback surveys allow birds present in nest sites to be detected when they respond to recordings of vocalisations. However, not all birds respond to playback on every occasion, response rate is likely to decline with increasing distance between the bird and the playback location, and the observer may not detect all responses. As a result, various analysis methods have been developed to measure and correct for these imperfect response and detection probabilities. We applied two classes of methods (calibration plot and hierarchical distance sampling) to acoustic survey data from the two largest colonies of breeding Leach's Storm Petrels in the northeast Atlantic: the St Kilda archipelago off the coast of northwest Scotland, and the island of Elliðaey in the Vestmannaeyjar archipelago off the southwest of Iceland. Our results indicate an overall decline of 68% for the St Kilda archipelago between 2000 and 2019, with a current best

estimate of ~8,900 (95% CI: 7,800–10,100) pairs. The population on Elliðaey appears to have declined by 40–49% between 1991 and 2018, with a current best estimate of ~5,400 (95% CI: 4,300–6,700) pairs. We also discuss the relative efficiency and precision of the two survey methods.

Introduction

Leach's Storm Petrel *Hydrobates leucorhous* is a widespread and highly pelagic seabird, breeding in burrows on islands across the Atlantic and Pacific Oceans. The global population is estimated at 6.7–8.3 million breeding pairs, but sharp declines have been detected at Atlantic colonies, leading to the species being up-listed from 'Least Concern' to 'Vulnerable' on the IUCN Red List in 2016 (BirdLife International 2020). The main eastern Atlantic Leach's Storm Petrel colonies are in Iceland and Scotland (Mitchell *et al*. 2004), but there are also up to 1,000 pairs breeding in Mykineshólmur in the Faroe Islands and smaller numbers breeding in Norway and Ireland (Bolton & Eaton 2020).

The Vestmannaeyjar archipelago contains almost all of Iceland's breeding Leach's Storm Petrels and, based on extrapolation of the densities measured on Elliðaey Island in 1991, is believed to hold the largest population in the eastern Atlantic (Hansen *et al*. 2009). The 1991 survey of Elliðaey revealed a strong positive association between the occurrence of Leach's Storm Petrel burrows and Atlantic Puffin *Fratercula arctica* (hereafter 'Puffin') habitat, which had been mapped across the whole of the Vestmannaeyjar archipelago (Hansen *et al*. 2009). Six other islands in the archipelago hold breeding colonies of Leach's Storm Petrels: Bjarnarey, Álsey, and Suðurey, which contain similar-sized areas of breeding Puffins to Elliðaey, and Brandur, Hellisey and Smáeyjar, which contain smaller areas of breeding Puffins (Hansen *et al*. 2011). The density of Leach's Storm Petrel Apparently Occupied Sites (AOS; i.e. estimated breeding pairs) within surveyed areas of Puffin habitat on Elliðaey was extrapolated across the Puffin habitat on the other islands in the archipelago, to produce a whole-archipelago estimate of 178,900 (± 34,100) AOS, including 44,100 (± 9,100) AOS for Elliðaey Island (Hansen *et al*. 2009).

The Seabird 2000 census (Mitchell *et al*. 2004) included the first attempt to produce accurate population estimates for Leach's Storm Petrels in Britain and Ireland. Mitchell *et al*. (2004) estimated the total British and Irish population of Leach's Storm Petrels to be 48,357 AOS (95% CI: 36,742–65,193), with 94% of these in the St Kilda archipelago. The largest sub-colony on St Kilda was on the island of Dùn, with an estimated 27,704 AOS (95% CI: 20,430–38,506) in 1999/2000 (Mitchell *et al*. 2004). Further surveys of Dùn in 2003 and 2006 produced estimates of 14,490 (95% CI: 12,110–17,439) and 12,770 (10,046–17,086) AOS respectively, suggesting a decline of 54% on the island since the Seabird 2000 survey (Newson *et al*. 2008).

Previous censuses of Leach's Storm Petrels in the northeast Atlantic have used the acoustic playback method described in Gilbert *et al*. (1998), which is based on techniques developed for surveying European Storm Petrels *H. pelagicus*

(Ratcliffe *et al*. 1998). The playback method involves playing recordings of storm petrel calls, which elicit responses from birds in nest sites. Not all storm petrels will respond to playback on every occasion, so the number of responses obtained during a survey is lower than the actual number of AOS in the surveyed area (Ratcliffe *et al*. 1998). Traditionally, storm petrel playback censuses use a multi-stage method. Playback is performed within a calibration plot, in which the actual number of AOS is known or estimated, in order to estimate the response rate, and thus obtain a correction factor. The total population size is then estimated by applying the correction factor to the number of responses detected in the main survey across a much wider area. Various analytical methods have been used to estimate response rates from the calibration plot (Mitchell *et al*. 2004; Bolton *et al*. 2010), which all rely on the assumption that there is an equal probability of response from all nests in the calibration area. Typically, the calibration area is divided into very small sub-plots (quadrats), with playback conducted in each, to satisfy this condition. Here, we term this approach the 'calibration plot method'.

Traditional acoustic playback methods for burrow-nesting seabirds are extremely time consuming. Detected response rate declines with increasing distance of AOS from the playback point (Ratcliffe *et al*. 1998) so, to maximise response rates, survey quadrats are typically very small (1–4 m^2). The ability to survey a larger area during each playback event, for example by using distance sampling methods which explicitly model the distance-detection function (i.e. the decline in detection probability as distance from the observer increases), has the potential to reduce the survey effort required to estimate a population size.

A key assumption of traditional distance sampling is that perfect detection occurs at distance = 0 (Buckland *et al*. 2001). However, the response rate of burrow-nesting seabirds to playback at distance = 0 tends to be substantially less than one, so there is a need to modify the method for these species. Hierarchical distance sampling (HDS) is a development of the distance sampling method that relaxes this assumption, by using repeat surveys of the same points to independently estimate (i) population density, (ii) detection probability and (iii) availability for detection (Sillett *et al*. 2012; Kéry & Royle 2016). The HDS method assumes that the population is closed, so all individuals are always present within the survey area, but allows for individuals to be unavailable for detection on some occasions, for example, if individuals move to unobservable locations at certain times of the day, or under particular weather conditions. For storm petrels, the probability of responding to playback can be treated as availability for detection, since it is not possible to detect birds when they do not respond. In traditional playback methods, the estimated 'response rate' is equivalent to the product of response rate (the probability of a bird responding to playback) and detection rate (the probability of the observer hearing an emitted response), but the HDS method estimates these components separately. As with the calibration plot method, HDS requires at least some points to be surveyed on more than one occasion, but it does not require individual AOS to be marked, as is the case with the calibration plot.

An additional advantage of HDS is that the density of birds can be modelled with respect to fine scale environmental covariates relating to habitat type. Although the calibration plot method can be used to estimate different densities in different habitat types, these tend to refer to broad areas, in which density is assumed to be homogeneous. A significant drawback of the calibration plot approach is that the colony area may be very difficult to delineate accurately, and errors in the assessment of colony area can hugely influence the resulting population estimate. This also applies to HDS to a degree, but an advantage of HDS is that models can incorporate covariates which explicitly represent the suitability of the habitat for the focal species.

In this study, our primary aim was to estimate current size and change of the largest Leach's Storm Petrel populations in the northeast Atlantic. We present the results of a 2017–18 survey of Leach's Storm Petrels on Elliðaey, and a 2019 survey of Leach's Storm Petrels in the St Kilda archipelago; the latter conducted as part of the fourth national breeding seabird census of Britain and Ireland, 'Seabirds Count'. At both colonies we used two playback survey methods, in an attempt to optimise the accuracy and precision of estimates in the time available, while also enabling back-compatibility and direct comparisons with previous surveys. On Elliðaey, two transects were surveyed in 1991, covering approximately 1% of the island's area. We repeated these transects in 2017 and 2018 and also analysed data from a whole-island census based on a grid of sample points, using HDS. We used insights from these analyses to re-evaluate likely population size in 1991. For St Kilda, we used HDS but also analysed the survey data using the calibration plot method that was used in the previous censuses. We also evaluated the field and analysis methods in terms of their efficiency of data collection and precision of the resulting population estimates.

Methods

Fieldwork

Field sites

Elliðaey Island (63°28'N 20°11'W) is a 45 ha uninhabited island of grass-covered volcanic tuff, with a maximum elevation of 145 m above sea level. Elliðaey is the northernmost island in the Vestmannaeyjar archipelago, lying approximately 7 km off the southwest coast of Iceland (Figure 1). The island is free of terrestrial mammals, except for Sheep *Ovis aries* and visiting humans.

The St Kilda archipelago (57°49'N 8°35'W) lies off the northwest coast of Scotland, 64 km west of North Uist (Figure 1). The four main St Kilda islands all hold breeding Leach's Storm Petrels. The largest sub-colony is on the island of Dùn, where dense vegetation and scattered boulders cover the steep slopes, and the maximum elevation is 178 m. Large areas of Dùn are densely burrowed by Puffins, and the ground is mostly unconsolidated and fragile. Smaller sub-colonies of Leach's Storm Petrels are found on the islands of Hirta, Boreray and Soay. All three of these islands are grazed by Sheep and have far more consolidated ground, with steep slopes of short grass sward, rocky outcrops and boulder fields. Aside from

Sheep and visiting humans, the only other mammal on the islands is the endemic St Kilda Field Mouse *Apodemus sylvaticus hirtensis*, which is present on Hirta and was known to be present on Dùn in 2008 (Bicknell *et al*. 2009). Harris and Murray (1978) report "a few pairs [of Leach's Storm Petrel] on Levenish and an unknown number on Stac an Armin", but these sea stacks are extremely difficult to access and these populations have never been systematically surveyed.

Figure 1. Red triangles show the locations of **(a)** the Vestmannaeyjar archipelago in relation to Iceland and **(b)** the St Kilda archipelago in relation to the Great Britain and Ireland.

Playback recording

Leach's Storm Petrels generally only respond to calls of the same sex when in the burrow (Taoka *et al*. 1989) and previous surveys of Leach's Storm Petrels on both Elliðaey and St Kilda used only the male chatter call in playbacks (Hansen *et al*. 2009; Mitchell *et al*. 2004). In the current study we used calls of both sexes, in an attempt to increase response rates (Perkins *et al*. 2017). Pilot work indicated that we achieved slightly higher response rates using a recording containing two female calls followed by an interval and then two male calls, compared with either a recording with no interval between female and male calls, or where a single male call was followed by an interval and then a single female call. We therefore use the former recording throughout (supplied in online Supplementary Material), with 10 second intervals after the calls of each sex in which to listen for responses. The total duration of the recording was 30 seconds, with a pure tone at the end to indicate the end of the survey period. Recordings were made on Elliðaey in 1991.

Playback method

We performed the playback by holding a portable speaker (EasyAcc model LX-839) facing towards the ground, approximately one metre above the survey point, and playing the recording at maximum volume (c. 75 dB). We only recorded responses from Leach's Storm Petrels if they occurred within the 30-second survey period for each playback trial. Once this period had finished, the observer measured the approximate distance to each response using a string (on Elliðaey) or a bamboo cane (on St Kilda) marked at 50 cm intervals. We recorded responses in eight 50 cm distance bands, from 0 m to 4 m. We noted any responses beyond 4 m but did not measure beyond the 4 m radius. On a small number of occasions, a high number of responses made it difficult to accurately locate individual responses, so the observer played the call again to elicit another response, while taking care to only record those individuals that responded on the first playback. On St Kilda, we carried out playback surveys for three species, but at each survey point playback for Leach's Storm Petrel was always carried out first, and responses recorded, before playback for the other species.

Timing of surveys

For both Elliðaey and St Kilda, we carried out fieldwork during the period when Leach's Storm Petrels were believed to be incubating, based on previous observations, so that an adult would normally have been present in every active burrow 24 hours a day (Mitchell *et al*. 2004; E. S. Hansen pers. obs.). Outside the incubation and brood-guard stage, the chick is usually left alone in the nest site, with adults making only brief nocturnal provisioning visits. Any burrows in which an egg had been laid but was not attended by an adult due to breeding failure or temporary egg neglect (Pollet *et al*. 2019) would not have been detected in our surveys, which could induce a relatively small underestimation of the number of AOS. We performed distance sampling surveys between 07:00 and 19:00 hours, and only when weather conditions were considered unlikely to impact the detection of bird vocalisations or estimation of distances (i.e. not in strong wind, heavy rain or fog). Although response rates of storm petrels to playback are generally higher at night (Ratcliffe *et al*. 1998; Mitchell *et al*. 2004), we performed the distance sampling surveys during daylight, as responses from birds in burrows can be difficult to distinguish from birds calling in flight at night and night surveys on rough terrain and near cliffs are more dangerous. We carried out the repeats of the 1991 survey transects on Elliðaey (described below) at night to replicate the previous survey method as closely as possible.

Elliðaey surveys

Four people performed the main census of Elliðaey on 24, 26 and 27 June 2018. We performed a point distance sampling survey across the whole island, using a pre-determined grid of 1,362 points at 16 m intervals (see Figure 2). During fieldwork, 208 of these points were found to be inaccessible and were excluded from the survey, but most of these excluded points fell in habitat unsuitable for Leach's Storm Petrel nesting (i.e. bare rock). Each of the remaining 1,154 points was surveyed once.

Calibration data

Fieldwork on Elliðaey was cut short due to poor weather, before we had collected sufficient calibration data to analyse the survey data using a calibration plot method (i.e. by applying a correction factor). However, we also performed a trial to quantify time of day variation in response rates, as storm petrel response rates are known to vary across the day (Ratcliffe *et al*. 1998). To do this, we surveyed 41 points every three hours between 08:00 and 23:00 (six times in total) on 27 June, using the same distance sampling method as the main survey. The calibration data showed no significant decrease in response rate across the first five daytime playbacks on the same day, suggesting there was no habituation effect to the playback (binomial repeated measures GLM, all pairwise comparisons with visit 1, $P > 0.342$). There was a significant increase in response rate on the sixth (night time) calibration playback (pairwise comparison between visit 1 and visit 6, $P < 0.0001$). The repeated playback at the same sites, combined with the distance sampling data collected in the main survey, therefore enabled us to analyse the survey data using the HDS method, although that had not been the original reason for the repeat samples.

Repeat of 1991 survey transects

To enable a direct comparison with the previous Elliðaey population estimate, we repeated the survey method used in 1991 (30 June to 1 July) between 00:00–02:00 hours on 27–30 June 2017 and 30 June 2018. In 2017, we performed playback along the two strip transects used in the 1991 survey: Hábarð (10 m wide x 160 m long) and Bunki (10 m wide x 300 m long; Figure 2). Sheep displaced the Bunki transect lines in 2017, shortening the transect to the upper 70 m, which contained higher AOS densities than the rest of the transect in 1991. In 2018, we repeated only the Hábarð transect, and the final 10 m of the transect line were not surveyed. As in 1991, each of these transects was split into quadrats of 2.5 x 2.5 m and a single playback was performed in each quadrat, using the same recording of a single male Leach's Storm Petrel chatter call as in the 1991 survey. We recorded the number of birds responding from below ground within each quadrat.

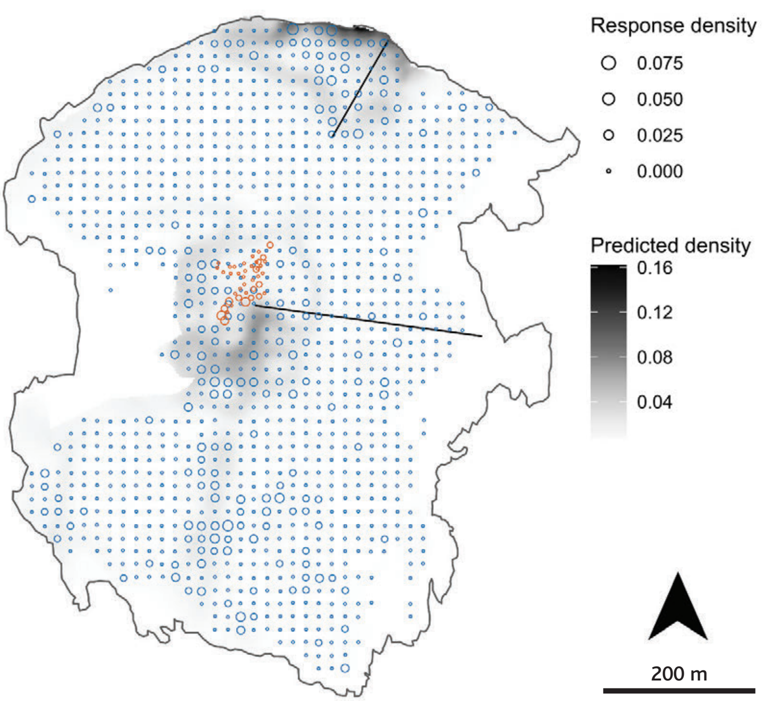


Figure 2. Map of Elliðaey Island, Vestmannaeyjar archipelago, Iceland. Blue open circles represent mean response density (responses per m²) for survey points. Orange open circles represent mean response density for points repeated during the time of day trial. Predicted density of Leach's Storm Petrel *Hydrobates leucorhous* (Apparently Occupied Sites per m²) from the top-performing hierarchical distance sampling model is shown. Black lines show the locations of the Hábarð (north) and Bunki (middle) transects, per-formed in 1991, 2017 and 2018. White areas without survey points are unsuitable habitat.

St Kilda surveys

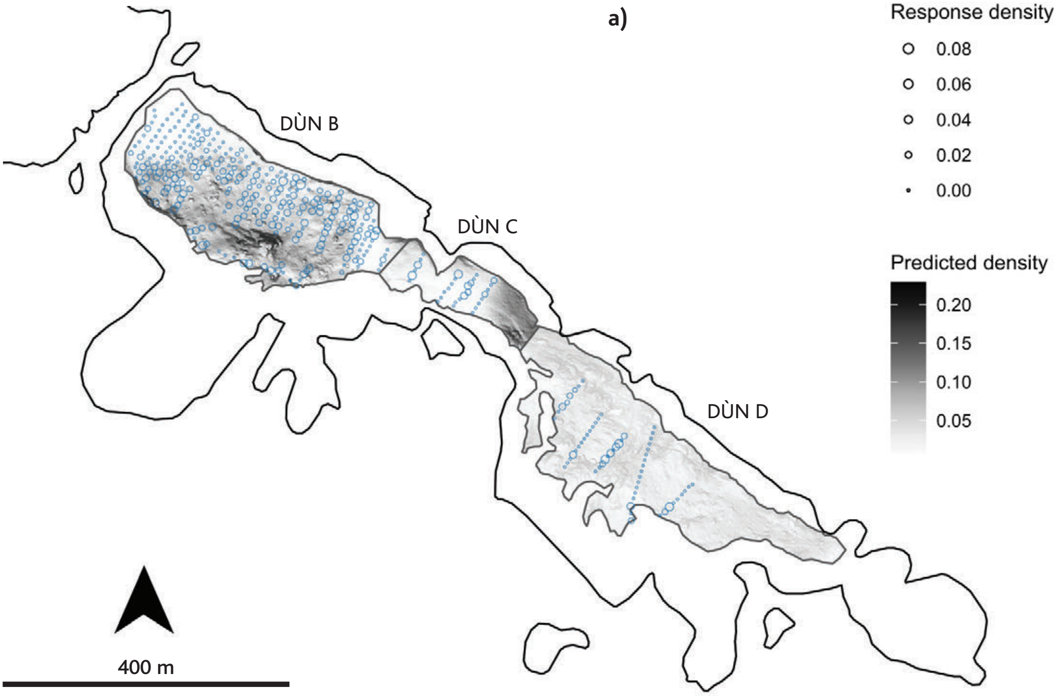
We surveyed Leach's Storm Petrel on Dùn, Hirta, Boreray and Soay between 18 June and 5 July 2019, alongside surveys for Puffins, Manx Shearwaters *Puffinus puffinus* and European Storm Petrels. We divided the islands into sectors of similar habitat based on those used in the Seabird 2000 census (Mitchell *et al*. 2000; following Harris & Murray 1977), although sector maps were only available as low-resolution photocopies so boundaries were not identical. On all islands, we ran rope transects down the slope and established playback survey points at 10 m intervals along each transect (Figure 3). The area surveyed by each playback point was larger than that used in previous surveys (see Mitchell *et al*. 2000, Newson *et al*. 2008 for details).

Dùn

Five people surveyed Dùn on 27–29 June, and 3 and 5 July 2019. On the northwestern section of Dùn (sector B), we laid transects at approximately 25 m intervals, and marked survey points with bamboo canes. We performed a playback survey at each point on each of the five survey days. On 3 July we laid out additional transects halfway between the original transects and on the remaining two survey days we also performed playback at points marked on these transects. The southeastern sector of Dùn (sector D) is densely burrowed by Puffins and the terrain is extremely fragile. To avoid causing damage to the habitat and disturbance to the Puffin colony, we limited the number of survey points and playback occasions in this area. We performed playback once on five transects in this southeastern sector on 27 June, alongside a Puffin census. We repeated a single transect in the southeastern sector on each of the additional four survey days. We surveyed the neck between the northwestern and southeastern sections (sector C) on 28 June, with transects laid vertically down the slope at approximately 25 m intervals. On two transects in the main northwest survey area, we marked all responses with individually-numbered flags to enable estimation of response rate for the calibration plot method. Large numbers of Northern Fulmars *Fulmarus glacialis* nest on Dùn, with eggs and small chicks present during the survey period. To avoid excessive disturbance to the Fulmars, we excluded some potentially-accessible areas of the island from the survey. We surveyed additional points along the ridge of the northwestern section of the island in an attempt to cover parts of this habitat, whilst avoiding areas occupied by nesting Fulmars. No attempt was made to visit the southwestern side of Dùn because of difficulties with safe access.

Boreray

Six people surveyed the island of Boreray on 18–22 June 2019. We performed playback along transects surveyed for Puffins. We laid out transects at 25 m intervals in areas of high Puffin density and less frequently in lower density areas. In the less accessible parts of the island (sectors BOR11 and BOR8) the number of transects was limited by time and safety constraints. On four transects, we marked survey points with metal pegs and repeated playback at these points on multiple days. On three transects, we marked responses with individually-numbered flags in order to obtain a response rate estimate for the calibration plot method. It became apparent that



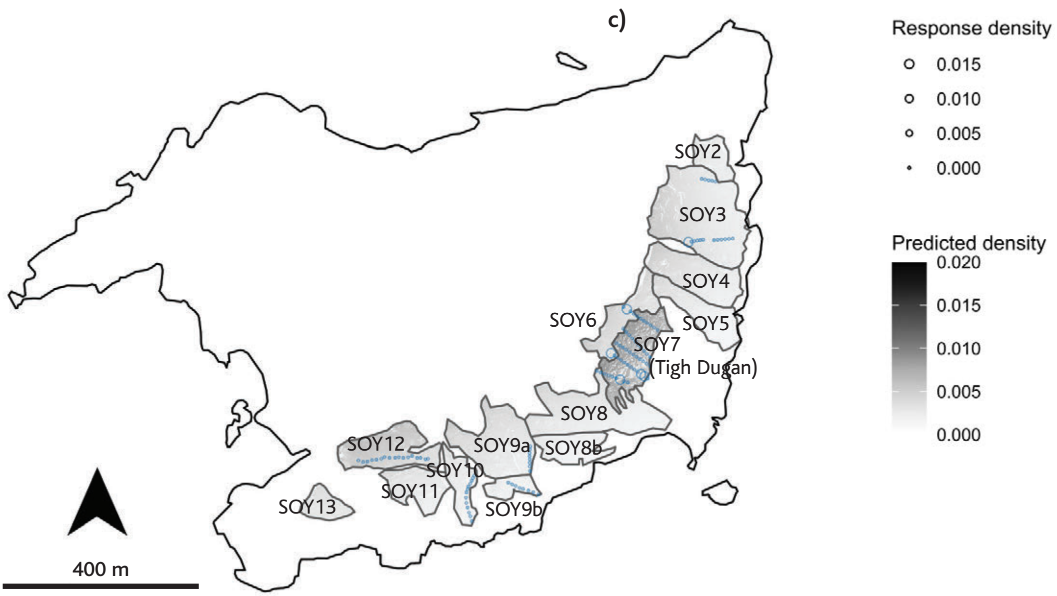
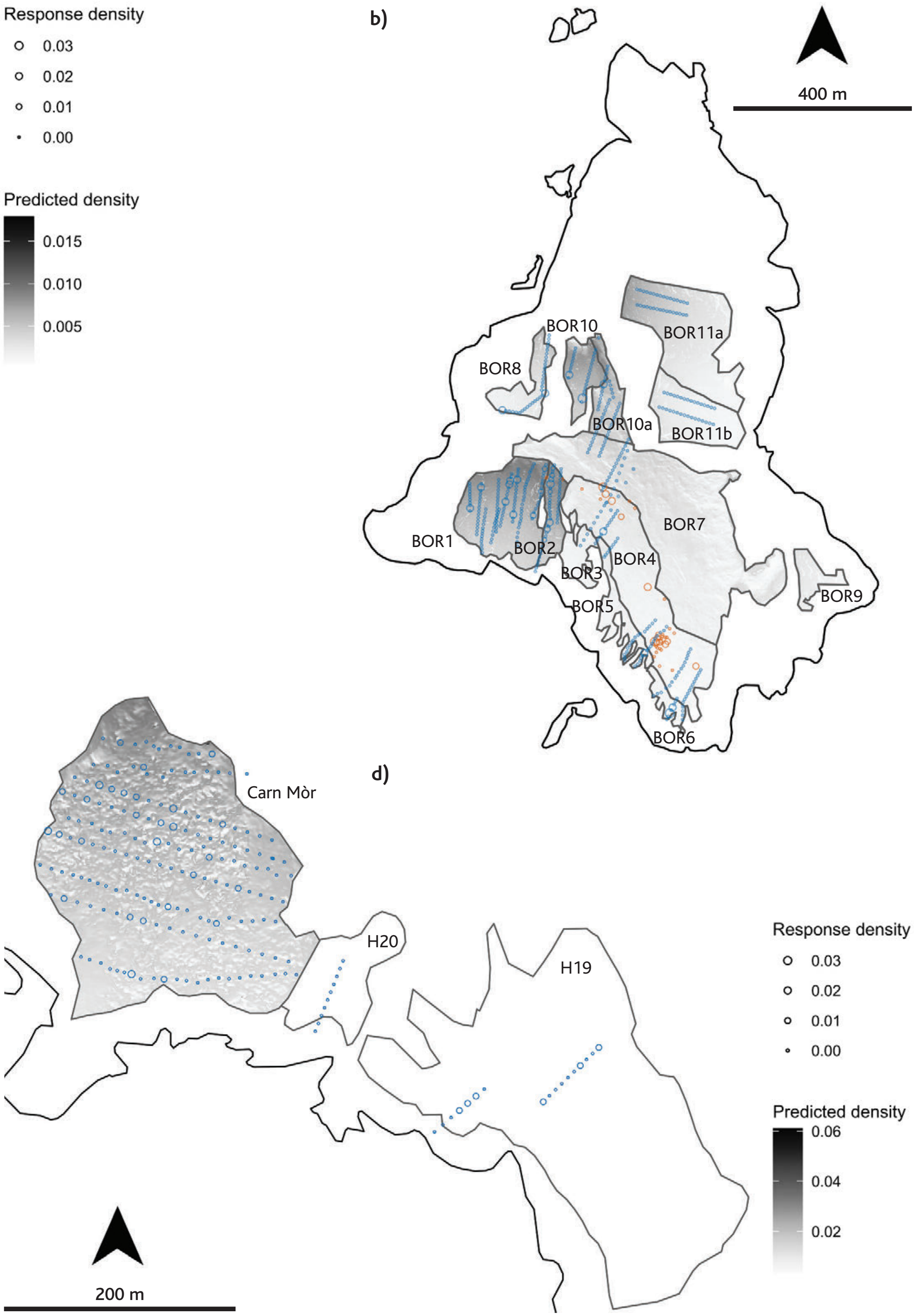


Figure 3. Maps of **(a)** Dùn, **(b)** Boreray, **(c)** Soay and **(d)** Carn Mòr, St Kilda, with sector outlines shown. Blue open circles represent mean response density (responses per m²) for survey points. Orange open circles represent response density for cleitean (drystone storage huts or bothies) on Boreray, which were treated as a separate 'sector'. Predicted density of Leach's Storm Petrel *Hydrobates leucorhous* Apparently Occupied Sites from the top-performing hierarchical distance sampling models is shown. Densities are based on topographical (3D) area.



Response density
0.03
0.02
0.01
0.00
Predicted density
0.015
0.010
0.005
b)
400 m
BOR10
BOR11a
BOR8
BOR10a
BOR11b
BOR7
BOR1
BOR2
BOR4
BOR3
BOR9
BOR5
BOR6
d)
Carn Mòr
H20
H19
Response density
0.03
0.02
0.01
0.00
Predicted density
0.06
0.04
0.02
200 m

there were very few petrels on most of the island but that they were concentrated in the cleitean (drystone storage huts or bothies, originally ~3 x 6 m but now in varying states of disrepair). In addition to the transects we therefore surveyed each cleit on up to five occasions; on each occasion using a single playback with the speaker held above the centre of the structure. Access difficulties meant we did not systematically survey areas of rockfall on coastal fringes, but we elicited responses in some of these areas using *ad hoc* playback, suggesting that they warrant further investigation in future surveys. These responses are not included in our population estimates and, as far as we are aware, these areas were not included in previous censuses.

Soay

Due to time and weather constraints, six people surveyed Soay on a single visit on 23 June 2019. On the grassy slopes, we surveyed Leach's Storm Petrels alongside Puffins, on six transects running down the slope. Five additional transects ran through the Tigh Dugan boulder field.

Hirta

In previous surveys of Hirta, the majority of Leach's Storm Petrels were found to be in the Carn Mòr boulder field on the southwest of the island. We focussed survey effort there in 2019, to make the most of the limited time available. Four people surveyed Carn Mòr on 25 June. We ran nine transects across the slope, parallel to the coastline, approximately 25 m apart. Two people surveyed three transects perpendicular to the coastline on the slopes adjacent to Carn Mòr on the same day. In an effort to determine presence/absence of Leach's Storm Petrels elsewhere on Hirta, we performed playbacks approximately every 2 m along the walls and cleitean above the village on 1 July, and at least one playback was performed at each cleit, other stone structures and natural boulder piles in the valley of Gleann Mòr on 30 June, although conditions were poor, with very strong winds.

On some St Kilda transects, GPS location data was not recorded for every survey point. In these cases, we used a straight-line interpolation to determine the locations of missing survey points, based on adjacent points.

Data Analysis

All analysis was performed using R (version 3.6.0, R Core Team 2019), implemented in R-Studio (www.r-studio.com). The code used in calculating the results, together with the archived data files, are available as online Supplementary Materials.

Due to time constraints, we were not able to survey every sector of every island on St Kilda, so to estimate whole-island populations we combined sectors of similar habitat and sufficient survey effort (Figure 3). Boreray was split into three 'combined sectors': (i) BOR1-2, which contained sectors BOR1 and BOR2, the terraced slopes with high Puffin density; (ii) BOR3+, which contained all other sectors; and (iii) the cleitean. Soay was split into (i) the Tigh Dugan boulder field (SOY7) and (ii) all other sectors (SOY), which generally comprised grassy slopes with scattered boulders. Dùn was split into (i) 'Puffin' (sector D) and (ii) 'non-Puffin' (sectors B and C) areas, due to the very high density of Puffin burrows in sector D. A small number of points fell outside the sector boundaries and these were allocated to the nearest sector by straight-line distance.

Calibration plot method - St Kilda only

Estimating response rate: In order to make direct comparisons of population size with the Seabird 2000 survey, we used the asymptote method to estimate response rate from the calibration transects, as described in Mitchell *et al*. (2004). The method involves fitting a curve to the cumulative number of AOS found on successive playback surveys of the calibration plot. The curve is fitted using an asymptotic regression model, of the form:

$$y = a(1 - e^{-b})$$

where y is the number of AOS detected on a visit, a is the asymptote of the regression curve (equivalent to the total number of AOS in the calibration plot) and b is the exponential proportional rate of increase to the asymptote. We fitted the asymptotic regression model using the 'nls' function of the 'stats' package.

We used the estimated value of b and its standard error to describe a gamma distribution, from which we drew 10,000 samples. A gamma distribution was chosen, as a zero-bounded but continuous distribution, so that the sampled values of the parameter b could not take negative values, reflecting the fact that the cumulative number of nests detected can only increase with further sampling, and not decrease. We converted these samples of b to response rates using the equation $1 - \exp(-b)$, and took the 2.5 and 97.5 percentiles of these as the 95% confidence interval.

Estimating response density: We calculated mean response density (number of responses per m^2) for each combined sector of St Kilda and used the 'boot' package (version 1.3-22, Davison & Hinkley 1997; Canty & Ripley 2019) to obtain 10,000 bootstrapped estimates of response density, which were used to calculate 95% confidence intervals.

Population estimates: We calculated population estimates for each combined sector by multiplying mean response density by the reciprocal of the mean response rate (i.e. the correction factor) and multiplying this value by the total area of the sector (Mitchell *et al*. 2004). For each combined sector we applied the 10,000 estimates of response rate to the 10,000 bootstraps of response density, to obtain confidence intervals for combined sector population estimates (Bolton *et al*. 2017).

We calculated whole-island population estimates by summing the estimates for each combined sector within an island. We obtained whole-island confidence intervals by summing randomly-combined population estimate bootstraps for each combined sector within an island. Similarly, we obtained the whole-archipelago population estimate by summing the estimates for each island, and its confidence interval by summing randomly combined bootstrap population estimates for each island.

Hierarchical distance sampling (HDS) models (all islands): We built HDS models using the 'gdistsamp' function of the 'unmarked' package (version 0.12-3, Fiske & Chandler 2011). We modelled Elliðaey separately from St Kilda due to differences in habitat types and the availability of covariate data. Since HDS requires at least some survey points to be surveyed more than once, we combined the main survey and time of day calibration data for the Elliðaey HDS models. For St Kilda, since the island of Dùn had a relatively high survey effort, we first built models for the Dùn data alone. For the rest of the St Kilda archipelago, we used data for all islands — including Dùn — in the models, since survey effort was not sufficient to model the other islands individually. While it is not currently possible to incorporate spatial autocorrelation effects within the 'unmarked' package, the potential biases are believed to be small, particularly if habitat covariates have good explanatory power (Kéry & Royle 2016).

For point distance sampling, it is recommended that the outermost ~10% of observations are truncated before analysis, to improve the estimation of the detection function (Buckland *et al*. 2001). We truncated our distance sampling data to 4 m, excluding any responses detected beyond this distance, which excluded 8.84% of detections for Dùn and 8.57% for St Kilda as a whole, but 21.71% for Elliðaey. This suggests that birds could more readily be detected beyond 4 m on Elliðaey than on St Kilda.

We initially constructed null models to test whether the hazard rate, half-normal, exponential or uniform detection functions best described the detection process, and whether a Poisson or negative binomial distribution best described abundance. We then used an information-theoretic approach to select the best-performing null models, based on Akaike's Information Criteria (Burnham & Anderson 2004).

Model covariates

Elliðaey

We extracted altitude, slope and aspect values for each survey point from a 2 m resolution digital elevation model (DEM) of Elliðaey (ArcticDEM version 2.0; Porter *et al*. 2018).

The dense tussocks of Red Fescue *Festuca rubra* that both Puffins and Leach's Storm Petrels nest in on Elliðaey are readily identifiable from satellite imagery. We classified all land on Elliðaey as either 'tussock' or 'non-tussock' habitat, using random forest supervised classification in the 'caret' package (version 6.0-84, Kuhn 2019). We extracted RGB colour values from polygons of known areas of tussock and non-tussock habitat that we identified visually from Bing Maps satellite imagery (dated 25 July 2016) to train the classifier, and then classified the whole of Elliðaey as either tussock or non-tussock habitat. We calculated the proportion of tussock habitat within 4 m, 8 m, 25 m and 50 m buffers around each survey point.

St Kilda

We used the 'grid_terrain' function of the 'lidR' package (Roussel *et al*. 2020) to create a digital terrain model (DTM) from 0.5 m resolution LiDAR data for the St Kilda archipelago (LiDAR data from Historic Environment Scotland). We then extracted altitude, slope and aspect values from the DTM for each survey point.

For Dùn, we used the 'caret' package (Kuhn 2019) to classify the habitat for each 1 m x 1 m pixel as 'rock', 'grass' or 'herb', based on RGB values from LiDAR imagery. We calculated the proportion of each habitat for 4 m, 8 m, 25 m and 50 m buffers around each survey point. The 'rock' category included cliffs, slabs and boulders. We used the term 'grass' for areas of more consolidated ground, observed in the field to be dominated by Red Fescue and Yorkshire Fog *Holcus lanatus*. We used the 'herb' category for areas of taller vegetation, observed in the field to be dominated by Sea Mayweed *Tripleurospermum maritimum* and Common Sorrel *Rumex acetosa*, where the ground tended to be tussocked. Note that Red Fescue covers most of Elliðaey, including the tussocked areas, whereas on Dùn, Red Fescue is more commonly found in non-tussocked areas.

We classified the southeast sector of Dùn (sector D) as 'Puffin' habitat due to its extremely high density of nesting Puffins (Luxmoore *et al*. 2018). Although Puffins nest elsewhere on Dùn, for modelling purposes we classified the rest of the island as 'non-Puffin' habitat, since Puffin burrows occur at much lower densities and are generally restricted to areas of boulders and the tops of the northeastern cliffs.

For St Kilda, we acquired daily windspeed data for the survey period, averaged across three weather stations on Hirta. Windspeed and direction can vary greatly around the archipelago, so it is important to recognise that the averaged values from Hirta may not be completely representative of the weather experienced at the time and location of each survey.

To help with model computation, we scaled all numerical covariates by subtracting the mean and dividing by the standard deviation, giving a standardised mean value of 0 and a standard deviation of 1.

Model structure

Elliðaey

We included altitude (linear and quadratic), slope (linear and quadratic), aspect (linear), and proportion of tussock habitat at 4 m, 8 m, 25 m and 50 m radius from each survey point as potential covariates of storm petrel abundance in the Elliðaey model set. We included time of day (linear and quadratic) as a covariate of availability for detection. We did not include date as a covariate of availability since the models use repeat sampling of the same sites to estimate availability and no sites on Elliðaey were sampled on more than one day. We included observer ID and date (linear, quadratic and categorical) as possible effects on detection probability. We included date as a detection covariate to account for differences in weather conditions between days, in the absence of weather data.

St Kilda

We included the following covariates as abundance effects for the Dùn-only model: Puffin/non-Puffin sector (categorical), altitude (linear and quadratic), slope (linear and quadratic), proportion of rock, grass, and herb habitat at 4 m, 8 m, 25 m and 50 m radius from each survey point (linear and quadratic). The all-island models included altitude (linear and quadratic), slope (linear and quadratic), island (categorical) and sector (categorical) as possible abundance effects. The set of all-island models also included a 'combined sector' effect on abundance, thereby reducing the total number of sectors in the model. Habitat was not included in the all-island models since habitat availability varied greatly between islands and the habitat with the highest density of Leach's Storm Petrels differed between islands. We included time of day (linear and quadratic), date (linear, quadratic and categorical), and windspeed (linear and quadratic) as covariates of availability for the Dùn-only and all-island model sets. For both model sets, we included windspeed (linear and quadratic) and observer ID as effects that may influence the detection probability. We included windspeed as an effect on both availability (i.e. response rate) and detection, since higher windspeeds could affect both the ability of a bird to hear the playback (and therefore the likelihood of it responding) and the ability of the observer to detect a response from the bird.

Model selection

Due to the large number of possible covariate combinations, we used a sequential approach to model selection (Arnold 2010; Sillett *et al*. 2012; Olson *et al*. 2017). First, we tested univariate models for each of the abundance, availability and detection covariates, while holding the other parameters constant. We retained covariates that ranked better than the null model by AIC. We checked variables for pairwise multicollinearity and where Pearson's r was > 0.7, we retained the variable with the lower univariate AIC.

Next, we combined the selected variables into additive, multivariate models. We started by testing detection models, while holding the availability and abundance components constant. We then used the top-performing detection model to test combinations of availability variables. Next, we tested combinations of abundance variables using the top-performing detection and availability models. Finally, we kept the top-performing combination of abundance covariates and removed a single variable at a time from the detection and availability components, to check whether the addition of abundance covariates made any other variables redundant. We evaluated goodness of fit of the overall top-performing model by parametric bootstrapping (Sillett *et al*. 2012). We used the 'parboot' function of the 'unmarked' package to simulate 100 new datasets from the model, refitting the model to each data set and calculating the Freeman-Tukey fit statistic for each iteration.

We used the top-performing model to predict Leach's Storm Petrel abundance for every 2 m x 2 m grid cell on Elliðaey and every 1 m x 1 m grid cell in each sector of the St Kilda archipelago, reflecting the resolution of the covariate data.

We used the sum of the expected abundance in all cells as the total population estimate for Elliðaey and at the levels of (i) sector, (ii) island and (iii) archipelago for St Kilda. The large number of cells made bootstrapping confidence intervals for sectors and islands unfeasibly time-consuming, so we calculated variances for combined abundance estimates (at the sector or island level) using the 'deltavar' function of the 'embdbook' package (version 1.3.12, Bolker 2008; Bolker 2020). Since confidence intervals for individual cells were asymmetric, we constructed confidence intervals for combined abundance estimates using a log-normal approach:

$$\lambda_{LCL} = \lambda / C$$

and

$$\lambda_{UCL} = \lambda * C$$

where λ is the mean abundance estimate, and

$$C = \exp\left\{1.96 * \sqrt{\log_e(1 + [cv(\lambda)]^2)}\right\}$$

Area calculations
Due to the steepness of the terrain across the islands, the slope-corrected (topographic) surface area was often much greater than the horizontal planar area, with an increase in area of more than 50% for some St Kilda sectors. We used the 'sp' package (version 1.3-1, Pebesma & Bivand 2005; Bivand *et al*. 2013) to calculate surface area from the DEM for Elliðaey and from the DTM for the St Kilda sectors. Where area estimates were given in previous analyses, we also used these values to produce current population estimates that are as comparable as possible, although we note that the area of available breeding habitat can change over time (Pollet & Shutler 2018).

Archived materials: datasets and script files
A limitation in assessing population trends across long periods of time (typically decades) is that field survey methods and analytical methods change, and it is not always clear how data were collected or analysed. The raw datasets and analysis script files used in the present study will be available to future researchers, to make explicit how we have arrived at the current population estimates, and to facilitate direct comparisons between population estimates across years.

Results

Elliðaey

Repeat of 1991 survey
Response density for the top 70 m of the Bunki transect was 67.5% lower in 2017 than 1991 (Table 1). For the Hábarð transect, response density in 2017 and 2018 was 46.0% and 39.8% lower than in 1991, respectively. Overall, there was a decline in response density of 48.8% between 1991 and 2017 and 39.8% between 1991 and 2018.

Table 1. Results from playback surveys on the Bunki and Hábarð Leach's Storm Petrel *Hydrobates leucorhous* transects on Elliðaey, Iceland, in 1991, 2017 and 2018. Response densities (number of Apparently Occupied Sites responding per m²) are given ± S.E.

Date	**1991 30 June to 1 July**			**2017 27–30 June**				**2018 29 June**			
Transect	**Area (m²)**	**Responses**	**Response density**	**Area (m²)**	**Responses**	**Response density**	**Change (%)**	**Area (m²)**	**Responses**	**Response density**	**Change (%)**
Bunki	2,975	110	0.037 ± 0.0057 (0.057)*	700*	13	0.019 ± 0.0064	-67.5*	-	-	-	-
Hábarð	1,600	257	0.161 ± 0.0123	1,600	139	0.087 ± 0.0108	-46.0	1,500	145	0.097 ± 0.0077	-39.8
Total	4,575	367	0.080 ± 0.0065 (0.129)*	2,300	152	0.066 ± 0.0080	-48.8	1,500	145	0.097 ± 0.0077	-39.8

* To estimate the change between Bunki transect in 1991 and 2017 only the top 70 m in 1991 are used for comparability (see Methods).

HDS method

In the main survey, we detected a total of 339 responses during 1,400 playbacks at 1,195 survey points on Elliðaey.

A half-normal detection function and negative binomial distribution for abundance produced the lowest AIC of all the null models, and were used in the subsequent model set. The full model set consisted of 72 models, in addition to the null models. The top five models are given in Table 2. The best-performing model for Elliðaey contained a linear effect of altitude and a quadratic effect of tussock habitat at a 50 m radius on abundance, a quadratic effect of time of day on availability, and a linear effect of date on detection probability. Graphs of covariate effects are provided as online Supplementary Material. The Freeman-Tukey P-value for the best-performing model was 0.537, suggesting an adequate fit to the data. The total population estimate was 5,356 (95% CI: 4,296–6,678) AOS.

St Kilda

We detected a total of 973 responses during 2,231 playbacks at 1,231 survey points on St Kilda. The size of each survey sector, the number of survey points and the number of playback responses for each combined sector are given in Table 3. Additional detail on the number of survey points and the number of repeated playbacks for each sector is provided as online Supplementary Material. Table 4 gives the results for the calibration plot and HDS methods for each of the surveyed St Kilda islands.

Calibration plot method

On Boreray, we only identified nine AOS on the calibration transects, which was not sufficient to reliably calculate a response rate. We identified a total of 52 AOS within a 4 m radius during the five playback occasions at the calibration sites on Dùn. We had intended to use only responses from a 1 m radius for the calibration plot method, but too few responses were obtained at this distance to produce a sufficiently precise response rate. We therefore used responses within a 3.5 m radius, since this produced narrower confidence intervals relative to the mean population estimates than any other radius (see online Supplementary Materials). The response rate calculated from the asymptote method was 0.208 (95% CI: 0.096–0.344). This represents the response rate calculated across all AOS within a 3.5 m radius of the playback point and the resulting correction factor was applied to response densities calculated for responses within 3.5 m of each survey point. The response rate from Dùn was used for the calibration plot method for all St Kilda islands.

On Hirta, no responses were obtained from the cleitean and walls above the village or in Gleann Mòr. Our survey effort for areas on Hirta other than Carn Mòr was not sufficient to estimate the population for the rest of the island, but based on the rate of decline observed at Carn Mòr, we estimate that other areas of Hirta currently contain fewer than 500 AOS.

HDS method

We removed 60 survey points from the HDS analysis for St Kilda, as the GPS data recorded were not sufficiently accurate (> +/- 5 metres) to extract environmental covariates for their locations and we could not reasonably interpolate their location from other points.

As for Elliðaey, for the St Kilda dataset a half-normal detection function and negative binomial distribution for abundance produced the lowest AIC of all the null models, for both the Dùn-only dataset and the all-island dataset, and we used these for the rest of the models in both sets.

The full model sets contained 133 models for Dùn and 114 models for all islands, in addition to the null models. The best Dùn-only model contained an effect of Puffin sector and quadratic terms for the proportion of herb habitat at a 25 m radius and slope on storm petrel abundance; quadratic effects of time of day and date, and a linear effect of windspeed on availability (i.e. the probability of a bird responding if it is present); and an observer effect on detection (Table 2). The best all-island model contained the following effects on abundance: 'combined sector', a linear effect of altitude and a quadratic effect of slope; a quadratic effect of time of day on availability; a linear effect of windspeed and an observer effect on detection probability (Table 2). Graphs of covariate effects are provided as online Supplementary Material. The top-performing models for Dùn and St Kilda had Freeman-Tukey P values of 0.366 and 0.238, respectively, suggesting adequate fits to the data.

Table 2. Top five hierarchical distance sampling models by AIC for Leach's Storm Petrels *Hydrobates leucorhous* on Elliðaey, Dùn and the St Kilda archipelago as a whole. As recommended by Arnold (2010), we have excluded models containing uninformative covariates from the model lists. Where quadratic effects are included, the model also included the corresponding linear effect. 'Tussock50' and 'Tussock25' refer to the proportion of habitat classified as "tussock" within a 50 m and 25 m radius of the survey point. 'Puffin habitat' is a binary variable, specifying whether a survey point was within the area of the island containing a very high density of Puffins. 'herb25' refers to the proportion of habitat classified as "herb" within a 25 m radius of the survey point.

Model rank	Abundance Covariates	Availability Covariates	Detection Covariates	No. of parameters	ΔAIC	Cumulative weight
Elliðaey						
1	Altitude + $Tussock50^2$	$Time^2$	linear date	10	0.00	0.91
2	Altitude + $Tussock50^2$	$Time^2$	-	9	4.61	1.00
3	Altitude + $Tussock50^2$	-	linear date	8	13.43	1.00
4	$Altitude^2$ + $slope^2$	$Time^2$	linear date	11	24.28	1.00
5	$Altitude^2$ + slope	$Time^2$	linear date	10	25.02	1.00
Dùn						
1	Puffin habitat + $herb25^2$ + $slope^2$	$Time^2$ + linear $date^2$ + windspeed	Observer	21	0.00	0.27
2	Puffin habitat + $herb25^2$ + $slope^2$	$Time^2$ + linear $date^2$	Observer	20	0.05	0.54
3	Puffin habitat + $herb25^2$ + $slope^2$	$Time^2$ + linear $date^2$	Observer + windspeed	21	1.23	0.69
4	Puffin habitat + $herb25^2$ + slope	$Time^2$ + linear $date^2$	Observer	19	3.02	0.75
5	Puffin habitat + $herb25^2$ + $slope^2$	$Time^2$ + linear date + windspeed	Observer	20	3.15	0.81
St Kilda						
1	Combined sector + altitude + $slope^2$	$Time^2$	Observer + windspeed	27	0.00	0.80
2	Combined sector + altitude + $slope^2$	$Time^2$	Observer	26	3.45	0.94
3	Sector + $altitude^2$ + $slope^2$ + aspect	$Time^2$ + linear $date^2$	Observer + windspeed	49	5.69	0.98
4	Combined sector + $slope^2$	$Time^2$ + linear $date^2$	Observer + windspeed	28	10.83	0.99
5	Combined sector + $altitude^2$ + slope	$Time^2$ + linear $date^2$	Observer + windspeed	29	11.46	0.99

Table 3. Summary of the areas, number of surveyed points, number of playbacks at those points (note that we surveyed some points multiple times), and number of responses (from all survey occasions, so including multiple responses from some Apparently Occupied Sites) in each sector or combined sector on St Kilda. Area refers to the topographical area; Seabird 2000 area is the area used in the previous survey, where available (Mitchell *et al*. 2000). For Dùn, the Seabird 2000 area of 147,396 m² has been divided between the sectors based on their proportion of the total area calculated in this study. Number of responses is given for a 4 m radius and 3.5 m radius as these are the radii used in the HDS and calibration plot methods, respectively. Numbers in brackets are those used in the HDS analysis, after some survey points were excluded due to GPS inaccuracies.

	Area	Seabird	No. of survey	No. of	No. of responses	
Dùn	**(m²)**	**2000 area**	**points**	**playbacks**	**4 m radius**	**3.5 m radius**
Dùn B+C	81,352	77,578	356 (314)	1,034 (983)	805 (767)	747
Dùn D	73,214	69,818	59	91	38	38
Boreray						
BOR1-2	59,715		184	352	33	29
BOR3+	353,113		305	324	11	11
Cleitean			40 (37)	143 (135)	46 (45)	46
Soay						
Tigh Dugan boulder field (SOY7)	18,067		44	44	3	3
Other areas (SOY)	227,796		72	72	3	3
Hirta						
Carn Mor	56,827	32,375	171	171	34	31

Discussion

We estimate the breeding population of Leach's Storm Petrels on Elliðaey to be in the region of 5,400 (95% CI: 4,300–6,700) pairs (based on the HDS estimate), following a decline of between 40–49% since 1991 (based on the repeats of the transects performed in 1991). The population in 1991 was therefore likely to have been in the region of 9,000–10,600 pairs; substantially lower than the previous estimate of 44,300 pairs, from the island-wide habitat-based extrapolation (Hansen *et al*. 2009). Results from the 2018 whole-island survey show that the 1991 transects at Hábarð and Bunki were positioned in the two densest areas of the colony (Figure 2), inflating the mean density and biasing the 1991 population estimate correspondingly. We also detected declines on all four of the main St Kilda islands, with reductions in AOS of 34–83% since the Seabird 2000 survey (Mitchell *et al*. 2004). Whilst we note that the field survey methods we used were not identical to those used in previous surveys (Mitchell *et al*. 2000; Newson *et al*. 2008), the population estimate for the entire St Kilda archipelago, derived from the same analytical methods used in 2000, is approximately 14,100 (95% CI: 10,500–23,600) pairs. This indicates an overall decline of 68% across surveyed areas since 1999. The HDS method produced a lower, but substantially more precise, estimate of 8,900 (95% CI: 7,800–10,100) AOS. Since the HDS approach accounts for the effects of several 'nuisance variables' on the likelihood of storm petrels responding to playback and detection of responses given, we consider the estimate derived from the HDS approach to be the more reliable of the two estimates.

Table 4. Leach's Storm Petrel *Hydrobates leucorhous* population estimates resulting from the calibration plot and hierarchical distance sampling methods for each of the St Kilda islands surveyed in 2019. For each sector or combination of sectors, density of Apparently Occupied Sites (AOS) is given, along with population estimates for topographical area and, where available, the area used in the Seabird 2000 census (Mitchell *et al.* 2004). Seabird 2000 estimates are given for comparison. For each island, the population change since the Seabird 2000 census is calculated using the estimate that is most comparable with the Seabird 2000 estimate. The change in density between Seabird 2000 and the current study is also given, where available.

	CALIBRATION PLOT METHOD			HDS METHOD		SEABIRD 2000	
	AOS per m^2	Total no. AOS	Total no. AOS Seabird 2000 area	Mean AOS per m^2	Total no. AOS	AOS per m^2	Total no. AOS
Dùn							
Dùn B+C	0.082 (0.049– 0.175)	6,675 (3,974–14,203)	6,365 (3,450–14,286)	0.051 (0.045–0.058)	4,148 (3,649–4,714)		
Dùn D	0.052 (0.023–0.121)	3,777 (1,688–8,891)	3,601 (1,151–7,072)	0.030 (0.022–0.042)	2,204 (1,586–3,063)		
Dùn total	0.068 (0.045–0.127)	**10,452 (6,899–19,614)**	**9,967 (6,569–18,506)**		**6,351 (5,507–7,324)**	0.188 (0.137–0.260)	**27,704 (20,430–38,506)**
Dùn population change (%)	-64%		-64%				
Boreray							
BOR1–2	0.007 (0.003–0.017)	419 (175–1,008)		0.006 (0.004–0.008)	328 (232–463)		
BOR3+	0.004 (0.002–0.011)	1,589 (554–4,021)		0.003 (0.002–0.004)	928 (598–1,438)		
Cleitean	1.358 (0.623–3.163) (per cleit)	57 (26–133)		0.975 (0.673–1.414) (per cleit)	41 (28–59)		
BOR1[a]	0.006 (0.002–0.015)					0.045 (0.028–0.062)	
BOR4[a]	0.002 (0.000–0.008)					0.110 (0.081–0.148)	

Boreray total		**2,065 (1,024–4,634)**			**1,297 (934–1,803)**		**12,093 (9,283–15,671)**
Boreray population change (%)	BOR1 -87% BOR4 -98%	-83%					
Soay							
Tigh Dugan boulder field (SOY7)	0.009 (0.000–0.026)	154 (0–465)		0.006 (0.003–0.013)	104 (48–227)		
Other areas	0.005 (0.000–0.016)	1,184 (0–3,626)		0.003 (0.001–0.006)	609 (283–1,314)		
Soay total		**1,338 (170–3,780)**			**713 (362–1,405)**		**2,031 (1,839–2,296)**
Soay population change (%)		-34%					
Hirta							
Carn Mòr	0.023 (0.009–0.070)	1,285 (662–2,902)	732 (377–1,653)	0.015 (0.012–0.020)	871 (655–1,158)	0.073 (0.052–0.109)	2,386 (1,680–3,527)
Carn Mòr population change	-68%		-69%				
Other areas	not surveyed						1,219 (1,077–1,398)
Hirta total							**3,605 (2,758–4,925)**
St Kilda total		**15,140 (11,315–25,412)**	**14,102 (10,454–23,554)**		**8,869 (7,787–10,102)**		**45,433 (34,310–61,398)**
St Kilda population change			-68%[b]				

[a] Densities are given for sectors BOR1 and BOR4 for comparison with those from Seabird 2000, but these sectors are included in the combined sectors BOR1–2 and BOR3+, respectively. [b] The overall population change for St Kilda is based on the difference between the total for the Seabird 2000 area in 2019 and the St Kilda total from Seabird 2000 minus the 'other areas' of St Kilda which weren't surveyed in 2019.

Assessment of population change

Our results from Elliðaey suggest the number of Leach's Storm Petrels breeding on the island in 2018 is much lower than the 1991 estimate. Our survey was much more extensive than the playback transects performed in 1991, since we surveyed points across the whole island, and is therefore likely to have produced a more accurate result. Our repeat in 2018 of the Hábarð transect surveyed in 1991 was performed on a single night of extremely poor weather, and the results of this should be treated with caution. Nevertheless, the 2017 survey of the 1991 transects produced similarly low estimates to that in 2018.

Since the previous population estimate for Leach's Storm Petrels breeding across all of the islands in the Vestmannaeyjar archipelago was entirely based on extrapolation of the 1991 Elliðaey survey results, the 2018 Elliðaey survey results indicate that the population of the archipelago is likely to be substantially lower than the previously estimated 178,900 pairs. Based on the assumptions used to produce the whole-archipelago estimate in 1991, we might expect the entire Vestmannaeyjar population to now be in the region of 21,900 pairs. However, Leach's Storm Petrel densities and habitat preferences may vary between islands within the same archipelago, as we found on St Kilda, so surveys of the other Vestmannaeyjar islands will be necessary to produce a more reliable estimate for this population, which is likely still the largest in the northeast Atlantic.

There also appear to have been significant declines in the number of Leach's Storm Petrels breeding in the St Kilda archipelago. Results suggest a decline of 22% on Dùn since the previous survey there in 2006 (Newson *et al*. 2008); a reduction of 2,800 pairs. While the reduction in breeding pairs since Seabird 2000 is large, the exponential rate of decline on Dùn appears to have slowed, from 15% per year between 1999 and 2003, to 2% per year if we compare our estimate of 9,967 AOS (which uses the closest method to previous surveys) to the 2006 estimate of 12,770 (Newson *et al*. 2008). However, the wide confidence intervals for the asymptote estimates on which these population estimates are based, suggest that the statistical power to detect within-island population changes is low.

Causes of population declines

As for many Leach's Storm Petrel colonies, the reasons for the apparent decline on Elliðaey are unclear. Until 2008, when human harvesting of Puffins ceased on Elliðaey, Herring *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* were controlled, reducing the gull population to < 10 breeding pairs, but snapshot counts during the Leach's Storm Petrel survey in 2018 estimated substantial numbers of gulls on the island (28 individual Herring Gulls and 135 Lesser Black-backed Gulls; Hey *et al*. 2019). Pellet analysis suggests that gulls on Elliðaey may consume approximately 200 Leach's Storm Petrels annually, although it is not known whether the predated storm petrels are predominantly breeding or non-breeding birds (Hey *et al*. 2019).

Leach's Storm Petrel.
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On St Kilda, predation by Great Skuas *Stercorarius skua* is a likely cause of the Leach's Storm Petrel decline (Votier *et al*. 2006; Miles 2010). The number of Great Skuas in the archipelago increased from 10 to 271 pairs between 1971 and 1997 (Phillips *et al*. 1999a), although the population has subsequently declined (Mitchell *et al*. 2004; Lawrence 2019). In 2019, we identified five Great Skua Apparently Occupied Territories with medium to large chicks in the northwest ('non-Puffin') sector of Dùn; one more pair than in 2007–09 (Miles 2010). We cleared one Great Skua territory of pellets and prey remains on 29 June and four days later found the remains of a minimum of three Leach's Storm Petrels (plus two Puffins and one Manx Shearwater) in the same territory. St Kilda's Great Skua population was estimated to consume 15,000 Leach's Storm Petrels in 1996 (Phillips *et al*. 1999b) and 21,000 a year in 2007–09 (Miles 2010), but with Dùn's Leach's Storm Petrel population apparently stabilising somewhat between 2003 and 2006 (Newson *et al*. 2008), it was assumed that the majority of predated individuals were non-breeders (Miles 2010).

The endemic St Kilda Field Mouse is present on Hirta and was known to be present on Dùn in 2008 (Bicknell *et al*. 2009). Seabirds form a significant part of the diet of Field Mice in Carn Mòr, but it is unclear whether these are predated or scavenged (Bicknell *et al*. 2009; Bicknell *et al*. 2020). Our results suggest declines in Leach's Storm Petrel populations on Soay and Boreray, where there are no Field Mice, so they are unlikely to be a major cause of population change in the archipelago and it seems likely that predation by Great Skuas has a much greater impact.

While large population declines at other Leach's Storm Petrel colonies have been attributed to predation pressure (Stenhouse *et al*. 2000; Wilhelm *et al*. 2015), the world's largest population (1.95 ± 0.42 (S.E.) million pairs) on Baccalieu Island, Newfoundland, is not subject to intense predation, yet has declined by 42% in 29 years (Wilhelm *et al*. 2019). Apparent adult survival rates in the western Atlantic and on Elliðaey are low (< 0.80, Fife *et al*. 2015; Greg Robertson & E. S. Hansen, unpubl. data 1983–2018) compared with those in the Pacific (0.975, Rennie *et al*. 2020), and reproductive success is high at some colonies and variable at others (Mauck *et al*. 2018; Wilhelm *et al*. 2019). It is likely that non-breeders make up a large proportion of the Leach's Storm Petrels depredated at colonies, since they tend to spend more time above ground than breeding adults, prospecting for nest sites and displaying to potential mates (Furness 1987). There is evidence of movement between populations within the Atlantic, and high levels of dispersal from natal colonies (Bicknell *et al*. 2012; Bicknell *et al*. 2014). The loss of large numbers of non-breeders through predation and other causes of population declines at the biggest colonies in the western Atlantic may therefore reduce the ability of compensatory recruitment to buffer against high mortality in eastern Atlantic colonies (Votier *et al*. 2008).

Several other threats may be causing or contributing to Leach's Storm Petrel declines. Storm petrels can be disorientated by artificial lights, and significant numbers may be killed in collisions with offshore oil and gas platforms and their gas flares (Ronconi *et al*. 2015), which are present in the recently-described foraging ranges of Leach's Storm Petrels from several declining colonies in the western Atlantic (Hedd *et al*. 2018). Storm petrels are also at risk from oil spills and discharges from such platforms, but the extent of overlap with the marine distribution of Leach's Storm Petrels from the studied colonies is unknown, and monitoring of the interactions between seabirds and these structures is currently very limited (Ronconi *et al*. 2015). Climate change is also likely to affect Leach's Storm Petrels, through impacts on prey distribution and abundance, direct impacts of severe weather events on foraging success and adult survival, and reduced reproductive success (Mauck *et al*. 2018). Leach's Storm Petrels in the northwest Atlantic have high mercury levels (Bond & Diamond 2009), although no association was found between mercury levels and reproductive success or survival (Pollet *et al*. 2017). The role of disease in the population dynamics of storm petrels is currently unknown, but infectious diseases have been implicated in the decline of other procellariiform species (Weimerskirch 2004).

The widespread decline of Leach's Storm Petrels across the Atlantic, and the extensive movement of birds within the ocean basin, suggest that the Atlantic's Leach's Storm Petrels should be viewed as a meta-population, and that any conservation actions for this highly mobile and dispersive species must take this into account. The foraging and migratory movements of Leach's Storm Petrels breeding in the northeast Atlantic are poorly known, but winter isotope values are similar to those from Baccalieu Island, Newfoundland (Hedd & Montevecchi 2006) and preliminary data from Elliðaey in 2020 indicate that their winter distribution overlaps with birds tracked from the western Atlantic (Pollet *et al*. 2014, 2019; A. Hedd *et al*. unpubl.). Further tracking of birds from Elliðaey is underway and could reveal important information on the threats they face at sea. Continued monitoring and demographic studies of breeding Leach's Storm Petrels on both Elliðaey and St Kilda, such as the ongoing monitoring of birds breeding in nest boxes on St Kilda, are also vital to improve our understanding of the processes causing the population declines.

Assessment of field and analytical methods

Accurately censusing burrow-nesting seabirds is challenging due to the generally low and variable rates of response to playback. Consequently, confidence intervals around population estimates tend to be large. We aimed to make population estimates as accurate and precise as possible, by optimising the type and amount of data that could be collected in the time available. We did this by using a distance sampling method, which enables a larger area to be surveyed for each playback than the calibration plot method (i.e. based on Ratcliffe *et al*. 1998), which assumes constant response and detection rates across the survey plot, meaning plots are necessarily small (typically < 4 m^2; Gilbert *et al*. 1998). It is important to note that implementation of the HDS analysis is far more complex and time-consuming than the calibration plot method and is unlikely to be practical in all survey situations.

Our field methods were largely optimised for the HDS analysis method, and this is reflected in the larger confidence intervals of the population estimates from the calibration plot method. Further assessment of the use of HDS to census burrow-nesting seabirds would, however, be useful, to ensure that the assumptions of this relatively complex type of model are met. For example, are there directionality effects in which observers are less likely to detect or accurately measure a response from a nest site behind them? For playback surveys, the probability that a bird responds to a playback is likely to decline with distance from the playback speaker, because the further a bird is from the stimulus, the less likely it is to hear it. While the 'gdistsamp' function of the 'unmarked' package does not enable 'availability' (i.e. the likelihood of a bird responding) to vary with distance from the observer, the models appear to be robust to situations where availability varies between individual animals based on their spatial distribution (Chandler *et al*. 2011; see online Supplementary Materials). Simulated datasets with known population size, response rates and detection rates, may be useful to confirm that this holds true for playback surveys.

It is not possible to give specific recommendations about sampling density, the number of points that should be repeated, or the number of occasions on which points should be repeated. The optimal survey design will depend on the extent of variation in the density of birds and in the magnitude and variation (in both time and space) in response rate. Simulations or the collection of pilot data could inform the most appropriate sampling strategy.

The accuracy of the population estimates obtained from the calibration plot method would be improved by surveying a greater number of points once with close-range playback (i.e. with a smaller survey radius) and using island-specific or sector-specific calibration, but this was not feasible in the time available in the field. Although we had originally intended to use only the responses within a 1 m radius for the calibration plot method, the low density of birds meant that insufficient responses were detected within that range for the asymptote to be estimated reliably. Therefore, responses from up to 3.5 m from the speaker were used to estimate the asymptote, even though our HDS analysis revealed that response rate (i.e. 'availability') may vary substantially across that distance. However, using data from different radii resulted in widely different population estimates. The density calculated using a 2 m radius was three times the density from a 3.5 m radius (see online Supplementary Materials), and the effect of survey radius for playback studies deserves further investigation. Given the diagnostics of the models fitted to the data collected, we believe that the HDS estimates are the most accurate assessment of the current Leach's Storm Petrel populations on Elliðaey and St Kilda, but that the calibration plot method estimates for St Kilda are most directly comparable with those from previous surveys. Estimates from the calibration plot method for St Kilda are higher than those for the HDS method, but the HDS estimates fall within the 95% confidence intervals of the respective estimates from the calibration plot method for each of the combined sectors.

Field methods for the HDS approach allowed us to cover more ground by increasing the survey radius for each playback. On Dùn, where the ground is unconsolidated and storm petrels often nest under vegetation, rather than in burrows, the distance sampling approach may have reduced the risk of trampling birds or nests, as surveyors remained on transect lines and did not need to walk over large areas, as was required in previous surveys where playback was performed every metre across 5 m x 5 m quadrats.

It is important that daytime playback surveys are performed when Leach's Storm Petrels are incubating or brooding small chicks, as this is the only period of the year when active nest sites will be consistently occupied by adults during the day, and therefore available to respond to playback. A mis-timed survey may result in an underestimate of the breeding population. In 2019, approximate laying dates were estimated for eight Leach's Storm Petrel pairs breeding in artificial nest boxes on Hirta. Nests were checked approximately weekly prior to laying and the laying date was taken as the median date between the date the egg was first seen and the date of the previous nest check. These estimated laying dates spanned a protracted period, from 1 June to 22 July, with a mean of 20 June (Lawrence 2019), so timing a survey when all birds are incubating or brooding would not be possible. Our surveys were performed between 18 June and 5 July and we found no evidence of a change in response rate with date for the islands overall, although the top Dùn model included a quadratic effect of date on availability (i.e. response rate). This date effect could, however, be a result of changes in weather conditions, rather than changes in the number of birds incubating.

An important consideration for future surveys is establishing colony extent. The limited fieldwork time available in this study and the difficulties of access meant that we could not survey every island in its entirety or attempt to determine the extent of the Leach's Storm Petrel distribution. Since the estimated densities are scaled up to the area of apparently suitable habitat, the size of habitat areas is important in estimating population sizes. The areas we used are based on apparently suitable habitat identified from aerial imagery. For St Kilda, sector boundaries were based on those used in the Seabird 2000 survey (Mitchell *et al*. 2000), although only poor-quality photocopies of the original sector maps were available. Our estimates of sector areas are slightly larger than those used by Mitchell *et al*. (2000) (Table 3). These differences can partially be explained by differing methods of estimating surface area on steep, rough topography, but may also be due to differences in delineating colony extent, or habitat change (Pollet & Shutler 2018). It is almost inevitable that areas outside of those identified as suitable habitat will contain at least some Leach's Storm Petrels. This is especially the case on St Kilda, where habitats form a complex matrix, and many areas are inaccessible. However, using the same areas in future surveys will enable population change to be assessed in a standardised manner. Provided remotely-sensed environmental data are available, all habitat types are sampled and models fit well, the HDS approach may be less susceptible to inaccuracies in estimation of habitat extent.

Leach's Storm Petrel.
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Notwithstanding the analytical challenges, and associated costs, of application of an HDS approach, the efficiency savings in terms of fieldwork effort, and improved precision of population estimates, lead us to conclude that HDS should be considered wherever possible for future surveys, especially those of nationally important colonies.

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