Resurvey reveals arrested population growth of the largest UK colony of European Storm-petrels *Hydrobates pelagicus*, Mousa, Shetland

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Abstract

Playback resurvey of the UK's largest breeding colony of European Storm-petrels *Hydrobates pelagicus* at Mousa, Shetland revealed that the substantial population growth achieved during previous decades has not been maintained. The estimated population size in 2015 was 10,778 apparently occupied sites (AOS) (95% confidence limits [CL] 8,857–13,207). The mean nesting density of birds breeding in natural habitat had declined substantially compared with 2008, but the area occupied by most sub-colonies had increased. Comparison with sub-colonies surveyed in 2008 indicated a 12.8% decline, though the lack of precision that surrounds both surveys renders the decline statistically non-significant. We discuss the possible causes of the observed change in trend. The use of a new playback recording that did not include alarm calls was associated with a substantial increase in response rate compared with previous surveys. Daily response rates from nests of known occupancy status declined during the course of the fieldwork period, associated with increasing absence of adults at the nest during daylight, as chicks acquired thermoregulatory independence and adults remained at sea by day. We therefore use a date-specific calibration factor to estimate AOS density. Methods of data analysis were improved for the current survey to allow estimation of the number of AOS and associated CL for each sub-colony separately. This resulted in a 51% reduction in the size of the confidence interval of the colony population estimate relative to the mean, compared with the 2008 survey. Playback surveys of burrow-nesting seabirds are typically characterised by low precision, which hinders statistically robust detection of population change, even when large declines are indicated. We recommend the adoption of a playback recording that does not include alarm calls, which may depress the frequency of responses or their detection by observers. Further, we suggest that for colonies where sub-colonies occur in discrete patches of habitat that are likely to vary in nesting density, the number of AOS should be estimated for each sub-colony separately. Adoption of these small modifications could substantially improve precision of playback surveys and hence the power to detect population change.

Introduction

European Storm-petrels *Hydrobates pelagicus* breed on islands of the northeast Atlantic and Mediterranean with the largest populations occurring in the Faroes, Iceland, Ireland and the UK. The global population is estimated at around 1.5 million individuals (Brooke 2004). Although the current status of many colonies is not well known, the species is suspected to be in decline globally owing to predation by invasive species, pollution and development at breeding localities (Birdlife 2016). The first comprehensive, quantitative assessment of the breeding status of European Storm-petrels in Britain and Ireland was conducted during the Seabird 2000 census (Mitchell *et al*. 2004), which concluded that Britain and Ireland jointly held around 83,000 pairs in 95 surveyed colonies, with other unsurveyed colonies probably supporting several tens of thousands of additional pairs. Together the populations of Britain and Ireland represent 14–54% of the biogeographic population of the subspecies *H. p. pelagicus*. Since the Seabird 2000 census, rat eradication programmes have led to the establishment of several further colonies in the UK on islands that were formerly unsuitable (Ramsey, Lundy, St Agnes and Gugh). Notwithstanding these successes, resurvey of some of the largest UK colonies in recent years have indicated declines, (e.g. Priest island, Ross and Cromarty, West Scotland; Insley *et al*. 2014). The largest UK colony at the time of the Seabird 2000 census was Mousa, Shetland, holding 5,410 pairs in 1996 (estimate recalculated by Bolton *et al*. 2010), representing about 22% of the UK population at that time. Resurvey in 2008 indicated a substantial increase to 11,781 pairs (Bolton *et al*. 2010). Here we report results of a census conducted in 2015 and consider possible causes of the changes observed since 1996.

Methods

Study site: Mousa (60°00’N, 01°11’W) is an uninhabited 180 ha sheep-grazed sandstone and limestone island lying 1 km off the southeast Shetland mainland. The island is designated as a European Special Protection Area (SPA) within the Natura 2000 network, reflecting the international importance of the site for breeding European Storm-petrels and Arctic Terns *Sterna paradisaea*. European Storm-petrels nest in crevices in storm beaches and under loose scattered boulders and piles of stone slabs from abandoned quarry workings, as well as in dry stone walls, ruined buildings and a 2000-year old Iron-age broch. Storm-petrels are highly vulnerable to predation and are active at the colony only during darkness, when males sing from their nest cavities. The only mammalian predator present on the island is the European Otter *Lutra lutra* (hereafter “otter”), with several active holts and evidence of predation on Storm-petrels in several parts of the island (M. Bolton, pers. obs.). Other predators of Storm-petrels present on the island are Great Skua *Catharacta skua* (30–40 pairs), Arctic Skua *Stercorarius parasiticus* (1–8 pairs), Herring Gull *Larus argentatus* (c. 5 pairs), Lesser Black-backed Gull *L. fuscus* (c. 1 pair) and Great Black-backed Gull *L. marinus* (c. 16 pairs).

Playback protocol: The standard survey protocol for Storm-petrels relies on diurnal playback of song at potential nesting locations to elicit responses from nesting birds (Ratcliffe *et al*. 1998). A recording of male purr call was played at approximately 75 dB for 10 seconds, and the number of apparently occupied sites (AOS) from which a vocal response of an adult was elicited within 30 seconds, was counted. Typically, adults respond to playback with a single brief alarm call, rather than purring song. The analogue recording of Storm-petrel song from Mousa that was used for both earlier surveys contained several alarm calls during the 10 seconds, which may have contributed to the low response rate recorded in earlier surveys, either by inhibiting responses from nest-holders, or by masking genuine alarm responses. For the present survey, a new digital recording was prepared, using a 10 second recording from Mousa of male purr song that did not contain any alarm calls. Any alarms heard by the observer would therefore be correctly attributed to a response, rather than to the playback recording. Playback recordings were presented using a LOGIC MP3 player (model L2GMP309) and RadioShack® 200 mW mini amplifier speaker (Model 2771008). Response rate is known to vary diurnally, with highest response frequencies close to sunrise and sunset. In common with previous surveys, fieldwork was conducted between 06:00 hrs and 18:00 hrs GMT, when response rate varies little (Ratcliffe *et al*. 1998).

Location and extent of sub-colonies and suitable habitat: The earlier resurvey in 2008 was conducted on the assumption that the location and extent of areas occupied by sub-colonies had not changed since the initial survey in 1996. For the present survey we conducted nocturnal fieldwork to reassess the location and extent of sub-colonies in natural habitat and quarry workings. Sub-colony boundaries were determined from the location of singing birds and marked by landscape features or by handheld GPS waypoints. To enable direct comparison with earlier work, we followed precisely the survey methods employed by Ratcliffe *et al*. (1997). Parallel survey transects, each 1 m wide and spaced at 5 m intervals, were orientated perpendicular to the long axis of each sub-colony, extending across the entire area occupied by breeding birds. The area enclosed by the sub-colony boundaries was estimated as the length of the long axis multiplied by the mean transect length. Some areas within sub-colonies comprised solid rock, or grass without cavities or fissures and were therefore unsuitable for nesting. To estimate the extent of suitable breeding habitat within each sub-colony we multiplied the total area by the proportion of survey points that contained suitable habitat. Measurement of the total length of dry stone wall on the island from aerial photos indicated that it had remained unchanged since the 1996 and 2008 surveys at 4,923 m.

Sampling strategy: Survey fieldwork was carried out between 22 July and 31 July 2015, when most birds were in the latter stages of incubation or brooding recently hatched chicks. To estimate the response density of birds nesting in dry stone walls, the same ten sample sections that had been selected for survey in previous years, each 100 m in length, were resurveyed. Playback was conducted at 1 m intervals along one side of each section and all AOS within 0.5 m of the survey point which elicited a response were counted.

For sub-colonies in natural habitat and quarry workings, playback was conducted every 1 m along each transect. Responses from adults within 0.5 m of the transect line were noted, representing a sample of 20% of the entire area. Sample points which fell in locations that did not contain any habitat suitable for nesting were not surveyed. In previous surveys all occupied areas of natural habitat have been surveyed in this manner except for the large area of boulder beach to the north of the broch, which has been surveyed using four 5 x 5 m quadrats. Nocturnal fieldwork indicated large variation in density of singing birds within this boulder beach and we considered that the use of just four quadrats may no longer adequately sample this sub-colony. We therefore used the same transect-based methodology as applied to other areas of natural habitat, which provided greater spatial representation in the sample. Although the broch has been known to hold breeding birds for many decades, it was not included in previous all-island surveys. Night-time fieldwork indicated that substantial numbers of birds were breeding there. It stands 13 m tall, with an external basal diameter of 15 m, tapering to 12 m at the top (Dryden 1890). It has a double-walled construction, with a stone staircase running between the two walls. The internal diameter is c. 6 m. We therefore considered the broch to represent 13 stacked external circular walls, each 1 m high, with a circumference (at the mid-line) of 39 m and a further 13 stacked inner circular walls with a circumference of 23 m. We conducted diurnal playback in a manner similar to that employed for the walls, at 1 m intervals at heights of 0.5 m and 1.5 m on both the inner and outer walls, and also at 12.5 m on the inner wall.

Estimation of response rate from calibration trials: The proportion of individuals that respond to playback is generally rather low (just 17% in the 2008 survey) and varies among colonies and years (Ratcliffe *et al*. 1998). Consequently, it is necessary to conduct calibration trials over the course of the survey period to estimate a correction factor to apply to the raw playback response data, in order to estimate the density of AOS (Ratcliffe *et al*. 1998). Calibration trials were conducted on each day of the survey, presenting recordings in the same manner as for survey points within 0.5 m of 54 nests known to be occupied by breeding birds and containing an egg or chick. The daily response rate was calculated as the number of nests from which a response from an adult was elicited, divided by the number of nests.

Data analysis: In common with previous surveys, we considered the ten sections of wall to represent a sample of all wall habitat and accordingly calculated a mean response density for all wall habitat, with associated confidence limits [CL] (Bolton *et al*. 2010). Previous surveys have adopted the same approach for areas of natural habitat, considering the overall response density in each sub-colony (i.e. the total number of responses divided by the surveyed area) as a single sampling unit of the island-wide response density for all areas of natural habitat. However, if sub-colonies differ greatly in breeding density, this will increase the sample variance and associated CL of the estimate of population size. In the present survey, analysis was conducted on data summarised at the level of each transect, rather than for each sub-colony, such that each transect represented a sampling unit for each sub-colony. Hence, we calculated a mean response density (and 95% CL) for each sub-

Figure 1. Location of survey areas and estimate of number of apparently occupied sites (AOS) for European Storm-petrels *Hydrobates pelagicus*, correcting for date-specific variation in response rate on Mousa, Shetland, UK. Data reproduced with the permission of RSPB. © Crown Copyright. Ordnance Survey licence number 100021787 (2017).

colony separately, potentially enabling a more precise estimate of total population size. It was not possible to adopt this approach for wall habitat, which unlike natural habitat did not occur in discrete patches.

The effect of survey date on response rate was investigated by fitting a linear regression to the response rate data obtained from the calibration trials, which revealed a significant decline in response rate during the course of the 10-day survey period (see results). Accordingly, the fitted line and 95% CL were used to calculate a daily correction factor (the reciprocal of the response rate). The fitted line correction factor was multiplied by the observed mean response density for each area to account for imperfect detection of occupied AOS and derive an estimate of mean AOS density (AOS/m for wall habitat and the broch and AOS/m^2 for areas of natural habitat). A bootstrap procedure (Davidson and Hinkley 1997; Canty and Ripley 2016) was used to generate 999 replicates of both daily response rate (and hence the daily correction factor) and response density. For each survey area, the 95% CL of AOS density were calculated by multiplying randomly paired estimates of response density and daily correction factors. These estimates were multiplied by the extent of suitable habitat available to derive the mean (±95% CL) number of AOS in each survey area. The whole-island population size was calculated as the sum of the estimates of the mean number of AOS for each survey area, and the 95% CL of the estimate of population size were calculated by summing 999 random bootstrap estimates of the number of AOS for each survey area. To determine whether the change in population size from 2008 was statistically significant, the 95% CL of population change was calculated from 999 randomly paired bootstrapped estimates of population size in 2008 and 2015. A change was deemed statistically different if the 95% CL of the estimate excluded zero.

Results

Extent of sub-colonies occupied by breeding birds: Nocturnal fieldwork identified a further sub-colony (West Pool Central), containing a total of 285 m^2 of suitable breeding habitat, occupied by breeding birds in 2015 which had not been surveyed in previous years. Among the 15 sub-colonies that were occupied in 1996, the extent of the area of suitable habitat occupied had increased from 9,596 m^2 to 15,640 m^2 (Table 1, see Figure 1 for location of sub-colonies). In 2015, the sub-colonies “Cellar” and “Loch” were each found to represent two discrete areas, so each was surveyed, and the data analysed, as two separate sub-colonies, making a total of 18 sub-colonies surveyed in 2015. For comparison with survey results from 2008 data were pooled in each case.

Calibration of survey data for non-response to playback: Mean daily response rates were considerably higher than in 1996 or 2008 (38% compared with 17% in 2008 and 25% in 1996, Bolton *et al*. 2010 and Ratcliffe *et al*. 1997 respectively) but declined significantly during the course of the 10-day survey period from 46% to 29% (Figure 2, fitted estimates). Although the survey was timed to coincide with the anticipated peak of nest attendance, and was conducted slightly earlier than in 1996, the decline in response was associated with increasing numbers of nests in

Table 1. Location and extent of natural habitat occupied by breeding European Storm-petrels *Hydrobates pelagicus* on Mousa in 1996 and 2015. Data for 1996 are from Table 3 of Ratcliffe *et al.* (1997).

Site	Sub-colony total area in 2015 (m^2)	Area of suitable habitat within sub-colony in 2015 (m^2)	Area of suitable habitat within sub-colony in 1996 (m^2)	Change in area occupied (m^2)
Boulder Beach	1,585	1,470	1,100	+370
Cairn	625	585	550	+35
Catti Geo	1,720	1,465	415	+1,050
Catti North	1,490	1,020	752	+268
Cellar	1,545	935	578	+357
East Ham	1,885	955	696	+259
Green Head	2,620	2,545	1,398	+1,147
Loch	1,360	690	842	−152
Masti Geo	590	395	730	−335
Muckle Bard East	1,275	1,060	491	+569
Muckle Bard North	1,970	1,830	709	+1,121
Muckle Bard West	395	310	261	+49
Underlee	835	565	336	+229
West Pool Central	365	285	0	+285
West Pool North	995	610	288	+322
West Pool South	1,045	920	450	+470
Total	20,300	15,640	9,596	+6,044

the calibration plot being unoccupied by adults during daylight as their chicks gained thermoregulatory independence and no longer required brooding. European Storm-petrels do not generally remain in the nest during daylight once their chicks have acquired thermoregulatory independence at the age of about seven days (Davis 1957). Among 28 nests within the calibration plot whose contents were checked daily after playback, chicks were hatched at 14 nests during the survey period and eight of these nests were unattended by adults during daylight in the latter stages of the survey. The absence of adults at these nests during daylight at this stage in the breeding cycle is entirely normal and does not indicate any effect of observer disturbance.

Nesting density, distribution and estimate of population size: The extent of survey effort, measured response density, and estimate of number of AOS for each sub-colony located in natural habitat, walls and the broch are shown in Table 2. A total of 801 responses to playback were recorded during the course of the survey, compared with totals of 343 in 2008 and 240 in 1996. The walls held a mean (± SD) of 0.84 ± 0.35 AOS/m, which represented a non-significant reduction in density since the 2008 survey (1.16 ± 0.74 AOS/m, paired t-test: t_9 = 1.680, P = 0.13, Figure 1). In total, the walls were estimated to hold 4,141(95% CL 2,628–6,212) AOS. In contrast, the nesting density of Storm-petrels in natural habitat had reduced very substantially compared with the level estimated in 2008 (mean ± SD of 0.63 ± 0.41 and 0.40 ± 0.13 AOS/m^2 in 2008 and 2015 respectively; paired t-test: t_{14} = 2.229, P = 0.043). However, the increase in total area occupied by sub-

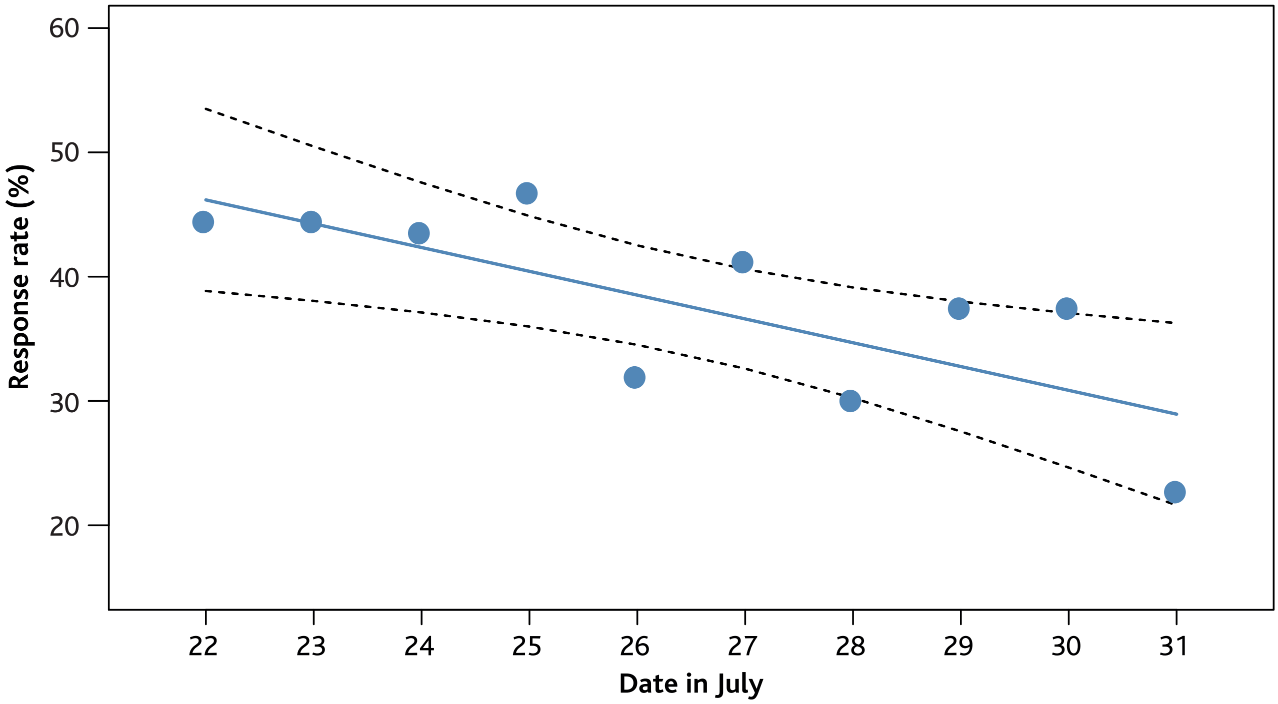

Figure 2. Decline during the survey period in the proportion of active apparently occupied sites (AOS) from which a vocal response from European Storm-petrels *Hydrobates pelagicus* was elicited by playback. The line fitted by least squares regression is shown with the associated 95% confidence limits ($P < 0.013$, $R^2 = 0.56$).

Table 2. Survey effort, response density and estimate of number of apparently occupied sites (AOS) of European Storm-petrels *Hydrobates pelagicus* in walls, natural habitat and the broch, Mousa, Shetland, UK, in 2015.

Location	Surveyed area	Number of responses	Mean Response density	Mean nest density	Estimated mean number of AOS (95% CL)
Walls	1,000 m	269	0.269 m^{-1}	0.84 m^{-1}	4,141 (2,628–6,212)
Broch	147 m	31	0.255 m^{-1}	0.63 m^{-1}	508 (139–1,252)
Boulder Beach	317 m^2	58	0.195 m^{-2}	0.46 m^{-2}	677 (413–989)
Cairn	125 m^2	24	0.191 m^{-2}	0.43 m^{-2}	252 (99–436)
Catti Geo	344 m^2	26	0.095 m^{-2}	0.22 m^{-2}	328 (194–471)
Catti North	298 m^2	26	0.106 m^{-2}	0.37 m^{-2}	374 (153–686)
Cellar	167 m^2	9	0.094 m^{-2}	0.26 m^{-2}	136 (39–288)
Cellar East	142 m^2	11	0.158 m^{-2}	0.43 m^{-2}	175 (92–248)
East Ham	377 m^2	11	0.036 m^{-2}	0.12 m^{-2}	118 (24–253)
Green Head	524 m^2	118	0.215 m^{-2}	0.47 m^{-2}	1,187 (738–1,819)
Loch North	173 m^2	5	0.062 m^{-2}	0.21 m^{-2}	96 (28–187)
Loch South	99 m^2	11	0.212 m^{-2}	0.73 m^{-2}	176 (52–370)
Masti Geo	118 m^2	20	0.233 m^{-2}	0.64 m^{-2}	251 (134–398)
Muckle Bard East	255 m^2	36	0.158 m^{-2}	0.43 m^{-2}	458 (260–688)
Muckle Bard North	394 m^2	58	0.154 m^{-2}	0.40 m^{-2}	730 (434–1,097)
Muckle Bard West	79 m^2	7	0.125 m^{-2}	0.33 m^{-2}	101 (45–159)
Underlee	167 m^2	17	0.162 m^{-2}	0.47 m^{-2}	265 (86–491)
West Pool Central	73 m^2	12	0.159 m^{-2}	0.39 m^{-2}	112 (16–249)
West Pool North	199 m^2	13	0.127m^{-2}	0.31 m^{-2}	192 (28–459)
West Pool South	209 m^2	39	0.220 m^{-2}	0.54 m^{-2}	501 (304–746)
Total					10,778 (8,857–13,207)

colonies in natural habitat largely offset the reduction in nesting density such that these sub-colonies combined held an estimated 6,129 AOS (95% CL 5,240–7,289) and the broch was estimated to hold a further 508 AOS. The whole-island estimate was 10,778 (95% CL 8,857–13,207, Table 2).

Survey precision: For the 2008 survey, where each sub-colony was considered as a single sample of all sub-colonies in natural habitat, the 95% confidence interval surrounding the whole-island estimate of the number of AOS in natural habitat was 92% of the mean (5,565/6,048). In contrast, for the present survey where the mean and CL were estimated for each sub-colony separately, the confidence interval for all sub-colonies in natural habitat combined was only 33% of the mean (2,049/6,129), representing a 64% reduction in the confidence interval/mean ratio. In 2015 wall habitat was surveyed, and AOS estimates calculated, in the same manner as in 2008, yet the confidence interval/mean ratio was lower (87% compared with 103% in 2008), suggesting that part of the improvement in survey precision was due to the higher response rate in 2015. When estimates for the number of AOS in natural habitat and walls were combined, the confidence interval/mean ratio for the whole-island estimate was 40%, representing a 51% reduction in the confidence interval/mean ratio compared with the value in 2008 (82%).

Changes in habitat use and size of sub-colonies since 2008: The estimate of the number of AOS located in wall habitat in 2015 (4,141) was lower than the number estimated in 2008 (5,733), whereas the number of AOS estimated in natural habitat was slightly higher in 2015 (6,129 and 6,048 respectively). However, the 95% CL for the estimates of AOS change in both of these habitats overlapped zero (−5,643 to 1,549 and −3,249 to 2,512 respectively) reflecting the uncertainty associated with the estimation of response rate and response density, and we conclude that there was no significant change in the total numbers of birds breeding in either of the two habitat types. However, there were very considerable changes in the number of AOS occurring within individual sub-colonies, with reductions in most of the sub-colonies located in the northeast of the island (Loch −617 AOS, Catti North −428 AOS, East Ham −168 AOS) and increases in many of those located in the southeast (Muckle Bard North +205 AOS, Muckle Bard East +119 AOS, West Pool Central +112 AOS, West Pool South +501 AOS and Green Head +200 AOS).

Has the colony declined significantly since 2008?: The estimate of population size in 2008, excluding the broch which, though known to be occupied, was not surveyed, was 11,781 (95% CL 8,100–17,728) AOS (Bolton *et al.* 2010). Exclusion of the broch in order to make direct comparison with the 2008 survey, yields a whole-island population estimate for 2015 of 10,270 AOS (95% CL 8,494–12,573). Whilst this represents a reduction since 2008 of 1,511 AOS (12.8% of the 2008 estimate), the 95% CL around the estimates of population change from 2008 to 2015 encompassed zero (−7,908 to 2,977) and we conclude, due to the level of imprecision associated with both surveys, the change in estimated population size is not statistically significant.

Discussion

Survey precision: Estimation of the number of AOS (and associated 95% CL) separately for each sub-colony resulted in a very substantial improvement in the precision of the estimate of the total number of AOS in all areas of natural habitat combined. Although the estimate of AOS in wall habitat was calculated in the same manner as the previous survey, and therefore had a larger associated confidence interval, the improvements achieved in precision of the estimate for natural habitat resulted in an overall increase in survey precision of 51% compared to 2008. We recommend that wherever Storm-petrels breed in discrete sub-colonies that may vary considerably in nest density, survey precision would be improved by estimating the mean density and associated confidence limits for each area separately, rather than regarding each as a single estimate of the mean density across the entire colony. Here, we did not apply this approach to the wall habitat, but maintained the same 100 m sample sections that have been surveyed in previous years. Further improvements in survey precision at this colony may result from improved sampling of wall habitats, and it would be instructive to examine the relationship between sample variance and (i) the length of wall that comprises a sampling unit and (ii) sample size (i.e. the number of wall sections surveyed), in order to determine the most efficient and effective deployment of survey effort in future years.

Response rates were considerably higher than those reported in the 1996 and 2008 surveys, possibility as a result of the use of a recording which did not contain any alarm calls. Higher mean response rates will result in improved precision of survey estimates if the confidence interval surrounding the estimate of response rate does not increase in direct proportion to the mean (see Perkins *et al*. 2017). We suggest that future playback surveys employ a recording with no alarm calls.

A recent comparison of infra-red filming and playback as survey methods for Storm-petrels (Perkins *et al*. In press) has shown that for similar levels of fieldwork effort, both methods have similar levels of accuracy and precision, though infra-red filming requires heavy and bulky equipment and time-consuming post fieldwork processing. Infra-red filming may be preferable for colonies or sub-colonies where close access to nesting locations is not possible for reasons of health and safety or disturbance.

Limitation of population growth: The survey conducted in 2008 revealed that the population had undergone a substantial increase, more than doubling in size since 1996. Clearly, the former population growth has not been sustained, for reasons that are currently unknown. Population trends are determined by the balance of demographic rates – productivity, mortality, immigration and emigration, each of which be influenced by both natural factors and human activity (Furness & Monaghan 1987). In closed systems, the limits to population growth are generally considered to be (i) food availability, (ii) nest site availability (iii) predation, or (iv) disease (Birkhead & Furness 1985).

Food availability. Whilst the declines of many seabird species in the North Sea have been driven by low productivity linked to reduced food, especially sandeel (*Ammodytes sp*.), availability (Monaghan 1992; Monaghan *et al*. 1992; Frederiksen *et al*. 2005; Frederiksen *et al*. 2007) there is currently no published information on the diet of Storm-petrels breeding on Mousa. DNA analysis of prey samples from migrating birds passing the coast of Portugal indicate a wide variety of prey may be taken including cephalopods, amphipods, isopods, mysidacea, fish, insects and even large bodied species such as Short-beaked Common Dolphin (*Delphinus delphis*) which must be scavenged from carcasses (Medeiros 2010). A wide potential prey base, coupled with an extensive potential foraging range (Thaxter *et al*. 2010) suggest that Storm-petrels may be less sensitive than some other seabirds to reductions in availability of any particular prey species (Furness & Tasker 2000). However, the degree to which Storm-petrels breeding in Shetland may have become food-limited in recent years is currently unknown.

Nest site availability. The reduction in nesting density observed in 2015 implies that suitable nest crevices occupied in 2008 have become vacant, which could be viewed as evidence that nest site availability is not currently limiting population size. However, lowered nesting density and expansion of sub-colony area could indicate a reduction in nest site quality due to external factors, or increasing parasite transmission as nest density increases (see below). Recent silting up of drainage channels has led to increase in ground water levels in some parts of the island, to the extent that study burrows and nest boxes that were known to have been used for breeding in previous decades are now water-logged and unsuitable for nesting, or associated with low rates of success. However, whilst there is a clear spatial pattern to the change in size of sub-colonies (increases in the south and southeast of the island and decreases in the northeast sub-colonies), this is not obviously associated with changes in the water table level of these areas, or other factors affecting nest site suitability.

Predation. Several studies have shown that predators can exert a large impact on breeding European Storm-petrels at colonies in the Atlantic and Mediterranean (e.g. Sanz-Aguilar *et al*. 2009). Matovic *et al*. (2017) estimated that mortality by predators amounted to 5% of breeders in some years and Libois *et al*. (2012) showed changes in breeding numbers reflected variation in predator pressure at a Storm-petrel colony in Benidorm, Spain. There has been a notable increase in two generalist predators observed to consume Storm-petrels on Mousa, namely Great Skuas and otters. Numbers of Great Skuas have fluctuated, tending to increase at about 4% p.a. from 20–24 pairs between 2001 to 2005, to 30–40 pairs between 2008 and 2015 (RSPB, unpubl. data). Several dozen regurgitated pellets examined in 2015 were found to consist entirely of European Storm-petrel remains (M. Bolton, pers. obs.). Similarly, the number of active otter holts and the level of predation on Storm-petrels have increased in the last decade (M. Bolton, pers. obs.), and remains of at least 15 Storm-petrels consistent with otter predation were located within the "Cairn" sub-colony during the course of survey fieldwork.

The population increase between 1996 and 2008 amounted to a mean annual growth rate of 6.7%. If predation had subsequently reduced this level of growth to zero, it would have amounted to the removal of 0.067 x 11,781 x 2 = 1,579 breeding individuals a year, on average. From the anecdotal information currently available, it seems unlikely that the level of predation exerted by either Great Skuas or otters at the colony is sufficient to fully account for the absence of population growth since 2008, though it would be instructive to quantify the predation exerted by these species. It is well known that Storm-petrels roam widely during their years of immaturity (Fowler *et al*. 1982; Harris *et al*. 1993; Okill & Bolton 2005), prospecting colonies that are remote from the natal colony. During this period they may be vulnerable to predation, and studies from St Kilda indicate that the majority of the thousands of Leach's Storm-petrel *Hydrobates leucorhous* consumed there annually by Great Skuas are prospecting immatures, many of which are likely to originate from other colonies in the North Atlantic (Bicknell *et al*. 2012; Miles *et al*. 2013). It is entirely plausible therefore that the decline in colony growth of European Storm-petrels on Mousa may result from predation impacts exerted elsewhere.

Disease and parasitism. Transmission of disease and parasites is considered one of the main costs of coloniality (Alexander 1974) and may be particularly high for species such as Storm-petrels that feed chicks by regurgitation. There is good experimental evidence from European Storm-petrels breeding in the Mediterranean that growth rates of chicks can be influenced by the size of ectoparasite loads (Merino *et al*. 1999). Further, Boulinier & Danchan (1996) found that among Kittiwake *Rissa tridactyla* colonies in the UK, chicks reared in declining colonies had higher burdens of ectoparasites than those at colonies with positive population trends. The authors suggested that by reducing local breeding success, ectoparasites could reduce both the recruitment of new breeders and breeders' site fidelity the following year, thereby influencing population trends. There is no information on historic or current levels of parasite burdens of Storm-petrels breeding on Mousa. The observed decline in nesting density and enlargement of sub-colonies into adjacent habitat is a response consistent with increasing parasite burdens in areas of high nesting density. One would also predict lower parasite transmission rates in one-dimensional wall habitat, where nesting densities have not declined, compared to two-dimensional natural habitat. It would be instructive to obtain information on the relationship between nesting density, parasite load size and breeding success for both habitat types.

Severe weather events: In addition to these four factors, which may regulate population growth in a density-dependent fashion, seabird population trends may be strongly influenced by severe weather events acting in a density-independent manner. For species which are particularly susceptible to severe environmental conditions, such as European Shag *Phalacrocorax aristotelis*, the increasing frequency of severe weather events resulting in mass mortality, may drive long term population trends (Frederiksen *et al*. 2008). Storm-petrels are also particularly susceptible to strong winds and driving rain, and "wrecks" of storm-driven birds, particularly Leach's Storm-petrels, occur regularly on the coasts of the NE Atlantic during autumn (Teixeira 1987). Matovic *et al*. (2017) relate the mortality of Storm-petrels breeding in Britany (France) to climatic indexes reflecting changing upwelling conditions in the Benguela current and heavy storms over their migratory route during La Niña events. These factors may also affect Storm-petrels breeding on Mousa, which are likely to share migratory routes. As the frequency of climate-induced severe weather events is predicted to increase, they may become an increasingly important cause of population limitation in Storm-petrels.

Anthropogenic impacts: Human activities may exacerbate many of the factors described above, and in addition may cause direct mortality of seabirds through fisheries' bycatch, pollution, recreational disturbance and collision with offshore structures. Storm-petrels appear to have low vulnerability to most of these threats (Furness *et al*. 2013; Williams *et al*. 1995), with the exception of a small documented impact of recreational disturbance (Watson *et al*. 2014) and attraction to gas flares associated with oil and gas platforms (see Ronconi *et al*. 2014 for a recent review).

Watson *et al*. (2014) found that the breeding productivity of Storm-petrels nesting in close proximity to visitor trails on Mousa was 25–35% lower than that of pairs breeding in undisturbed areas. However, given the low number of pairs nesting in areas accessed by visitors, they concluded that recreational disturbance resulted in only minor (≤ 1.6%) reduction in productivity at the colony level.

Storm-petrels are susceptible to attraction to, and incineration by, the flares caused by combustion of associated gases released during drilling for the extraction of hydrocarbons (see Weise *et al*. 2001 and references therein). There is a high density of oil and gas fields in the North Sea, many within the potential foraging range and feeding areas of European Storm-petrels. A reported incident of "several hundred" Storm-petrel mortalities was associated with collision and incineration at a flare stack in the North Sea (Sage 1979) but the identification of the species concerned has been subsequently questioned (Bourne 1979, 1982). Whilst the quantities of associated gas released in the extraction of oil in the UK North Sea has reduced in recent years (Oil and Gas UK, 2015), the proportion of gases combusted (flared) rather than vented, has increased (Stewart 2014). Further, several fields which have begun operation since 2005 have both high monthly oil yield and high flaring rates (e.g. Chestnut, Burghley, Don SW, West Don) (Stewart 2014) and lie within the potential foraging range of the colony. It is important to establish the foraging locations of Storm-petrels from Mousa and asses the risk posed by gas flares.

Emigration: Additionally, the cessation of population growth at the colony on Mousa could potentially result from an increase in emigration. A small colony of breeding Storm-petrels has recently become established on the island of Noss, some 18 km from Mousa, since the extirpation of feral cats in 1987 (SNH 2007). Colonisation of Noss was first reported in 2008 and 18 AOS were detected by playback in 2010 and again in 2016 (Denton & Nisbet 2016). Whilst it is probable that recruits originating from Mousa have contributed to the establishment of this colony, the modest numbers of individuals involved would not account for the recent change in population trend on Mousa.

Regional and UK trends: It is not possible to relate the change in population growth at Mousa to wider regional trends due to the absence of resurvey of other Storm-petrel colonies in the Northern Isles of Scotland. Both playback surveys and long-term ringing and recapture of European Storm-petrels on Priest Island, Ross and Cromarty, West Scotland, which held around 17% of the UK population during the Seabird 2000 census (Mitchell *et al*. 2004), indicated a steep decline of around 50% between 2001 and 2012 (Insley *et al*. 2014). However, more recent information based on playback survey suggests some population recovery subsequently (RSPB, unpubl data). The colony on Skokholm (Wales) which held almost 10% of the UK population at the time of Seabird 2000 (2,450 AOS, 95% CL 2,300–2,600; Mitchell *et al*. 2004) was estimated to hold only 1,910 AOS (95% CL 1,640–2,095) in 2016 (Wood *et al*. 2017). Although the 95% confidence intervals do not overlap, indicating a significant decline, differences in survey methodology and analysis led Wood *et al*. (2017) to conclude that the colony had probably remained stable. There is an urgent need to update the population estimates of all colonies in Britain and Ireland that have not been resurveyed since the Seabird 2000 census, in order to establish the current conservation status of the species.

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