Playback re-survey and demographic modelling indicate a substantial increase in breeding European Storm-petrels *Hydrobates pelagicus* at the largest UK colony, Mousa, Shetland

Bolton, M.[1*], Brown, J. G.[1,4], Moncrieff, H.[1], Ratcliffe, N.[2] and Okill, J.D.[3]

* *Correspondence author. Email: Mark.Bolton@rspb.org.uk*
[1] *RSPB, UK Headquarters, The Lodge, Sandy, Bedfordshire SG19 2DL, UK;*
[2] *British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 OET, UK;*
[3] *Heilinabretta, Trondra, Shetland ZE1 0XL, UK.*
[4] *Scottish Natural Heritage, Ground Floor, Stewart Building, Alexandra Wharf, Lerwick, Shetland ZE1 0LL, UK.*

Abstract
The island of Mousa, Shetland, is designated as part of the European Natura 2000 reserve network as a Special Protection Area (SPA) for breeding European Storm-petrels *Hydrobates pelagicus*. In 1996 the population was censused using playback methods and reported as 6,800 (95% CI 4,800–8,800) apparently occupied sites (AOS), c. 26% of the UK breeding population. Re-examination of the 1996 data highlighted some calculation inaccuracies, resulting in a reduced population estimate for 1996 of 5,410 AOS (95% CI 3,932–7,022). Resurvey of the colony in 2008 using identical methods revealed a 118% increase to 11,781 AOS (95% CI 8,100–17,728). A sample of c. 90 nest sites in natural crevices has been monitored annually since 1990 to determine breeding productivity. A deterministic population model, incorporating observed annual productivity estimates, annual survival rates and age of first breeding, also indicates a population increase of similar magnitude (95%) between 1996 and 2008. The similarity in trend estimates from the two independent approaches is perhaps surprising, given the large potential sources of error associated with each, and suggests that both the playback survey method and productivity monitoring from a single annual visit provide reliable demographic estimates. The large increase in population size of European Storm-petrels contrasts starkly with the trends of many other seabird species in the region, and likely results from aspects of Procellariiform foraging and reproductive strategies that confer resilience to unpredictable and scarce food supplies.

Introduction
Due to their vulnerability to predation, nearly all species of storm-petrels nest on remote islands, visit the colony only under the cover of darkness and nest out of sight in deep crevices. These characteristics severely hinder the estimation of population size, and prior to the Seabird 2000 census (Mitchell *et al.* 2004) few reliable quanti-

tative survey data were available for any British or Irish colonies. Earlier estimates (e.g. Lloyd *et al*. 1991) had been based largely on subjective judgement and, in preparation for the Seabird 2000 census, considerable research effort was invested in the development of a reliable, quantitative survey method for storm-petrels. This resulted in the establishment of the diurnal playback technique (Ratcliffe *et al*. 1998), where responses are elicited from birds occupying nest holes during daylight, in response to playback of recordings of burrow calls. A colony- and year-specific correction factor is required to account for variation in the proportion of birds that respond. Since no previous quantitative estimates of population size existed for most storm-petrel colonies, data collected during Seabird 2000 could not be used to derive population trends. Here we report a playback re-survey, following a 12-year interval, of the largest European Storm-petrel *Hydrobates pelagicus* colony in the UK, and provide one of the first quantitative estimates of population trend for the species in UK. In addition, we derive a second, independent estimate of population trend from a simple population model parameterised with empirical estimates of annual productivity and age of first breeding from the colony. The extent of similarity between the two estimates of population trend was used to assess the reliability of the playback survey method, which has recently been questioned (e.g. Brown 2006).

Methods

Study site and survey protocols: Mousa (60°00'N 01°11'W) is a 180 ha sheep-grazed sandstone and limestone island lying 1 km off the southeast Shetland Mainland. It has a long history of human occupation, stretching back several thousand years. The famous Mousa broch (an Iron Age fortification) dates from around 100 BC and the remains of several burnt mounds on the island indicate even earlier occupation. Mousa was relatively well populated in the eighteenth and nineteenth centuries, as evidenced by the remains of several homesteads, and in 1774 was "tolerably well cultivated", with 11 families on the island (Low 1879). By 1841 the population had fallen to just 12 inhabitants and none were left by 1861 (Schei & Moberg 1988). Given such a long history of human occupation and cultivation, it is noteworthy that no rodents now occur on the island, and the only mammalian predator of European Storm-petrels is the European Otter *Lutra lutra*.

The island has been designated under the EU Wild Birds Directive as a Special Protection Area (SPA) within the European Natura 2000 reserve network. European Storm-petrels are one of the designated features of the reserve, due to the international significance of the breeding population. Since 2001 the island has been managed by the Royal Society for the Protection of Birds, which has led to a reduction in livestock densities and control of visitor access. European Storm-petrels nest within the 4.9 km of stone walls and scattered areas of loose rocks and boulders, which total 0.96 ha (Ratcliffe *et al*. 1997a). The stone walls lack any mortar or in-filling and in many places have partially collapsed, resulting in low-standing tumbles of rock slabs which are particularly suitable as storm-petrel nesting habitat. Except for one area of boulder beach by the broch, the areas of loose rocks lie above the inter-tidal zone, and comprise a variety of rock sizes and shapes, from large rounded boulders to quarried flat slabs.

A playback survey was carried out between 24 and 26 July 2008, following precisely the methods employed by Ratcliffe *et al.* (1997a) during their 1996 survey, conducted between 26 July and 9 August. The same ten sections (each 100 m in length) of stone wall that had been randomly selected for the 1996 census were re-surveyed. A recording of a male purr call (the same recording used for the 1996 survey) was played at approximately 75 dB for 10 seconds at each survey point using a portable tape recorder. The playback recording was presented at 1 m intervals along one side of each section and any vocal response elicited during 30 seconds following the playback was noted. For areas of loose rocks and boulders, playback was carried out at 1 m intervals along parallel transects lying 5 m apart, covering the entire area of habitat. The number of responses elicited within 0.5 m from the transect line were recorded. The boulder beach was surveyed by playback conducted at the intersections of a 5 m x 5 m grid within each of four randomly located 25 m^2 quadrats (as for the 1996 census). For each sample area, the number of responses from adult European Storm-petrels was divided by the length of wall, or area of natural habitat surveyed to give an estimate of response density for the two nesting habitats (responses per m of wall and responses per m^2 of natural habitat).

Estimation of response rate to playback for survey calibration: The response to playback is generally low (typically responses are obtained from fewer than half the occupied sites on any single occasion) and variable (mean response rate varied from 25% to 59% among 16 sites and habitats reported in Mitchell *et al.* (2004)). It is therefore important to estimate the daily response rate (the proportion of occupied sites from which a response is obtained), in order to calibrate the number of responses recorded during the survey to estimate population size. To determine the daily response rate, blind calibration trials were performed on seven days between 21 and 30 July. Playback was conducted at 44 sites where the nest chamber was visible, which included 24 known to be occupied from visual inspection, but for which the occupancy status was unknown to the observer. For calibration analysis, we did not include data from sites where the nest chamber was not visible and the presence of a bird was only detected from a bird calling, since this could have introduced bias towards more vocal individuals. We did not remove or disturb birds present at the nest during daylight to verify the presence of an egg and the survey unit is therefore an 'Apparently Occupied Site'(AOS). We calculate that only 3% of the sites detected on any given day during our survey were not used for breeding, as follows: from visual inspections of nests over the course of the season, Ratcliffe *et al.* (1998) found that 16% of occupied sites were not used for breeding, but the daily probability of non-breeders occupying such sites during the survey period was lower than the corresponding daily attendance probability at breeding sites (0.23 and 0.83 respectively on 25 July, the mid-point of the 2008 survey). Further, the daily probability of eliciting a response to playback from a bird in a non-breeding site was also lower than at a breeding site (0.18 and 0.32 respectively). Assuming the same values for this study, the proportion of detected sites not used for breeding is therefore given by:

$$(0.16 \times 0.23 \times 0.18) / ((0.84 \times 0.83 \times 0.32) + (0.16 \times 0.23 \times 0.18)) = 0.029$$

We also examined the accuracy of various analytical methods that have been employed in other surveys, where no sample of sites of known occupancy was available and the total number of AOS within the calibration plot therefore must be estimated. A variety of methods have been employed to estimate the total number of AOS within the calibration plot, which are well summarised in Mitchell *et al.* (2004, Appendix II). The simplest method continues daily calibration trials until no further AOS are detected and assumes that all AOS in the plot have therefore been located. However, detection of all AOS may require many days of fieldwork, which may be impractical in many situations. Consequently several analytical methods have been employed to estimate the total number of AOS as the asymptotic value from a plot of the cumulative number of AOS detected against survey number (Mayhew *et al.* 2000; Fowler 2001). A third method uses du Feu's mark-recapture method (du Feu *et al.* 1983) to estimate the total number of AOS within the calibration area. This approach makes use of information concerning the number of sites from which responses are repeatedly obtained over the course of the multi-day trial (which constitute 'recaptures') and might therefore be expected to be the most reliable, since the other methods waste such recapture information. This method may also be the most efficient, since calibration trials do not need to be conducted for the more extended periods required for the other methods. We compared the performance of these alternative methods using the sample of nests judged to have been occupied from visual inspection.

Estimation of population size from playback survey: A bootstrapping procedure was used to estimate the 95% confidence intervals of the response densities in sampled sections of wall and areas of natural habitat. The mean response densities and confidence intervals were extrapolated to the total extent of these two habitats to derive a habitat-specific estimate of the total number of responses for the whole island. A calibration factor (the reciprocal of the daily response rate) was then applied to account for the number of birds that did not respond to playback. In calculating the confidence intervals for the resulting whole-island population estimate for each habitat, 999 bootstrapped replicates of the number of whole-island responses for each habitat were randomly paired with 999 bootstrapped replicates of the calibration factor. The confidence intervals for total population estimate for wall and natural habitats combined was similarly calculated from summing 999 random pairings of bootstrapped estimates of the whole-island wall and natural habitat populations. The means of all parameters were calculated directly from the sample values, rather than the bootstrapped values, since bootstrapped means will tend to the sample means, and have no significance. This approach differs from that adopted in the analysis of the 1996 survey data, where bootstrapped means (which differed substantially from the sample means) were applied. Furthermore, the analysis of the 1996 data incorrectly calculated the lower and upper confidence intervals of the whole-island number of AOS in each habitat (the product of the whole-island number of responses and the calibration factor) as the product of the lower and upper confidence levels respectively, of the two components. This resulted in an overestimate of the magnitude of the confidence intervals, resulting in reduced power to detect future population change. Similarly, the confidence intervals of the 1996 whole-island estimate, itself the sum of the wall and natural habitat estimates, were incorrectly calculated by adding the lower and upper confidence intervals respectively of the two components.

Estimation of population trend from demographic data: A second, independent estimate of population trend was obtained from a deterministic demographic model parameterised using empirical data on annual breeding success from 1995 to 2009 and an estimate of age of first breeding obtained from recaptures of known-age European Storm-petrels ringed as nestlings on Mousa (Okill & Bolton 2005). From 1995, approximately 90 accessible nests located in wall crevices have been monitored annually in early September. The number of nests showing signs of breeding activity (presence of unhatched eggs, eggshell fragments, shed down, a dead chick etc.) was recorded, together with the number containing a well-grown chick. The timing of the visits was judged to coincide with the peak in numbers of well-grown chicks, but before any had fledged.

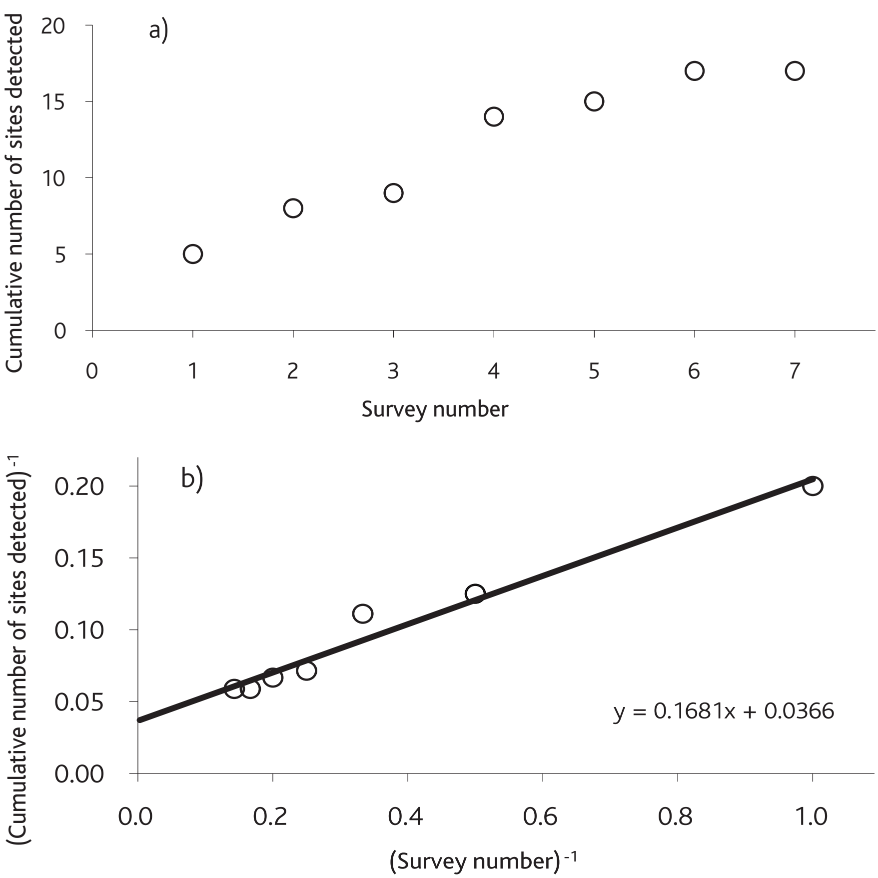

Figure 1. Estimation of the number of occupied European Storm-petrel *Hydrobates pelagicus* nest sites within the calibration area. a) Cumulative number of sites detected with number of surveys. b) Reciprocal plot of cumulative number of sites detected and number of surveys. Twenty-four nest sites were known to be occupied.

Annual breeding success was calculated as the number of nests containing well-developed chicks, divided by the number of nest sites showing signs of breeding activity. Nests where adults were still incubating or brooding small chicks were judged to fail, since detailed monitoring of nests at this colony has shown that breeding attempts at these stages in early September usually fail (MB unpubl. data). Annual breeding success between 1995 and 2009 averaged 0.74 (range 0.50–0.90). The model assumed adult annual survival was 0.88; Scott (1970) estimates a value of 0.895 and Hounsome *et al.* (2006) give a value of 0.87. To our knowledge, there is no reliable estimate of first year survival for any storm-petrel species (Brooke 2004), so we used the value of 0.70 derived for another Procellariiforme, the Henderson Petrel *Pterodroma atrata*, where survival rates of adults are very similar to those of European Storm-petrels (de L. Brooke *et al.* 2010). We also ran the demographic model with first year survival values of 0.6 and 0.8 to determine the sensitivity of the resulting population trend to variation in this parameter. We assumed that survival rates of second-year birds was equal to that of adults and that birds bred in their third year (Okill & Bolton 2005). The model was scaled to yield a population equivalent to the revised 1996 census estimate, and forecast the expected population size in 2008, given the observed annual productivity and assuming no net immigration or emigration.

Further data on annual productivity, obtained by detailed nest monitoring between 1990 and 1994 by D. Suddaby and MB (reported in Osborn 1994), were used to estimate population trends between 1992 and 1996. Since European Storm-petrels first breed at three years of age, this extension of the model required an estimate of productivity in 1989 (to estimate the size of the cohort recruiting in 1992). We assumed a value equivalent to the mean of the remaining 20 years, as no empirical estimate for 1989 was available. The estimate of population size in 1992 was obtained from Suddaby (1992), though note this was obtained by locating singing birds at night, not diurnal playback. Finally, we also forecast likely population change from 2009 to 2012, on the basis of productivity in 2006 to 2009, since these cohorts will provide the recruits for the years to 2012.

Results

Estimation of the number of AOS within the calibration plot: Twenty-four sites within the calibration plot were known from visual inspection to be occupied, but only 17 of these were detected over the course of seven days' playback trials (Figure 1a); no response was obtained during this period from the remaining seven occupied sites. A plot of the reciprocals (Figure 1b) yielded a significant linear regression ($y = 0.1681x + 0.0366$) which indicated that the asymptote of the cumulative AOS plot (given from the value of the y-intercept) was $1 / 0.0366 = 27$ (Fowler 2001). Responses were obtained from a further six locations where visual inspection had previously failed to detect the presence of a bird during daylight, and we interpret these responses as either birds breeding in unknown sites close to study nests where the nest chamber was not visible, or daytime occupation of study nests by non-breeders which had not been present during the visual inspection. These sites were excluded from further analysis due to their ambiguous status.

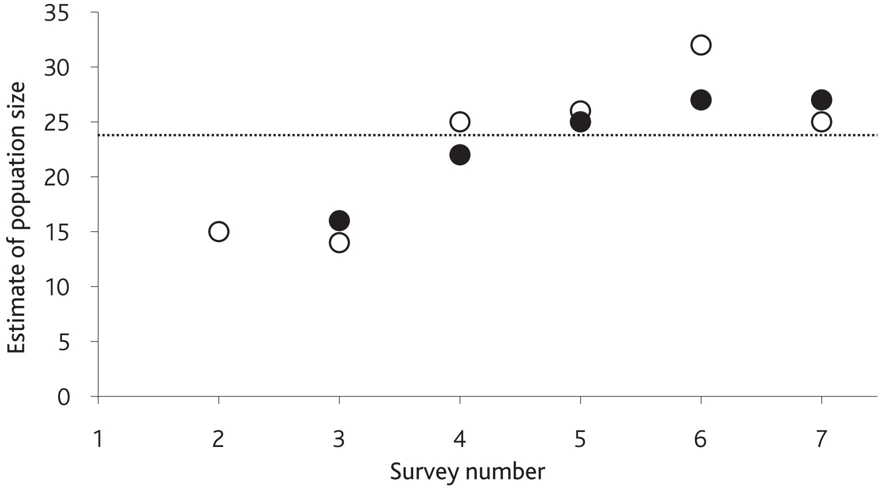

Figure 2. Effect of number of calibration surveys on accuracy of estimate of total AOS within the calibration plot. Filled circles: estimate of the cumulative AOS asymptote from the reciprocal plot (as Fig 1b); Open circles: du Feu mark-recapture estimate.

The du Feu mark-recapture yielded an estimate of 25 AOS among the sites known to be occupied, and was therefore the most accurate of the three methods considered. We further investigated the relationship between the number of calibration surveys carried out and the accuracy of the estimates obtained by the du Feu method and the cumulative AOS asymptote (following the method outlined in Figure 1b). This analysis indicated that whilst the du Feu method provided the most accurate estimate after seven calibration surveys, both methods provided similarly reliable estimates following four days of trials (Figure 2). Indeed, the du Feu estimate obtained after six trials (32 AOS) was substantially poorer than that obtained after six trials by the asymptote method (27 AOS). Since the number of occupied sites was known from visual inspection to be 24, this was the value used in subsequent analyses.

Correction of survey data for non-response to playback: The mean daily response rate at sites known to be occupied was 0.166 and the boot-strapped 95% confidence intervals were 0.119–0.220. The very wide confidence intervals reflect large day-to-day variation in the numbers of birds responding within the calibration plot over the course of the seven-day trial. The corresponding correction factors (the reciprocal of the response rates) are therefore 6.00 (95% CI = 4.54–8.40). The mean response rate is substantially lower than the value of 0.25 reported for the 1996 survey, and the confidence intervals substantially wider, with the result that for a given response density (number of AOS per unit of habitat area), the extrapolated population size will be larger in 2008 compared with 1996, and the confidence intervals much wider, reducing the power to detect population changes.

Estimate of population size: A total of 343 responses to playback were obtained during the course of the entire survey, compared with 240 from the same survey plots in 1996. The survey of ten 100 m sections of walls yielded a sample mean of

0.194 detected AOS/m, rather higher than the mean frequency detected in the 1996 survey (0.150 AOS/m). The analysis of the 1996 data was incorrectly conducted on an erroneous bootstrapped mean value of 0.193 AOS/m. The overestimate of the response density from wall habitats in 1996 necessarily resulted in an overestimate of the island population size, and the 1996 survey data are reanalysed here to provide a more reliable estimate. The recalculated population estimate for 1996 used the correction factor given in Ratcliffe *et al*. (1997a, 1997b; mean = 4.0, 95% CI = 3.7–4.3). Confidence intervals for the whole-island estimates were calculated by bootstrapping pairwise combinations of the response estimate and correction factors drawn at random from their respective frequency distributions. Extrapolating the response density to estimate the total number of AOS detected along the total length of walls on the island (4,923 m) yields an estimate of 955 detected AOS in 2008 (95% CI = 630–1,359), compared to a recalculated value of 738 detected AOS (95% CI = 458–1,044) in 1996. The revised estimate of the total number of AOS in wall habitats in 1996 (accounting for those occupied sites where no response was detected) was 2,954 (95% CI = 1,731–4,196) and for 2008 the corresponding estimates were 5,733 AOS (95% CI = 3406–9,304).

In natural habitats the mean density was 0.105 responses/m^2 in 2008 (95% CI = 0.007–0.136), higher than the mean density of 0.064 responses/m^2 (95% CI = 0.044–0.087) found in the 1996 survey (though incorrectly reported as 0.08 in Ratcliffe *et al*. (1997a)). The extrapolated estimate of the total number of detected AOS in all areas of natural habitat was 1,008 (95% CI = 681–1,305) in 2008 compared with a recalculated value of 614 AOS (95% CI = 422–835) in 1996. Correcting these estimates for those occupied sites where no response was detected, using the same methods as for the wall habitat, gave estimates of 6,048 AOS (95% CI = 3,847–9,412) in 2008 and 2,457 (95% CI = 1,705–3,383) in 1996.

Combining the estimates of the number of AOS in both wall and natural habitats yields an estimate of total population size for the entire island in 2008 of 11,781 AOS (95% CI = 8,100–17,728). This compares with a revised estimate of 5,410 AOS (95% CI = 3,932–7,022) in 1996. The absence of overlap in the confidence intervals of the two estimates suggests that the population has increased significantly between 1996 and 2008 (Figure 3).

We considered the possibility that the low estimate of population size in 1996 resulted from the slightly later survey period (extending up to 7 August), which could have resulted in more nests being unattended by adults later in the survey period. However, there was no evidence of a relationship between survey date and the density of AOS detected for either wall or natural habitat in the 1996 survey (Spearman R = -0.431, n = 10, P = 0.21; R = 0.151, n = 10, P = 0.59 respectively).

Estimate of population trend by demographic modelling: The demographic model predicted that the initial population of 5,410 breeding pairs would have grown by 95.2% to 10,561 breeding pairs by 2008 (Figure 3). This estimate accords with the playback survey estimate of population increase from 5,410 to 11,781 AOS.

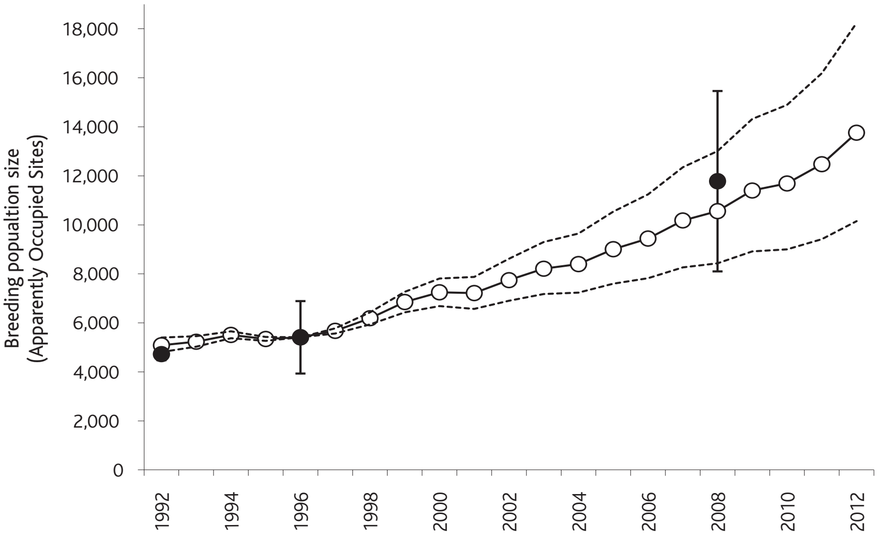

Figure 3. Population trend of European Storm-petrels *Hydrobates pelagicus* breeding on Mousa, Shetland. Filled circles represent survey data, though note that the 1992 survey was conducted using different methods (mapping singing birds at night (Suddaby 1992)). Open circles show population trend calculated from a demographic model, incorporating observed annual breeding success and age of first breeding. Dotted lines indicate the modelled trends based on higher (0.8) and lower (0.6) estimates of first year survival. Note the models were scaled to yield the observed population estimate in 1996.

Discussion

Re-survey using playback methods has shown that the internationally important population of European Storm-petrels breeding on Mousa has maintained favourable status, having doubled in size between 1996 and 2008. Re-analysis of the data from the 1996 survey shows that at the time of the Seabird 2000 census, the population breeding on Mousa represented around 22% of the UK population (Mitchell *et al*. 2004). Assuming the size of the remaining colonies have remained unchanged (and there is some evidence to suggest that the third-largest UK colony, on Priest Island, has actually declined (Hounsome *et al*. 2006; S. Elliott pers. comm.)), in 2008 the Mousa colony represented 38% of the UK population, and 2% of the midpoint estimate of the world population (Mitchell *et al*. 2004). The similarity in population trend obtained by demographic modelling suggests that both methods provide a reliable assessment of population change. The late-season single-visit method used to assess productivity might be expected to overestimate breeding success, through an inability to identify nests where breeding attempts fail early in the season, and unhatched or damaged eggs are subsequently removed or displaced from view. The correspondence between trends estimated by playback and demographic modelling suggests that either such overestimation is minor, or alternatively, if breeding success is substantially overestimated, another demographic parameter, such as adult or first year survival has been correspondingly underestimated. A further possibility is that there has been net immigration into the population, resulting in a rate of population growth that is coincidentally similar with that predicted by overestimated breeding success.

The large increase in population size of European Storm-petrels reported here contrasts starkly with the trends of many other seabird species in the Shetland Islands, and likely results from the ability of storm-petrels to forage over very considerable areas, and at great distance from the breeding colonies (Stone 1995; Pollock *et al*. 2000), which confers resilience against local food scarcity. Additionally, both eggs and nestlings are tolerant of considerable periods of parental neglect, enduring periods of up to seven days without parental attendance (Davis 1957; Scott 1970). These physiological adaptations further enable the species to withstand temporal scarcity of food resources.

The two alternative methods of estimating the number of AOS within the calibration plot both performed reasonably satisfactorily, with both estimates falling within 13% of the true value, and sub-setting of the data indicated that both methods would have performed to a similar degree of accuracy after four or five days of calibration trials, rather than the customary seven days. However, it would be premature to conclude on the basis of this study, that only four or five days' calibration trials are required, and we encourage others with similar datasets to conduct these analyses to determine the generality of this finding. It should also be noted that a 13% error in estimation of the number of AOS within the response rate calibration plot will lead to an error of the same magnitude in the estimate of the total population size, and associated confidence intervals. The close approximation of the du Feu estimate to the true value suggests that birds are equally likely to respond, and the lack of any response from seven sites resulted not from the existence of 'mute' individuals, but rather from the generally low daily response rate and the relatively short duration of the calibration trial.

Storm-petrels are highly vulnerable to predation when on land, and the occurrence of breeding colonies in the Northern Isles of Scotland is known to be highly dependent on the absence of Brown Rats *Rattus norvegicus* (de León *et al*. 2006), which can take eggs, nestlings and adults. The likelihood of human-mediated introduction of rats to seabird islands is linked to the extent and type of traffic from rat sources. Rats have extremely high fecundity and may increase in numbers rapidly, yet their nocturnal and subterranean habits render them likely to escape detection in the absence of dedicated monitoring. In consequence, introduced rats may exert a considerable impact on native seabirds long before their presence is recognised. It is imperative therefore that the routine monitoring of rat-status at important colonies, such as Mousa, is maintained as a high priority, and that there is an effective contingency plan in place to ensure a rapid eradication response in the event of rat occurrence on the island.

Acknowledgements
We thank Tom Jamieson for provision of boat access to Mousa for the 2008 playback survey and for the ongoing provision of transport to the island for annual nest monitoring. This work was funded by the Royal Society for the Protection of Birds and Scottish Natural Heritage. We thank Iain Nicol, Robert Smith and Ewan Ellis who assisted with the calibration study under the Nuffield School Bursary scheme and Mike Hounsome and Hugh Insley for helpful comments on an earlier draft of the manuscript.

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