Perrins, C M and Wood, Matthew J and Garroway, C J and Boyle, D and Oakes, N and Revera, R and Collins, P and Taylor, C (2012) A whole-island census of the Manx Shearwaters Puffinus puffinus breeding on Skomer Island in 2011. Seabird, 25. pp. 1-13.

A whole-island census of the Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island in 2011

Chris M. Perrins[1*], Matt J. Wood[2], Colin J. Garroway[1], Dave Boyle[1], Nick Oakes[3], Rose Revera[3], Phil Collins[3] and Chris Taylor[3]

*Correspondence author. Email: chris.perrins@zoo.ox.ac.uk

[1] *Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK;*

[2] *School of Natural and Social Sciences, University of Gloucestershire, Francis Close Hall, Cheltenham GL50 4AZ, UK;*

[3] *The Wildlife Trust of South and West Wales, The Welsh Wildlife Centre, Cilgerran, Cardigan SA43 2TB, UK.*

Abstract

Skomer Island, Pembrokeshire, Wales is believed to have one of the largest colonies of Manx Shearwaters *Puffinus puffinus* in the World. In 1998 a census was made of the whole island, and the adjacent islands of Skokholm and Middleholm, in order to try to establish the size of the breeding population; the Skomer population was estimated to be just over 101,000 breeding pairs. A second census was carried out in 2011. First, a set of study burrows was opened and a tape of the male call (normally only males respond to these) was played down each burrow several times during the course of incubation in order to establish the male response rate. Then the same tape was played down all the burrows in each of 288 randomly selected plots across the island and the number of responses recorded. Extrapolating responses from census plots to the whole island yielded an estimate of 125,112 (CI ± 16,445) responses. Adjusting this figure to take account of the response rate yielded an estimate of 316,070 (SE ± 41,767) breeding pairs. This figure is greatly in excess of the estimate made just 13 years earlier. Possible reasons for this are discussed.

Introduction

The Manx Shearwater *Puffinus puffinus* is a burrow-nesting seabird which is very vulnerable to predation when on land. To minimise this, it comes ashore only at night and nests in burrows; all its major colonies are on islands which lack mammalian predators. Because of these habits, it is difficult to census, especially since in many of the colonies varying proportions of the burrows may be occupied, not by the shearwaters, but by European Rabbits *Oryctolagus cuniculus* and Atlantic Puffins *Fratercula arctica*. In recent years estimates of the number of breeding pairs have often been based on counting responses to a tape of the male call, played down the burrows. Normally only the male responds to the call, but not all males respond (Brooke 1978), so a correction factor based on the response rate must be used to arrive at an estimate for the whole population; in previous studies this response rate has been about 0.42, but has varied from study to study with consequent effects on the estimates of population size (Newton *et al.* 2004).

The two islands, Skomer and Skokholm, Pembrokeshire, Wales, are noted for their large populations of Manx Shearwaters. In 1998 a census of the two islands, plus the much smaller Middleholm, estimated a total population of 150,000 pairs with about 101,000 pairs on Skomer (Smith *et al.* 2001). With the caveat that numbers are poorly known and using the maximum figures quoted by Newton *et al.* (2004), some 90% of the of the World population (370,000 of 410,000 pairs) nest in the UK and Ireland, a higher proportion of the World population than is the case for any other bird species breeding in Britain and Ireland. Again using Newton *et al.* (2004) this means that some 40% of the UK and Irish population (150,000 of 370,000 pairs) breed on the Pembrokeshire islands. There is little information on the status of any population; on Skomer one study has attempted to measure changes in population size in a series of fixed plots each year (Taylor *et al.* 2011).

The whole-island census on Skomer in 1998 (Smith *et al.* 2001) was very labour-intensive and hence expensive because, in addition to the breeding season census, it also involved whole-island counts of burrows in winter when the vegetation, particularly Bracken *Pteridium aquilinum*, had died down and the burrows were more easily located. This part of the census took 600 person-hours to complete (149,507 burrows were counted). The number of shearwaters was estimated by revisiting a number of these burrows the following spring and determining the proportion that were occupied. One assumption made at the time was that burrow numbers remained substantially unchanged between the winter burrow count and the spring playback study.

Funding for a repeat census using the 1998 technique was not available, so a less labour-intensive, more cost-efficient system was developed for 2011. Also, in view of the importance of the two islands for Manx Shearwaters it was desirable to design a method that would be applicable to both Skomer and Skokholm, and which could be repeated as required. Furthermore, such a method might have wider application for the census of other burrow-nesting populations of seabirds on islands.

Methods

A protocol was devised (Perrins 2010) to estimate the breeding population on Skomer in 2011.

Selection of census plots: For the 1998 census, the island was divided up into 334 one-hectare squares aligned with the British National Grid and marker posts were put in at the corners of each hectare; these are referred to as 'squares' (Figure 1). This layout aids the use of Geographical Information Systems for mapping and data analysis, and was maintained for the 2011 census. Squares were defined as *Coast* where the hectare square cut or touched the perimeter of the island, as *Near coast* if they were in the next ring of hectare squares adjacent to the *Coast* ones; all the rest were defined as *Inland*. Not every square contained land suitable for nesting shearwaters; many *Coast* squares were part land and part sea, and much of the land part of some of these was composed largely of rock, while some *Inland* squares were located in boggy ground where burrowing was impossible. In 1998

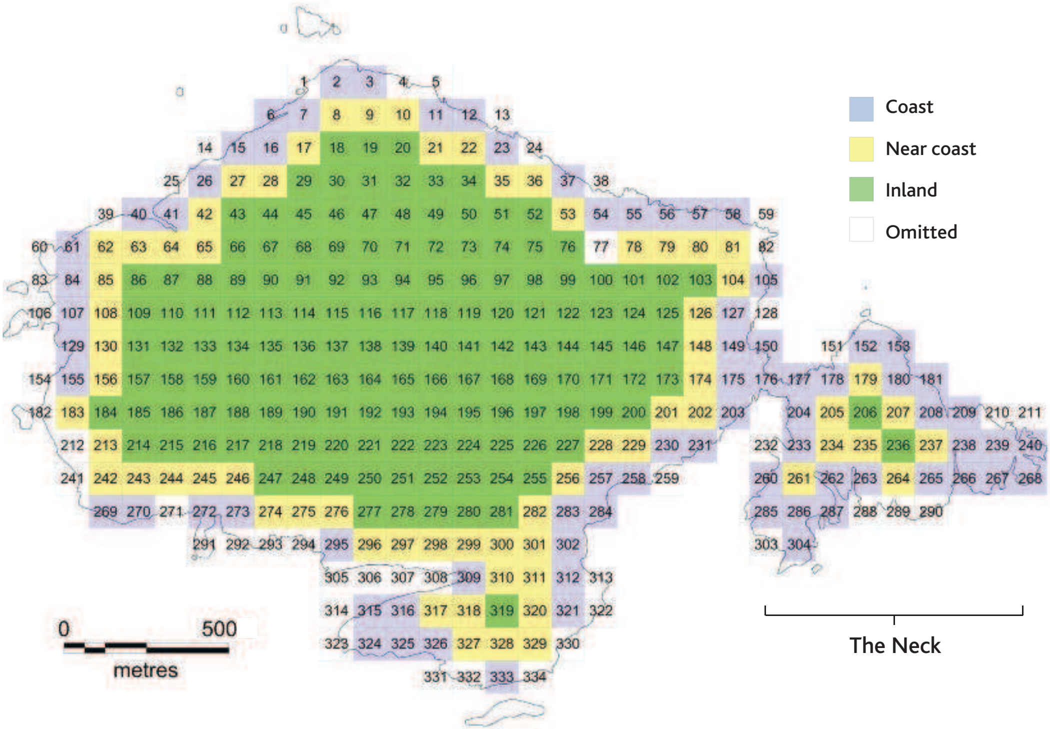

Figure 1. Map of Skomer showing the hectare squares and their category (see text for explanation)

the proportion of each of the *Coast* squares that was land was roughly estimated; we retained the same proportions for these squares in 2011. In 2011, a point was selected within each hectare square using the island GIS, without reference to the underlying terrain. Usually this was the centre of the square, but in some, mainly *Coast*, squares where the central point was clearly in the sea, a point closer to an inland corner of the square was selected: the field worker selected the nearest accessible point within 25 m of the preselected point (half way to the closest edge of the hectare square), again without reference to the terrain. This objectivity in the selection of census points avoided the introduction of bias due to the subjective selection of sites which appeared more (or less) suitable for shearwaters. Twenty-one *Coast* squares, which were mostly sea, were not covered in either census because they were on steep slopes and could not be visited safely and a further 25 squares visited in 1998 were not visited in 2011, again for safety reasons.

Estimating the total number of playback responses on the island: Each square was visited once during the period 4–15 June 2011 by a single observer. The observer went to the preselected point in the square which was located with the use of a GPS (Garmin Etrex-H: Garmin International Inc., Olathe, KS, USA), accurate to within 3–4 m; the high degree of accuracy was due to the open ground and lack of tree cover. To mark out the plot area, a bamboo cane was pushed into the ground at this point and two 10 m ropes attached to it. These were laid out so as to form a slice of a pie in which the observer examined the ground for burrows. The size of the slice was varied to suit the terrain and the burrow density. Each successive slice was examined until the circle had been completed. The area covered was therefore a circle of 10 m radius (= 314 m^2) and is referred to as a 'plot'.

Within the plots, the observer examined each burrow and if it continued beyond arm's reach, the burrow was considered to be potentially deep enough to be used by shearwaters for nesting; any burrow that could be felt to divide was counted as two (or occasionally more). The number of potential burrows in each plot was noted. A tape was played down each potential burrow, using a recording of a male shearwater call recorded on Skokholm in the 1970s (supplied by Dr. M. Brooke). The tape was played on a small cassette recorder, sealed in a plastic bag, which was dropped into the mouth of the burrow and played for 3–4 call cycles (or less when a bird responded quickly). The speed of response is very variable and some birds do not reply (see below). The number of responses per plot was noted.

If the position of the plots has been randomly selected, it should be possible to calculate the expected number of responses from the whole area covered. A circle with a 10 m radius covers an area of 314 m^2. Hence multiplying the mean number of responses in a plot by 10,000/314 should give the expected number of responses per square. For some squares, almost only *Coast* ones, the size of the land portion of the square is less than a hectare and so the expected number of responses has been amended to take account of this.

Response rate to call playback: A study plot was set up by DB in early spring. Forty-three burrows were opened and inspection hatches fitted; these were visited regularly until an egg was laid. No egg was ever found in ten of these; since we define the number of breeding pairs as those burrows in which an egg is laid, these were not used in the study plot. In the remaining 33 nests the pairs were located and marked, and when the egg was laid the pair were sexed (after laying the large egg, the female has a distended cloaca). Then, when most of the population had laid (late May), the tape was played eight times to each burrow on alternate days from 3 June, except that there was a three-day interval between the penultimate and the final playback session on 18 June. After noting whether or not there was a response, the burrow contents were inspected to determine which, if any, birds were present. This is a laborious operation and so, as in other studies, it was not possible to use a larger sample of burrows due to time constraints in the field.

Data from the playback trials conducted in both census years (1998 and 2011) were pooled to maximise the data available for analysis. To this end, we selected those trials carried out during approximately overlapping dates, when shearwaters were expected to be present in their burrows while incubating eggs: 1–16 June in 1998 (245 trials at 49 burrows) and 3–18 June in 2011 (264 trials at 33 burrows), a total of 509 trials (Table 1).

In 2011, all of the 33 burrows chosen for the control playback trial contained an egg at some point during the trial; on the first inspection (3 June) one contained an unincubated egg and the pair in another burrow had yet to lay; these were regarded as active nests and retained in the analysis, even if they failed at a later stage. On the final visit (18 June), two burrows contained a newly hatched chick. On 36 occasions, inspected burrows contained no adult shearwater; these were also retained since the aim was to measure the response rate from all active burrows, as would be the case for an observer who did not open the burrows to check whether a bird was inside, the method used in the whole-island census. In considering sex as a factor in analysis, the small number of burrows containing both males and females (n = 9) were classified as containing males only: since females respond so infrequently, it is unlikely to bias the detection of male responses. The exclusion of these nine trials in which male and female were occupying a burrow did not influence the results of analyses.

Table 1. Comparison of playback trials conducted in 1998 and 2011. (N.B. these are raw data not corrected for sex, date and burrow identity; see Results).

	1998	**2011**
Number of nests in which an egg was laid	49	33
Mean number of males per visit	25.8	15.5
Mean number of responses per visit	21.4	12.3
Proportion of males present responding	0.83	0.79
Proportion of males present per visit	0.53	0.47
Mean proportion of nests at which male responded	0.44	0.38

Estimating the number of breeding pairs: From the product of the estimated total number of responses on the island and the response rate per burrow (controlling for other factors), we extrapolated an estimate of the total number of occupied burrows, and hence the number of breeding pairs on Skomer Island.

Statistical analysis: In estimating the response rate to call playback in study plots, the sex of the shearwater occupying a burrow and trial year were examined for their influence on the response to the taped call: sex and year were treated as fixed effects (sex*year). Burrow identity was included as a categorical random effect, nested within trial date as a continuous random effect in order to control for temporal pseudoreplication (random effect structure: date|burrow). Using this combination of random effects essentially fits a slope for response rate against date within each individual burrow. The potential for response rate overall to vary with trial date was examined by modelling 'date' as fixed linear and quadratic effects: no significant variation was detected and the random effect structure described previously was retained. Using the function 'lmer' from package 'lme4' (Bates *et al*. 2011) in R version 2.13.0 (R Development Core Team 2011), data were analysed using a generalized mixed effects model (GLMM) with binomial errors, a logit link and Laplace approximation, fitted by maximum likelihood to allow comparison of fixed effects. The full model was optimised by backward stepwise deletion beginning with the fixed effects (sex*year). Random effects were similarly optimised (date|burrow). A predictor was deleted if its removal from the model made a non-significant change in model deviance (Analysis of deviance, $P > 0.05$). Response rates were calculated by back transformation (from logits to proportions) using model predictions (Crawley 2007), refitted using REML before extraction of parameter estimates.

To assess whether the number of plots sampled was sufficient to estimate the total population responses, we examined the stability of population estimates at different sampling intensities. To verify that a sufficient number of plots were sampled we calculated bootstrapped estimates of the total number of responses for 10 sampling regimes, beginning at 29 plots (10% of plots sampled) and increasing by intervals of approximately 29 (Davison & Hinkley 1997). For each sampling regime, we randomly selected the number of plots with replacement 1,000 times. For each sample, we estimated the number of responses for the island and we present the median and 2.5–97.5 percentile intervals for each sampling regime. If the population estimate was to stabilise before the entire sample of plots were resampled it would be likely that sampling had been sufficient. If the estimate was to increase on each occasion that more plots were resampled, it would be unlikely that we could reliably estimate the number of responses without sampling every plot on the island. Bootstraps were calculated using code written for R version 2.13.0 (R Development Core Team 2011).

Results

A total of 4,475 responses were recorded from the 288 plots, an average of 15.54 responses per plot. Three observers completed 256 plots within the time available for the project, and a further 32 were completed with assistance from other fieldworkers at the end of the census period. There were differences in the mean number of responses per plot recorded by the three main observers. This might have happened if the observers had varied in the amount of time that they played the tape down each burrow and if this, in turn, affected the likelihood of a response. However, examination of the data showed that one observer visited markedly more of the plots with very high response rates (40+). When this is taken into account, the means of the three observers are closely similar, suggesting that observer bias is unlikely to have affected the results.

It is possible to find nesting shearwaters in almost all the hectare squares on the island, the only exceptions being places that are too wet or too rocky for shearwaters to dig burrows. Nevertheless, across the island, the number of responses per plot has a very strong negative binomial distribution; there were no responses from 81 of the plots and 190 from one plot. The most obvious cause of this variation is that those plots with the highest response rates are those nearest to the coast (Figure 1); these tend to have the deepest soil where burrowing is easiest. Usually also, the land slopes towards the sea making it easier for the birds to take to the air. One possible disadvantage of such sites is that they are also favoured by Atlantic Puffins; we can expect inter-specific as well as intra-specific competition for sites in these localities.

Table 2. Number of responses in plots in relation to proximity to the coast.

Habitat type	Number of plots	Total Number of Responses	Land area (ha)
Coast	75	2,548	59.31
Near coast	66	983	65.70
Inland	147	944	146.45
Total	288	4,475	271.46

Table 2 shows the relationship between plots and habitat type. *Coast* plots produced 57% of the responses although they accounted for only some 22% of the land area and the two habitat types *Coast* and *Near coast* yielded almost 80% of the responses although they represented less than 50% of the land area.

Estimating the total number of playback responses on the island: The numbers of playback responses are shown in Table 2. Even allowing for the different approaches in 1998 and 2011, there was a highly significant correlation between the numbers of responses in the same plot in the two surveys ($r^2 = 23.6\%$, $P < 0.001$).

Time did not permit measuring more than a one plot per square, so it was not possible to simply estimate the variance within squares. To overcome this, we have paired squares and measured the variance in the two plots in adjacent squares. The three habitat divisions used in Table 2 were retained and within these, pairs of adjacent squares selected. In almost all cases these were contiguous squares (including some that only met at corners). Four plots had to be omitted, one *Inland* plot was not surveyed, so another did not have a matching partner, and two *Coast* plots were geographically isolated after the other pairs had been selected.

Using P = Number of responses in a Plot and S = Size of Squares, and the area of each plot (a circle of 10 m radius) being 314 m^2, the total number of responses was estimated as:

$$\sum[(P1+P2)/2 \times (S1+S2/314)] = 125114\ (E(x))$$

The sampling standard error was estimated as:

$$\sqrt{\sum\left[\frac{(\text{abs } P1-P2) \times \sqrt{(1-(314/S1+S2))}}{2} \times \frac{S1+S2}{314}\right]^2} = 8{,}222$$

And so the 95% Confidence Intervals are ± (2 x 8,222) = ± 16,445.
And hence the estimated total number of responses lies between 108,669 and 141,559.

Response rate to call playback: Table 1 compares the results from burrow study plots in 1998 and 2011, examined to calculate the response rate of shearwaters to call playback. The sample of nests with eggs was smaller in 2011 than 1998 (33 *vs* 49), but the proportions of those males present that responded were similar in the two studies (2011: 0.79, 1998: 0.83). However, the proportion of males present on each visit was slightly lower in 2011 than in 1998: (0.46 *vs* 0.53). Also, the proportion of burrows from which a male response was recorded was slightly lower in 2011 than in 1998 (0.37 *vs* 0.44). It is important to examine this apparent difference in the raw data, because this feature is used to calculate the response rate. Before doing so, we controlled for trial date, burrow identity and the sex of the responding shearwater.

The degree of temporal pseudoreplication in playback trials was not of concern, as trial date had no detectable effect on shearwater response rate (change in model deviance $P > 0.05$, either before or after the optimisation of fixed effects). Therefore, only burrow was included as a random effect in subsequent analyses. Sex had a highly significant effect on the probability of a shearwater responding to playback, males responding much more frequently than females (Analysis of Deviance: $\chi^2 = 58.6$, df = 1, $P < 0.0001$): the mean response rate of males was 92.9 ± 4.6%, that of females 0.3 ± 0.3%. We found no significant difference in playback response rate between trial years (1998 *vs* 2011: $\chi^2 = 0.25$, df = 1, $P = 0.62$). Overall, and controlling for variation in response rate between burrows, the mean response rate of shearwaters was 40.3 SE ± 2.5%.

Estimating the number of breeding pairs: The estimate of the total population requires the following:

i) E(x) Estimate of number of responding burrows = 125,114 (see above)
ii) Var(x) Sampling variance of number of responding burrows = $8{,}222^2$
iii) E(y) Estimate of fraction of occupied burrows that respond = 0.403
iiii) Var(y) Sampling variance of fraction of occupied burrows that respond = $p(1–p)/n = .002934$

The estimate of the number of breeding pairs E(Z) is calculated as follows (Lynch & Walsh 1997: A.1.19a):

$$
\begin{aligned}
E(Z) &= E(x)/E(y) \times [1+Var(y)/E(y)^2] \\
&= 125114/0.403 \times [1+ 0.002934/0.4033^2] \\
&= 310456.5757 \times 1.018065501 \\
&= 316{,}065.1294
\end{aligned}
$$

The sampling variance of the estimate Var(Z) is calculated as follows (Lynch & Walsh 1997: A.1.19b):

$$
\begin{aligned}
Var(Z) &= [E(x)/E(y)]^2 \times [Var(x)/E(x)^2 + Var(y)/E(y)^2] \\
&= [125114/0.403]^2 \times [(8222/125114^2) + 0.002934/(0.403)^2] \\
&= 96383285384 \times 0.0181 \\
&= 1744537465
\end{aligned}
$$

The s.e. of the estimate = $\sqrt{Var(Z)} = 41767$

$$
\begin{aligned}
CI &= +/- 41767 \times 2 \\
&= 83534
\end{aligned}
$$

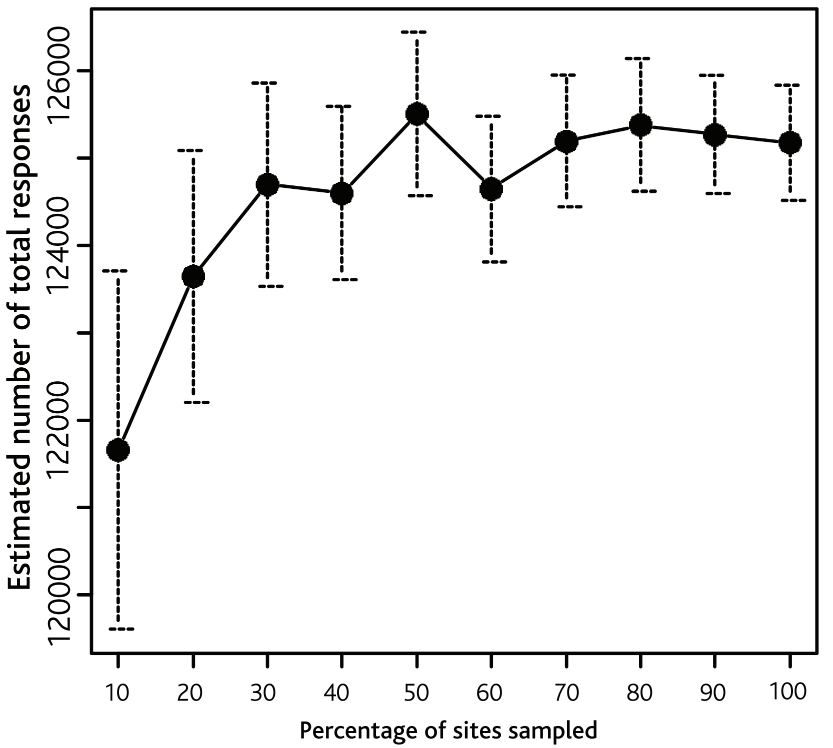

Figure 2. The effect of varying the number of plots (in which the number of responses was counted) on the estimate; the dotted bars show the 95% Confidence Intervals.

So the population is estimated to be 316,000 breeding pairs and the 95% Confidence Intervals to lie between 232,536 and 399,604 breeding pairs.

This estimate excludes a number of birds in areas that were not covered by the census. In both years, "21 squares/part squares totalling c 7.15 ha, mostly of rock, but containing at least 371 burrows were not sampled" (Smith *et al*. 2001), for safety reasons (the burrows were counted from a distance). In addition, in 2011 a further 25 squares/part squares which yielded 164 responses in 1998 were not covered. The one plot not censused and the three 'unpaired' plots are also not included. One of the latter may have contained 4,500 pairs, but it is unlikely that the rest of them together contained a further 1,000 pairs.

Figure 2 shows the effect of the number of plots sampled on the estimated total number of responses. The estimate increases slightly until 30% of the plots are counted, then stabilises; as expected the Confidence Intervals continue to decrease. Hence it seems that the number of plots surveyed should have been more than adequate to achieve a reliable estimate.

Discussion

Estimated Numbers and Confidence Intervals: It is inevitable that a population estimate of this type will have a number of sources of error. This estimate is derived from combining two measurements, the responses to playback in the plots and the response rate, each of which has errors.

Figure 3. Censussing a *Coast* plot in fairly open vegetation, June 2012. © J. C. Gonzalez.

Nevertheless, the results seem reasonable. We obtained 4,475 responses from 9.04 ha (288 plots of 314 m^2). Simple arithmetic suggests that if the plots are representative, then the total number of responses expected from the whole area (272 ha) would be the number of responses obtained, 4,475, x 272/9.04 or 134,727, a number not very different from the 125,114 calculated above. The number of responses then has to be adjusted for the response rate. Since the two sexes take roughly equal shares of incubation, a response rate of 0.5 might be expected. However, other factors lower the response rate: the male may be present, but not respond, both birds may be absent for a day or two or the egg may be lost and both birds cease to visit. Response rates of 0.32–0.55 have been reported by Newton *et al*. (2004), so the rate of 0.403 used here is in line with other studies. Hence it is not at all surprising that the estimate of the total number of breeding birds is not simply twice, but about 2½ times the number of responses.

Two features of the measure of response rate have important effects on the final population estimate. First, the response rate itself is important. For example, if we used uncorrected response rates (without controlling for sex) for each census (0.44 in 1998, 0.38 in 2011) to estimate the 2011 population size, this would make a substantial difference to the population estimate (284,345 *vs* 329,242). Because of this, it is important to control statistically for the effect of sex in response rate calibration trials if it is possible to do so. The uncorrected response rate was higher in 1998 than 2011, because a higher proportion of male shearwaters were found in calibration burrows in the 1998 census. Once the effect of sex is controlled for, we found no significant difference in response rate between 1998 and 2011; this allows us to use the pooled response data from 1998 and 2011. There is also the risk that, being obtained from one small set of study burrows, the response rate is not representative of the whole island. It would be preferable to have the sample plots dispersed around the island, to increase the probability of their being fully representative of the whole population.

Second, the size of the sample of burrows used in the responses has a large effect on the Confidence Intervals. Increasing the number of burrows from around 40 to 80 or more would roughly halve the Confidence Intervals. In this study the 95% Confidence Intervals indicate that the true figure lies within 25% of the estimated total. Both the spread of the number of responses observed in each plot and the distribution of these, with many plots with no responses, contribute to this. Nevertheless the bootstrap calculations (Figure 2) indicate that sufficient plots were visited to produce a reliable estimate.

Comparison with earlier counts on Skomer: Apart from the 1998 census, earlier estimates of the numbers of pairs of shearwaters on Skomer have been based on measures made of sample areas, multiplied up to the whole area of the island. Because of the very different densities in different areas, there were thought to be large potential errors in these and no attempt was made to calculate Confidence Intervals. Sutcliffe (1989), extrapolating from data collected from the Neck (see below), calculated that the population for the whole island might be as high as 165,000 pairs. Brooke (1990) made detailed surveys of the numbers of pairs in 31 one-hectare squares in 1981–84 and estimated that the breeding population might be around 100,000 pairs.

Comparison with the 1998 census: The results presented here differ strikingly from the results recorded in 1998 (Smith *et al.* 2001). A change from 101,000 to 316,000 pairs in the estimated population size requires an increase of approximately 9% p.a. For a bird with a low reproductive rate and a long period of deferred maturity, this is a very high rate. The UK and Irish population of the Northern Gannet *Morus bassana* has been increasing steadily for many years, but the rates have largely been of the order of 2% p.a., though the population at the Bass Rock has increased by 4.8% p.a. for 35 years (Wanless *et al.* 2005). During the period when it was spreading rapidly around the UK the Northern Fulmar *Fulmarus glacialis* achieved rates of increase of some 8% p.a. (Tasker 2004), but this may also have included some immigration.

The only previous attempt to estimate the population size of Manx Shearwaters on Skomer using playback was made in 1995 by Gibbons & Vaughan (1998). They restricted their study to the Neck, a 23 ha area on the east of the island (Figure 1), and obtained a figure of 26,500 pairs (95% CI 21,000–32,000). In comparison, the number of responses on the Neck in 2011 was 22,891 and the estimated population size 56,801 pairs, again very much larger than the earlier estimate.

Possible reasons for this difference include:

i That the population has increased during the 13-year interval. There is some evidence to suggest that there has been an increase. Surveys of 18 0.1 ha plots have been made annually by MSc students from Oxford (Taylor *et al*. 2011). From 767–1,113 males have responded in the different years, with the numbers showing a significant increase with time. However, at the most, this increase has been only about 2.5% per year, not nearly enough to explain the difference recorded between 1998 and 2011.

ii That the local population has been augmented by large numbers of immigrants. This seems unlikely since, even before the 2011 survey, the Pembrokeshire islands were thought to house 40 % of the UK and Irish population; an increase through immigration in a smaller population might well occur, but for Skomer this seems unlikely.

iii That there has been a sharp decrease in the age of first breeding. There is no evidence one way or the other, but it seems an unlikely explanation.

iv That the methods used in one (or both) of the surveys were sufficiently flawed to account for the difference, or part of it.

One difficulty with comparing the 1998 estimate with the current one is that the methods used were so different. One possible explanation for the disparity is that the technique used in 1998, of counting all the burrows in mid-winter and visiting a known percentage of these in summer, is faulty. It assumes that the 'population' of burrows remains the same throughout the year, whereas there is very heavy digging in spring by all three species - shearwaters, puffins and rabbits. In 2011, the number of burrows counted in the 288 plots was 13,863 and this, correcting for area (as done for responses in Table 2), yields a burrow number of 417,368, almost three times the number counted in winter 1997/98. [Burrows dug in spring are not normally used for breeding that same year - M. Brooke pers. comm.]

Differences in tape quality or observer behaviour are other possible sources of discrepancy. However, it seems unlikely that these can explain the differences between the two studies since the response rates were similar: 1998 3,218 responses in 11,320 burrows tested (28.4%), 2011 4,475 in 13,863 (32.3%).

While the reasons for the discrepancy between the two censuses needs to be better understood, we suggest that the method used here provides a fast, relatively low-labour way of making estimates of shearwater populations. We believe that the labour involved in establishing the response rate could be greatly reduced by searching for burrows with eggs at the end of May and simply marking and playing the tapes down these without trying to establish who the occupants were. This assumes no significant egg loss prior to the end of May. All that is needed is a response rate from a known number of burrows with eggs. This would potentially enable larger samples to be made and would not only increase the accuracy of the response rate but also reduce the Confidence Intervals.

Acknowledgements

Dr. M. de L. Brooke kindly made the tapes used in playback. Several members of the Edward Grey Institute of Field Ornithology, together with some MSc students from the Zoology Department at Oxford University who were present on the island, completed the remaining census plots: we are grateful for their assistance at such short notice. Prof. Alan Grafen advised on calculating the estimates and Confidence Intervals and Drs Rhys Green and David Gibbons made useful comments on an early draft, while comments by Annabel Knipe, Roddy Mavor, Norman Ratcliffe and the editor improved the submitted manuscript. Costs were borne by the Countryside Council for Wales.

References

Bates, D., Maechler, M. & Bolker, B. 2011. Linear mixed-effects models using S4 classes. *The Comprehensive R Archive Network*: http://cran.r-project.org

Brooke, M. de L. 1978. Sexual differences in the voice and individual recognition in the Manx Shearwater (*Puffinus puffinus*). *Animal Behav*iour 26: 622–629.

Brooke, M. de L. 1990. *The Manx Shearwater*. Poyser, London.

Crawley, M. J. 2007. *The R Book*. Wiley, Chichester.

Davison, A. C., Hinkley, D. V. 1997. *Bootstrap Methods and Their Application*. Cambridge University Press, New York.

Gibbons, D. W. & Vaughan, D. 1998. The population size of Manx Shearwater *Puffinus puffinus* on "The Neck" of Skomer Island: a comparison of methods. *Seabird* 20: 3–11.

Lynch, M. & Walsh, B. 1997. *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Sunderland, Massachusetts.

Newton, S. F., Thompson, K. & Mitchell, P. I. 2004. Manx Shearwater *Puffinus puffinus*. In: Mitchell, P. I., Newton, S. F., Ratcliffe, N. & Dunn, T. E. (eds.) *Seabird Populations of Britain and Ireland*: 63–80. Poyser, London.

Perrins, C. M. 2010. *Censussing the Manx Shearwater populations on Skomer and Skokholm*. Report to Countryside Council for Wales (Regional Report No: CCW/WW/10/3).

R Development Core Team. 2011. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Smith, S., Thompson, G. & Perrins, C. M. 2001. A census of the Manx Shearwater on Skomer, Skokholm and Middleholm, West Wales. *Bird Study* 48: 330–340.

Sutcliffe, S. J. 1989. *Seabird Studies on Skomer Island NNR in 1989*. Report to the Dyfed Wildlife Trust.

Tasker, M. L. 2004. Northern Fulmar *Fulmarus glacialis*. In: Mitchell, P. I., Newton, S. F., Ratcliffe, N. & Dunn, T. E. (eds.) *Seabird Populations of Britain and Ireland*: 49–62. Poyser, London.

Taylor, C. J., Boyle, D., Perrins, C. M, and Kipling, R. 2011. *Seabird monitoring on Skomer Island in 2011*. JNCC Contract Report.

Wanless, S., Murray, S. & Harris, M. P. 2005. The status of Northern Gannet in Britain and Ireland in 2003/04. *British Birds* 98: 280–94.