

MONITORING EUROPEAN STORM-PETRELS *HYDROBATES PELAGICUS*: A COMPARISON OF THE RESULTS PROVIDED BY MARK/RECAPTURE AND TAPE RESPONSE METHODS

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Hounsome, M.V., Insley, H., Elliott, S. Graham, K.L. & Mayhew, P. 2006. Monitoring European Storm-petrels *Hydrobates pelagicus*: a comparison of the results provided by mark/recapture and tape response methods. *Atlantic Seabirds* 8(1/2): 5-20. *Two techniques for estimating the size of breeding populations of European Storm-petrels Hydrobates pelagicus were carried out on two Scottish islands: the tape response method (in 1999 and 2004) and three types of mark/release/recapture method (in each year since 1998). The tape response method gave lower estimates than the MRR methods, raising questions about the assumptions and limitations of the techniques for monitoring European Storm-petrel populations. An apparent fall in population on Priest Island in 2004, indicated by the tape response method, is discussed.*

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INTRODUCTION

Breeding storm-petrels are difficult to census accurately (Ratcliffe *et al.* 1998) but the tape response method has become the accepted technique for censusing both storm-petrel species that breed in the British Isles (Gilbert *et al.* 1999). It is labour intensive and time consuming, requiring a minimum of seven days to calibrate the counts in each colony, making it expensive for frequent monitoring. Mark/recapture methods have been suggested as an alternative, but the results can be difficult to interpret, largely because of uncertainty about the origin and distribution of the population they are estimating.

Storm-petrels have been monitored on two small islands off the north and west coast of Scotland during the last nine years using two different methods (Hounsome *et al.* 2002, Hounsome *et al.* 2003, Insley *et al.* 2004a, 2004b). The work on Eilean Hoan started in 1996 and that on Priest Island in 1998. Both islands are Royal Society for the Protection of Birds (RSPB) reserves and Special Protection Areas designated under the European Union Natura 2000 programme, Priest being specifically designated for its European Storm-petrel

breeding colony, which is thought to be the third biggest in Britain (Mitchell *et al* 2004).

METHODS

Mark/recapture Throughout the study European Storm-petrels have been caught after dark using mist nets. Tape-luring attracts non-breeders as well as breeders and Fowler & Hounsome (1998) have shown that very few non-breeders are present before the beginning of July so catches, without tape lures, have been taken in the second and third weeks of June. Both of these measures were a deliberate attempt to minimise the number of non-breeding wandering birds trapped and to focus the study on the breeding population at each colony. Captured birds were processed in the order in which they were caught and times were recorded in 10 minute intervals. The processing rate of up to three birds a minute on Priest precluded any close examination of the birds, but on Eilean Hoan there was time to assess the extent and vascularisation of the brood-patch and to measure the wing and weight of the birds.

After initial work to measure the extent of population mixing at sites across Priest Island (Hounsome *et al* 2002), from 2002 onwards catching efforts were focussed on one core site (labelled as MSS in this paper). Eilean Hoan is small enough for most if not all of the population to be caught at the main colony area in a ruined stone fank (sheep holding pen). Exploratory catching was done elsewhere on the island in 2003 and 2005 and this confirmed that birds from the core site were quickly being re-caught elsewhere and that the mixing assumption was reasonable.

Analysis of the mark/recapture results has been carried out using three separate statistical methods. The du Feu method (du Feu *et al* 1983) considers only the retraps caught within each yearly session so that each year's estimate is independent of all other years. The Fisher and Ford and Jolly methods (Fisher & Ford 1947, Jolly 1965) consider only year-to-year retraps ignoring any multiple recaptures within the yearly session. Thus, there are three methods using two completely independent types of mark/recapture analyses which use separate sets of recapture data.

Tape response survey The first full tape response survey at Priest Island was carried out in 1999 with a second in 2004. Both surveys were carried out in July to ensure that the work was done at the optimal period (Ratcliffe *et al.* 1998; Gilbert *et al.* 1999). The tape response survey was carried out and analysed using the methods described by Gilbert *et al.* (1999) and Mayhew *et al.* (2000). To calibrate response rates (i.e. establish what proportion of birds respond to the tape stimulus), a series of 'calibration plots' were repeatedly visited. Tape response surveys require a separate calibration plot for each season and habitat,

and a separate calibration exercise for each survey year. Calibration requires repeat surveying and recording of response over the same plots for a minimum seven-day period.

On Priest Island four habitat types were recognised (boulder beach, stone walls, scree and heath/grassland). One calibration plot was established in each habitat and the same calibration plots for each type were used in 1999 and 2004 to determine the response rate of European Storm-petrels in each of these habitats (map and site descriptions in Mayhew *et al.* 2000). Over the seven visits to each calibration plot, an increasing number of responses occurred, with the cumulative number of burrows from which a response had been heard increasing with number of visits. A curve was fitted to the relationship between visit number and cumulative number of responses, and this was used to estimate (i) the eventual number of responses that would have occurred after a large number of visits; and (ii) the response rate on the first visit ^a. The results from all calibration plots in both years were further analysed using a single generalised linear model ^b. The aim of this was to test the degree of association between response rate, and the year, habitat and visit number.

Population estimation broadly followed the procedure used in Mayhew 2000. This was in two stages, firstly the extrapolated number of responses, had the whole island been surveyed, was estimated. Then the population was estimated, as the extrapolated number of responses, divided by the appropriate response rate.

For the boulder beach, scree and stone wall areas, the extrapolated number of responses was the same as the uncorrected number of responses, as these areas were surveyed in their entirety. However, the surveyed area in heath/grass habitats was only 20 quadrats, or 20ha out of a possible 94.68ha. So the extrapolated number of responses, had this whole area been surveyed, was estimated as 94.68/20 times the number of responses from the sampled quadrats. Confidence intervals of the extrapolated number of responses were estimated using bootstrapping ^c (Table 2).

To calculate the population estimates, the extrapolated number of responses in each habitat was divided by the habitat-specific response rate for that year (Table 3). For boulder beach, scree and stone wall habitats, the confidence intervals of the population were taken as the number of responses divided by the lower and upper confidence intervals of the response rate for that habitat in that year (Table 3). For heath/grass habitats, the lower confidence interval of the population was estimated as the lower confidence interval of the extrapolated number of responses, divided by the upper confidence interval of the response rate, and vice versa for the upper confidence interval. For the whole island population, the population estimates in the different habitats were summed. The confidence intervals were estimated using the confidence

intervals of the global response rate across all habitats in that year^d. Population estimates (number of birds) were calculated as twice the number of corrected responses, assuming one pair for each occupied burrow.

The significance of the difference in population estimates between the two years was tested using a resampling procedure used by Sim *et al.* (2005)^e. Essentially this creates a distribution of differences under a null hypothesis that the years are equivalent, and compares this with the observed difference. Note that for this test, the data we used were the corrected responses, using the mean response estimate for each habitat. The uncertainty in the response rate was not modelled in the analysis.

RESULTS

Mark/recapture The du Feu population estimates (du Feu *et al.* 1983) from this survey are presented in Table 1. Comparison with the estimates presented in earlier years (Hounsoms *et al.* 2002 and 2003, Insley *et al.* 2002, 2004a, 2004b) will show some minor differences. Both the Jolly and Fisher and Ford methods (Jolly 1965, Fisher & Ford 1947) incorporate data for birds caught in previous years. As the study progresses and more birds from earlier years are recaptured there is a progressive updating and improvement of population estimates by these year-to-year methods. On the other hand, the du Feu estimates are unaffected by captures in previous or subsequent years because the method considers only captures and recaptures within each year. The data sets have been cleaned several times over the course of the work so that there may be some small changes from previously published du Feu estimates.

The du Feu estimates for Eilean Hoan show the population fluctuating between about 250 to 800 birds, with an apparent fall in 2004 (Table 1). The estimates for the MSS site on Priest Island range from about 8,000 to about 12,000 but show little indication of a fall in 2004 (Table 1).

The Fisher & Ford method is an old deterministic approach (Fisher & Ford 1947) and assumes a constant survival rate; it consequently gives a smoothed series of population estimates. It is included here only because it can give estimates in the early stages of a study, which this is, considering that some of these birds live for thirty years. The accepted modern method is that of Jolly (1965) and its subsequent developments and the computer programs MARK and POPAN5 have been used to determine the optimal model for these data. Both programs agree that the general model is the best i.e. the model that assumes that both the survival rate and the probability of capture vary with time (Φ, p). For Priest this model was the most parsimonious, with an AICc weight of 0.99; it was also the best fit, with a deviance of 132.8. The next most parsimonious model was one in which the survival rate was constant but the probability of

capture varies with time (Φ, p_t), with an AICc weight of 0.01; this was also the second best fit, with a deviance of 149.7. The same pattern was seen in the Eilean Hoan data, with the Φ, p_t model being both the most parsimonious and the best fit (AICc weight = 0.85 and the deviance = 246.7); the next best model was again Φ, p_t (AICc weight = 0.15 and deviance = 262.5). The program MARKREC (Hounscome 1978) was used to produce the population estimates (Table 1, and Figures 1 and 2).

Table 1. Summary of mark/recapture population estimates \pm = standard error.

Tabel 1. Samenvatting van populatieschattingen met behulp van vangst/terugvangst. \pm = standaardfout.

Island	Method	Survival	1998	1999	2000	2001	2002	2003	2004
Eilean Hoan									
	duFeu	-	-	-	-	464 ± 73	391 ± 80	775 ± 210	267 ± 39
		0.7206	296	308	621	474	362	685	454
	Jolly	± 0.1294	± 74	± 51	± 109	± 77	± 63	± 168	± 129
		0.8386							
	F&F	± 0.0262	324	271	546	490	523	628	816
Priest MSS									
	duFeu	-	-	-	-	11,514 $\pm 3,024$	8,036 ± 918	11,804 $\pm 1,601$	9,450 $\pm 1,624$
		0.8484				8,141	7,929	8,439	6,718
	Jolly	± 0.0820	-	-	-	$\pm 1,460$	± 841	± 846	± 808
		0.8448							
	F&F	± 0.0158	-	-	-	11,638	8,500	7,477	7,279

The estimates of the overall survival rate are, with the exception of the Jolly estimate for Eilean Hoan, consistent both within themselves and with published estimates of 0.86 (Dagys 2001) and 0.87 (Scott 1970). Note that the standard error for the Jolly survival estimate for Eilean Hoan is very large; it is expected that in future years this estimate will come into line with the others. Most published survival estimates are derived from recoveries of dead birds, but mark/recapture estimates must necessarily include emigration so they are usually much lower than those derived from recoveries of dead birds only. The fact that our estimates are only slightly below those for dead birds indicates that there is little emigration from our breeding populations. This, together with the agreement of three mark/recapture methods gives us confidence that the population estimates are reasonable and that the captured birds are breeders not non-breeding birds. There is also some synchronicity between the estimates for the two islands which might reflect real natural processes and which add a degree of confidence to the population estimates.

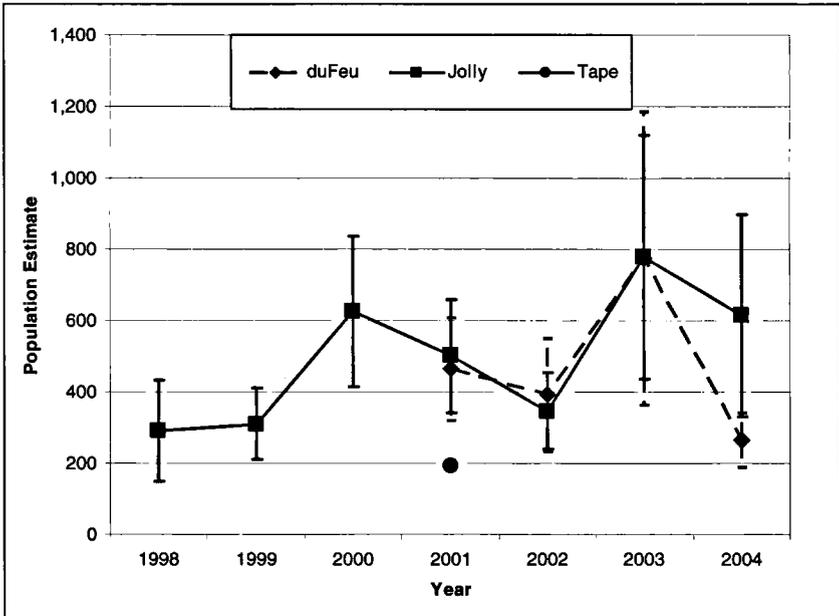


Figure 1. Eilean Hoan Storm Petrel population estimates for the period 1998-2004, with 95% confidence limits (the limits for the tape response estimate in 2004 are too small to show on this graph).

Figuur 1. Populatieschattingen van Stormvogeltjes op Eilean Hoan, 1998-2004, inclusief 95%-betrouwbaarheidsintervallen (resultaten van playback-methode in 2004 zijn te klein om in de grafiek zichtbaar te zijn).

Table 2. Response rate to taped call playback by European Storm-petrels in each of the habitat types surveyed on Priest Island in 1999 and 2004.

Tabel 2. Antwoordfrequentie van Stormvogeltjes bij playback-methode per habitattyp, zoals onderzocht is op Priest Island in 1999 en 2004.

Habitat	1999		2004	
	Response rate	95% C.I.	Response rate	95% C.I.
Boulder Beach	0.47	0.40 - 0.54	0.21	0.17 - 0.27
Stone Walls	0.42	0.38 - 0.45	0.17	0.04 - 0.29
Scree	0.48	0.45 - 0.50	0.26	0.17 - 0.34
Heath/Grassland	0.36	0.27 - 0.44	0.21	0.10 - 0.31
All Habitats	0.41	0.24 - 0.59	0.27	0.21 - 0.34

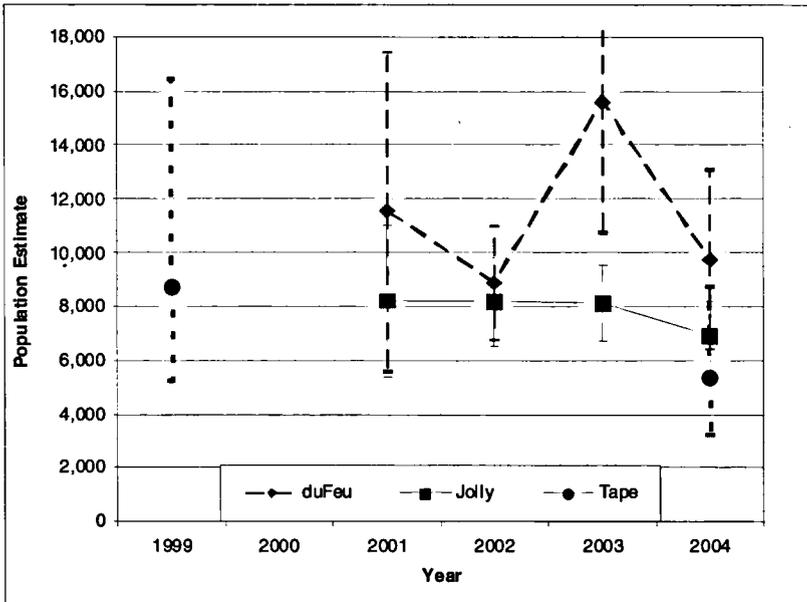


Figure 2. Priest Island European Storm-petrel population estimates for the period 1999-2004, with their 95% confidence limits. It is important to note that the tape response estimates are for the whole island, whereas those for Jolly and du Feu are for a single site (MSS). Also note the very large 95% limits of the tape response estimates compared with those for Eilean Hoan (fig.1).

Figuur 2. Populatieschattingen van Stormvogeltjes op Priest Island, 1999-2004, inclusief 95%-betrouwbaarheidsintervallen. Nota bene: de schattingen aan de hand van de playback-methode zijn voor het gehele eiland, terwijl die van Jolly en du Feu betrekking hebben op één (studie)gebied (MSS). Let ook op de zeer ruime 95%-marges van de playback-methode in vergelijking met die van Eilean Hoan (fig.1).

Tape response survey On Priest Island twenty 1ha plots of heath/grassland were surveyed, representing only 21% of the total area of this habitat type so this was extrapolated to give a total number of European Storm-petrels recorded in that habitat area, before the response rate was applied. All the areas of boulder beach, stone wall and scree were surveyed, so no extrapolation was needed.

Table 2 shows the response rates (with upper and lower 95% confidence intervals) for each habitat in each of the two years, 1999 and 2004, and the mean

response rates across all habitats in the two years. Habitat specific estimates of response rate are taken from the curve-fitting as described in the Methods. The modelling analysis of response rate data from the calibration plots (see Methods) suggested that the difference in response rates between years was significant ($p=0.03$), and that the response rate in 1999 was about 1.5 times higher than that in 2004. The model simplified to one suggesting that only 'year' was significantly associated with response rate, implying that differences in response rate between habitats and visits were minor. The response rates for all habitats combined, in each year, and their confidence limits, were taken as the estimates for the two levels, 1999 and 2004, of the categorical variable 'year', in this model (Table 2).

Table 3. Tape response calculation of AOS by European Storm-petrels from the main survey for the four breeding habitats and the total population estimates for Priest Island in 1999 and 2004.

Tabel 3. Berekening aan de hand van de playback-methode van het aantal AOS van de belangrijkste inventarisatie van de vier broedhabitats en populatieschattingen voor Priest Island in 1999 en 2004.

Habitat	Number of responses		Extrapolated responses		AOS (after correction for response rate)		95% confidence limits (after bootstrapping)		95% confidence limits of correction factors	
	1999	2004	1999	2004	1999	2004	1999	2004	1999	2004
Boulder Beach	25	24	(25)	(24)	53	112			47-63	88-144
Stone Wall	72	34	(72)	(34)	172	198			159-190	119-879
Scree	679	230	(679)	(230)	1,429	900			1,358-1,516	685-1,388
Heath/Grassland	206	64	975	303	2,716	1,458	2,149-3,270	819-2,139	1,774-4,300	555-4,684
All Habitats	982	352	1,751	591	4,370	2,670	3,800-4,920	2,030-3,350	2,610-8,220	1,590-4,370
Population Estimate					8,740	5,340	7,600-9,850	4,060-6,700	5,220-16,440	3,180-8,740

The responses and population estimates on Priest Island for 1999 and 2004 are shown in Table 3. It is clear that, with the exception of the boulder beach and walls, the responses to the taped calls were many fewer in 2004 than in 1999. Overall population estimates in the two years were 8,740 (95% cIs: 5,220-16,440) birds in 1999 and 5,340 (95% cIs: 3,180-8,740) birds in 2004.

The between years difference in corrected responses was strongly significant ($p=0.006$) using the randomisation test described in Methods. It must be emphasised that these are estimates for the whole island whereas the mark/recapture estimates are for only the MSS site.

A tape response survey has been carried out comprehensively on Eilean Hoan only once during the study period, in 2001, when the whole island was surveyed over a seven day period. The much smaller size of both the island and European Storm-petrel colony made this possible rather than having a sample and calibration survey as employed on Priest Island.

The tape response population estimate for Eilean Hoan in 2001 was 194 (95%CI 188-200) (Insley *et al* 2002). Note that this is much less than the mark/recapture estimates between 1998 and 2004; indeed, it is close to the numbers actually caught in each of these years. In 2001 the mark/recapture estimates were: du Feu, 464, Jolly, 474 and Fisher & Ford, 490, with 150 birds being caught (Figure 1). It is clear that there were many more birds present than would be expected from the tape response estimate.

DISCUSSION

There are two main questions raised by these results: why are the tape response estimates lower than the mark/ recapture ones, particularly for Priest Island where the latter measured only one section of the island? And, was there a genuine reduction in the breeding population in 2004? A subsidiary question might be: if there really was a reduction in 2004 does it represent a true reduction in the colony size, or just an exceptional bad year?

There are four possible answers to the first question:

- 1) mark/recapture is falsely high, possibly because it is including pre-breeders or because it includes birds that are alive but not actually breeding or because it is a flawed statistical method or at least, is not suited to these circumstances.
- 2) tape response is falsely low, possibly because it is not detecting all the occupied nests even after calibration or because of surveyor error or because it is a flawed method.
- 3) both methods are giving inaccurate estimates.
- 4) both methods are correct, but they are estimating different aspects of the population.

The fact that the two quite independent types of mark/recapture analysis give similar results and that the estimated survival rates are so close to the published ones means that the population estimates are not likely to be seriously biased. Also, the data are ideal for such analysis, with so many extensive individual recapture histories and such a high proportion of retraps (around 30%). So, answer 1) does not seem likely. The fact that tape lures were not used

and that very few immatures are present in mid June means that these estimates are likely to be of adults only.

The tape response method has become the standard way of estimating apparently occupied sites and has been extensively used and refined. There is no reason to suspect that it is a flawed method. It is, however, more dependent upon the skill of the surveyors than is the mark/recapture method (although trained ringers are needed for mark/recapture projects), so it is just possible that the surveys themselves were flawed rather than the method itself. The teams on Priest and Eilean Hoan were experienced and dedicated, and the differences in response rate on Priest were so obvious that it is unlikely that this was significant observer error. So answer 2) does not seem likely. It is also unlikely that both well-tried and tested methods are giving wrong estimates.

So we are left with the possibility that the different methods are estimating different components of the population. The tape response method is explicitly estimating the number of apparently occupied sites, in a particular year. This estimate can be doubled to give an estimate of the number of birds occupying burrows. What does the Jolly mark/recapture method estimate? The answer is simple: it is the number of birds in the 'pool' from which the samples have been taken. In other words, it estimates the number of birds in the population, *whether they are present on the sampling nights or not*. It would include birds taking a year off and not present as well as birds present but not actually breeding in that year. So it is estimating the breeding population of the islands, not the numbers actually occupying burrows during the survey. As noted in the Methods section, it is thought that there are very few immature birds present at these colonies this early in the breeding season so the estimate is of the mature, potentially breeding, population. Later in the season up to half the birds in the burrows can be non-breeders (Cramp & Simmons 1977), and these birds are known to sing (*op. cit.*) and may respond to taped calls and thus be included in estimates made by the tape-response method.

The mark/recapture estimates show a modest fall in the population on both Eilean Hoan and Priest Island in 2004, but only as part of the normal fluctuations over the period (Figures 1 and 2). No tape response estimates were made on Eilean Hoan in 2004, but those for Priest Island show a considerable fall – from a population of 8,740 in 1999 to 5,340 in 2004. If the suggested reason for the differences between the estimates by the two methods, above, is correct then it could be said that, yes, there were fewer occupied burrows in 2004 than in 1999, but that does not necessarily mean that the breeding population had fallen. The birds could be alive but conditions were such that many of them chose not to breed or they were in too poor a condition to breed.

Another possibility might be that normal numbers were present early in the season when the mark/recapture estimate was made, but that conditions were

such that many of them abandoned their breeding attempts. Thus, birds might have returned to the breeding colony but had either laid and failed, or were simply not in good enough condition on their return to lay and were therefore not occupying the nesting burrows later in July, when the tape response survey was carried out.

It is difficult to know whether the fall in the tape response estimates from 1999 to 2004 indicates a genuine decline in the breeding population of European Storm-petrels on Priest Island, or whether it is just a sign of a poor breeding season. It has been well documented that other seabirds around Scotland have had a generally poor breeding season in 2004 (Mavor *et al.* 2005). This may be related to the increased Atlantic inflow changing the species composition and timing of the bloom and/or to rising sea temperatures causing a shift northwards in plankton populations. On the other hand it might be that the surveys were conducted too early in 2004. We go on the dates recommended in Gilbert *et al.* (1999) which is based on the normal peak of responses, but if laying was delayed and all the birds were not yet on eggs when we carried out the survey it might result in an underestimate of the number of apparently occupied sites. Laying date has been shown to vary by up to a month in work done in Brittany (Cadiou, 2001) with the date by which 50% of eggs had been laid varying from mid May to mid July. So it is possible that the low population estimate in 2004 is because not all the birds were yet incubating. We propose to install nest boxes so that we can determine the breeding status of the colony on our visits; this will help us interpret future tape response estimates.

Continued monitoring over the next five years will answer some of these questions. Mark/recapture estimates can be made in every year and trends may become apparent. So far there have been only two tape response estimates on Priest Island and one on Eilean Hoan and it is impossible to identify trends from only two estimates. Even if the survey on Priest Island is repeated in another five years (2009) there will be only three points.

So, which method is best for monitoring European Storm-petrel populations? The tape response method has the advantage in that it is widely used and is standardised so that comparisons can be made not only within years on one island but among other islands. Other advantages are that it can be done in daylight, you don't need a ringing license or ringing equipment, it's spatially explicit which enables sampling, it can be applied irrespective of colony size and it can map breeding distribution within islands. It is also likely to give good estimates of the number and distribution of occupied sites, but these do not necessarily correspond to the number of birds available to breed. It also suffers from the fact that it is hard to calibrate for birds that don't respond and it can be very laborious for large islands/colonies. In most circumstances it is not practical to carry out a survey every year so that the normal annual fluctuation

in the number of pairs attempting to breed will be obscured. In 2005 a trial was begun on Priest Island to assess whether annual monitoring of a sample of tape response plots can be used to assess annual population fluctuations on the island.

The mark/recapture estimates refer to a more nebulous concept of the population – the number of potential breeders in the wider population using each island. It has the advantage that it is less labour-intensive and so is practical to carry out annually. This is likely to give a better indication of the annual population fluctuations and will highlight trends with a finer resolution. The Jolly method also gives estimates of survival rate and, crucially, recruitment rate and it thus allows diagnosis of the aspects of the life history that are driving population change which has the potential to inform conservation management. The disadvantages are that personnel have to stay overnight, they need to be trained ringers and they need ringing equipment. It is worthwhile only for colonies over a certain size, the proportion of large colonies sampled is often unknown and there is a risk of including non-breeders if the visits are not correctly timed.

At present it is not possible to say which method is best for European Storm-petrel monitoring as they are estimating slightly different things. It could be said that it is best to continue using the tape response method because most other seabird populations are estimated on the basis of the number of occupied nests. On the other hand, mark/recapture methods give annual estimates not only of the population but of survival and recruitment. Another five years of mark/recapture estimates, annual tape response estimates for selected plots and another full tape response estimate in 2009 will go a long way towards resolving the issue and hopefully will lead to the development of more robust monitoring methods for these internationally important populations of European Storm-petrels.

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MONITORING VAN STORMVOGELTJES *HYDROBATES PELAGICUS*:
EEN VERGELIJKING VAN DE RESULTATEN VAN
VANGST/TERUGVANGST- EN PLAYBACK-METHODEN

Op twee Schotse eilanden werden twee technieken gebruikt om de grootte van de broedpopulatie van Stormvogeltje *Hydrobates pelagicus* te bepalen: playback-methode (in 1999 en 2004) en drie typen van vang/terugvangmethoden (jaarlijks sinds 1998; vangen, merken, vrijlaten en terug vangen). De playback-methode leverde lagere schattingen op dan de vang/terugvangmethode, hetgeen vragen oproept over de aannames en beperkingen van de technieken om Stormvogeltjes te monitoren. Een opgeschijnde afname in een populatie op Priest Island in 2004, aangetoond met de playback methode, wordt bediscussieerd.

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ENDNOTES

a. The formula used in the curve-fitting program was as Mayhew *et al.* (2000), i.e.:

$$\text{CUMULA} = a * (1 - \exp(-1 * b * \text{VISNUM}))$$

where CUMULA is cumulative total number of responses and VISNUM is visit number to the calibration plot (1-7). The value 'a' estimates the asymptote - the 'true' total no. birds in the plot; while the value for 'b' estimates the shape of the curve. The 'visit 1 response rate' (v1rr) is estimated as the value of CUMULA for VISNUM=1, divided by the true total (a). This simplifies to:

$$\text{v1rr} = 1 - \exp(-1 * b)$$

From this equation, and the confidence intervals of the 'b' parameter from the curve-fitting, the confidence intervals of the response rate were calculated. The curve-fitting was carried out using the NLIN procedure in SAS version 8 which uses least squares to fit a curve to the function specified by the user. At one calibration plot in one year, it was impossible to fit a curve as there was a large jump in the cumulative number of responses between two visits. In this case, the cumulative total number of responses (12) after seven visits was used directly as the estimate of the 'true' total no. birds in the plot. The mean and 95% cIs of the visit one response rate were estimated by bootstrapping: 1000 'bootstrap samples' each of seven values, were selected at random, with replacement, from the seven numbers representing the responses from the seven visits. The mean response rate of each sample was calculated, as the mean number of responses divided by 12. The mean and confidence intervals of these 1000 means was used as the mean and confidence intervals of the response rate for this habitat in this year.

b. The model fitted was a GLM with repeated measures (proc Genmod in SAS, using a GEE approach to model correlation between repeated measures), with (responses)/(estimated total no. occupied burrows (i.e. the parameter 'a' from curve-fitting exercise) as the y variable in a binomial model. Each trial (i.e. visit to a calibration plot) contributed a separate row of data, the repeated trials at each stratum in each year were modelled as correlated with each other using a repeated command which assumes that visits closer together were more strongly correlated than visits further apart. The explanatory variables were Year (1999 or 2004), Habitat (a four-level categorical variable representing boulder beach, scree etc), and TrialNumber (1-7), and all their interactions. Using backwards deletion and a threshold p value of 0.05, only 'year' remained in the model (p=0.03) suggesting that response rates differed between years but not between habitats or between trials at each stratum.

This involved selecting, at random, with replacement, 20 values from the list of observed responses for the 20 quadrats in this stratum, taking the mean of each sample, and multiplying up (by 94.68/20) to give an estimate for the whole heath/grass area. This was repeated 1,000 times and the 25th largest and 25th smallest values of the estimated number of responses for the whole area were taken as the 95% confidence intervals.

d. The total population estimate, calculated from the sum of estimates of the different habitats, was multiplied by the global mean response rate for that year, then divided by the upper confidence limit of this response rate to give the lower population confidence limit (and vice versa to calculate the upper confidence limit).

Briefly, this involves selecting, for each survey plot, one of the two year's data at random. The data for the other year is then placed beside this in a second column. This is done for all plots. The difference in population is then calculated for the two years. This process is repeated 1000 times and the resulting distribution (based on the null hypothesis that the years are equivalent) is compared with the observed difference. If differences as large as that observed, are rare within this distribution, then the observed difference is unlikely under the null hypothesis, with a level of significance which can be estimated from the distribution. Further details in Sim *et al.*