

**Fisheries risks to the population viability of black petrel  
(*Procellaria parkinsoni*)**

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## EXECUTIVE SUMMARY

Francis, R.I.C.C.; Bell, E.A. (2010). Fisheries risks to the population viability of black petrel (*Procellaria parkinsoni*).

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Data on the main population of black petrel (*Procellaria parkinsoni*), which breeds on Great Barrier Island, were analysed. Three types of data were available. The most useful was abundance data, from which it was possible to infer that the population was probably increasing at a rate between 1.2% and 3.1% per year. Mark-recapture data were useful in estimating demographic parameters, like survival and breeding success, but contained little information on population growth rates. Fishery bycatch data from observers were too sparse and imprecise to be useful.

The fact that the population is probably increasing shows that there is no evidence that fisheries currently pose a risk to this population. However, this does not imply that there is clear evidence that fisheries do not pose a risk to this population.

The mean age of first breeding for black petrel is estimated to be 6.7 y. Before this, new adults spend an average of 1.2 y in the colony as pre-breeders, with only 3% skipping the pre-breeder phase. Of birds that appear in the study area as pre-breeders and survive to breed, only 68% do so in the study area. Once birds start breeding, their annual survival rate is 0.89, 80% breed each year, and of those, 77% are successful (i.e., produce a fledgling). Survival rates before the pre-breeder stage are not well determined because we can't distinguish mortality from emigration (birds that breed in an area away from where they were hatched).

Two recommendations for further monitoring of this population are: periodic repeats of the transect-based abundance estimation last done in 2005 (to determine whether the population is increasing or declining); and the use of data loggers to improve our knowledge of the birds' foraging range and thus help to identify fisheries that might be affecting this population.

## 1. INTRODUCTION

The work described in this report was carried out as part of the five-year Ministry of Fisheries project PRO200602, whose specific objectives are as follows.

1. Model the effects of fisheries mortality on population viability compared with other sources of mortality or trophic effects of fishing to allow an assessment of the risk posed to population viability by fishing.
2. Assess the ability of alternative management strategies to: a) avoid, remedy or mitigate the adverse effects of fishing on seabird population viability; and b) to reduce mortality to a negligible level, measured in population terms, for selected species.
3. Examine the overlap of fishing activity with species distribution at sea for different stages of the breeding and life cycle and for different sexes and provide an assessment of the risk posed to seabird species from different fisheries (by target species fisheries, fishing methods, area and season).
4. Assess population status of selected seabird populations in relation to fisheries risks to population viability.

Previous work in the first two years of this project involved the developing and testing of the computer program SeaBird (Francis et al. 2007), and the evaluation of the effects of fishing on southern Buller's albatross (Francis et al. 2008). The work described in this report was aimed at the analysis of data on the main population of black petrel (*Procellaria parkinsoni*), which breeds on Great Barrier Island.

### 1.1 The species

The black petrel (*Procellaria parkinsoni*) is a medium-sized endemic seabird that was once the dominant muttonbird of the North Island Maori, being found on most North Island ranges over 400 m (Scofield 1989) and also in the northern South Island (Imber 1987). The only known current breeding locations are on Hauturu/Little Barrier Island and Great Barrier Island (Aotea Island) (Heather & Robertson 1996). The colony on Hauturu/Little Barrier Island is of long standing, dating back to at least 1885 (Scofield 1989), but that on Great Barrier Island seems to be more recent, being first reported by Bell & Braithwaite (1964) despite there having been "intensive natural history investigation on the island in both the 19th and 20th centuries" (Scofield 1989). Imber (1987) estimated the total Great Barrier Island population (500–1000 breeding pairs) to be about 10 times as big as that on Little Barrier Island (50–100 breeding pairs).

Between 1986 and 1990, 249 fledglings were transferred from Great Barrier Island to Little Barrier Island, but most of those that were subsequently seen as pre-breeders or breeders had returned to Great Barrier Island (Imber et al. 2003).

Black petrels nest in burrows, usually above 400 m in altitude, and within 50 m either side of ridge lines (Scofield 1989). The breeding season starts in October, when males prepare burrows and try to attract a mate. Eggs are laid in December, and the peak period for hatching is early February (the typical incubation period is 57 days). Chick rearing takes about 107 days, with chicks fledging in April. During the breeding season adults forage mostly to the west and east of northern New Zealand (Bell et al. 2009). Both adult and newly fledged birds spend the winter off the west coast of North and South America.

This species is rated as Vulnerable by the IUCN (<http://www.iucnredlist.org/details/144872/0>). The Department of Conservation (DoC) classification for black petrel was recently upgraded from Gradual

Decline to Range Restricted, with the comment ‘Although formerly in decline, there is no current evidence that this continues’, and the qualification HI, indicating that the species’ loss of range was human induced (Hitchmough et al. 2007). Different threat categories were used in DoC’s most recent classification (Miskelly et al. 2008), in which the term Range Restricted was retained for black petrel, but used as a qualifier to the risk category Nationally Vulnerable. In their assessment of risks to New Zealand seabirds from commercial fishing Baird & Gilbert (2008) found black petrel to be the only species in their high risk category. However, they noted that the degree of risk to this species was highly uncertain because of the low level of fishery observer coverage in FMA 1, the area of primary concern.

## 1.2 The study population

The population studied here is that in the main breeding area on Great Barrier Island, around the summit of Mount Hobson (Hirakimata, altitude 627 m). More specifically, it is that in the 35 ha rectangle (Figure 1) that was defined in a study that began in 1996 (Bell et al. 2007). Most of the data analysed here come from that study. In each breeding season, there have been two or three visits to the study area at key times of the breeding cycle (Table 1). Throughout this report breeding seasons are labelled by the year of fledging (e.g., the season from October 1995 to April 1996 is labelled 1996).

**Table 1: Timing of visits to the study area in each breeding season. Note that, for example, the 1995–96 season is labelled 1996.**

Seasons	December (egg laying)	Jan./Feb. (hatching)	April (fledging)
1996 to 2001	No	Yes	Yes
2002 to 2009	Yes	Yes	Yes

## 2. DATA

Three types of data were available for the present study: fisheries bycatch data from observers, abundance estimates, and mark-recapture data.

### 2.1 Bycatch data

The bycatch data were found to be too sparse to be of use in modelling in the present project.

Baird & Gilbert (2008) found that the main bycatch threat to this species in New Zealand waters occurred in FMAs 1 and 2 in the surface (SLL) and bottom (BLL) longline fisheries during the breeding season. However, observer coverage is typically very low for these fisheries in this time and area: 2.5% for SLL and 0.3 % for BLL (these values are averages for the October–March period over the years 2001–04, calculated from the *bycatch1* data set described by Francis et al. (2008)). Over the period 1997–2008, observers in the SLL fishery (in all areas) reported an average of only 2.2 black petrels caught per year. This very low number, combined with the low observer coverage, means that estimates of annual bycatch will be extremely uncertain.

The lack of bycatch data is exacerbated by occasional misidentification (wrong species code) or incomplete identification (e.g., black petrel recorded as unidentified petrel, or small seabird). This occurred with 4 of the 15 black petrel necropsied between 1999–2000 and 2007–08. The published necropsy reports do not detail the incidence of the reverse misidentification: birds wrongly identified by observers as black petrel. However, a spreadsheet giving data for the last three fishing years (2005–06 to 2007–08) showed 1 such bird in 2006–07 and 10 in 2007–08 (Stephanie Rowe, Department of Conservation, pers. comm.).

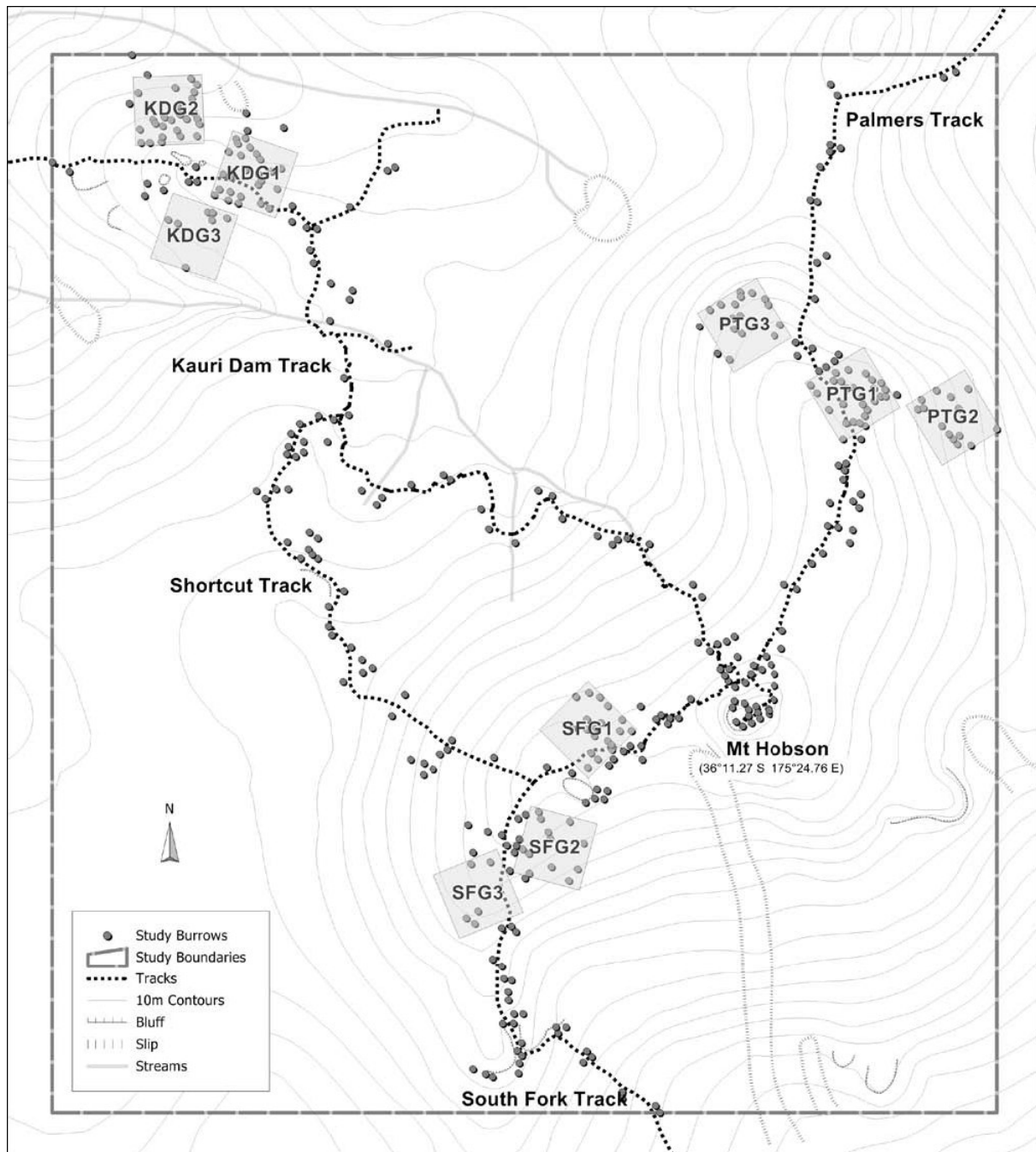


Figure 1: Location of the study area on Great Barrier Island showing study burrows, census grids and other features. The peak of Mt Hobson is 627 m above sea level. KDG, Kauri Dam Grid; SFG, South Forks Grid; PTG, Palmers Track Grid.

## 2.2 Abundance estimates

### 2.2.1 Early estimates

There are three early, but informal, abundance estimates for black petrel on Great Barrier Island. Bartle (1967) said the “consensus of opinion as to the numbers and distribution of Black Petrels on Mt Hobson is that they are confined to the summit pyramid (1600–2038 ft [=488–621 m]) and that there are about fifty occupied burrows in this area”. However, Reed (1976), from a visit in 1972, estimated a much bigger population of 300–400 birds, and reported (as a pers. comm. from Bartle) that Bartle had revised his earlier estimate upwards to be more consistent with this. It is unclear whether this

estimate refers to all birds, or just breeders. Imber (1987) estimated an even larger population of 1000–2000 breeders (500–1000 breeding pairs) on Great Barrier Island.

### 2.2.2 Scofield's estimate

The first formal estimate of abundance on Great Barrier Island was by Scofield (1989), who estimated a population of 2600 breeders in the area above 400 m adjacent to Mt Hobson. He divided this area into five strata defined by vegetation type (Figure 2), of which only three (11, 21, and 23) were considered to be suitable habitat for black petrel. Ten 50 m x 10 m transects were randomly located within these three strata, and searched for burrows. Of the 26 burrows found within these transects, 16 were identified as being used by breeding birds. The estimate of 2600 breeders was obtained by multiplying the average density of breeding burrows within the transects in each stratum (burrows/ha) by the stratum area (ha), summing across strata, and multiplying by 2 (breeders per burrow) (see original estimates in Table 2). The estimate of 48 breeders in stratum 22 came from a search of the entire stratum, which was not possible in the other strata because of dense undergrowth (R.P. Scofield, Canterbury Museum, pers. comm.).

An attempt to compare the area covered by Scofield's population estimate with the current study area (as shown in Figure 1) revealed two problems with Scofield's map. First, the scale bar seemed to be wrong. When Scofield's stratum boundaries were digitised and georeferenced (using Quantum GIS [<http://qgis.osgeo.org>] and the assumption that his scale bar and the location of Mt Hobson/Hirakimata were correct), the total area within his strata 11, 21, and 23 was found to be almost four times as large as he claimed (150.7 ha, rather than 40 ha). The second problem was that the shape of Scofield's 400 m contour line was found to be very different from that in the LINZ 2005 1:50 000 topographic dataset. Nor did it resemble contours in various earlier topographic maps of Great Barrier Island (those examined were 1973, 1978, and 1986 editions of the NZMS 259 map; the 1973 edition of the NZMS 252/8 map; and the 1953 edition of the NZMS 1 map; the last of which has no contours near Hirakimata). Some resolution of these problems might be found in the unpublished N.Z. Forest Service report (titled 'Forest Map of Great Barrier Forest Park') that was cited as a source for Scofield's map. However, a search for this report (in the libraries of DoC, Scion, MAF, and Landcare) was unsuccessful.

Scofield's map was rescaled on the assumption that the area inside his presumed 400 m contour line is the same as that within this contour line in the LINZ 2005 1:50 000 topographic dataset (estimated, using Quantum GIS, to be 121.5 ha). With this assumption, the distance marked 1 km on Scofield's scale bar was actually 0.544 km, and the current study area lies almost wholly inside Scofield's (see heavy dashed line in Figure 2). Also, the total area within strata 11, 21, and 23 is 44.6 ha, which is close to the 40 ha claimed by Scofield, though the areas of the individual strata are quite different (Table 2). Seven of Scofield's 10 transects lie inside the current study area (the exceptions are transects d [in stratum 11], f [stratum 21], and j [stratum 23]). A recalculation of Scofield's population estimate using the adjusted stratum areas of Table 2, and correcting some minor calculation errors (see Appendix 1), produced an adjusted estimate of 2780 breeders (Table 2).

This 'adjusted' estimate is for the area inside Scofield's assumed 400 m contour. The estimated number of breeders within the current study area (referred to in Table 2 as the 'restricted' estimate) is 1598 [this was calculated by multiplying, for each stratum, Scofield's estimated burrow density (corrected following Appendix 1) by the area of the part of the stratum that was inside the current study area.]. This restricted estimate must be treated as much less certain than is implied by the estimated standard errors because (A), there is great uncertainty about the correct scaling of Scofield's map, and (B), it is unclear whether it is appropriate to assume that Scofield's burrow densities (calculated from transects throughout his strata) are correct for the parts of the strata inside the current study area.

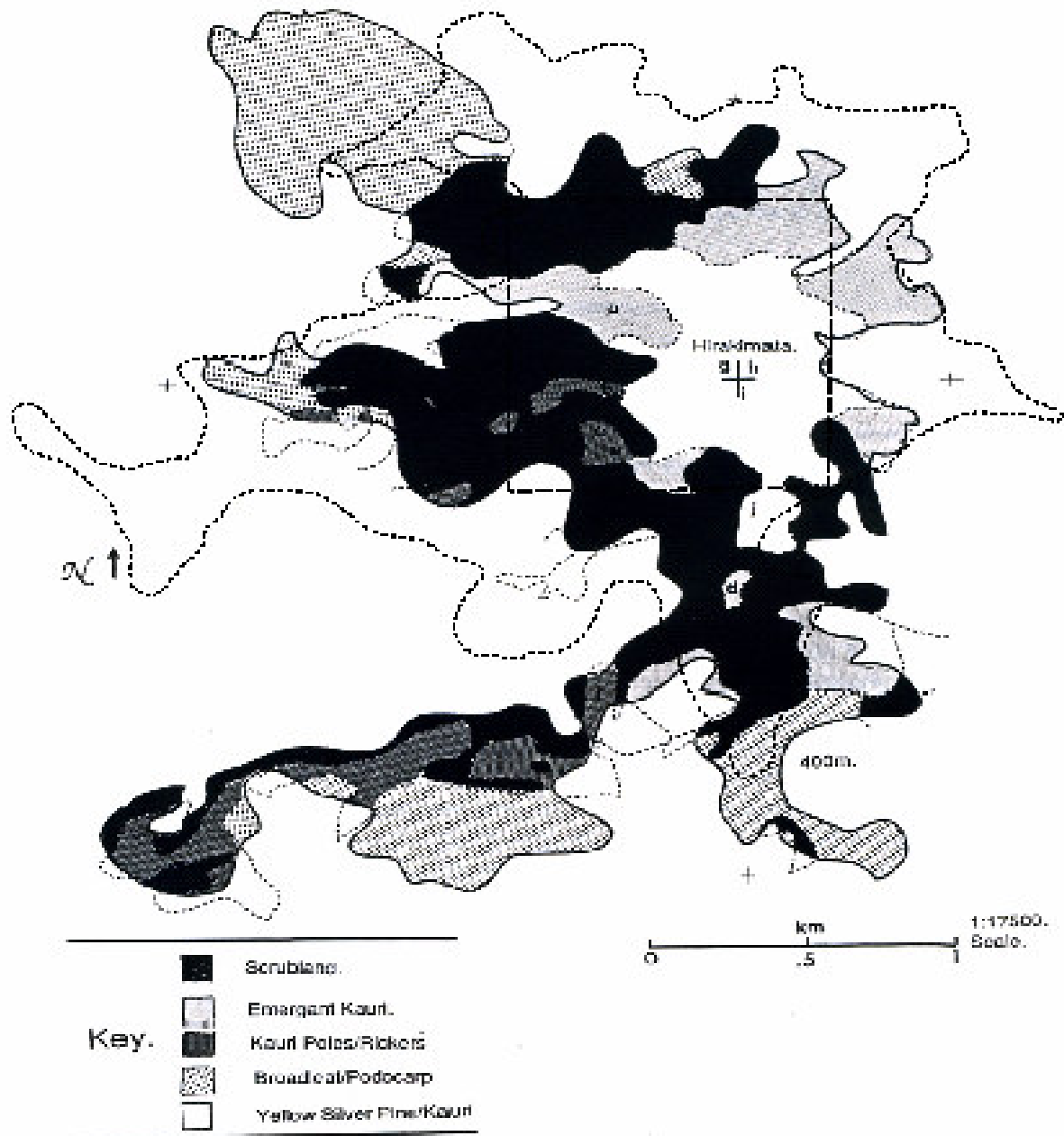


Figure 2: The area adjacent to Mt Hobson/Hirakimata associated with the black petrel population estimate of Scofield (1989). This is a reproduction of his figure 2, showing his assumed 400 m contour line (solid line bounding shaded areas), strata (shaded areas), and transects (letters, a-j), and two added lines: the official 400 m line (heavy dotted line, from the LINZ 2005 1:50 000 topographic dataset) and the boundary of the current study area (heavy dashed line) as shown in Figure 1. The two additional lines were added after the map scale was adjusted so that the area inside the assumed 400 m contour was equal to that inside the official 400 m contour (121.5 ha); with this adjustment Scofield's scale bar represents 0.544 km, rather than 1 km.



**Table 2: Original, adjusted, and restricted stratum areas and breeding population estimates for black petrel near Mt Hobson. Original values are from table 2 of Scofield (1989). The adjusted stratum areas were calculated from a digitised and rescaled version of Scofield’s fig. 2 (Figure 2); the adjusted population estimates for strata 11, 21, and 23 used these adjusted areas and corrected burrow density estimates (see Appendix 1). For each stratum, the restricted estimates apply to the part of that stratum that lies within the current study area (bounded by the heavy dashed line in Figure 2).**

Stratum <sup>1</sup>	Vegetation type	Stratum area (ha)			Number of breeders (s.e.s)		
		Orig.	Adj.	Restr.	Orig.	Adj.	Restr.
10	Scrubland	–	45.5	12.2	–	–	–
11	Emergent kauri	10	15.1	6.7	200 (400)	604 (604)	268 (268)
21	Kauri poles/rickers	10	13.2	1.2	500 (172)	660 (132)	60 (12)
22	Broadleaf/podocarp	–	31.4	0.0	48 (–)	48 (–)	0 (0)
23	Yellow silver pine/kauri	20	16.3	14.1	1800 (172)	1468 (164)	1270 (142)
All			121.5	34.2	2600 (1500)	2780 (640)	1598 (304)

<sup>1</sup>These stratum numbers were referred to by Scofield (1989) as Forest Service codes

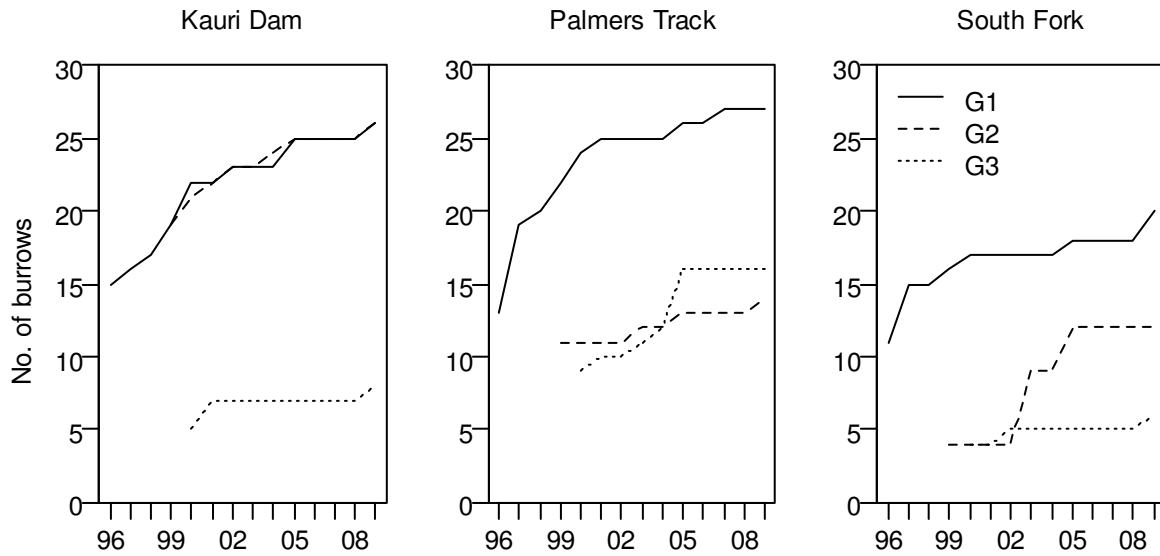
### 2.2.3 Census grid counts

There have been two approaches to abundance estimation in the present study. The first approach used annual counts of burrows in 40 m x 40 m census grids within the study area. These census grids were not randomly positioned. The first three were established in 1996 ‘in areas that had an historical presence of black petrels, different strata, vegetation types and topography and that were near known launch sites’ (Bell et al. 2007). A second grid was added in each area in 1999, and a third grid in 2000. In each year, each known burrow in the grids was classified as breeding, non-breeding, or empty. The burrow counts (listed in full in Appendix 2) show strong spatial heterogeneity (i.e., counts are consistently higher in some grids than in others) and a strong upward trend (Figure 3).

In interpreting this upward trend we need to be aware that the burrow counts should not be considered as complete, or as independent between years. They are incomplete because the terrain and dense vegetation make it quite possible to miss some burrows; they are not independent because once a burrow was found its position was marked, so it would be counted in all succeeding years. A four-level classification of burrows (Table 3) was devised to help in the interpretation of the upward trend. Between 2000 and 2009, the number of census-grid burrows increased by 38, or 32% (Table 4). Of these additional burrows, 70% were coded as 3 or 4, so we know they weren’t overlooked in previous years. Thus the increase in burrows between 2000 and 2009 probably lies between 22% (70% of 32%) and 32%, which corresponds to an average increase of 2.2%–3.1% per year. Further, because there has been no trend in the percentage of these burrows that have been used for breeding (Table 4), we can estimate that the breeding population within the census grids has increased at an average rate of between 2.2% and 3.1% per year. For the former estimate, we are assuming that all the burrows that were found after 2000 but designated as established (i.e., code 2) were already established in 2000 but not seen in that year; for the latter estimate we assume that all these burrows were created after 2000.

**Table 3: Description of codes assigned to burrows observed in census grids. Burrows with code 4 were examined every year after they were first seen, but were not included in burrow counts until they were deemed sufficiently developed to be suitable for breeding.**

Code	Seen in first year grid surveyed?	Burrow status when first seen	Percentage of burrows
1	yes	new or established	60
2	no	established (likely to have existed in previous years)	20
3	no	new (unlikely to have existed in previous years)	12
4	yes	potential (new burrow, not yet sufficiently developed to be suitable for breeding)	8



**Figure 3: Counts of burrows between 1996 and 2009 in nine census grids, with three grids (G1, G2, G3) in each of three locations: Kauri Dam, Palmers Track, and South Fork.**

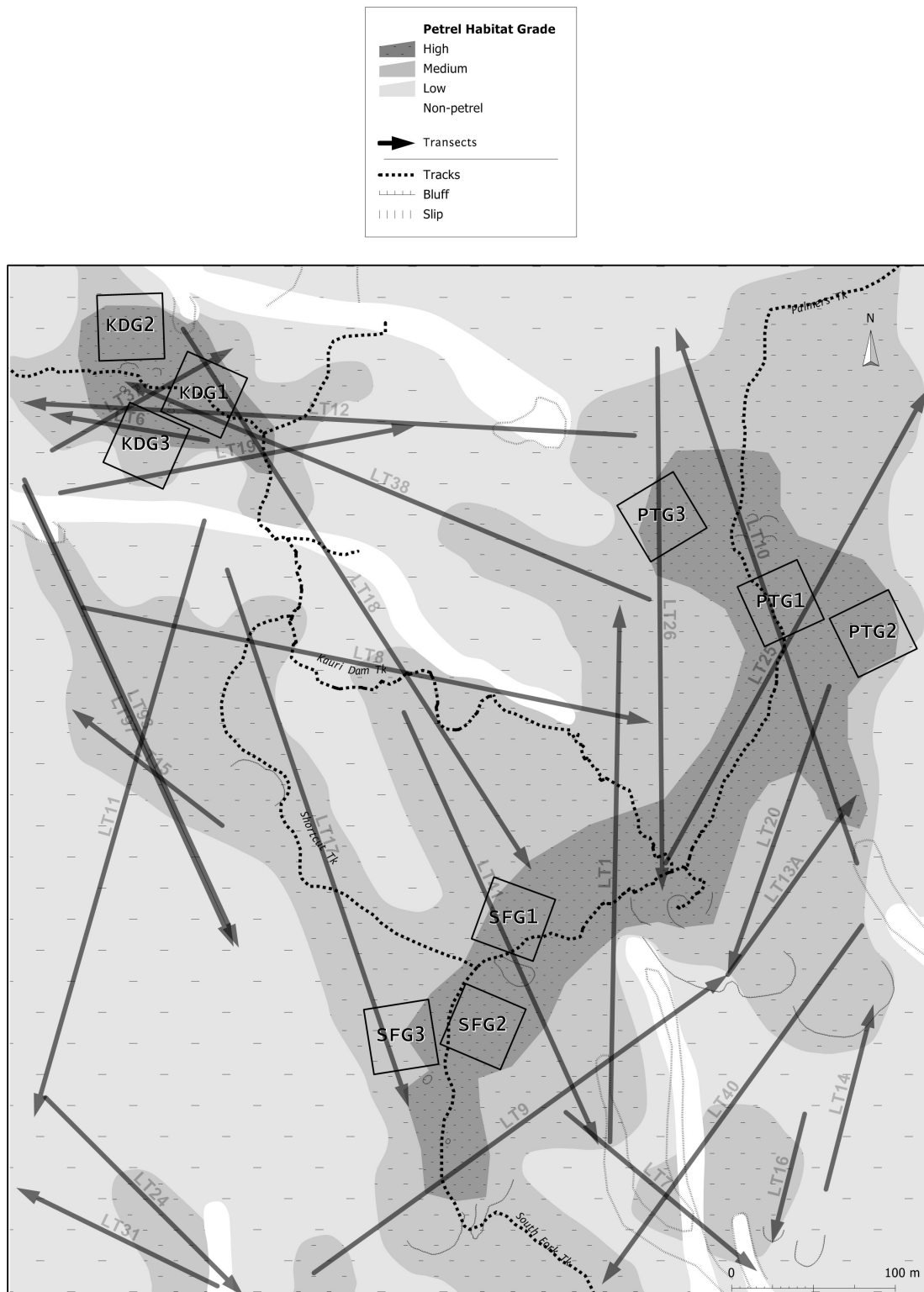
**Table 4: Total number of burrows in all nine census grids from 2000, and the percentage of them that were used for breeding.**

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
All burrows	117	122	125	132	134	147	147	148	148	155
Percentage breeding	69.2	62.3	64.8	58.3	58.2	55.8	63.3	64.9	57.4	61.9

## 2.2.4 Transect counts

The second approach to abundance estimation in the current study was applied only in 2005. In that year, 26 transects, of width 4 m and length up to 400 m, were randomly located by choosing a random starting point and direction within the study area (Figure 4). From the 112 breeding burrows counted within these transects, together with a stratification of both the transects and the study area into two habitat grades (optimum and poor), an estimate of 3551 breeders (s.e. 555) was produced for the study area (Bell et al. 2007). Bell et al. (2009) subsequently re-stratified into four habitat grades (high, medium, low, and non-petrel) and revised this estimate to 2595 breeders (s.e. 288).

A drawback to these two analyses is that the stratification procedure was inconsistent. For example, Bell et al. (2009) used information about all known burrows (from transects, census grids, and others) to classify 7 ha of the 35 ha study area as high grade habitat (containing more than 100 burrows/ha). They also classified 5 of the 26 transects as high grade habitat (again because they contained more than 100 burrows/ha). They then calculated the number of breeding pairs in the high-grade stratum by (i) dividing the number of breeding burrows in each high-grade transect by the transect area, (ii) averaging the resulting densities across the 5 high-grade transects, and (iii) multiplying by the stratum area (7 ha). What makes this procedure inconsistent is that most transects crossed two or more strata. Thus, the burrow densities calculated at step (i) were derived from burrows in several strata, and yet they were scaled up at step (iii) by the area of just one stratum.



**Figure 4:** A new stratification of the study area into four habitat grades (high, medium, low, and non-petrel). Also shown are the 26 random transects (LT1–26) and 9 census grids (PTG1-3, SFG1-3, KDG1-3).

The transect data were reanalysed using a new approach that avoided this inconsistency, and used a new stratification of the study area (Figure 4) which substantially changed the stratum areas (Table 5). The new stratification used all known data from the area including two new transects (as well as the existing 26), aerial photographs (to confirm position and size of slips, streams, cliffs and rocks and identify vegetation and terrain (i.e., slope)) and census grids. These data were entered into

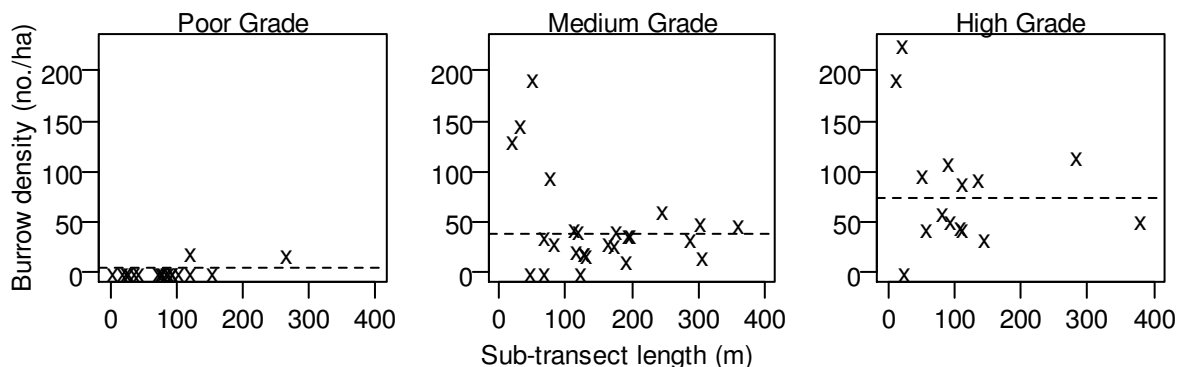
Manifold™ (GIS mapping software) which produced the habitat boundaries and calculated the area of each habitat. This altered the level of both high and medium density petrel areas as well as adding more non-petrel habitat to the 35-ha study area as it was apparent that that optimum habitat was restricted to the ridges and steep slopes of the summit area and that there had been a previous underestimate of low quality habitat. Each transect was subdivided, using the new stratum boundaries, into sub-transects, each of which lay wholly within a single stratum (note that some sub-transects consisted of two or more spatially separated parts). We denote the length of the  $i$ th sub-transect in stratum  $s$  by  $L_{is}$ , and the associated number of breeding burrows by  $n_{is}$  (see Appendix 2 for a complete listing of the sub-transect data, including counts of non-breeding and empty burrows, which are not analysed here). Sub-transect breeding burrow densities (no./ha) were calculated as  $d_{is} = 10^4 n_{is} / (4L_{is})$  (recall that the transect widths were all 4 m, and  $1 \text{ ha} = 10^4 \text{ m}^2$ ). As might be expected, the within-stratum variability in these densities decreased with increasing sub-transect length (Figure 5). Because of this, it was assumed that the sampling variance of the sub-transect burrow counts was proportional to sub-transect length, which means that the mean burrow density for each stratum should be calculated as a weighted mean  $d_s = (\sum_i d_{is} L_{is}) / (\sum_i L_{is})$  and its s.e. as

$$\text{s.e.}(d_s) = \frac{\left[ \sum_i (d_{is} L_{is}^{0.5} - (\sum_j d_{js} L_{js}^{0.5}) / m_s)^2 / (m_s - 1) \right]^{0.5}}{(\sum_i L_i)^{0.5}}$$

where  $m_s$  is the number of sub-transects in stratum  $s$ . These densities were doubled (to convert from burrows to birds) and multiplied by stratum area to get estimated population sizes by stratum (Table 6).

**Table 5: Comparison between two stratifications of the study area.**

Stratum	Burrow density (no./ha)	Stratum area (ha)	
		table 7, Bell et al. (2009)	New (Figure 4)
High grade	$\geq 100$	7	4.67
Medium grade	50–99	17	15.3
Poor	1–49	10	13.6
Non-petrel habitat	0	1	1.75



**Figure 5: Sub-transect densities of breeding burrows plotted by habitat stratum. Mean densities for each stratum are shown by broken horizontal lines.**

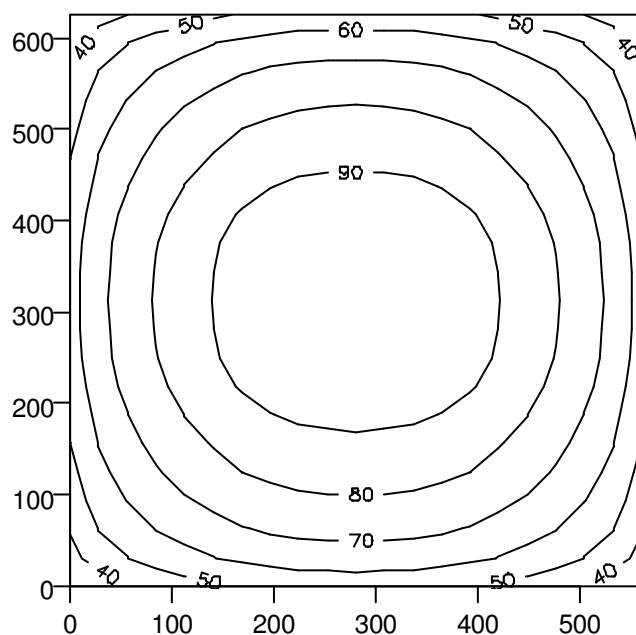
**Table 6: Estimated burrow densities and population numbers for breeding birds by stratum (with s.e.s in parentheses), using the new stratification of Figure 4.**

Stratum	Burrow density (no./ha)	Population number
Poor grade	4.9 (2.2)	134 (61)
Medium grade	37.6 (5.4)	1150 (166)
High grade	72.8 (11.0)	680 (103)
All	–	1964 (204)

The new estimate of 1964 breeders in 2005 (Table 6) is 23% higher than the comparable estimate based on the data of Scofield (1989) (1598 breeders – see Table 2). If we assume that the latter estimate is for 1988 (it was based on observations in November 1987, October 1988, and April 1989) this implies an average population increase of 1.2% per year  $[(1964/1598)^{1/17} = 1.012]$ .

There are three factors that affect the estimates of Table 6. First, as illustrated in the above discussion of the census grids, some burrows may have been overlooked, and this would cause an under-estimate in densities and population numbers. Second, the procedure for generating random transects suffers from an edge effect, in that burrows near the edges of the study area are less likely to lie within a transect (Figure 6). It is difficult to quantify the extent of the biases caused by these two factors, but it does not seem unreasonable to assume their combined effect is relatively small. The third factor is uncertainty in the stratification, which is not accounted for in the calculation of the s.e.s in Table 6. This will cause the s.e.s to be under-estimated. Considering how much the stratum areas changed when revised (see Table 5), this under-estimation may be substantial.

It would be advisable, when applying the random transect method to other colonies to use shorter transects to reduce the bias caused by edge effects (see Figure A3.2). However, future surveys in the present study area should retain the 400 m transect length used here to ensure comparability with the existing survey.



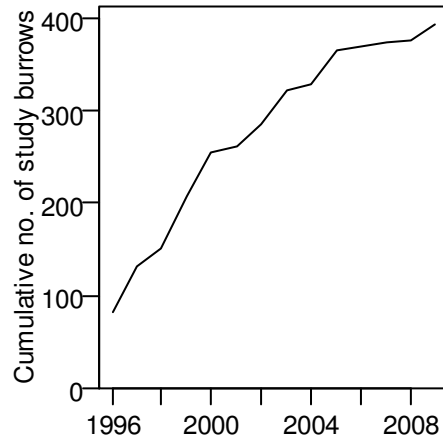
**Figure 6: Contours of the probability that a point in the study area will lie within a random transect, expressed as a percentage of the maximum probability (which occurs at the centre of the study area). Values on the x- and y-axes are distances (in m) from the south-west corner of the study area. (Details of the calculation of these contours are given in Appendix 3.)**

### 2.2.5 Counts from South America

Also of interest is a study by Spear et al. (2005) who surveyed 14 277 km<sup>2</sup> of ocean from the shoreline to 1500 km off the coast from Chile north to Panama in a series of 15 cruises from 1980 to 1995. They found that black petrel were most abundant along the coasts of Ecuador and Peru and, from observations of only 159 birds, estimated a population of 38 000 birds (95% confidence interval, 28 000 – 50 000) during the austral autumn.

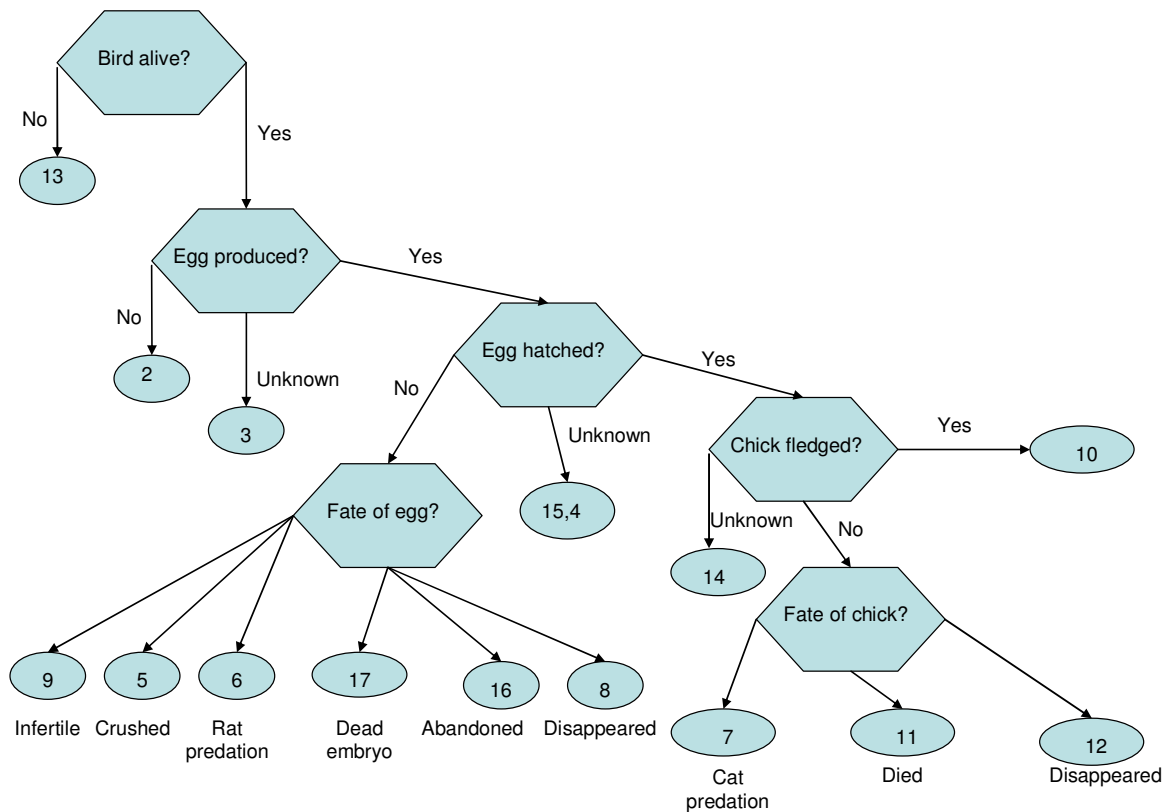
### 2.3 Mark-recapture data

During each visit to the study area (see Table 1 for timing of visits), a series of study burrows was inspected, often several times, all unbanded birds encountered were banded, and the location and status of each bird encountered was recorded. The study burrows, whose number has increased by almost 400% since 1996 (Figure 7), fall into two groups: those near tracks, and those in census grids. Currently it takes about 3 days to inspect all study burrows.



**Figure 7: Cumulative number of study burrows.**

A great amount of detail in the mark-recapture data set has been ignored here because, although it would be useful for more behaviour-focussed research, it did not seem likely to contribute to the aims of the present analysis. Adult survival does not seem to be sex-specific (Bell et al. 2009) so sex (which is known with some confidence for only about a third of breeding birds) was ignored. Information about which birds breed together, and in which burrow, was also ignored. Finally, the data were annualised so that for each banded bird a single code was used to represent its status in each season since it was banded. A code of 0 indicated the bird was not seen; 1 indicated that the bird was a fledged chick (this code was used only in the season of banding); and codes 2–17 described the breeding status and outcome for adult birds (Figure 8).



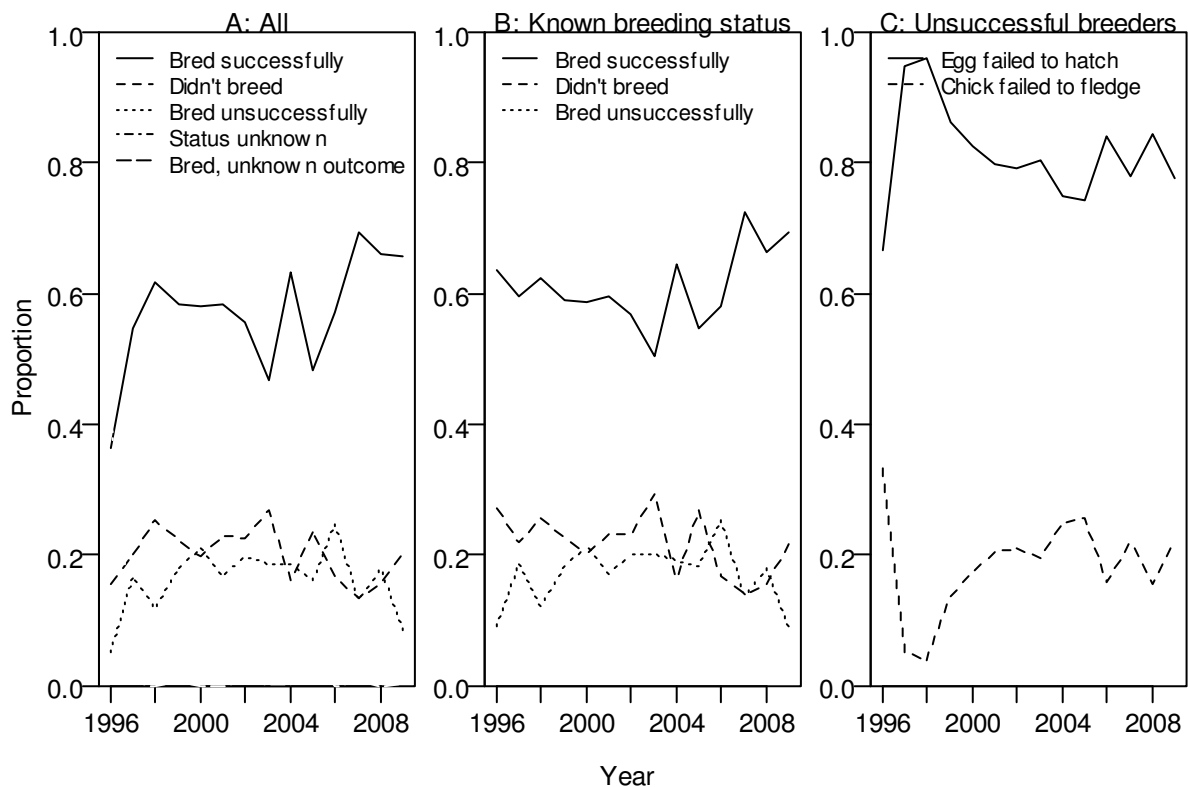
**Figure 8: Flow diagram illustrating the codes used to designate the breeding status and outcome for each banded adult bird in each season that it was seen. Other codes used were 0 (not seen) and 1 (chick). Codes 4 and 15 have the same meaning.**

In each season about 60% of adults with known breeding status bred successfully, 18% bred unsuccessfully, and 22% didn't breed (Figure 9B). The egg hatched in only about 20% of instances of unsuccessful breeding (Figure 9C). None of the nine identified causes of breeding failure was dominant (Figure 10).

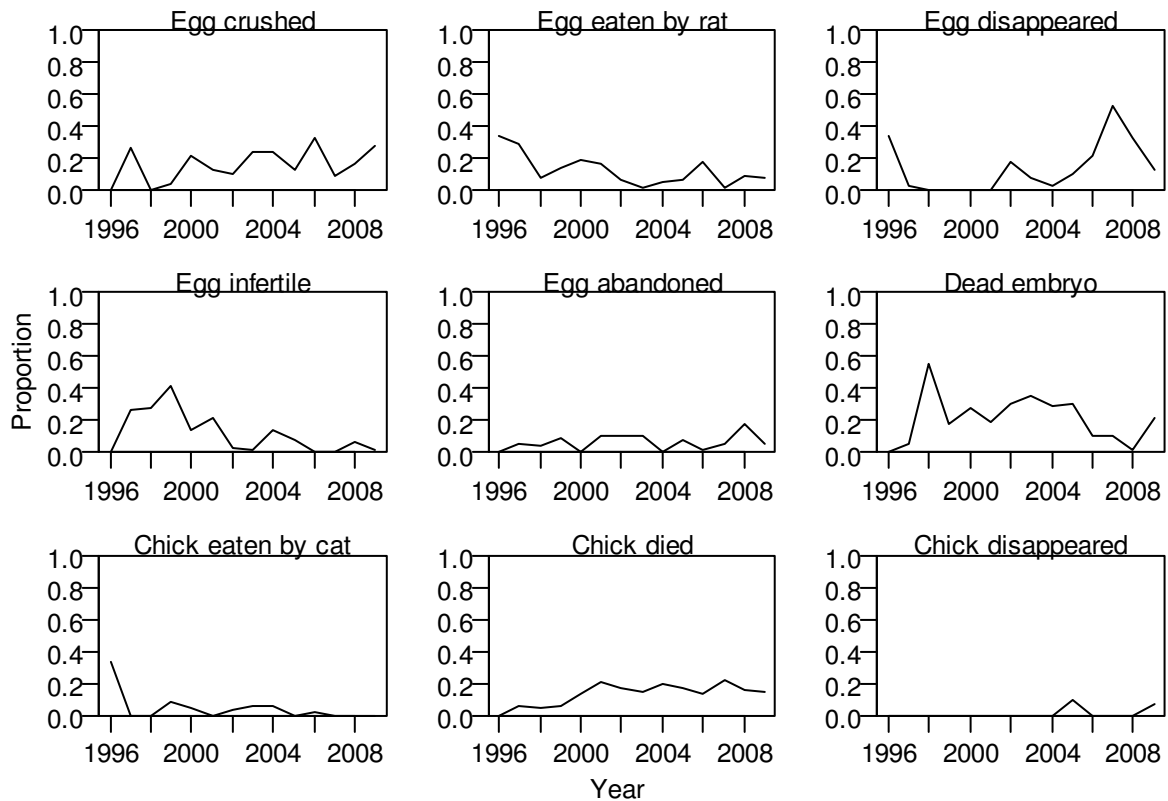
The data set available for analysis included 3324 banded birds, 98% of which were banded during the study period (the rest were banded before the study period but have been resighted during it), and 89% of which were banded in study burrows (a few birds were banded on the surface or in non-study burrows) (Table 7). Because resighting probabilities for non-study birds were extremely low (Figure 11) these birds have been excluded from any further analysis.

**Table 7: Classification of the 3324 birds in the mark-recapture data set by type (study/non-study) and date and age of banding. 'Non-study' birds are those that were banded on the surface or in non-study burrows.**

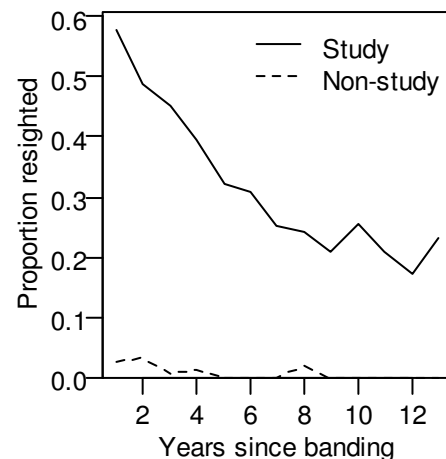
Type	Banded before study		Banded in study	
	Banded as chick	Banded as adult	Banded as chick	Banded as adult
Study	11	41	1583	1329
Non-study	6	16	86	252



**Figure 9: Breeding status or outcome of live adults by year for: A, all birds; B, all birds for which breeding status was known; and C, birds which bred unsuccessfully.**



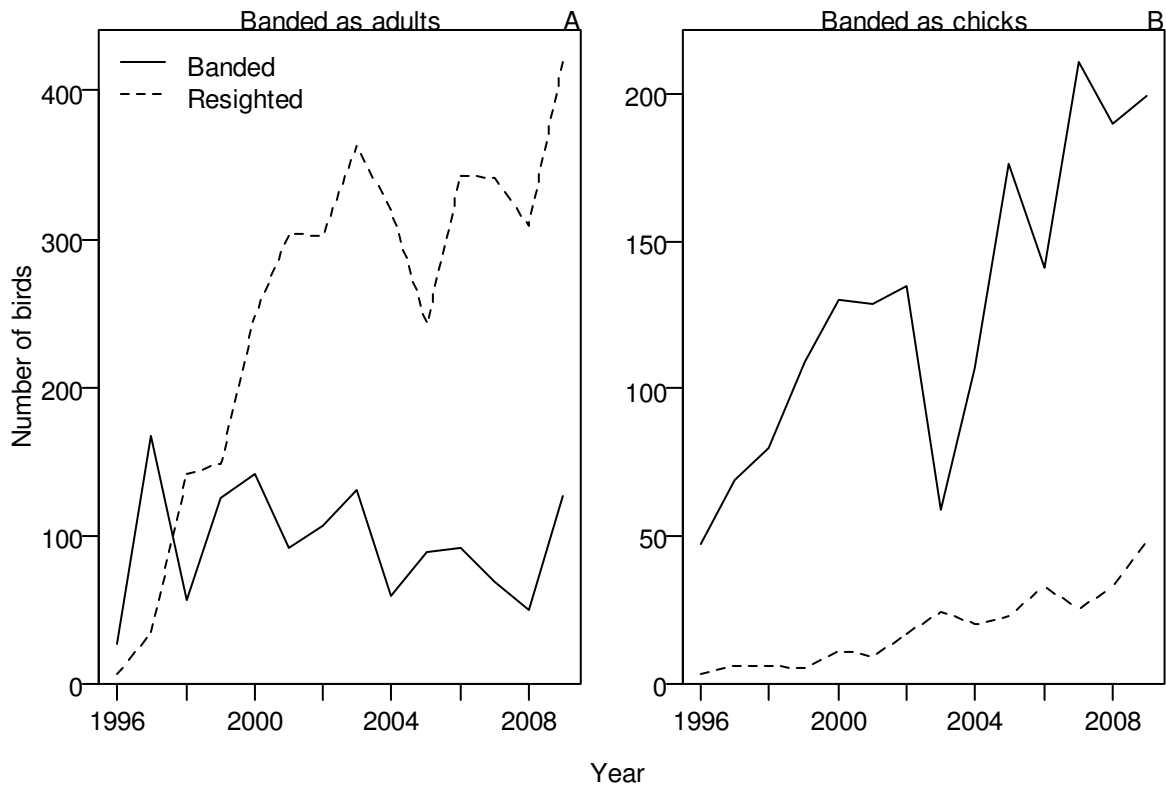
**Figure 10: Causes of breeding failure where this was known. The top six panels concern eggs that didn't hatch; the bottom three panels concern chicks that hatched but did not fledge.**



**Figure 11: Proportion of banded birds seen by years since banding for study ('s') and non-study ('n') birds. Only birds banded as adults since 1996 are included in this plot.**

An average of 95 adults has been banded each season since 1996 and because of this the number of these birds resighted each year has grown steadily, reaching 420 in 2008–09 (Figure 12A). The number of chicks banded each year has also grown substantially (Figure 12B), mostly (presumably) because of the increase in number of study burrows.





**Figure 12: Number of birds banded and resighted by year: A, birds banded as adults; B, birds banded as chicks. Non-study birds were excluded from this plot.**

### 2.3.1 Birds banded before 1995–96

Only limited use can be made of the data associated with the 74 birds that were banded before 1995–96. Additional information would be needed before these data could be used to estimate survival in years before 1995–96. This would need to include numbers of birds banded before 1995–96 but resighted in the study period, and also precise banding locations for all birds (because, as shown by Figure 11, resighting probabilities are strongly dependent on whether birds were banded in a study burrow). Because of these limitations, these birds were all treated as if they were banded in the season of their first resighting during the study period.

### 2.3.2 Observations of dead birds

Eight banded study birds have been found dead (Table 8). Of these, only five were found during study observations.

**Table 8: Summary of information on the 8 study birds that were found dead after banding.**

A, Banded as a chick			
Died before seen breeding?	Number	Age at death	
Y	4	1, 1, 1, 3	
N	1	21	
B, Banded as an adult			
Number	Years to death after banding		
3	1, 4, 5		

### 2.3.3 First breeding for known-age birds

Of the almost 1700 birds banded as chicks, only 54 have since been observed breeding, all of which were study birds. No bird was observed breeding before age 4, and the most common age when first observed breeding was 6 y (Table 9). The maximum age at first breeding appears to be about 10 y (we exclude observations of birds banded before 1990, since these birds could well have bred before the sampling programme started in 1996). Almost all of the birds not yet seen breeding (94% = 1540/1632) were study birds.

It appears that the great majority of chicks in the study area either do not survive to breed or breed outside the study area. Note that any chick banded between 1996 and 1999 that was going to breed in the study area should have started breeding by now, but only 5% (17/328) of these have been observed breeding.

**Table 9: Tabulation, for all study birds banded as chicks before 2005, of the age they were first observed breeding, and the number not yet observed breeding, by year of banding (birds that were observed dead (code=13) or with uncertain breeding status (code=3) before being seen breeding were excluded from this table) ‘-’ = impossible combinations.**

Year banded	Age when first observed breeding											All	Not seen breeding
	4	5	6	7	8	9	10	11	12	13	15		
1986	-	-	-	-	-	-	0	0	1	0	1	2	0
1987	-	-	-	-	-	0	0	0	0	1	0	1	1
1988	-	-	-	-	1	1	0	0	1	0	0	3	0
1989	-	-	-	0	1	0	0	1	0	0	0	2	0
1990	-	-	0	1	0	0	0	0	0	0	0	1	0
1992	0	1	0	0	0	0	0	0	0	0	0	1	0
1996	0	1	1	0	0	0	0	0	0	0	-	2	45
1997	0	1	0	1	2	1	0	0	0	-	-	5	64
1998	0	1	2	0	0	0	0	0	-	-	-	3	74
1999	0	0	2	2	2	0	1	-	-	-	-	7	100
2000	0	2	3	3	2	2	-	-	-	-	-	12	115
2001	0	1	0	0	1	-	-	-	-	-	-	2	126
2002	0	0	4	2	-	-	-	-	-	-	-	6	129
2003	0	1	1	-	-	-	-	-	-	-	-	2	57
2004	1	1	-	-	-	-	-	-	-	-	-	2	105
All	1	9	13	9	9	4	1	1	2	1	1	51	816

### 2.3.4 Observations of pre-breeders

At first resighting, about 70% (53/73) of birds banded as chicks were not breeding (Table 10). Since this percentage is much higher than the percentage of non-breeders in birds banded as adults (Figure 9) it seems likely that at least some juvenile birds returning to the colony go through a pre-breeder stage of one or more years. From the banding data the average duration of this pre-breeding period was just less than 1 year, and never exceeded 4 years (Table 11).

**Table 10: Age and status at first resighting for birds banded as chicks and since resighted alive.**

Age at first resighting	Status		
	Non-breeder	Unknown	Breeder
3		1	0
4		14	4
5		19	1
6		9	0
7		8	0
8		0	0
9		1	0
10		1	0
All		53	5

**Table 11: Number of years between first resighting and first resighting as a breeder for the 41 birds that were banded as chicks and subsequently seen breeding.**

Age at 1st resighting	No. of years before seen breeding				
	0	1	2	3	4
3	0	0	0	1	0
4	1	3	1	1	0
5	5	5	3	2	0
6	6	2	1	0	1
7	2	1	0	0	0
8	3	0	0	0	0
9	3	0	0	0	0
All	20	11	5	4	1

Since less than half of the birds banded as adults were known to be breeders when banded (Table 12), it seems quite likely that some of these were banded as pre-breeders.

**Table 12: State of bird at banding for those birds banded as adults.**

Breeder	Non-breeder	Unknown
774	646	218

### 2.3.5 Disturbance of breeders?

Bell et al. (2009) noted a gradual decline in the annual percentage of burrows that are used for breeding (see light solid line in Figure 13) and postulated that this might have been an unfortunate consequence of study observations. The disturbance caused by the handling of breeding birds and the digging of observation hatches in burrows could possibly be causing breeding birds to move to non-study burrows. A re-analysis of the revised and updated data showed no evidence of such an effect

The current data set differs somewhat from that plotted by Bell et al. (2009) and no longer shows a significant trend in the percentage of burrows used for breeding (see heavy lines in Figure 13). Moreover, a more detailed examination of the data showed that this plot could be misleading. Since any effect of disturbance is presumably cumulative, it seemed sensible to re-plot the data with the x-variable changed from year of observation to number of years a burrow has been a study burrow. This produced a strong upward trend in the percentage of burrows used for breeding (Figure 14A) which, if taken at face value, would suggest that the more a burrow is disturbed, the more likely it is to be used for breeding. However, a third way of plotting the data showed an unsuspected heterogeneity. There were some years (e.g., 1996) in which a high proportion of newly-discovered burrows were of high quality (i.e., likely to be used for breeding in successive years), and other years (e.g., 2001) in which they were of low quality (Figure 14B). This heterogeneity biases Figure 14A because points on the right side of the plot derive only from burrows first observed in the early years of the study, whereas those on the left side derive from most burrows. To avoid this bias, the data were replotted in the same format as in Figure 14A, but with the burrows grouped by year of first observation. In this new plot, only one of the plotted lines (that for burrows seen in 1996) showed a significant trend, and that trend was slight and upward (Figure 15). Thus, we find no evidence that repeated disturbance of breeders tends to make them abandon study burrows.

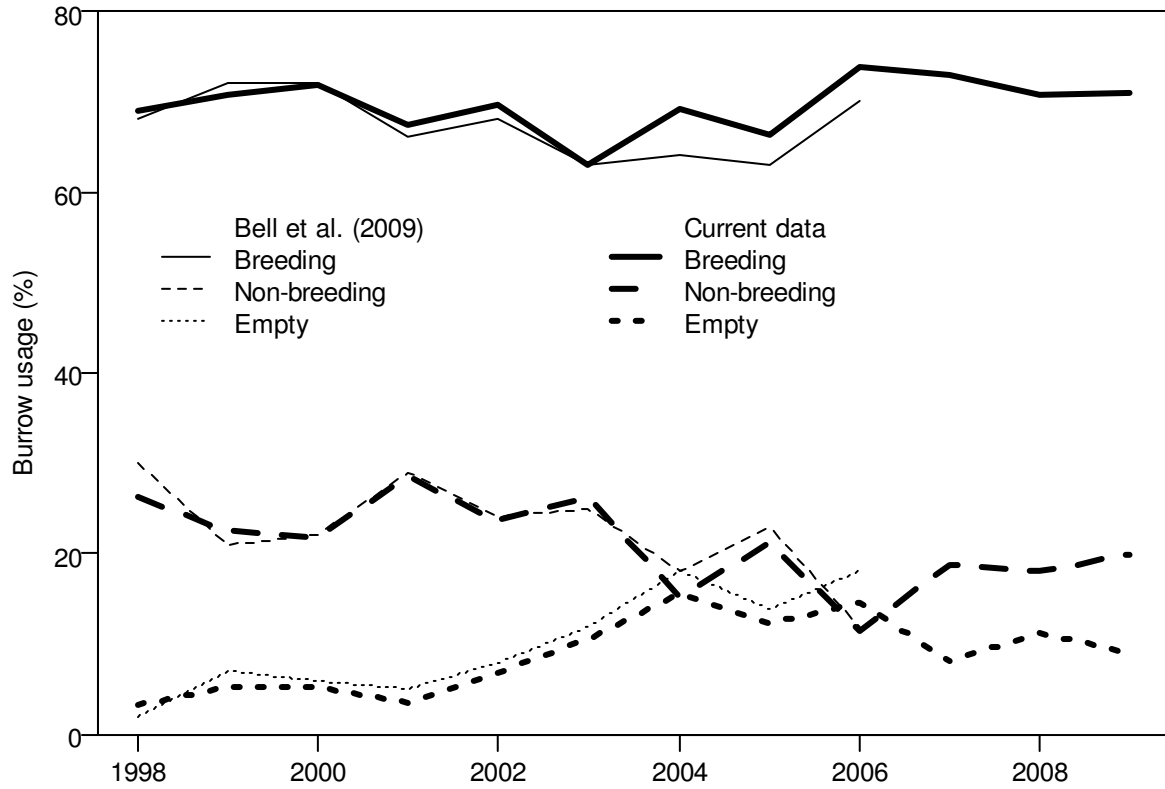


Figure 13: Estimated burrow use by year since 1998 from current data (heavy lines) and that of Bell et al. (2009) (light lines; see their table 2 and figure 5).

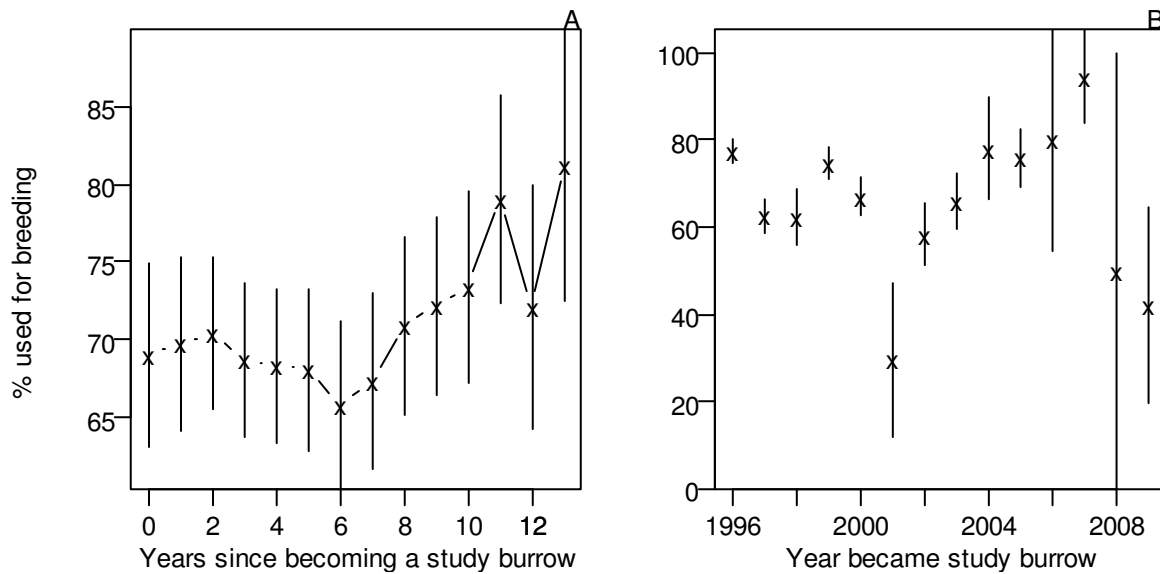
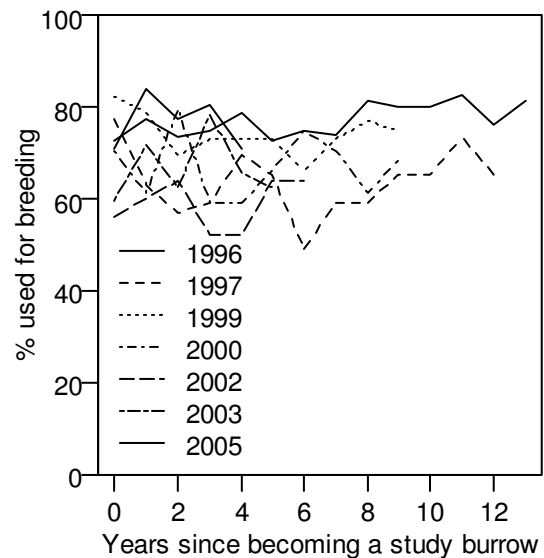


Figure 14: Percentage of burrows used for breeding plotted against A, the number of years since becoming a study burrow; and B, the year in which the burrow became a study burrow. Vertical bars are approximate 95% confidence intervals.

**Figure 15: Percentage of burrows used for breeding plotted against the number of years since becoming a study burrow. Each line corresponds to a group of burrows that first became a study burrow in the same year; lines are plotted only for years in which at least 20 new study burrows were discovered.**



### 3. Modelling results

In order to illustrate important features of the available data, and of the inferences that can be drawn from these data, we present results from a series of models of increasing complexity. All were built and analysed using NIWA's modelling software, SeaBird (Francis et al. 2008) and input files for the most important models are given in Appendix 4. The models fall into the following four groups, according to the data used:

1. Adult mark-recapture data (Section 3.1)
2. Juvenile mark-recapture data (Section 3.2)
3. All mark-recapture data (Section 3.3)
4. Mark-recapture and abundance data (Section 3.4)

All these models assumed the same order of processes within each year:

- Recruitment (chicks are added to the model partition)
- Observations (birds are banded or resighted)
- Mortality (some birds die)
- Transition (birds move between classes in the partition)

and no attempt was made to distinguish between 'natural' and fishery-induced mortality. Observations of dead birds were ignored because they are so rare and nearly half of them were not made as part of the study resighting effort (see above).

Up to four types of parameters were estimated in these models (Table 13).

**Table 13: Details of the four types of parameters that were estimated in the SeaBird models.**

Type	Varies from	Description
Survival	year to year	Proportion of birds surviving in each year <sup>1,2</sup>
Resighting	Yes	Proportion of banded birds that are seen
Transition	Not initially <sup>3</sup>	Proportion of birds in one state (e.g., non-breeder) in one year that will change to another state (e.g., breeder) in the next year
Abundance <sup>4</sup>	–	Initial population size

<sup>1</sup>Survival rates labelled 1996, say, refer to the period between observations in 1996 (the 1995–96 season) and 1997 (the 1996–97 season)

<sup>2</sup>Survival rates for 2008 were always assumed equal to those for 2007 (since survival and resighting rates for the last year of mark-recapture data are always confounded)

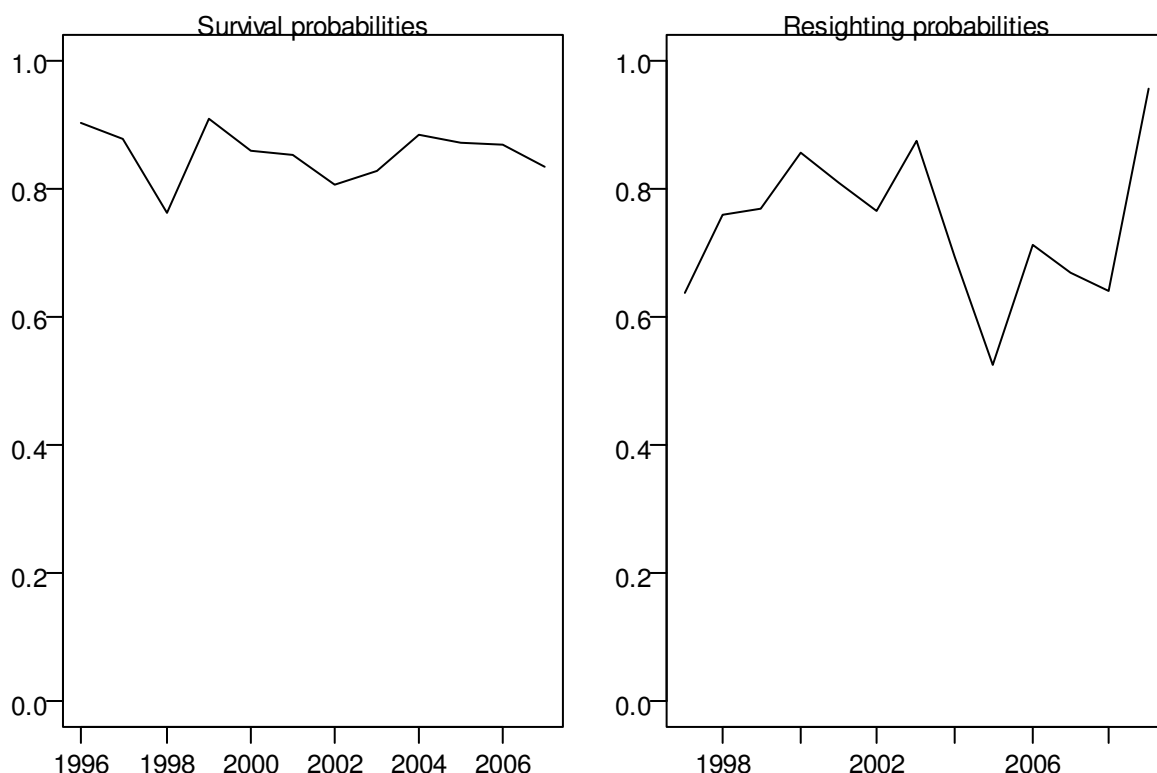
<sup>3</sup>Year-to-year variation in these parameters was investigated only in the final models

<sup>4</sup>Estimated only in models using abundance data

### 3.1 Models for adult birds

In all adult models, data from birds banded as chicks were used just for the years after the first resighting as an adult (for these models that first resighting was treated as a banding observation).

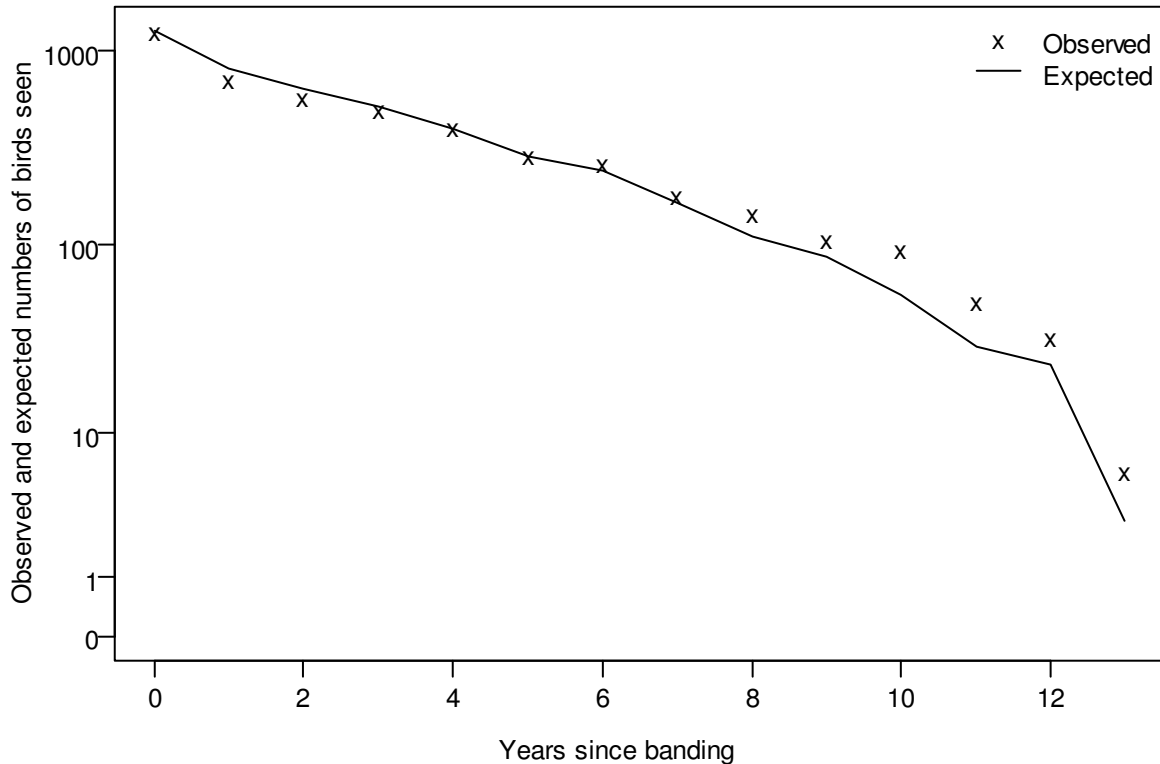
The first model, BPET2, simply analysed the presence or absence of banded birds each year. The status of each bird, at banding or resighting, was ignored, which means that no transition parameters were estimated. Estimated survival was about 0.86 (median), with no obvious trend; resighting probabilities varied widely from 0.53 to 0.96 (Figure 16).



**Figure 16: Survival and resighting probabilities estimated in model BPET2.**

To check for evidence of band loss, the observed and expected numbers of birds seen were plotted against the number of years since banding. If there is any substantial band loss then the expected numbers will tend to exceed the observed numbers as the number of years since banding increases

(e.g., see figure 5 of Francis (2008)). The opposite pattern was seen with BPET2, with expected numbers being less than observed numbers after about 5 years following banding (Figure 17). This suggested that band loss was not a problem but that the model was ignoring some important structure in the data.



**Figure 17: Observed (‘x’) and expected (line) numbers of birds seen from model BPET2, plotted as a function of the number of years since banding.**

The next model, BPET4, categorised birds into three types each time they were observed: non-breeder (nbr), failed breeder (fbr), or successful breeder (sbr). A series of variants of this model was investigated to determine the best parameterisation, as determined by the Akaike Information Criterion, AIC (Akaike 1974). Each model had three or four transition parameters, two or three categories of resighting probability, and between one and three vectors of survival probabilities (Tables 14, 15). The aim was to determine A, did transition and resighting probabilities for breeders depend on whether their breeding was successful?; and B, to what extent survival probabilities depended on breeding status.

**Table 14: Parameters estimated in one or more of the variants of model BPET4. For a description of which parameters were estimated in each variant see Table 15.**

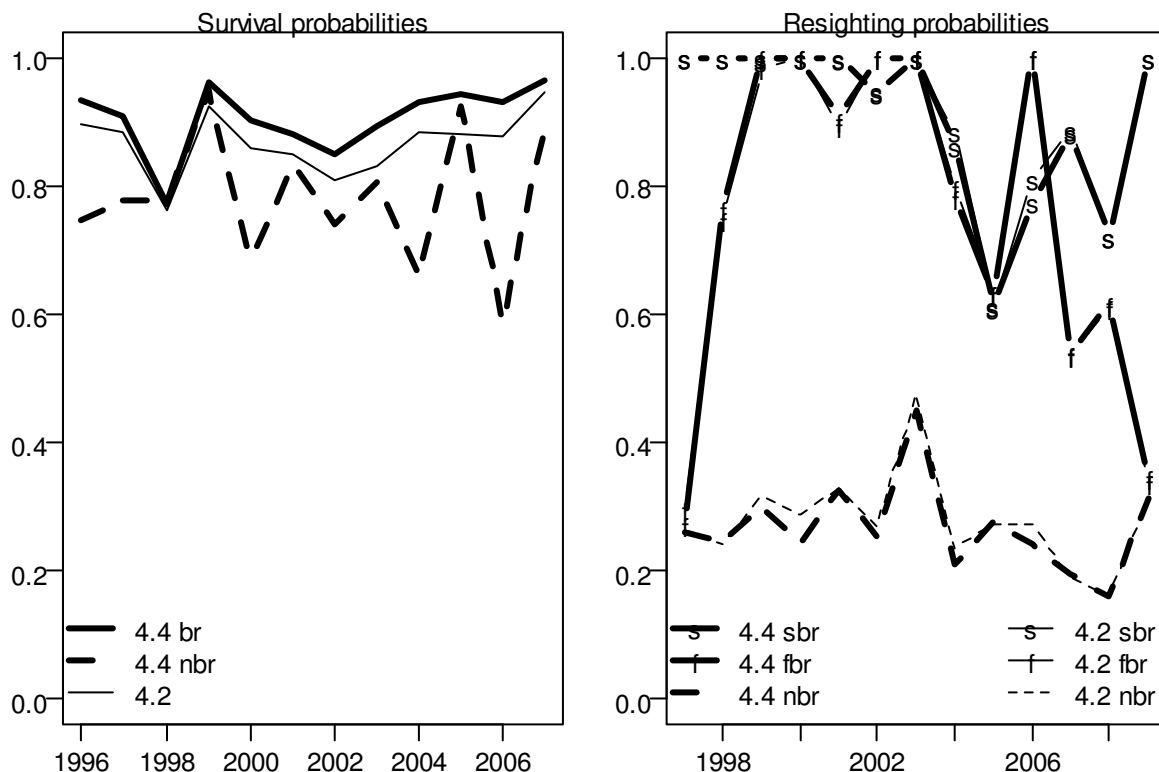
Parameter(s)	Description
Tnbrbr <sup>1</sup>	Probability a non-breeder in year y will breed in year y+1
Tbrbr	Probability a breeder in year y will breed in year y+1
Tfbrbr	Probability a failed breeder in year y will breed in year y+1
Tsbrbr	Probability a successful breeder in year y will breed in year y+1
Psuccess <sup>1</sup>	Probability a breeder will be successful
Prnbr <sup>1</sup> , Prbr, Prfbr, Prsbr	Resighting probabilities for non-breeders, breeders, failed breeders and successful breeders, respectively
nbrsurv, brsurv, fbrsurv, sbrsurv, surv	Survival probabilities for non-breeders, breeders, failed breeders, successful breeders, and all birds, respectively

<sup>1</sup>Parameters included in all variants of BPET4

The AIC values (Table 15) suggest three conclusions in decreasing order of strength: A, survival rates are clearly different for breeders and non-breeders (cf models 4.4 and 4.2, which differ by 60.4 in AIC); B, resighting probabilities for breeders depend on breeding success (cf models 4.4 and 4.3; AIC difference = 33.6); and C, survival rates for breeders do not depend on breeding success (cf models 4.4 and 4.5; AIC difference = 7.5). In the best model (BPET4.4), estimated survival rates for breeders were typically 0.10 higher (median value) for breeders than non-breeders and resighting probabilities were very high for successful breeders (median 1.00), lower for failed breeders (0.78) and much lower for non-breeders (0.25) (Figure 18). When, in model BPET4.2, survival was forced to be the same for breeders and non-breeders the estimated values were intermediate between the two values estimated in BPET4.4 but the resighting probabilities differed very little from those for BPET4.4 (compare heavy and light lines in Figure 18).

**Table 15: Description of the differences between some variants of model BPET4 in terms of parameterisation and AIC (Akaike Information Criterion). All variants used exactly the same data, differing only in parameterisation. The best model, BPET4.4, was that with the lowest AIC.**

Model	Transition		Resighting		Parameterisation		AIC – min(AIC)
	of breeders	of breeders	of breeders	of breeders	Survival	Number of parameters	
4		Tbrbr		Prbr	surv	41	102.5
4.1	Tfbrbr, Tsbrbr			Prbr	surv	42	93.8
4.2	Tfbrbr, Tsbrbr	Prfbr, Prsbr			surv	55	60.4
4.3	Tfbrbr, Tsbrbr			Prbr	nbrsurv, brsurv	54	33.6
4.4	Tfbrbr, Tsbrbr	Prfbr, Prsbr			nbrsurv, brsurv	67	0.0
4.5	Tfbrbr, Tsbrbr	Prfbr, Prsbr			nbrsurv, fbrsurv, sbrsurv	79	7.5
4.6		Tbrbr	Prfbr, Prsbr		nbrsurv, brsurv	66	12.0



**Figure 18: Survival and resighting probabilities estimated in models BPET4.4 (heavy lines) and BPET4.2 (light lines).**

Two other features of the resighting probabilities for model BPET4.4 stand out in Figure 18. First, the estimated probabilities of resighting failed breeders in the first and last years may be unreliable,



because they are much lower than in other years. Second, for all three categories of bird, resighting probabilities were typically lower in the second half of the study, particularly for breeders.

The estimated differences in resighting probabilities were not surprising, but those for survival were. We expect non-breeders to be less easily seen than breeders because they are not constrained by parental duties to remain in the colony. Also, since breeding failure is usually caused by non-hatching of the egg (see Figure 9C), failed breeders are less likely to be seen than successful breeders because most of them are not constrained to remain in the colony after early February (the typical hatching date). As to survival, since non-breeders do not have to dedicate resources to breeding we might expect that they would be in better condition than breeders at the end of the breeding season, and thus have higher rates of survival to the next season. But this is the opposite to what was estimated in both BPET4.4 and in the model of Fletcher et al. (2008) (see their figure R.2.21).

One hypothesis that could explain this unexpected result concerns that fact that neither our data status codes (see Figure 8) nor our models distinguish between pre-breeders and non-breeders, labelling both as non-breeders (where pre-breeders are defined, as in Section 2.3.4, as birds that have returned to the colony as adults but not yet bred). Under this hypothesis, non-breeders have similar or higher survival rates to breeders, but pre-breeders appear to have a lower survival rate because they have not yet chosen where to breed as adults. If they are sighted in the study area as pre-breeders but subsequently choose to breed outside that area they will appear, from the point of view of the model, to have died. Two alternative models were used to test this hypothesis: BPET4p and BPET4b.

Model BPET4p had four states: pre-breeder (pbr), non-breeder (nbr), failed breeder (fbr), and successful breeder (sbr), although the observations did not always distinguish between these states (Table 16). A comparison of six variants of this model (Table 17) did not support our hypothesis. In the best of these variants, BPET4p, pre- and non-breeders were found to have similar rates of survival, which were consistently less than those for breeders (Figure 19). In this model, the anomalously low estimates of resighting probabilities for failed breeders in the first two years (right panel, Figure 19) presumably arise from the fact that there were no observations of non-breeders in the first two years (Table 18).

**Table 16: Correspondence between the breeding-status codes in the data set (see Figure 8) and the four states (pbr, nbr, sbr, fbr) of model BPET4p, where this correspondence was sometimes ambiguous. This ambiguity was dealt with in SeaBird by defining four composite states: pbr/nbr, fbr/sbr, nbr/fbr/sbr, pbr/nbr/fbr/sbr.**

Code	Model state	Condition
2	pbr	If banded as chick and not previously seen breeding
	pbr/nbr	If banded as an adult and not previously seen breeding
	nbr	Otherwise
3	pbr/nbr/fbr/sbr	If not previously seen breeding
	nbr/fbr/sbr	Otherwise
4, 14, 15	fbr/sbr	

**Table 17: Description of the differences between some variants of model BPET4p in terms of parameterisation and AIC (Akaike Information Criterion). All variants used exactly the same data, differing only in parameterisation. The best model, BPET4p, was that with the lowest AIC. Interpretation: e.g., for model 4p1 there were three vectors of survival parameters, one for pbr, one for nbr, and one for both fbr and sbr.**

Model	<u>Survival parameters</u>				<u>Resighting parameters</u>				Number of parameters	AIC – min(AIC)
	pbr	nbr	fbr	sbr	pbr	nbr	fbr	sbr		
4p	1	1	2	2	1	1	2	3	68	0.0
4p1	1	2	3	3	1	1	2	3	80	20.5
4p2	1	1	2	2	1	2	3	4	81	7.7
4p3	1	2	3	3	1	2	3	4	93	25.6
4p4	1	2	2	2	1	1	2	3	68	72.7
4p5	1	1	1	1	1	2	3	4	69	70.9

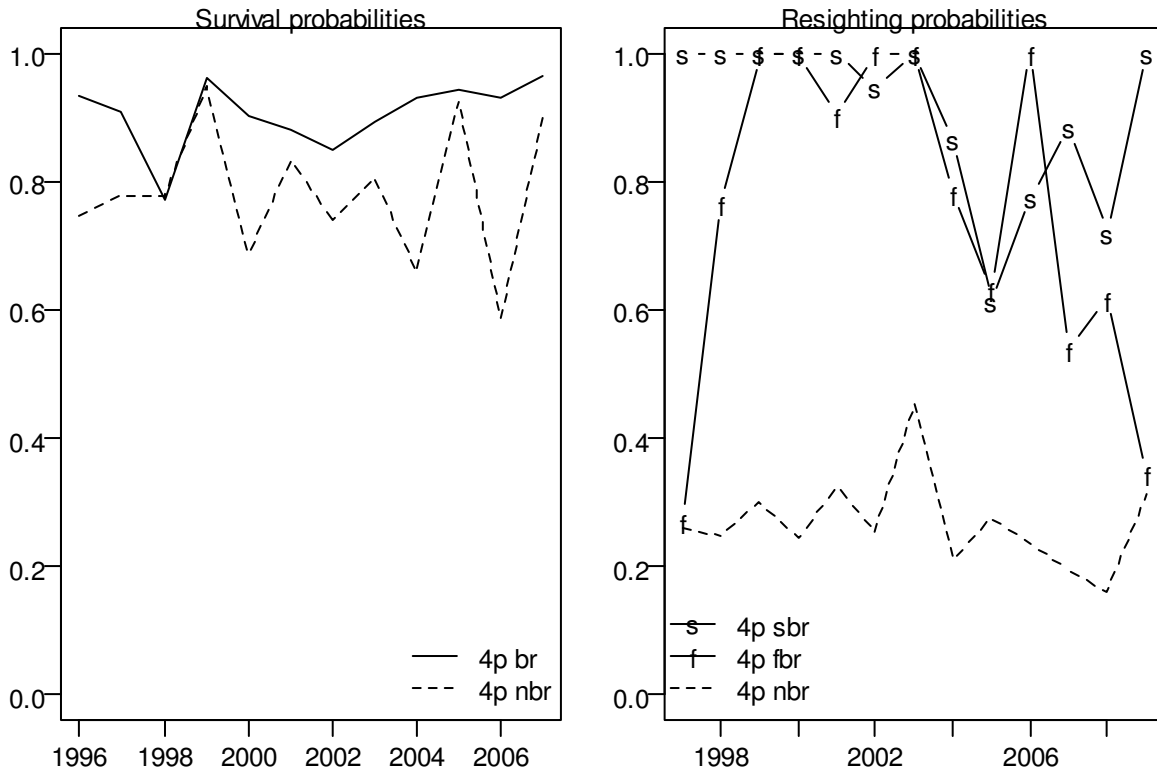


Figure 19: Survival and resighting probabilities estimated in model BPET4p.

Table 18: Summary of the status of observed birds in the first two years of the study (1996–97) and in subsequent years (1998–2008).

Years	Status known				Status partially known			Status unknown
	pbr	nbr	fbr	sbr	pbr/nbr	nbr/fbr/sbr	fbr/sbr	
1996-1997	40	0	36	121	0	0	1	10
1998-2008	549	216	766	2415	58	5	2	26

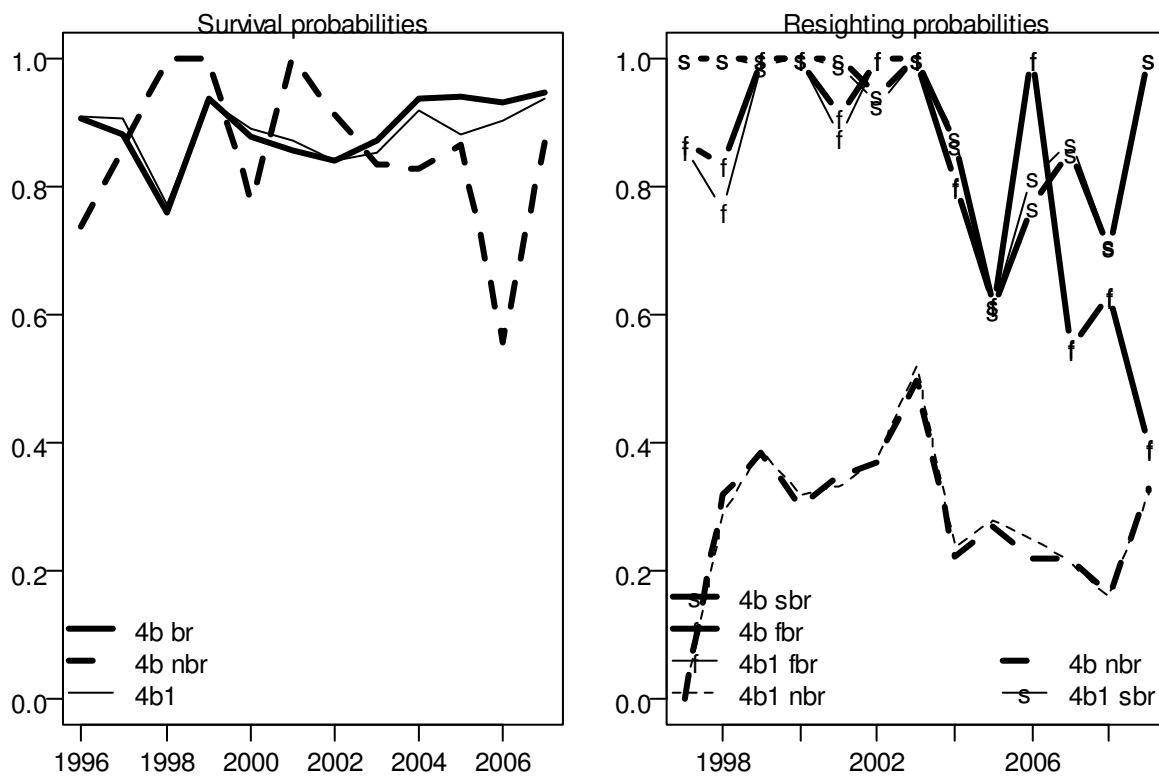
It seemed possible that some inferences from model BPET4p, and its variants, were confused by observations in which the distinction between pre- and non-breeders was not certain. A simpler model, BPET4b, with just three states (nbr, fbr, sbr), was devised to avoid this potential confusion. The pre-breeding phase was removed from the data by removing, for each banded bird, all observations before the first breeding observation (i.e., the first breeding observation was treated as the banding observation). This reduced the number of post-banding observations by about 25% (from 9119 observations on 1269 birds for BPET4 and BPET4p to 6920 observations on 988 birds for BPET4b). Again, a comparison of several variants of this model (Table 19) did not support our hypothesis. In the best of these variants, BPET4b, survival rates were found to differ between breeders and non-breeders and, more often than not, to be lower for the latter birds (Figure 20). However, this result wasn't as strong as for BPET4p in that the difference between breeder and non-breeder survival rates was smaller (compare left panels in Figures 19 & 20) and the contrast in AIC was smaller (BPET4b is better than BPET4b1 by only 3.4 AIC points, whereas in the corresponding comparison, between BPET4p and BPET4p4, the difference is more than 70 points).

On the basis of models BPET4p and BPET4b we reject our hypothesis that survival rates for non-breeders should be similar to, or greater than, those for breeders. On the contrary, survival rates tend to be lower for non-breeders than for breeders. One reason for this may be that adults that are in poor condition, and thus at greater risk of dying, choose not to breed because they have insufficient reserves.

The agreement between observed and expected numbers seen is markedly better for model BPET4p than it was for BPET2, and even better for BPET4b (Figure 21). The transition matrices for models BPET4p and BPET4b both show that the probability that a bird will breed successfully, given that it survives, is least if it was a pre- or non-breeder in the previous year, higher if it was a failed breeder, and higher again if it was a successful breeder (Table 20).

**Table 19: Description of the differences between some variants of model BPET4b in terms of parameterisation and AIC (Akaike Information Criterion). All variants used exactly the same data, differing only in parameterisation. The best model, BPET4b, was that with the lowest AIC.**

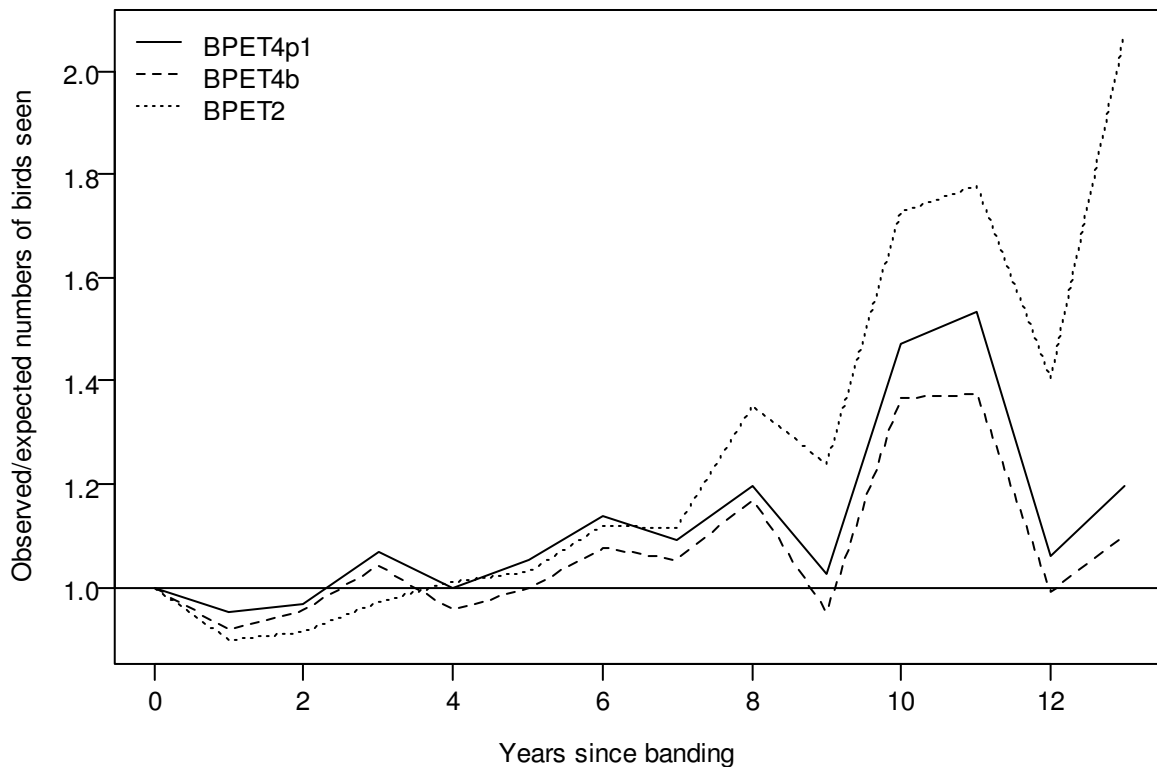
Model	Parameterisation			Number of parameters	AIC – min(AIC)
	Transition of breeders	Resighting of breeders	Survival		
4b	Tfbrbr, Tsbrbr	Prfbr, Prsbr	nbrsurv, brsurv	67	0.0
4b1	Tfbrbr, Tsbrbr	Prfbr, Prsbr	surv	55	3.4
4b2	Tfbrbr, Tsbrbr	Prbr	surv	42	19.5
4b3	Tbrbr	Prbr	surv	41	27.8
4b4	Tfbrbr, Tsbrbr	Prbr	nbrsurv, brsurv	54	16.3



**Figure 20: Survival and resighting probabilities estimated in models BPET4b (heavy lines) and BPET4b1 (light lines).**

**Table 20: Estimated transition probabilities for models BPET4p and BPET4b. Interpretation: e.g., the value 0.12 in row nbr and column fbr of the transition matrix for BPET4p means that for a bird which is a non-breeder (nbr) in year y, there is a probability of 0.12 that it will be a failed breeder (fbr) in year y+1, given that it survives.**

	BPET4p				BPET4b		
	pbr	nbr	fbr	sbr	nbr	fbr	sbr
pbr	0.57	0.00	0.10	0.33			
nbr	0.00	0.50	0.12	0.38	0.48	0.11	0.41
fbr	0.00	0.24	0.17	0.58	0.22	0.17	0.62
sbr	0.00	0.16	0.19	0.65	0.14	0.18	0.68



**Figure 21: Ratio of observed and expected numbers of birds seen, plotted as a function of the number of years since banding, for models BPET4p, BPET4b, and BPET2.**

### 3.2 Models for juveniles

All juvenile models used only observations from birds banded as chicks, and ignored all observations after the first sighting as a breeder.

For simplicity, the first model, BPET5, ignored the pre-breeder period. That is, sightings before the first sighting as a breeder were ignored. This model classified birds into 11 states (chick, age1-age9, and adult), estimated only three parameters (Table 21A), and had a simple transition matrix most of whose entries were 0 or 1 (Table 21B). The other entries of the transition matrix were calculated from parameters P1stbr6 and oddsmult as follows.

$$\begin{aligned} \text{logit}(P1stbra) &= \text{logit}(P1stbr6) + (a-6)\text{oddsmult} \\ Pnbra &= 1 - P1stbra \end{aligned}$$

for age  $a = 4, \dots, 9$ . The first equation assumes that P1stbra varies linearly with age  $a$  in logit space.

From this model, it was estimated that the annual survival rate of juveniles was only 0.68 and, for those chicks that survive to breed, the mean age of first breeding was 6.9 y and the most common ages were 7 y (25% of birds) and 8 y (23%) (Figure 22). BPET5.1 was a variant of this model in which the linearity assumption for P1stbra was dropped, so that 7 parameters were estimated: P1stb4, ..., P1stbr9, and juvsurv. This model was slightly worse than BPET5 (Table 22) but produced a similar distribution of ages at first breeding, with mean 7.0 y (compare solid and broken lines in Figure 22).

**Table 21: Parameters and transition matrix for model BPET5. Resighting probabilities were assumed to be 1 for adults and 0 for all other stages.**

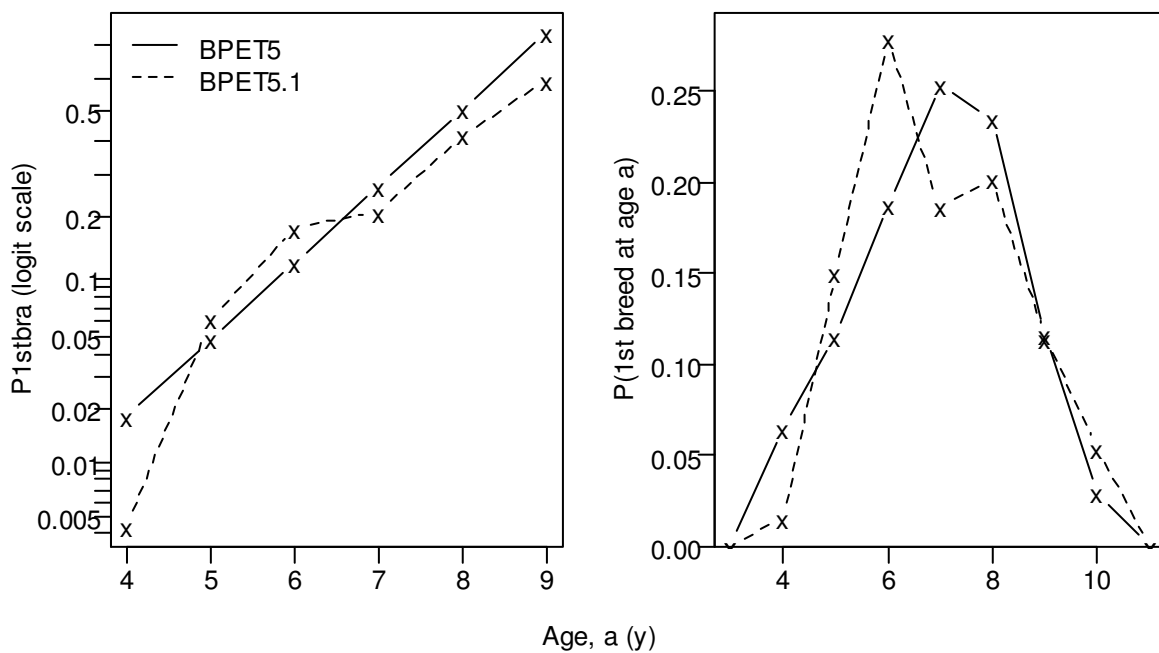
A, Parameters

Parameter	Description
P1stbr6	Probability a bird first breeds at age 6, given that it survives to that age without breeding
oddsmult <sup>1</sup>	Slope of linear relation between logit(P1stbra) and age a
juvsurv	Annual probability of survival for chicks

B, Transition matrix

	chick	age1	age2	age3	age4	age5	age6	age7	age8	age9	adult
chick	0	1	0	0	0	0	0	0	0	0	0
age1	0	0	1	0	0	0	0	0	0	0	0
age2	0	0	0	1	0	0	0	0	0	0	0
age3	0	0	0	0	Pnbr4	0	0	0	0	0	P1stbr4
age4	0	0	0	0	0	Pnbr5	0	0	0	0	P1stbr5
age5	0	0	0	0	0	0	Pnbr6	0	0	0	P1stbr6
age6	0	0	0	0	0	0	0	Pnbr7	0	0	P1stbr7
age7	0	0	0	0	0	0	0	0	Pnbr8	0	P1stbr8
age8	0	0	0	0	0	0	0	0	0	Pnbr9	P1stbr9
age9	0	0	0	0	0	0	0	0	0	0	1
adult	0	0	0	0	0	0	0	0	0	0	1

<sup>1</sup>The name of this parameter derives from the fact that if  $o_a$  is the odds that a bird first breeds at age  $a$ , given that it survives to that age without breeding, then  $o_{a+1} = \text{oddsmult} \times o_a$



**Figure 22: Comparison of estimates of age at first breeding from models BPET5 & BPET5.1. Both panels show the probability of first breeding at age  $a$ : in the left panel the probabilities are conditional on survival to that age without breeding and are plotted on a logistic scale; in the right panel they are conditional only on survival to breed and are on a natural scale.**

**Table 22: Comparison of models BPET5 and BPET5.1**

Model	Number of parameters	AIC – min(AIC)
BPET5	3	0.0
BPET5.1	7	1.0

Model BPET5p was like BPET5 but included a pre-breeding stage (so pre-breeding observations were not ignored). This model required six parameters (Table 23A) and the transition matrix probabilities (Table 23B) were calculated from these parameters as follows

$$\begin{aligned} Ppra &= P1stappa \times (1 - Pbr1st) \\ Pada &= P1stappa \times Pbr1st \\ Pjva &= 1 - Ppra - Pada \\ \text{logit}(P1stappa) &= \text{logit}(P1stapp6) + (a-6)\text{oddsmult} \end{aligned}$$

**Table 23: Parameters and transition matrix for model BPET5p. Resighting probabilities for adults were assumed to be 1.**

A, Parameters

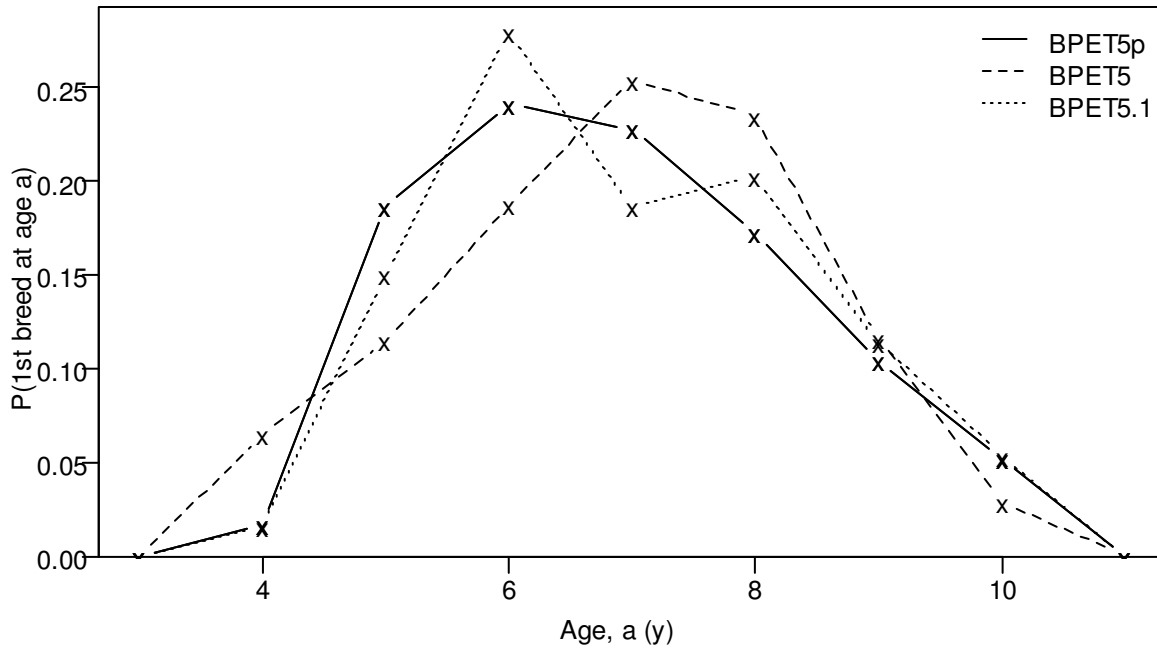
Parameter	Description
P1stapp6	Probability a bird first appears in the colony at age 6, given that it survives to that age without previously appearing
oddsmult	Slope of linear relation between $\text{logit}(P1stappa)$ and age $a$
Pbr1st	Probability a bird breeds in the first year it returns to the colony
Tprad	Probability a bird that is a pre-breeder in year $y$ becomes an adult (first breeds) in year $y+1$ , given that it survives
surv	Annual probability of survival
Prprbr	Probability of resighting a pre-breeder

B, Transition matrix

	chick	age1	age2	age3	age4	age5	age6	age7	age8	age9	prbr	adult
chick	0	1	0	0	0	0	0	0	0	0	0	0
age1	0	0	1	0	0	0	0	0	0	0	0	0
age2	0	0	0	1	0	0	0	0	0	0	0	0
age3	0	0	0	0	Pjv4	0	0	0	0	0	Ppr4	Pad4
age4	0	0	0	0	0	Pjv5	0	0	0	0	Ppr5	Pad4
age5	0	0	0	0	0	0	Pjv6	0	0	0	Ppr6	Pad4
age6	0	0	0	0	0	0	0	Pjv7	0	0	Ppr7	Pad4
age7	0	0	0	0	0	0	0	0	Pjv8	0	Ppr8	Pad4
age8	0	0	0	0	0	0	0	0	0	Pjv9	Ppr9	Pad4
age9	0	0	0	0	0	0	0	0	0	0	0	1
prbr	0	0	0	0	0	0	0	0	0	0	1-Tprad	Tprad
adult	0	0	0	0	0	0	0	0	0	0	0	1

The estimated distribution of ages at first breeding from BPET5p were similar to those from BPET5.1, with mean 6.9 y. (Figure 23) and the estimated survival rate for juveniles (0.69) was similar to that for BPET5 (0.68). About 44% of pre-breeders in year  $y$  become adults in year  $y+1$  if they survive ( $Tprad = 0.44$ ) and about 3% of birds breed in the first year they return to the colony ( $Pbr1st = 0.029$ ).

It is easy to misinterpret the observations and gain a wrong impression about the duration of the pre-breeding stage. Of banded chicks that were subsequently seen breeding, 49% (20/41) bred in the first year they were seen as adults (see Table 11). Thus we might conclude that about 49% of birds skip the pre-breeding stage, which is very different from the model estimate of 3% ( $Pbr1st = 0.029$ ). The reason for this large difference is the comparatively low probability of resighting pre-breeders ( $Prpre=0.466$ ). We showed this by simulating observations that could have been made on the banded chicks in the present data set if the assumptions and estimated parameters of model BPET5p were correct. The simulated observations had the same structure (i.e., the same number of birds, dates of banding and years of observation) as the real observations. For each bird, two sets of simulated observations were created: the first assumed the estimated value of the resighting probability,  $Prpre$  (0.466), and the second assumed  $Prpre=1$ .



**Figure 23: Comparison of estimates of age at first breeding from model BPET5p with those from BPET5 and BPET5.1.**

Each set of observations for a bird fell into one of 7 categories as follows

Category	Description
Unseen	Never resighted after banding
pbr	Resighted, but only as a pre-breeder
0pbr	First resighted as a breeder
xpbr, for x=1,...,4	Resighted as breeder x years after first sighting as a pre-breeder

With  $P_{pre} = 1$ , only 4% (2/51) of the birds seen breeding were breeding when first resighted, which is reasonable given the low value of  $P_{br1st}$ . However the comparable value with  $P_{pre} = 0.466$  was 47% (24/51), which is much closer to the figure of 49% in the real observations (Table 24). The average duration of the pre-breeding period estimated from the observations (and ignoring the probability of resighting pre-breeders) is 0.9 y. A more realistic estimate, obtained from the simulated observations with  $P_{pre}=1$ , is 1.5 y.

**Table 24: Comparison of the categories assigned to birds banded as chicks on the basis of the real observations and of simulated observations in which  $P_{pre}$ , the probability of resighting a pre-breeder was either 0.466 (as estimated in BPET5p) or 1.**

	Category						
	Unseen	pbr	0pbr	1pbr	2pbr	3pbr	4pbr
Real observations	961	32	20	11	5	4	1
Simulated observations, $P_{pre}=0.466$	958	25	24	16	7	3	1
Simulated observations, $P_{pre}=1$	932	51	2	29	15	3	2

### 3.3 Models for all mark-recapture data

BPET6p was the first model using all the mark-recapture data. It was structured like a combination of models BPET5p and BPET4p (for the pre-adult and adult parts of the data, respectively). As well as the ten pre-adult states in BPET5p (chick, age1, ..., age9) and the four adult states of BPET4p (pbr, nbr, fbr, sbr), BPET6p contains an additional state, labelled oth, for adults living outside the study area. This is to allow for chicks born in the study area that grow up to breed elsewhere. The treatment of ambiguous observations was the same as for BPET4p (see Table 16). The model parameters and transition matrix are given in Table 25 and the SeaBird input files are given in Appendix 4.

In this model, three parameters control the first appearance of a bird in a breeding colony as an adult. The age at which this happens is, as with BPET5p (see above), determined by parameters P1stapp6 and oddsmult, and the appearance is in the study colony, with probability Pappstd, or elsewhere (i.e., state oth) with probability 1-Pappstd.

This first appearance in the study area is either as a pre-breeder (with probability 1-Pbr1st) or as a breeder (with probability Pbr1st). Thus, for birds of age  $a$  from 4 to 9, there are five possibilities, as follows

Location	Stage	Status	Probability
other	adult		$P_{otha} = P1stappa(1-Pappstd)$
study	adult	pbr	$P_{pbra} = P1stappa \times Pappstd(1-Pbr1st)$
study	adult	fbr	$P_{fbra} = P1stappa \times Pappstd \times Pbr1st(1-Psuccess)$
study	adult	sbr	$P_{sbra} = P1stappa \times Pappstd \times Pbr1st \times Psuccess$
	juvenile		$P_{jva} = 1-P_{otha}-P_{pbra}-P_{fbra}-P_{sbra}$

Juveniles that have not bred before age 10 must breed at that age, so they have only three possibilities:

Location	Stage	Status	Probability
other	adult	oth	$P_{oth10} = 1-Pappstd$
study	adult	fbr	$P_{fbr10} = Pappstd(1-Psuccess)$
study	adult	sbr	$P_{sbr10} = Pappstd \times Psuccess$

When a bird that has been a pre-breeder in the study area first breeds, it does so either in the study area (with probability Pbrstd) or elsewhere (with probability 1-Pbrstd). Thus, birds that have become pre-breeders in the study area have four options for the following year:

Location	Status	Probability
study	pbr	$T_{pbrpbr} = 1-T_{pbrbr}$
study	fbr	$T_{pbrfbr} = T_{pbrbr} \times Pbrstd(1-Psuccess)$
study	sbr	$T_{pbrsbr} = T_{pbrbr} \times Pbrstd \times Psuccess$
other	oth	$T_{pbroth} = T_{pbrbr} \times (1-Pbrstd)$

Once a bird starts breeding in the study area it moves between states nbr, fbr, sbr in the same way (and controlled by the same parameters) as in BPET4p. Birds that choose to move to state oth never leave it.



**Table 25: Parameters and transition matrix for model BPET6p. Resighting probabilities were assumed to be zero for both juveniles and adults in state oth.**

A, Parameters

Parameter	Description
P1stapp6	Probability a bird first appears as an adult in a breeding colony at age 6, given that it survives to that age
oddsmult	Slope of linear relation between logit(P1stappa) and age a
Pappstd	Probability, for a chick banded in the study area and surviving, that their first appearance in a breeding colony be within the study area
Pbr1st	Probability, for a chick that survives to breed, that it will breed in the first year it appears in a breeding colony as an adult (i.e., it is never a pre-breeder)
Pbrstd	Probability, for a pre-breeder in the study area that survives to breed, that breeding will happen in the study area
Tpbrbr/Tnbrbr/Tfbrbr/Tsbrbr	Probability that a pre-breeder/non-breeder/failed breeder/successful breeder in the study area in one year will breed the next year, given that it survives
Psuccess	Probability that a bird that breeds is successful (produces a fledgling)
juvsurv/pbrsurv/nbrsurv/brsurv	Annual probability of survival for juveniles/pre-breeders/non-breeders/breeders
Prpbr/Prnbr/Prfbr/Prsbr	Probability of resighting a pre-breeder/non-breeder/failed breeder/successful breeder

B, Transition matrix

	chick	age1	age2	age3	age4	...	age9	pbr	nbr	fbr	sbr	oth
chick	0	1	0	0	0	...	0	0	0	0	0	0
age1	0	0	1	0	0	...	0	0	0	0	0	0
age2	0	0	0	1	0	...	0	0	0	0	0	0
age3	0	0	0	0	Pjv4	...	0	Ppbr4	0	Pfbr4	Psbr4	Poth4
...	...	...	...	...	...	...	...	...	...	...	...	...
age8	0	0	0	0	0	...	Pjv9	Ppbr9	0	Pfbr9	Psbr9	Poth9
age9	0	0	0	0	0	...	0	0	0	Pfbr10	Psbr10	Poth10
pbr	0	0	0	0	0	...	0	Tpbrpbr	0	Tpbrfbr	Tpbrsbr	Tpbroth
nbr	0	0	0	0	0	...	0	0	Tnbrnbr	Tnbrfbr	Tnbrsbr	0
fbr	0	0	0	0	0	...	0	0	Tfbrnbr	Tfbrfbr	Tfbrsbr	0
sbr	0	0	0	0	0	...	0	0	Tsbrnbr	Tsbrfbr	Tsbrsbr	0
oth	0	0	0	0	0	...	0	0	0	0	0	1

As with previous models, several variants of BPET6p were considered to determine the best parameterization of survival and resighting parameters (Table 26). In the best model, BPET6p2, estimates of the juvenile parameters were similar to those from BPET5p, but with slightly lower mean age at first breeding (6.7 y, compared to 6.9 y from BPET5p) (Figure 24). However, there were two marked differences in estimates of adult parameters, compared to those from BPET4p: survival rates for non-breeders were markedly higher, and resighting rates for pre-breeders were estimated to be greater than those for non-breeders (Figure 25).

**Table 26: Description of the differences between some variants of model BPET6p in terms of parameterisation and AIC (Akaike Information Criterion). All variants used exactly the same data, differing only in parameterisation. The best model, BPET6p2, was that with the lowest AIC. Interpretation: e.g., for model 6p there were two vectors of survival parameters, one for both pbr and nbr, and one for both fbr and sbr.**

Model	<u>Survival parameters</u>				<u>Resighting parameters</u>				Number of parameters	AIC – min(AIC)
	pbr	nbr	fbr	sbr	pbr	nbr	fbr	sbr		
6p	1	1	2	2	1	1	2	3	74	16.8
6p1	1	2	3	3	1	1	2	3	86	22.0
6p2	1	1	2	2	1	2	3	4	87	0.0
6p3	1	2	3	3	1	2	3	4	99	5.8
6p4	1	2	2	2	1	1	2	3	74	24.6
6p5	1	1	1	1	1	2	3	4	75	2.8

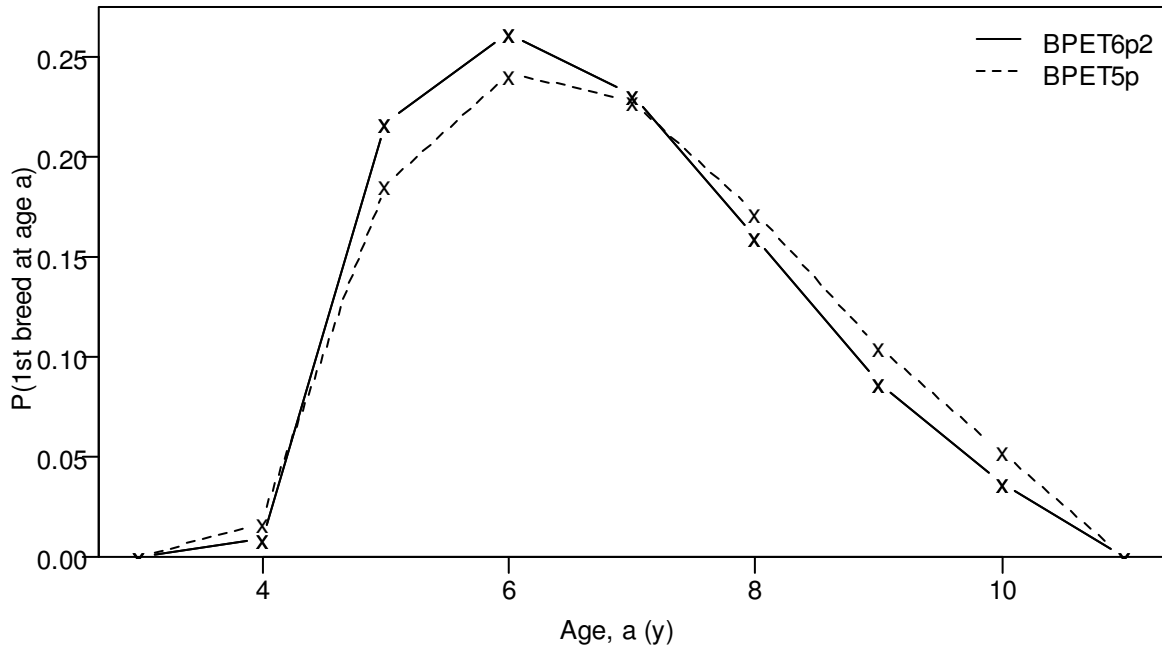


Figure 24: Comparison of estimates of age at first breeding from models BPET6p2 and BPET5p.

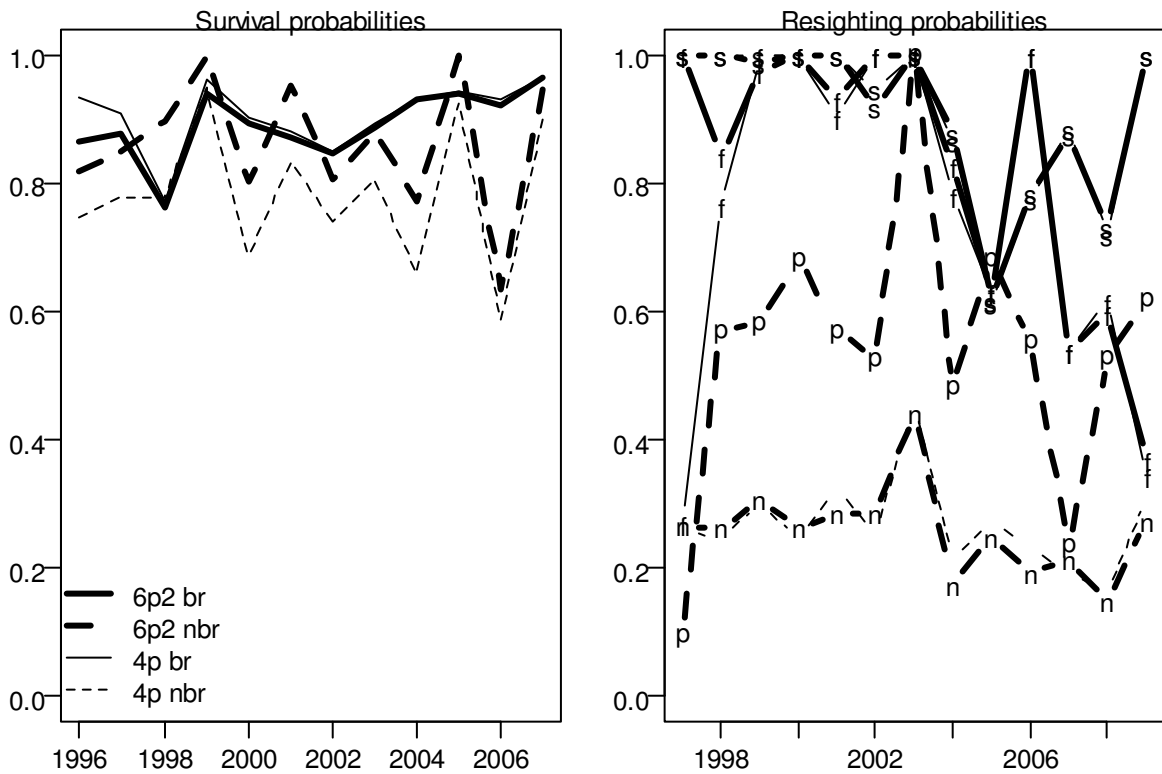


Figure 25: Comparison of survival and resighting probabilities estimated in models BPET6p2 and BPET4p.

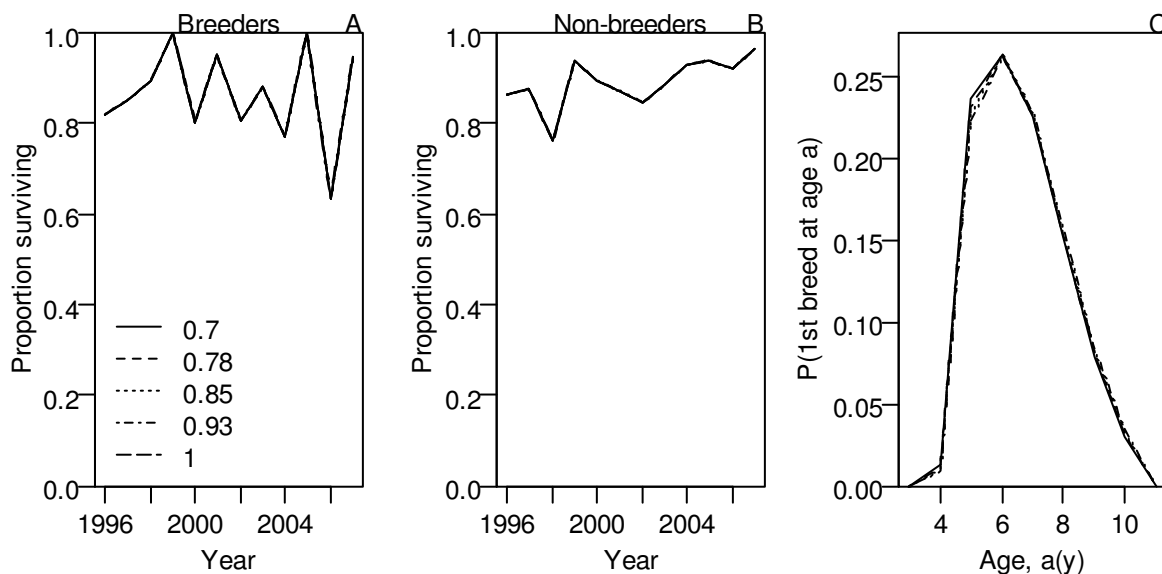
It is unclear why non-breeder survival estimates in BPET6p2 were more like those in BPET4b than BPET4p. The mean difference between survival rates for breeders and non-breeders was 0.03 in BPET6p2 and 0.04 in BPET4b, compared to 0.12 in BPET4p. Further, an alternative model assuming these rates was close to optimal compared to BPET6p2 and BPET4b, but clearly suboptimal compared to BPET4p (the relevant AIC differences are 2.8 for BPET6p5 in Table 26; 3.4 for BPET4b1 in Table 19; and 70.9 for BPET4p5 in Table 17). A close investigation of the fits to BPET4p and BPET6p2 found no evidence that either model had failed to converge, and the difference

in parameter estimates was not found to be attributable to outlier observations (i.e., a few banded birds whose likelihoods were markedly different for the two models).

In BPET6p2, juvenile survival was estimated to be 1, but a posterior profile on this parameter showed that it was completely confounded with the parameter Pappstd (Table 27). Thus the available data do not allow us to distinguish between one extreme, in which all juveniles survive but most appear as pre-breeders outside the study area (juvsurv = 1 and Pappstd = 0.12), and the other, where only 70% of juveniles survive each year (juvsurv=0.7) but almost all are pre-breeders in the study area (Pappstd=0.98). Across this range of values of juvsurv there is essentially no change in adult survival rates (Figure 26A,B). The other two parameters that change with juvsurv (see P1stapp6 & oddsmult in Table 27) do so in a compensatory way, so that the estimated distribution of ages at first breeding is little changed (Figure 26C). It is estimated that about two-thirds of birds that appear in the study area as pre-breeders will breed there (as opposed to elsewhere), given that they survive (Pbrstd = 0.66).

**Table 27: Results of a posterior profile on the parameter juvsurv in model BPET6p2 showing the values of the only parameters whose values changed substantially and also of the objective function.**

juvsurv	P1stapp6	oddsmult	Pappstd	Objective function
0.70	0.345	1.784	0.979	7463.41
0.78	0.387	1.716	0.523	7463.40
0.85	0.425	1.662	0.302	7463.40
0.93	0.459	1.620	0.185	7463.40
1.00	0.490	1.586	0.120	7463.39



**Figure 26: Estimates of A, survival of breeders, B, survival of non-breeders, and C, age at first breeding from the posterior profile on juvsurv for model BPET6p2. In each panel there are five lines corresponding to the five values of juvsurv in the profile (see Table 27).**

### 3.4 Models for mark-recapture and abundance data

The models developed so far have included only one type of observation: mark-recapture. This type of observation allows us to estimate vital rates (e.g., survival and breeding success), and thus infer the rate of growth of the population, but they give us no information about absolute population size.

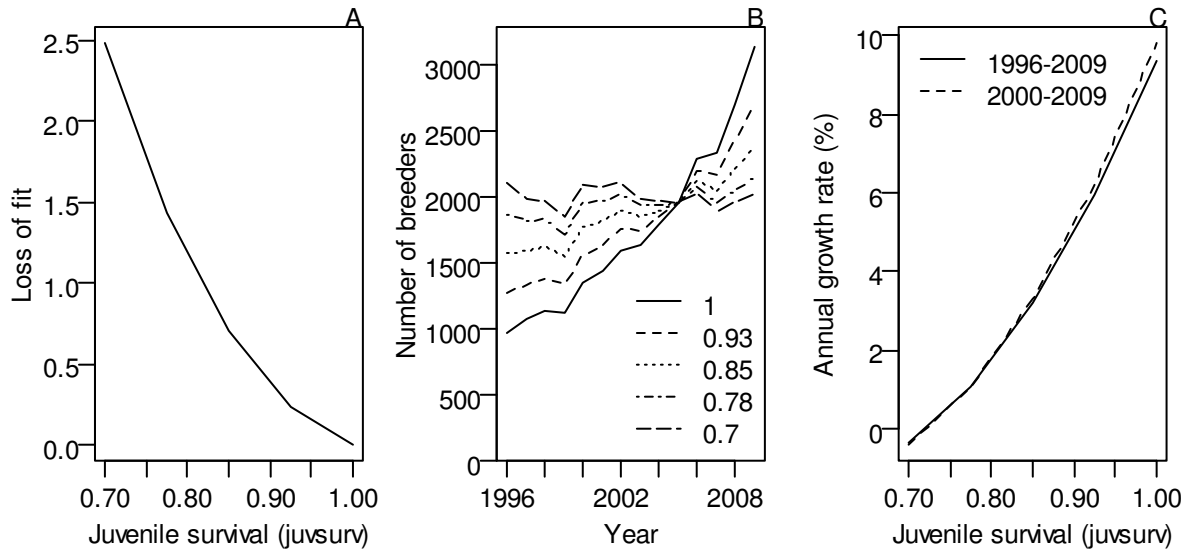
The next model, BPET7, was a small extension of BPET6p2 to include the 2005 population estimate (of 1964 breeders – see Table 6) and thus allow the estimation of absolute population numbers in any year. The 2005 estimate was arbitrarily assigned a c.v. of 0.05 so that the model fitted it well. Two

other changes were made. First, the number of chicks fledged in each year was assumed to be  $0.5[Nsbr + Nsbr \times Noth / (Nnbr + Nfbr + Nsbr)]$ . The first term relates to chicks born in the study area, and the second to those born elsewhere (with the assumption that the proportion of adults that breed successfully is the same as in the study area). [In previous models the number of fledglings each year was arbitrarily assumed to be 1000, because the data did not allow estimation of absolute numbers of birds]. The second change was that an additional parameter was estimated: the initial (1996) population size,  $N_0$  (see Appendix 4 for a description of the differences in SeaBird input files between BPET6p2 and BPET7).

### 3.4.1 Inferred population growth rates

As with BPET6p2, juvenile survival was, unrealistically, estimated to be 1 with model BPET7, but a posterior profile on this parameter showed that lower values were almost as plausible, with the objective function value being only 2.5 points higher when  $juvsurv = 0.7$  (Figure 27A). Over this range of values, the estimated population trajectory ranged from a steep increase at an average rate of 9.4% per year for  $juvsurv = 1$  to a slow decline (-0.4% per year) for  $juvsurv = 0.07$  (Figure 27B,C). These average growth rates are almost the same whether they are calculated over the entire study period (1996–2009) or the shorter period of 2000–09 (Figure 27C) (this shorter period is of interest here because it is associated with the growth-rate estimate of Section 2.2.3 based on census grids). As with BPET6p2, adult survival rates were virtually unaffected by changes in  $juvsurv$  but this parameter was strongly confounded with  $Pappstd$ . Thus the mark-recapture data do not, by themselves, provide clear grounds to distinguish between one extreme, in which the population is increasing substantially, all juveniles survive, but only 12% are pre-breeders in the study area ( $juvsurv=1$ ,  $Pappstd=0.12$ ) and the opposite, in which the population is slowly declining, 30% of juveniles die each year, but 90% of those that survive appear as pre-breeders in the study area ( $juvsurv=0.7$ ,  $Pappstd=0.90$ ). We can reduce this range of uncertainty if we assume that juvenile survival will not exceed 0.88, the mean estimated survival rate for non-breeders. With this assumption, the estimated annual growth rate for the population (as shown in Figure 27C) should not exceed 4.5% (if calculated from 2000 to 2009) or 4.3% (if from 1996 to 2009).

An obvious question to ask is how consistent this model is with the two population growth rate estimates from above: 2.2%–3.1% per year between 2000 and 2009 (from the census grid data in Section 2.2.3) and 1.2% per year between 1988 and 2005 (from the two transect-based abundance estimates of Section 2.2.4). Within the posterior profile of Figure 27, the range of growth rates from 1.2% to 3.1% per year corresponds to the range 0.78 to 0.84 for juvenile survival. The loss of model fit at these values of  $juvsurv$ , compared to the fit when  $juvsurv = 0.88$ , is only 0.9 and 0.2 objective function points, respectively. Thus we can conclude that BPET7 is not inconsistent with these estimated growth rates.



**Figure 27: Results of a posterior profile on juvsurv for model BPET7, showing, as functions of juvsurv, A, the loss of fit; B, population trajectories; and C, the estimated annual growth rate in the number of breeders (between 1996 and 2009, solid line; and between 2000 and 2009, broken line).**

### 3.4.2 Transition parameter estimates

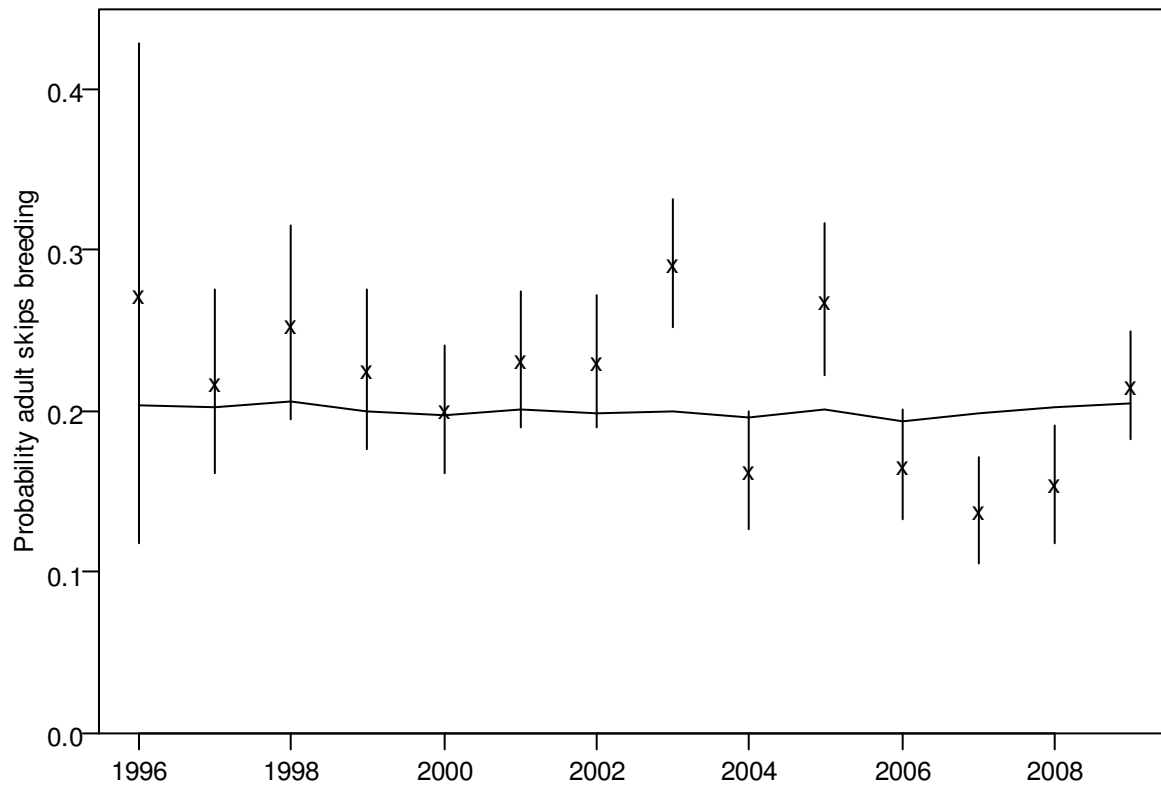
The estimated transition matrix for BPET7 (Table 28) may be thought of as made up of three groups of rows. Those in the first group (rows for states chick, age1, age2, and oth) are fixed by definition (see Table 25 for their definitions). The second group (age3–age9) concerns the transition from chick to pre-breeder. This group appears not to be well determined because it changes substantially with juvsurv, which we have seen is not well estimated. However, all the uncertainty in these rows concerns the proportion of birds that first appear as pre-breeders in the study area. The estimated distribution of ages at first breeding is virtually the same as for BPET6p2 (see Figure 24), and this is virtually unchanged by changes in juvsurv. The third group of rows, concerning adulthood (pbr, nbr, fbr, sbr), is also stable with respect to uncertainty about juvsurv, as are the following three probabilities. The probability a bird will skip the pre-breeding phase and breed in its first season back at the breeding colony is still estimated to be low ( $P_{br1st} = 0.03$ ); about two-thirds of birds seen as pre-breeders in the study area will breed in that area, given that they survive ( $P_{brstd} = 0.68$ ); and about three-quarters of breeders are successful each year ( $P_{success} = 0.77$ ).

**Table 28: Estimated transition matrix for model BPET7. Rows and columns consisting of only 0s and 1s are omitted to save space (see Table 25 for information about these).**

	age9	pbr	nbr	fbr	sbr	oth	age4	age5	age5	age5	age8
age3	0.71	0	0	0	0	0	0.03	0	0	0	0.25
age4	0	0.61	0	0	0	0	0.04	0	0	0	0.34
age5	0	0	0.50	0	0	0	0.06	0	0	0	0.44
age6	0	0	0	0.39	0	0	0.07	0	0	0	0.54
age7	0	0	0	0	0.29	0	0.08	0	0	0	0.63
age8	0	0	0	0	0	0.20	0.09	0	0	0	0.70
age9	0	0	0	0	0	0	0	0	0.03	0.09	0.88
pbr	0	0	0	0	0	0	0.24	0	0.12	0.40	0.25
nbr	0	0	0	0	0	0	0	0.57	0.10	0.33	0
fbr	0	0	0	0	0	0	0	0.21	0.18	0.60	0
sbr	0	0	0	0	0	0	0	0.15	0.20	0.65	0

About 20% of adults (excluding pre-breeders) skip breeding each year (Figure 28), which is similar to the estimate of 22% by Hunter et al. (2001), which was based on burrow observations, rather than banding data.

We have seen that one parameter determining the rate of emigration from the study area (Pappstd) is not well determined, but the other (Pbrstd) appears to be. In model BPET7c we fixed Pbrstd = 1 to evaluate the strength of the information about this parameter. In this model Pappstd was estimated to be 1 (which means that there is no emigration from the study area), juvsurv was 0.69, and the breeding population was estimated to be decreasing at 7.5% per year. Since the fit to the data was significantly worse in this model, compared to BPET7 (AIC difference = 24.9), we can conclude that there is clear evidence that some pre-breeders in the study area will breed elsewhere. [Strictly speaking, this evidence concerns only those birds that were also chicks in the study area, since we used no observations on birds banded as chicks outside the study area].



**Figure 28: Comparison of estimates of skipping rates from BPET7 (solid line) and from direct observations Observed ('x', with 95% confidence intervals as vertical bars).**

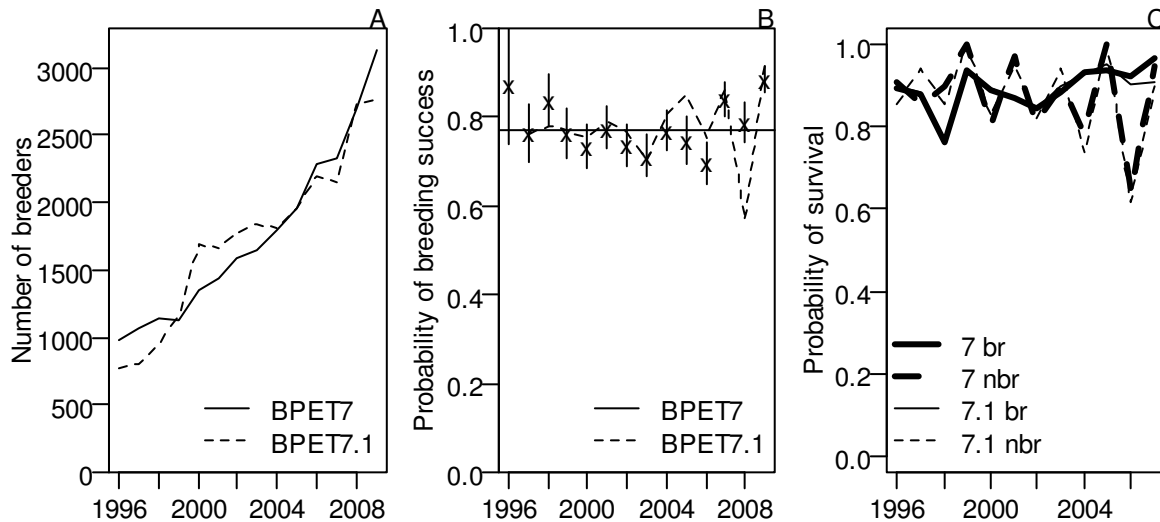
### 3.4.3 Effect of year-to-year variation in transition parameters

In all models so far we have, for simplicity, assumed that all transition parameters were time-invariant. The effect of allowing year-to-year variation in the adult transition parameters (Tpbrbr, Tnbrbr, Tfbrbr, Tsrbrbr, Psuccess) was explored in model BPET7.1 (see Table 25 for definitions of these and other transition parameters referred to in this section). No time variation was considered for parameters concerning the transition from juvenile to adult (P1stapp6, oddsmult, Pappstd, Pbr1st, Pbrstd) because of lack of data (recall that only 54 birds banded as chicks have so far been observed breeding)

The following procedure was used to construct BPET7.1, starting with model BPET7. The aim was to allow time variation in the adult transition parameters only where this significantly improved model fit (i.e., produced a lower AIC). A stepwise procedure was used in which one more transition parameter was converted to time-varying at each step, with the procedure stopping when the AIC no longer dropped. The order in which the parameters were converted to time varying (Psuccess, Tnbrbr, Tpbrbr, Tfbrbr, Tsrbrbr) was found by fitting models in which only one parameter was time varying

and ranking the parameters by the improvement of fit (from most to least) compared to BPET7. In the final model, BPET7.1, all but *Tsbrbr* were time varying.

The estimated population trajectory from BPET7.1 was broadly similar to that for BPET7 (Figure 29A), though the comparison is sensitive to the range of years considered (the mean annual growth rate estimated from BPET7.1 is greater than that from BPET7 when calculated from 1996 to 2009 [10.3% compared to 9.4%] but less over the period 2000 to 2009 [5.7% compared to 9.8%]). Breeding success, as estimated in BPET7.1, showed increasing variation with time, but no trend, compared to the estimate from BPET7 (Figure 29B). Estimated survival rates were little affected by time variation in the transition parameters (Figure 29C).



**Figure 29:** Effect of allowing some time-varying transition parameters on A, the population trajectory; B, estimates of breeding success ( $P_{\text{success}}$ ); and C, survival probabilities for breeders and non-breeders. All transition parameters were time-invariant in model BPET7; some are time-varying in BPET7.1 (see text for details). Also shown in panel B are direct estimates of  $P_{\text{success}}$  ('x', with 95% confidence intervals as vertical bars) from the observed numbers of successful and failed breeders in each year.

#### 4. COMPARISONS WITH OTHER STUDIES

Table 29 compares some estimates from the present study with those from other studies on the same species (all of which used a subset of the data used here) or congeners. Mean ages at first breeding are all quite similar. It is difficult to draw any conclusion about estimates of juvenile survival because they vary so widely. The present estimate of 0.89 for adult survival (averaged over breeders and non-breeders over all years) is higher than the other estimates for the same species but close to the average of those for other *Procellaria* petrels.

It is notable that the difference in survival between breeders and non-breeders in the present study (0.02) is much smaller than that previously estimated for black petrel (0.11 by Fletcher et al. 2008) and the value of 0.23 for the Westland petrel (Waugh et al. 2006). We have not been able to explain why we estimated a small difference in some models (0.02 in BPET7, 0.03 in BPET6p2, 0.04 in BPET4b) and a larger difference in others (0.12 in BPET4p and BPET4.4) – see discussion in Section 3.3 – but note that for BPET4.4, the model which is most similar to that of Fletcher et al. (2008), our estimate is similar to theirs.

**Table 29: Comparison of some parameter estimates from the present study with those from other studies on the same species (*Procellaria parkinsoni*) or other species of the same genus. nbr = non-breeders, br = breeders.**

Age at 1st breeding (y)	Annual probability of survival					Procellaria species	Source
	no emig. <sup>1</sup>	juveniles adj. <sup>2</sup>	nbr	br	adults all		
6.7	0.69	0.78–0.84	0.88	0.89	0.89	<i>parkinsoni</i>	Present study
8.5 <sup>5</sup>	–	–	–	–	0.88	<i>parkinsoni</i>	Hunter et al. (2001) <sup>3</sup>
7.3	0.65	–	0.75 <sup>6</sup>	0.86	0.85	<i>parkinsoni</i>	Fletcher et al. (2008) <sup>3</sup>
–	0.86 <sup>4</sup>	–	–	–	0.79	<i>parkinsoni</i>	Bell et al. (2009) <sup>3</sup>
–	–	–	0.73	0.96	0.85	<i>westlandica</i>	Waugh et al. (2006)
6.1	0.39	0.7	–	–	0.90	<i>aequinoctialis</i>	Barbraud et al. (2008)
7.0	–	–	–	–	0.94	<i>cinerea</i>	Barbraud et al. (2009)

<sup>1</sup>Assumed to be under-estimates because emigration was ignored

<sup>2</sup>Estimates adjusted to be consistent with an estimated population growth

<sup>3</sup>Based on a subset of the data used in the present study

<sup>4</sup>Equivalent annual value over 6 years

<sup>5</sup>Preliminary estimate, believed to be an over-estimate

<sup>6</sup>Inferred from figure R.2.2.1 because the value of 0.83 given on p. 49 seemed inconsistent with this plot

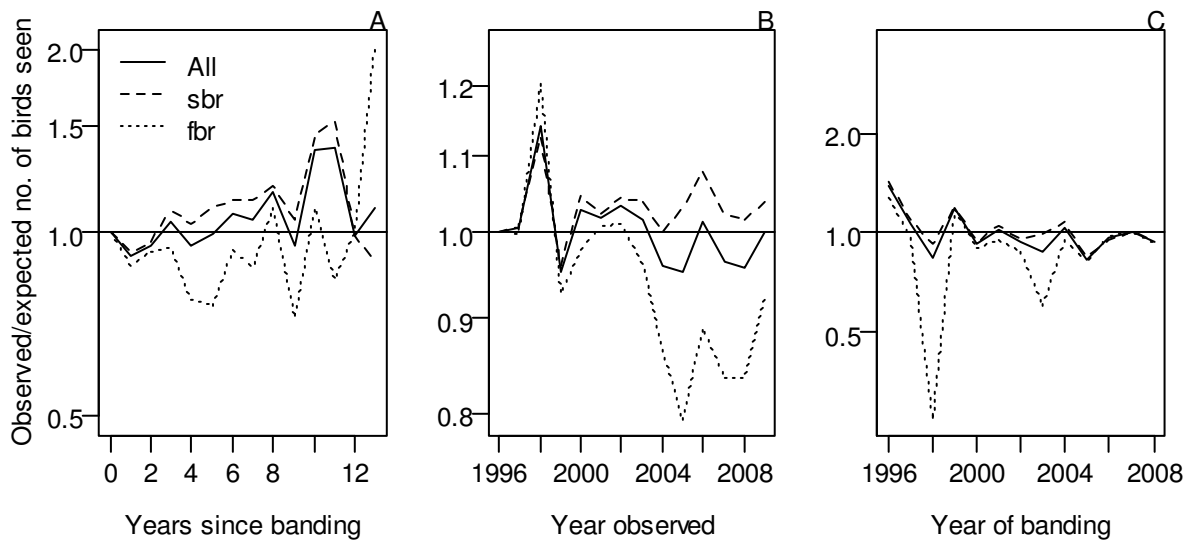
## 5. THE PROBLEM OF DIAGNOSTIC PLOTS

In many types of modelling (e.g., for fisheries stock assessment) it is common to present a range of diagnostic plots as a way of demonstrating how well the model fits the data. Each type of plot is intended to detect a specific way in which the fit may be poor. When such plots show a lack of fit there are sometimes (though not always) obvious ways of modifying the model to try to achieve a better fit. During a presentation of some initial results from this project the relative lack of diagnostic plots was commented on (only one type was presented). In this section, we discuss the problem of diagnostic plots for seabird mark-recapture data.

The type of diagnostic plot that was presented earlier (and can be seen, in slightly different forms, in Figures 17 and 21) was intended to detect band loss. Francis et al. (2008) showed what can be done when band loss is detected by such a plot. However, it is not at all clear what should be done when, as happened in the present study, these plots showed a pattern opposite to what would be expected if bands were being lost (in the case of Figure 21, we see an upward trend, but band loss would produce a downward trend).

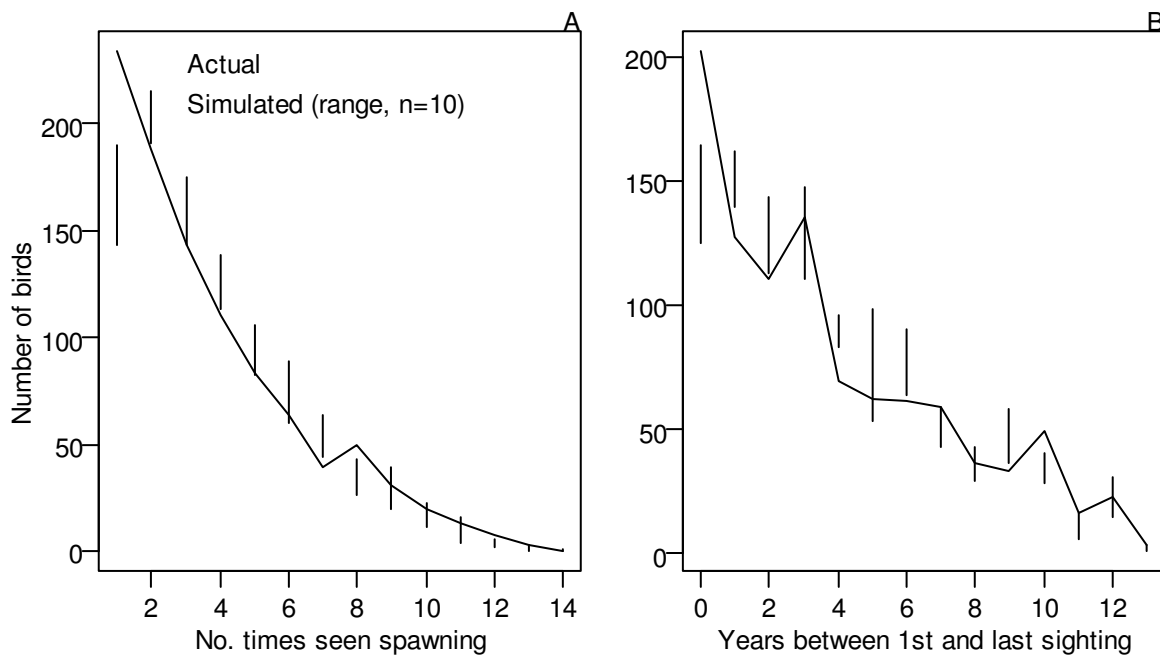
One approach to detecting lack of fit involves dividing all banding observations into groups. For each group we calculate the actual (what we observed) and expected (according to the parameters and assumptions of the fitted model) number of observations. This was the approach used in Figure 21, where the grouping was by number of years since banding and we plotted the ratio of observed and expected numbers. Figure 30 illustrates three variations on this approach applied to model BPET4b. Panel A is similar to Figure 21, except that we have grouped by both years since banding *and* state at banding (sbr or fbr) (the solid line in this panel is exactly the same as the dashed line in Figure 21). In panel B, we grouped by year of observation and state at banding; in panel C, the grouping was by year of banding and state at banding. All three panels show a clear pattern: birds that were banded as successful (or failed) breeders tended to be resighted more (less) than would be expected, according to the fitting model. Though the pattern is clear, there is no obvious way we might modify our model to remove this pattern.





**Figure 30:** The ratio of observed to expected numbers of birds seen for model BPET4b, plotted by state at banding, against A, years since banding; B, year observed; and C, year of banding. In each panel, the solid line is for all birds and the other two lines relate to birds grouped by state at banding: successful breeder (sbr, dashed line), or failed breeder (fbr, dotted line).

Another approach to diagnostics is to compare actual and simulated data. We simulated 10 mark-recapture data sets which had exactly the same structure as the data used in BPET4b (i.e., the same number of birds, with the same banding years and state at banding), except that we omitted 3 birds with composite banding states. Figure 31 shows two ways in which the actual and simulated data appear to differ. In this figure there are strong suggestions of lack of fit, which is shown when the jagged line (for the actual data) fails to cross the vertical lines (from the simulated data). To give a specific example, from the left-hand side of panel A, there were 234 birds in the actual data set that were seen breeding only once, whereas in the 10 simulated data sets this number was much less, ranging from 143 to 190.

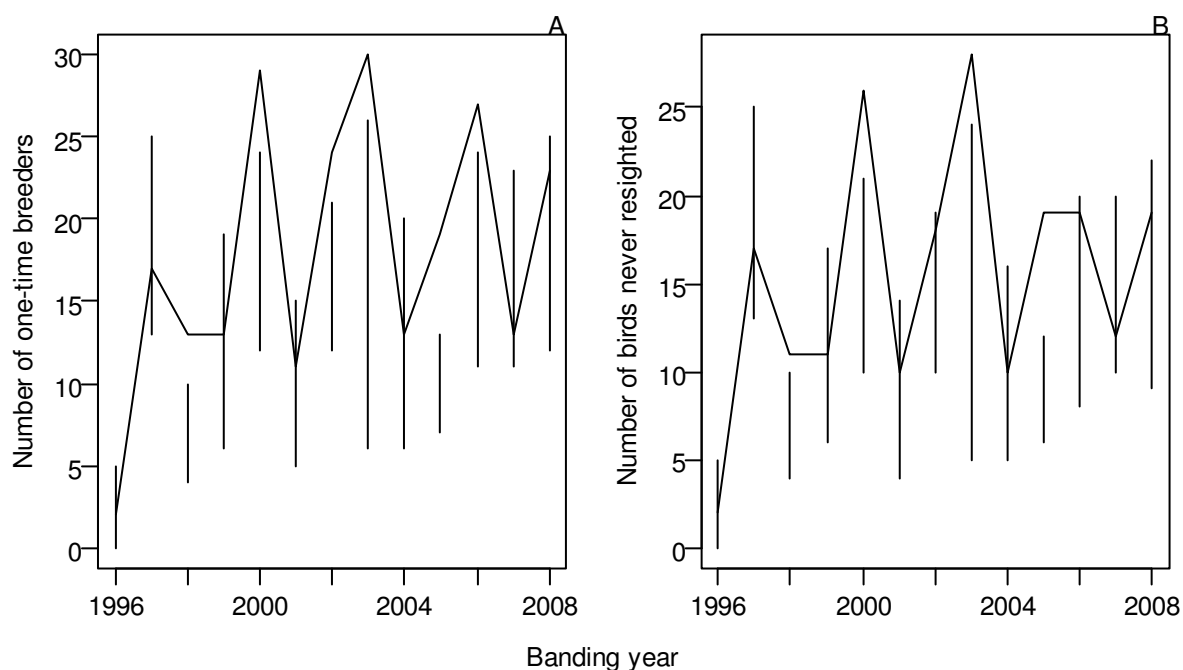


**Figure 31:** Comparison between the actual data used in model BPET4b and 10 simulated data sets with the same structure. The birds in each data set are grouped by A, the number of times they were seen breeding, and B, the number of years between the first and second sighting. In each panel, the jagged line shows the number of birds in each group for the actual data, and the vertical lines show the range, amongst the 10 simulated data sets, of numbers of birds in each group.

Another way of plotting the same data (Figure 32) illustrates strong temporal heterogeneity in the differences between actual and simulated data, and thus temporal heterogeneity in lack of fit. None of the patterns shown in Figures 31 & 32 suggest simple ways of modifying the model so as to improve its fit to the data.

The point we wish to make is that it is not difficult to construct plots which show some sort of lack of fit. We could easily have shown others. However, what we did not find in the present study was a diagnostic plot which illustrated a lack of fit that was easily corrected by a simple modification of model assumptions.

It is also worth saying that lack of model fit is not always a matter of great concern. For example, our model assumes that all transition probabilities are the same for all birds. This is almost certainly not true, in that some birds are likely to be consistently ‘good’ breeders, as was shown for southern Buller’s albatross by Francis et al. (2008). However, it does not seem very likely that this type of lack of fit would materially bias the parameters of key importance: rates of survival and breeding success.



**Figure 32: Illustration of temporal heterogeneity in differences between the actual data used in model BPET4b and 10 simulated data sets with the same structure. The birds in each data set are grouped by banding year. The vertical axis shows the number of birds in each group that A, bred only once, or B, were never resighted. In each panel, the jagged line shows the number of birds in each group for the actual data, and the vertical lines show the range, amongst the 10 simulated data sets, of numbers of birds in each group.**

## 6. CONCLUSIONS

### 6.1 Status of the Great Barrier Island population of black petrel

We will discuss the status of this population in the context of the four objectives for this project (see Section 1).

The main conclusion from this year’s work is that there is no evidence that fisheries currently pose a risk to this population (Objectives 1 and 4). This conclusion depends primarily on the abundance estimates of Section 2.2, which suggest that the population has been growing at an average rate of

between 1.2% and 3.1% per year. These growth rates are consistent with the mark-recapture data, though these data do not contain strong information about growth rates (because they can't distinguish emigration from mortality in young birds).

However, we can not go so far as to say that we have clear evidence that fisheries do not pose a risk to this population. The best evidence we have indicates that the population is increasing, but that evidence is not strong. There is great uncertainty about the comparability of the two transect-based estimates of abundance. Also, population trends within the nine census grids (which cover only 1.44 ha) may differ from those in the whole study area (35 ha). Although there are grounds for believing that the study area includes a substantial proportion of the breeding population on Great Barrier Island, we have no formal estimates concerning trends outside this area.

Because of the lack of evidence of risk from fisheries no attempt has been made to evaluate alternative management strategies for this population (Objective 2).

With regard to the risks posed by different fisheries (Objective 3) we have no reason to modify the conclusion of Baird & Gilbert (2008) that the main New Zealand bycatch threat to this species occurs in FMAs 1 and 2 in the surface and bottom longline fisheries during the breeding season. However, this conclusion is based on very sparse bycatch data and says nothing about risks from non-New Zealand fisheries. Geolocator data loggers offer a means of refining our knowledge about the foraging range of breeding birds, and thus the potential for interactions with fisheries. Initial results, from 11 birds, showed high variability in foraging range (including movement outside the New Zealand EEZ) (Bell et al. 2009), making it difficult to draw general conclusions at this stage.

## **6.2 Demographic parameters**

The mean age of first breeding for black petrel is estimated to be 6.7 y. Before this, new adults spend an average of 1.2 y in the colony as pre-breeders, with only 3% skipping the pre-breeder phase. Of birds that appear in the study area as pre-breeders and survive to breed, only 68% do so in the study area. Once birds start breeding, their annual survival rate is 0.89, 80% breed each year, and of those, 77% are successful (i.e., produce a fledgling). Survival rates before the pre-breeder stage are not well determined because we can't distinguish mortality from emigration (birds that breed in an area away from where they were hatched).

## **6.3 Recommendations for further monitoring**

The most effective way of monitoring this population to determine whether it might be at risk is to repeat the transect-based abundance estimation last done in 2005. This would provide information about the likely rate of population growth or decline. Mark-recapture studies are valuable in producing estimates of many demographic parameters, but they are not useful in estimating changes in population abundance because they can not reliably estimate juvenile survival.

Deployment of more data loggers would improve our knowledge of foraging range and thus help to identify fisheries which might be affecting this population.

## **7. ACKNOWLEDGMENTS**

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### **Appendix 1: Some minor errors in Scofield (1989)**

This appendix describes some minor calculation errors relating to breeding burrows ('BR') and birds in tables 1 and 2 of Scofield (1989) (errors relating to non-breeders are ignored here). It is assumed here that the burrow counts (i.e., the line labelled 'No. of breeding burrows' in table 1) are correct.

There are three errors in Scofield's table 1. First, the variance formula used in the calculation of the s.e.s was that for a population, rather than for a sample (i.e., the sum of squared residuals was divided by  $n$ , rather than  $n-1$ ). Second, for stratum 11, it appears that a value of  $n = 4$  transects/stratum was used (for both the mean and the s.e.), rather than the correct  $n = 2$ . The third error concerns the parenthetic values in table 1, which are not labelled. The values presented are  $2 \times$  s.e., but it is clear from the way they are used to produce the corresponding parenthetic values in table 1 (which are labelled as s.e.s) that they are intended to be s.e.s. When these three errors are corrected the last line of table 1 becomes 1.0 (1.00), 1.25 (0.25), and 2.25 (0.25).

Dividing these numbers by 0.05 (the transect area in ha) produces corrected values for the first column of table 2: 20 (20), 25 (5), and 45 (5). Multiplying this column by the stratum areas produces corrected values for the population estimates (number of breeding pairs) in the penultimate column of table 2: 200 (200), 250 (50), and 900 (100). Summing these estimates produces an overall estimate of 1350 breeding pairs with an s.e. of 229 (note that s.e.s should be added as squares, i.e.,  $229 = (200^2 + 50^2 + 100^2)^{0.5}$ ; Scofield's s.e. for his overall estimate is a simple sum of his stratum s.e.s).

## Appendix 2: Detailed data for census grids and transect counts

This appendix contains the detailed data used in the estimation of abundance in Section 2.2.3 based on census grids (see Figure 3, Table 4) and transect counts (see Figure 5, Table 6).

**Table A2.1: Census grid burrow counts, by grid, type (br, breeding; nbr, non-breeding; emp, empty), and year.**

Grid	Year	Number of burrows								
		Kauri Dam			Palmers Track			South Fork		
		emp	br	nbr	emp	br	nbr	emp	br	nbr
G1	1996	1	10	4	3	7	3	2	5	4
G1	1997	1	10	5	0	13	6	1	12	2
G1	1998	0	8	9	0	13	7	1	11	3
G1	1999	1	12	6	1	15	6	0	11	5
G1	2000	3	11	8	1	18	5	1	10	6
G1	2001	1	12	9	0	16	9	3	10	4
G1	2002	4	11	8	1	19	5	4	8	5
G1	2003	2	16	5	3	15	7	4	6	7
G1	2004	3	18	2	3	14	8	6	7	4
G1	2005	1	17	7	5	14	7	4	11	3
G1	2006	3	20	2	6	16	4	5	11	2
G1	2007	3	16	6	3	20	4	1	13	4
G1	2008	3	15	7	6	17	4	0	10	8
G1	2009	5	16	5	2	20	5	3	10	7
G2	1999	0	15	4	0	10	1	1	2	1
G2	2000	0	16	5	0	10	1	1	1	2
G2	2001	0	13	9	0	10	1	1	3	0
G2	2002	1	16	6	0	10	1	0	3	1
G2	2003	2	16	5	2	8	2	0	3	6
G2	2004	4	16	4	1	7	4	5	2	2
G2	2005	3	16	6	2	7	4	2	4	6
G2	2006	6	15	4	3	9	1	5	7	0
G2	2007	2	19	4	1	9	3	1	4	7
G2	2008	5	17	3	0	8	5	0	6	6
G2	2009	1	20	5	2	9	3	5	6	1
G3	2000	2	3	0	0	9	0	1	3	0
G3	2001	1	3	3	2	6	2	0	3	1
G3	2002	1	4	2	3	6	1	0	4	1
G3	2003	1	3	3	2	6	3	1	4	0
G3	2004	2	4	1	4	7	1	1	3	1
G3	2005	2	4	1	6	5	5	1	4	0
G3	2006	2	4	1	9	7	0	1	4	0
G3	2007	1	5	1	6	7	3	1	3	1
G3	2008	1	4	2	9	5	2	1	3	1
G3	2009	2	4	2	5	6	5	1	5	0

**Table A2.2: Breakdown of transect lengths and burrow counts by stratum (non, non-petrel habitat; lo, poor grade; med, medium grade; hi, high grade – see Figure 4) and burrow type (br, breeding; nbr, non-breeding; emp, empty).**

Transect	Transect length (m)				Number of burrows									
	total	non	lo	med	hi	in lo stratum			in med stratum			in hi stratum		
						br	nbr	emp	br	nbr	emp	br	nbr	emp
LT1	400	0	0	308	92	0	0	0	2	2	0	4	2	0
LT6	130	0	0	47	83	0	0	0	0	2	0	2	1	0
LT7	200	40	36	124	0	0	0	0	0	1	1	0	0	0
LT8	400	53	44	303	0	0	0	0	6	3	1	0	0	0
LT9	320	17	86	166	51	0	0	0	2	3	0	2	1	0
LT10	400	0	0	116	284	0	0	0	1	0	0	13	6	0
LT11	400	6	265	129	0	2	0	0	1	1	0	0	0	0
LT12	380	34	123	115	109	0	0	0	2	2	0	2	1	0
LT13A	150	0	0	128	22	0	0	0	1	2	1	2	1	0
LT14	138	0	104	34	0	0	0	0	2	0	0	0	0	0
LT15	120	0	0	120	0	0	0	0	2	1	0	0	0	0
LT16	110	0	27	83	0	0	0	0	1	0	1	0	0	0
LT17	400	0	26	361	13	0	0	0	7	3	0	1	0	0
LT18	400	22	74	193	111	0	0	0	1	3	0	4	1	0
LT19	250	0	156	69	25	0	0	0	0	0	0	0	0	0
LT20	190	0	0	133	57	0	0	0	1	1	0	1	1	0
LT24	180	24	78	78	0	0	0	0	3	1	0	0	0	0
LT25	400	0	0	19	381	0	0	0	1	0	0	8	9	2
LT26	400	0	20	245	135	0	0	0	6	2	1	5	2	0
LT31	170	7	95	68	0	0	0	0	1	0	0	0	0	0
LT37	150	0	3	52	95	0	0	0	4	0	0	2	2	0
LT38	400	0	76	178	146	0	0	0	3	1	0	2	1	1
LT40	330	34	122	174	0	1	2	0	2	4	1	0	0	0
LT41	400	0	0	288	112	0	0	0	4	6	0	2	1	0
LT93	330	35	96	199	0	0	0	0	3	0	0	0	0	0
LT97	320	35	90	195	0	0	0	0	3	1	0	0	0	0

### Appendix 3: Edge effect calculations

This appendix provides some documentation of the calculations behind Figure 6, which demonstrates the edge effect associated with the random transect survey carried out in the present study. Also shown, in Figure A3.2, is how this edge effect lessens when the transect length is reduced.

The R function, ‘Pinclbur’, listed below calculates the probability,  $P$ , that a burrow at location  $(x_0, y_0)$  will lie inside a transect of maximum length  $R$  and width  $2w$  in the rectangle between  $(0,0)$  and  $(X,Y)$ , if the transect is generated by selecting a random starting point within the rectangle and a random direction (the transect length will be less  $R$  if it reaches a boundary of the rectangle). Figure 6 was generated by evaluating this probability at a grid of points inside the study area and using the R function ‘contour’ to plot contours of the probabilities, expressed as a percentage of the maximum probability (which occurs at the centre of the rectangle). For this figure,  $X = 560$ ,  $Y = 625$ ,  $R = 400$ , and  $w = 2$ .

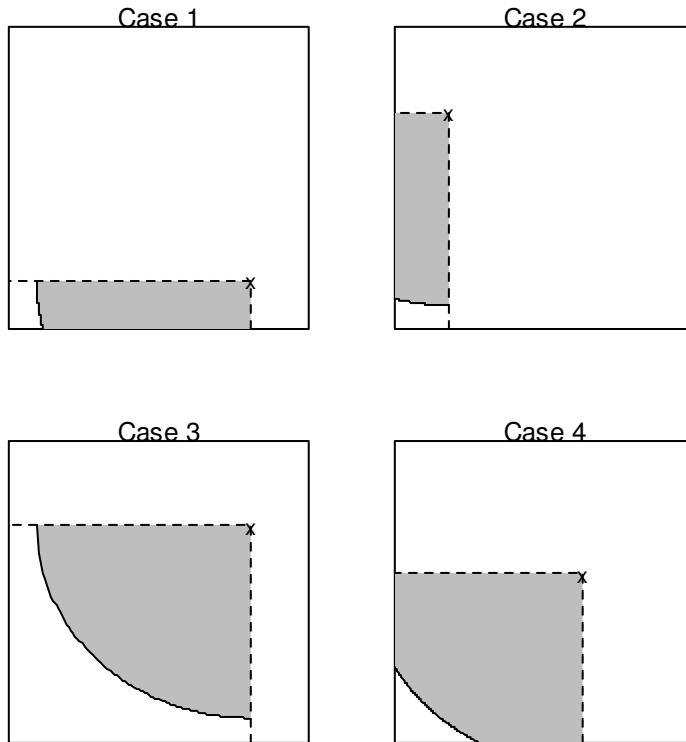
The probability may be written as  $P = (1/XY) \int_0^R h(r) A'(x_0, y_0, r) dr$ , where  $h(r)$  is the probability that a random transect starting at distance  $r$  from a burrow will include that burrow,  $A(x_0, y_0, r)$  is the area of the intersection of the rectangle and a circle of radius  $r$  centred at  $(x_0, y_0)$ , and  $A'$  is the derivative of  $A$  with respect to  $r$ .

Evaluation of function  $h$  is straightforward:

$$h(r) = \begin{cases} (1/\pi) \sin^{-1}(w/r) & r > w \\ 0.5 & r \leq w \end{cases}$$

The evaluation of  $A'$  is much more complex, and we provide only a brief guide to the steps involved. It is calculated as a sum of four parts, which correspond to the four quadrants of the rectangle bounded by the horizontal line  $x = x_0$  and the vertical line  $y = y_0$ . Within each of these quadrants, the equation used for  $A'$  depends on how, if at all, the circle of radius  $r$  centred at  $(x_0, y_0)$  intersects the parts of the rectangle boundary within that quadrant. There are five ways that intersection can occur. Four of these are illustrated in Figure A3.1, and these correspond, in that order, to the four calculations of the variable ‘sel’ in the function ‘Aprimefn’ defined inside ‘Pinclbur’. The fifth case, which occurs when  $(x_0, y_0)$  lies close to the corner, so that the boundary of the circle lies wholly outside the quadrant, need not be considered, because for this case  $A' = 0$ .



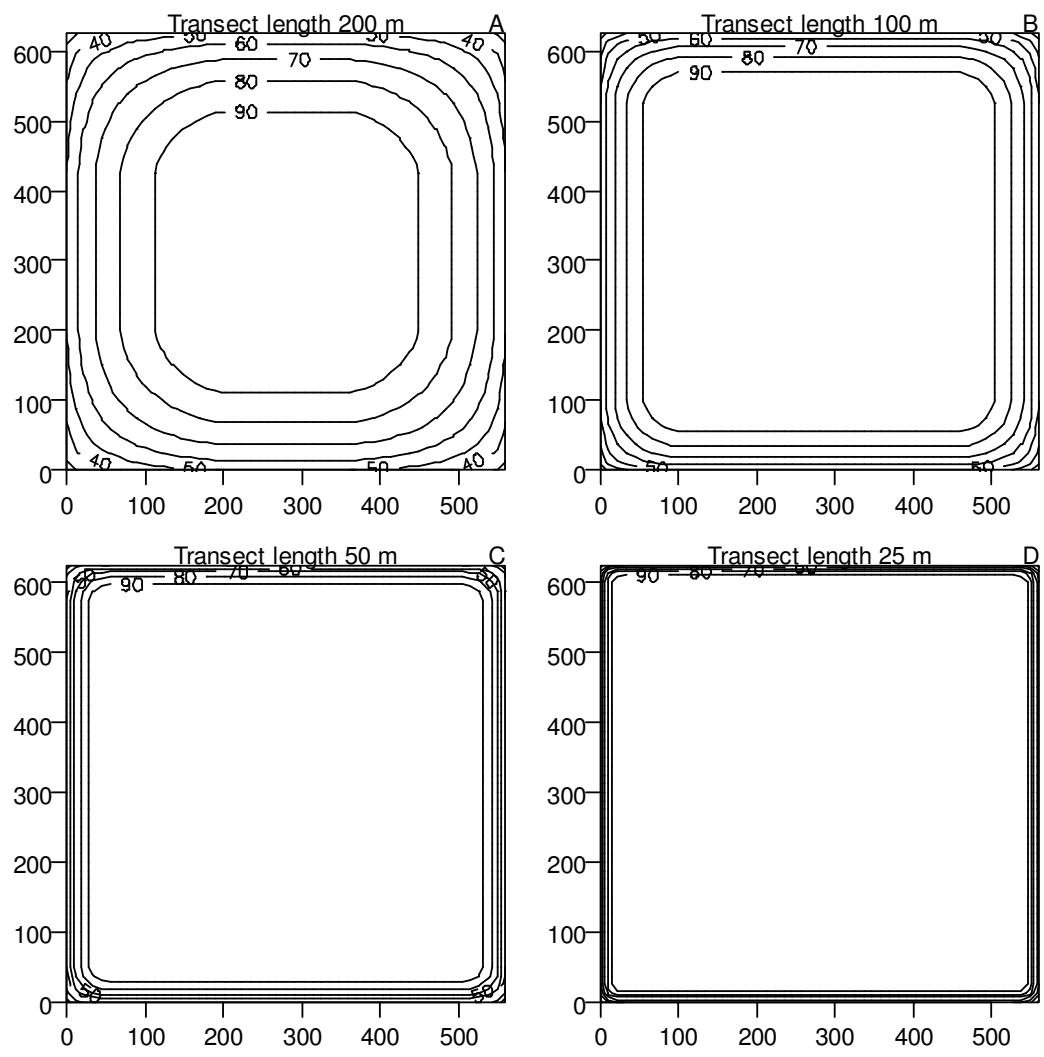


**Figure A3.1:** Illustration of the four cases considered in evaluating the part of the function  $A'$  associated with the lower left quadrant of the rectangular region. The point  $(x_0, y_0)$  is plotted as 'x' and the shaded area is the part of the area  $A(x_0, y_0, r)$  that lies within the quadrant.

```

Pinclbur <- function(x0,y0,X,Y,R,w){
  Aprimefn <- function(u,v,U,V,svec){
    out <- rep(0,len(svec))
    for(i in 1:4){
      u2 <- ifelse(i<3,u,U-u)
      v2 <- ifelse(is.in(i,2:3),V-v,v)
      sel <- u2>=svec & svec>v2
      out[sel] <- out[sel]+svec[sel]*(0.5*pi-acos(v2/svec[sel]))
      sel <- v2>=svec & svec>u2
      out[sel] <- out[sel]+svec[sel]*(0.5*pi-acos(u2/svec[sel]))
      sel <- u2>=svec & v2>=svec
      out[sel] <- out[sel]+svec[sel]*0.5*pi
      sel <- u2<svec & v2<svec & (u2^2+v2^2)>(svec^2)
      out[sel] <- out[sel]+svec[sel]*(0.5*pi-acos(v2/svec[sel])-
        acos(u2/svec[sel]))
    }
    out
  }
  fn <- function(rvec,x0,y0,X,Y,R,w){
    h <- asin(w/ifelse(rvec>w,rvec,w))/pi
    Aprime <- Aprimefn(x0,y0,X,Y,rvec)
    out <- h*Aprime/(X*Y)
    out
  }
  out <- integrate(fn,0,R,x0=x0,y0=y0,X=X,Y=Y,R=R,w=w)$value
  out
}

```



**Figure A3.2:** Demonstration of how the edge effect, demonstrated for transects of length 400 m in Figure 6, changes for different transect lengths: A 200 m; B, 100 m; C 50 m; and D, 25 m. Each panel shows contours of the probability that a point in the study area will lie within a random transect, expressed as a percentage of the maximum probability (which occurs at the centre of the study area). Values on the x- and y-axes are distances (in m) from the southeast corner of the study area.



```

parameter_names Prjuv Prpbr Prnbr Prfbr Prsbr Proth
## USER-DEFINED BASE PARAMETERS
@base_parameter
  name Const1
  values 1
@base_parameter
  name Psuccess
  values 0.7
@base_parameter
  name juvsurv
  values 0.95
## Next block only for BPET6p1, 6p3, 6p4
{@base_parameter
  name pbrsurv
  values 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
  year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007
}
## Next block only for BPET6p, 6p1, 6p2, 6p3
@base_parameter
  name nbrsurv
  values 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
  year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007
## Next block only for BPET6p, 6p1, 6p2, 6p3, 6p4
@base_parameter
  name brsurv
  values 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
  year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007
## Next block only for BPET6p5
{@base_parameter
  name adsurv
  values 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
  year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007
}
@base_parameter
  name Plstapp6
  values 0.1
@base_parameter
  name oddsmult
  values 3
@base_parameter
  name Pappstd
  values 0.5
@base_parameter
  name Pbrlst
  values 0.1
@base_parameter
  name Pbrstd
  values 0.5
@base_parameter
  name Tfbrbr
  values 0.5
@base_parameter
  name Tsbrbr
  values 0.5
@base_parameter
  name Tnbrbr
  values 0.5
@base_parameter
  name Tpbrbr
  values 0.5
@base_parameter
  name Prjuv
  values 0
@base_parameter
  name Proth
  values 0
## Next block only for BPET6p2, 6p3, 6p5
@base_parameter
  name Prpbr
  values 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
  year_blocks 1996 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
@base_parameter
  name Prnbr
  values 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
  year_blocks 1996 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
@base_parameter
  name Prfbr

```

```

        values      0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
        year_blocks 1996 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
@base_parameter
  name Prsbr
  values      0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9 0.9
  year_blocks 1996 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
##      USER-DEFINED DERIVED PARAMETERS (SAME FOR ALL RUNS)
@derived_parameter
  name Nrec
  formula     1000
## Define Ppbrx
@derived_parameter
  name Ppbr4
  formula     P1stapp4*Pappstd*(1-Pbr1st)
@derived_parameter
  name Ppbr5
  formula     P1stapp5*Pappstd*(1-Pbr1st)
@derived_parameter
  name Ppbr6
  formula     P1stapp6*Pappstd*(1-Pbr1st)
@derived_parameter
  name Ppbr7
  formula     P1stapp7*Pappstd*(1-Pbr1st)
@derived_parameter
  name Ppbr8
  formula     P1stapp8*Pappstd*(1-Pbr1st)
@derived_parameter
  name Ppbr9
  formula     P1stapp9*Pappstd*(1-Pbr1st)
## Define Pfbrx
@derived_parameter
  name Pfbr4
  formula     P1stapp4*Pappstd*Pbr1st*(1-Psuccess)
@derived_parameter
  name Pfbr5
  formula     P1stapp5*Pappstd*Pbr1st*(1-Psuccess)
@derived_parameter
  name Pfbr6
  formula     P1stapp6*Pappstd*Pbr1st*(1-Psuccess)
@derived_parameter
  name Pfbr7
  formula     P1stapp7*Pappstd*Pbr1st*(1-Psuccess)
@derived_parameter
  name Pfbr8
  formula     P1stapp8*Pappstd*Pbr1st*(1-Psuccess)
@derived_parameter
  name Pfbr9
  formula     P1stapp9*Pappstd*Pbr1st*(1-Psuccess)
@derived_parameter
  name Pfbr10
  formula     Pappstd*(1-Psuccess)
## Define Psbrx
@derived_parameter
  name Psbr4
  formula     P1stapp4*Pappstd*Pbr1st*Psuccess
@derived_parameter
  name Psbr5
  formula     P1stapp5*Pappstd*Pbr1st*Psuccess
@derived_parameter
  name Psbr6
  formula     P1stapp6*Pappstd*Pbr1st*Psuccess
@derived_parameter
  name Psbr7
  formula     P1stapp7*Pappstd*Pbr1st*Psuccess
@derived_parameter
  name Psbr8
  formula     P1stapp8*Pappstd*Pbr1st*Psuccess
@derived_parameter
  name Psbr9
  formula     P1stapp9*Pappstd*Pbr1st*Psuccess
@derived_parameter
  name Psbr10
  formula     Pappstd*Psuccess
## Define Pothx
@derived_parameter
  name Poth4
  formula     P1stapp4*(1-Pappstd)

```

```

@derived_parameter
  name Poth5
  formula      P1stapp5*(1-Pappstd)
@derived_parameter
  name Poth6
  formula      P1stapp6*(1-Pappstd)
@derived_parameter
  name Poth7
  formula      P1stapp7*(1-Pappstd)
@derived_parameter
  name Poth8
  formula      P1stapp8*(1-Pappstd)
@derived_parameter
  name Poth9
  formula      P1stapp9*(1-Pappstd)
@derived_parameter
  name Poth10
  formula      1-Pappstd
## Define Pjvx
@derived_parameter
  name Pjv4
  formula      1-Poth4-Ppbr4-Pfbr4-Psbr4
@derived_parameter
  name Pjv5
  formula      1-Poth5-Ppbr5-Pfbr5-Psbr5
@derived_parameter
  name Pjv6
  formula      1-Poth6-Ppbr6-Pfbr6-Psbr6
@derived_parameter
  name Pjv7
  formula      1-Poth7-Ppbr7-Pfbr7-Psbr7
@derived_parameter
  name Pjv8
  formula      1-Poth8-Ppbr8-Pfbr8-Psbr8
@derived_parameter
  name Pjv9
  formula      1-Poth9-Ppbr9-Pfbr9-Psbr9
## Define Tpbrxxx
@derived_parameter
  name Tpbrpbr
  formula      1-Tpbrbr
@derived_parameter
  name Tpbrfbr
  formula      Tpbrbr*Pbrstd*(1-Psuccess)
@derived_parameter
  name Tpbrsbr
  formula      Tpbrbr*Pbrstd*Psuccess
@derived_parameter
  name Tpbroth
  formula      Tpbrbr*(1-Pbrstd)
## Define Tnbrxxx
@derived_parameter
  name Tnbrnbr
  formula      1-Tnbrbr
@derived_parameter
  name Tnbrfbr
  formula      Tnbrbr*(1-Psuccess)
@derived_parameter
  name Tnbrsbr
  formula      Tnbrbr*Psuccess
## Define Tfbrxxx
@derived_parameter
  name Tfbrnbr
  formula      1-Tfbrbr
@derived_parameter
  name Tfbrfbr
  formula      Tfbrbr*(1-Psuccess)
@derived_parameter
  name Tfbrsbr
  formula      Tfbrbr*Psuccess
## Define Tsbrxxx
@derived_parameter
  name Tsbrnbr
  formula      1-Tsbrbr
@derived_parameter
  name Tsbrfbr
  formula      Tsbrbr*(1-Psuccess)

```

```

@derived_parameter
  name Tsbrsbr
  formula Tsbrbr*Psuccess
## Define P1stapp4-5,7-9
@derived_parameter
  name P1stapp4
  formula 1/(1+(1-P1stapp5)*oddsmult/P1stapp5)
@derived_parameter
  name P1stapp5
  formula 1/(1+(1-P1stapp6)*oddsmult/P1stapp6)
@derived_parameter
  name P1stapp7
  formula 1/(1+(1-P1stapp6)/(oddsmult*P1stapp6))
@derived_parameter
  name P1stapp8
  formula 1/(1+(1-P1stapp7)/(oddsmult*P1stapp7))
@derived_parameter
  name P1stapp9
  formula 1/(1+(1-P1stapp8)/(oddsmult*P1stapp8))

```

## A4.2 Population file for BPET7

This file was exactly the same as for model BPET6p2 except that the @derived\_parameter command block for Nrec was changed to the following.

```

@derived_parameter
  name Nrec
  step 1
  formula 0.5*Nsbr*(1+Noth/(Nnbr+Nfbr+Nsbr))

```

## A4.3 Estimation file for BPET6p2

The following file is the estimation file for model BPET6p2, except that the mark-recapture observations (which would fill 32 pages!) have been removed to conserve space. The file includes comments showing how it should be modified to apply to the variants of this model described in Table 26.

```

@estimator Bayes # Use the Bayes estimation method
@max_iters 2500
@max_evals 4000
@grad_tol 1e-6
@profile
  parameter juvsurv
  n 5
  l 0.7
  u 1.0
@mark_recapture bandfrom1996
  step 1
  proportion_mortality 0
  resight_p Presight
  composite_class_indices 16 17 18 19
  composite_class_16 11 12
  composite_class_17 12 13 14
  composite_class_18 13 14
  composite_class_19 11 12 13 14
[mark-recapture observations removed to conserve space]
## Next block only for BPET6p1, 6p3, 6p4
{@estimate
  parameter pbrsurv
  lower_bound 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
}
@estimate
  parameter juvsurv
  lower_bound 0
  upper_bound 1
  prior uniform

```

```

## Next block only for BPET6p, 6p1, 6p2, 6p3
@estimate
  parameter nbrsurv
  lower_bound 0 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
## Next block only for BPET6p, 6p1, 6p2, 6p3, 6p4
@estimate
  parameter brsurv
  lower_bound 0 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
## Next block only for BPET6p5
{@estimate
  parameter adsurv
  lower_bound 0 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
}
## Next block only for BPET6p2, 6p3, 6p5
@estimate
  parameter Prpbr
  lower_bound 0 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
@estimate
  parameter Prnbr
  lower_bound 0 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
@estimate
  parameter Prfbr
  lower_bound 0 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
@estimate
  parameter Prsbr
  lower_bound 0 0 0 0 0 0 0 0 0 0 0 0
  upper_bound 1 1 1 1 1 1 1 1 1 1 1 1
  prior uniform
@estimate
  parameter Plstapp6
  lower_bound 0.01
  upper_bound 0.99
  prior uniform
@estimate
  parameter oddsmult
  lower_bound 1
  upper_bound 5
  prior uniform
@estimate
  parameter Pappstd
  lower_bound 0.1
  upper_bound 1.0
  prior uniform
@estimate
  parameter Pbrlst
  lower_bound 0
  upper_bound 1
  prior uniform
@estimate
  parameter Pbrstd
  lower_bound 0
  upper_bound 1
  prior uniform
@estimate
  parameter Tfbrbr
  lower_bound 0
  upper_bound 1
  prior uniform
@estimate
  parameter Tsbrbr
  lower_bound 0
  upper_bound 1
  prior uniform
@estimate
  parameter Tnbrbr

```



```

        lower_bound 0
        upper_bound 1
        prior uniform
@estimate
        parameter Tpbrbr
        lower_bound 0
        upper_bound 1
        prior uniform
@estimate
        parameter Psuccess
        lower_bound 0.3
        upper_bound 1
        prior uniform

```

#### A4.4 Estimation file for BPET7

This file was exactly the same as for model BPET6p2 except that the following two command blocks were added.

```

@abundance census
        years 2005
        step 1
        proportion_mortality 0
        selectivity selbr
        2005 1964
        dist normal
        cv 0.05
@estimate
        parameter initialisation.NO
        prior uniform
        lower_bound 1000
        upper_bound 15000

```

#### A4.5 Parameter estimates for BPET6p2

```

juvsurv 1 nbrsurv 12 brsurv 12 Prpbr 13 Prnbr 13 Prfbr 13 Prsbr 13 Plstapp6 1 oddsmult 1
Pappstd 1 Pbrlst 1 Pbrstd 1 Tfbrbr 1 Tsrbr 1 Tnrbr 1 Tpbrbr 1 Psuccess 1
0.999998 0.819915 0.850706 0.896524 1 0.803498 0.953043 0.807169 0.882463 0.772149 0.999965
0.633696 0.945526 0.864412 0.876852 0.763013 0.939571 0.892697 0.872528 0.846689 0.88602
0.931656 0.939764 0.921343 0.965509 0.0959561 0.570183 0.584002 0.683956 0.571304 0.526355 1
0.482648 0.681918 0.555854 0.235523 0.528177 0.618784 0.264799 0.261218 0.306004 0.261958
0.283414 0.283801 0.441098 0.17302 0.247079 0.192342 0.211613 0.147697 0.272399 0.999995
0.843994 0.97497 1 0.932507 1 1 0.829088 0.629318 1 0.538179 0.599735 0.369833 1 1 0.98844 1 1
0.918606 1 0.877176 0.616154 0.782889 0.875433 0.732175 1 0.48959 1.58628 0.119805 0.0299616
0.660485 0.780598 0.846716 0.446674 0.764866 0.769633

```

#### A4.6 Parameter estimates for BPET7

```

initialisation.NO juvsurv 1 nbrsurv 12 brsurv 12 Prpbr 13 Prnbr 13 Prfbr 13 Prsbr 13 Plstapp6
1 oddsmult 1 Pappstd 1 Pbrlst 1 Pbrstd 1 Tfbrbr 1 Tsrbr 1 Tnrbr 1 Tpbrbr 1 Psuccess 1
1228.98 1 0.910293 0.853713 0.897397 1 0.804946 0.973112 0.811397 0.901559 0.787217 1 0.641885
0.946446 0.892201 0.87766 0.764334 0.938339 0.89087 0.871645 0.844895 0.884013 0.932149
0.938609 0.922666 0.965825 0.0869972 0.512434 0.540131 0.604599 0.550408 0.418028 1 0.449128
0.668832 0.525752 0.244637 0.507798 0.631182 0.264338 0.264104 0.313624 0.268985 0.292409
0.304268 0.447784 0.177238 0.246493 0.195617 0.214135 0.148382 0.269847 0.999999 0.836047
0.974899 1 0.93427 0.999999 1 0.825222 0.625746 1 0.534492 0.597101 0.368036 1 1 0.985144 1
0.994501 0.911529 1 0.872174 0.611886 0.776117 0.868448 0.727567 1 0.498288 1.57573 0.117517
0.0294258 0.67766 0.785075 0.849387 0.433562 0.760258 0.769983

```