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Tini a Tangaroa

Demographic assessment of black petrels (*Procellaria parkinsoni*) on Great Barrier Island (Aotea Island)

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EXECUTIVE SUMMARY

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The management of incidental fishery-related mortalities to New Zealand seabird species is guided by a multi-species spatial risk assessment, which has consistently identified takoketai/black petrel (*Procellaria parkinsoni*) as the highest risk species. The spatial risk assessment utilises estimates of key demographic rates for the Great Barrier Island (Aotea Island) population, including recent annual survival rate and age at first breeding, obtained from demographic assessment models. New demographic assessment models were developed using updated mark-recapture data and population estimates from stratified transect surveys.

The previous base case model for this population was updated with new field-based mark recapture observations and a population size estimate from 2016. Alternative model runs differed with respect to their parameterisation of pre-breeder survival (i.e., grouped with immature survival, previously grouped with non-breeders) and recapture probability of breeders (i.e., this model run assumed all were seen, previously estimated). In addition, a greatly simplified model run ignored observations collected prior to an individual's first breeding. All models produced good fits to mark-recapture observations and adequate fits to line transect population size estimates. Model estimates of adult survival (i.e., of individuals that have bred) ranged from 0.857 (95% CI = 0.832–0.872) for the simple model to 0.883 (95% CI = 0.872–0.902) for the previous base case model structure. Survival rates for pre-breeders were not well determined, because the model could not distinguish mortality of this stage from emigration (i.e., birds born in the study area that did not return to breed there). The model assuming all breeders were seen produced plausible estimates of annual breeding rate and produced the best model fits to mark-recapture data (the new base case model), though estimates of adult survival (0.880; 95% CI = 0.871–0.888) and age at first breeding (6.89; 95% CI = 6.59–7.16) were very similar to alternative models.

A conflict between mark-recapture and line transect data with respect to population trajectory is likely to be caused by slower population growth in high-quality habitat (where most mark-recapture study bird burrows are located) relative to low-quality habitat in recent years. Further research could account for this by either: collecting mark-recapture information in low quality habitat; or re-weighting the transect data based on the habitat quality of the study burrows from which the mark-recapture data were collected. Additionally, once there are sufficient observations of mark-recapture study birds breeding outside the study area, a two-area model could be considered to account for the potentially biasing effect of emigration on adult survival estimates.

1. INTRODUCTION

1.1 Background

Black petrels or takoketai (*Procellaria parkinsoni*) are medium-sized (c. 700 g), burrow-nesting seabirds that breed during the austral summer in colonies located on Great Barrier Island (Aotea Island) (GBI) and Te Hauturu-o-Toi/Little Barrier Island (LBI) in the Hauraki Gulf, near Auckland, New Zealand (Figure 1). The breeding season starts in October, when males prepare burrows and try to attract a mate. Eggs are laid in late November/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 late April/May. During the breeding season, adults forage along the shelf break of the north coast of the North Island and into deeper oceanic waters (Freeman et al. 2010). Outside the breeding season, black petrels migrate to western waters off Central and South America (Cabezas et al. 2012). Black petrels forage both on the surface and by making shallow dives to a maximum of 34 m depth (Bell 2016), preying mostly on squid and occasionally on tunicates, crustaceans, cyclostomes, and fish (Imber 1976). Breeding seabirds are central-place foragers, meaning that their foraging efforts are restricted in space by the need to return to their nests (Ropert-Coudert et al. 2004). Black petrels formerly bred on many forested mainland mountain ranges in the North Island and northwest South Island (Imber 1987). A relict population totalling about 15 000 birds is now confined to GBI and LBI with most (c. 4500 pairs) breeding on GBI and c. 620 pairs on Little Barrier (Richard & Abraham 2015, Bell et al. 2016a). The species is currently listed as Nationally Vulnerable by the New Zealand Threat Classification system (Robertson et al. 2013).

The population risk of direct fishery-related mortalities on New Zealand seabirds is estimated by a multi-species spatially-explicit fisheries risk assessment (SEFRA) model. The SEFRA model estimates species-specific annual deaths and relates them to a population-sustainability threshold (PST) – the annual number of individuals that can be caught as bycatch without threatening the maintenance of the population above 50% of carrying capacity with high certainty (Richard et al. 2011, Richard & Abraham 2013, Richard et al. 2015). According to this analysis and the above criterion, black petrels were ranked as the highest risk seabird species to fishery-related mortality around NZ (Richard & Abraham 2020).

1.2 Demographic assessment

The latest iteration of the seabird risk assessment (Richard & Abraham 2020) utilises a specified adult survival as a constraint on the total numbers of annual potential fatalities that can occur. That assessment used a current adult survival of 0.90, estimated by Bell et al. (2011), which used mark-recapture and population size estimates up to 2010. This was found to constrain adult captures for this species, markedly reducing the risk ratio posterior (Richard & Abraham 2020). Recent field studies of black petrels on GBI have estimated a steady increase in numbers since a low point in 2003/04 (hereafter referred to by the end year, i.e., 2004) (Bell et al. 2016b), suggesting that adult survival may have increased. Estimates of adult survival from mark-recapture data only using MARK (White & Burnham 1999) are consistent with an increasing trend in adult survival through time (Bell et al. 2016b).

The specific research objective of this study was to update the previous population modelling of black petrels at GBI to produce an updated population trend and estimate of adult survival. In response, this study updated the previous base case demographic assessment model for the GBI population with new mark-recapture observations collected during field seasons from 2015 to 2017 to update the current adult survival estimate for the seabird risk assessment. In addition, the sensitivity of key demographic rates was explored in response to new model structures informed by improved understanding of black petrel behaviour and population dynamics at GBI.

2. DATA AND METHODS

2.1 Field-based methods and population estimates

Field-based mark-recapture observations and population size estimates of black petrels were obtained from a 35 ha study area around the summit of Mount Hobson (Hirakimata) on GBI and study burrows located near to a system of walking tracks (see Figure 1) (Bell et al. 2007). Between 1996 and 2001, field observations were collected during two visits to the study area each year (during egg hatching in January/February and check fledging in April), and this was extended to three visits each year since 2002 (including a visit during egg laying in the previous December) (see Table 1). During the first visit (i.e., December), the breeding status of study burrows was checked, and any adults were identified or banded and returned to the burrow. During the second trip in mid-late January to February, any adults present were identified or banded and returned to the burrow and the breeding status of study burrows was confirmed with the presence of eggs, eggshell fragments, or chicks noted, and the absence of this evidence used to identify non-breeding birds. The study burrows were monitored again in April and all surviving fledgling chicks were banded. This information was then used to determine the individual breeding success of banded birds.

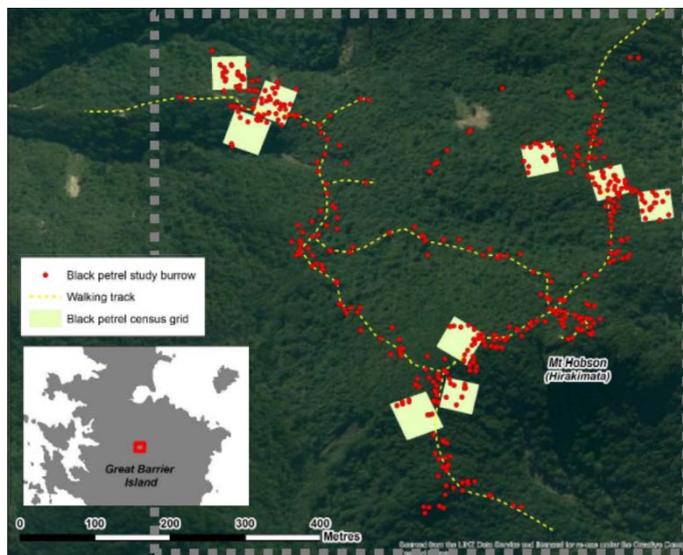


Figure 1: The location of the black petrel (*Procellaria parkinsoni*) study burrows and census grids within the study area on Great Barrier Island (Aotea Island) (left) with spatial extent of right-hand plot highlighted by grey dashed line; and example of line transect survey random transects and habitat grades from the 2010 survey (right). These figures were modified from figure 1 of Bell et al. (2016b) and figure 5 of Bell et al. (2011), respectively. A spatial plan of the 2016 line transect survey is shown in Appendix 2.

Table 1: The timing of visits to the study area in each breeding season. Note that, for example, the 1995–96 season is labelled 1996. In the 2009 season only, the study area was also visited in October to check during the pre-mating phase.

Field seasons	Dec (egg laying)	Jan/Feb (hatching)	Apr (fledging)
1996 – 2001	No	Yes	Yes
2002 – 2017	Yes	Yes	Yes

Three types of demographic data were made available to the present study:

1. census grid burrow counts,
2. transect survey population estimates, and
3. mark-recapture observations of banded birds (in study burrows).

Census grid burrow counts

Census grid burrow counts are annual counts of all black petrel burrows in nine 40 m x 40 m census grids within the study area (as shown as yellow squares in Figure 1). The first group of three census grids was established in 1996, in each of three habitat types that had a historical presence of black petrels, with different vegetation types and topography, and that were near known launch sites (Bell et al. 2007). A second census grid was established in each block in 1999, and third added in 2000, giving nine in all, or three in each of three blocks. The second and third grids were located randomly within the same habitat areas as the first grid. Their location and extent have remained the same throughout the study period after being established. In each census year, each known burrow in a grid was checked and classified as breeding, non-breeding, or empty during the survey trips in December and again in January (Bell et al. 2016b). Searches through the grids occur annually to determine whether any new burrows have been created by black petrels (or burrows that may have been missed during earlier surveys). Census grids were mostly located in high-quality habitat areas and, so, resulting counts have historically not been incorporated into demographic assessments.

Transect survey population estimates

Stratified line transect surveys of black petrel population size were undertaken in 2005 (Bell et al. 2007), 2010 (Bell et al. 2011), 2013 (Bell et al. 2013) and 2016 (Bell et al. 2018), to estimate black petrel population size across high-, medium-, and low-grade habitat areas. A total of 26 random transects were completed in 2005, 2010, and 2013, and 20 were completed in 2016. All transects were surveyed using the same methods reported by Bell et al. (2007). Breeding burrows were treated as having two resident birds present and any non-breeding burrows were treated as having 1.25 birds present (because in any non-breeding burrow there is a 25% chance of capturing more than one bird in the burrow when the resident male attracts a female to that burrow).

The line transects were stratified into four habitat grades along the transect length: high-grade petrel habitat (4.67 ha), medium-grade (15.30 ha), low-grade (13.56 ha), and non-petrel habitat (1.75 ha) (Bell et al. 2013) (see Figure 1). In June 2014, a severe storm event caused significant damage to the black petrel study area (Bell et al. 2016b). No study burrows were affected, but major slips within the boundaries of the study site caused a reduction in the spatial extent of suitable breeding habitat. Consequently, for the 2016 survey, the area of medium-grade, low-grade, and non-petrel habitat was updated to 14.86 ha, 12.69 ha, and 3.06 ha, respectively. These updated habitat areas were used in the latest population estimation (i.e., 2016 onwards).

Burrow densities were calculated for each habitat grade within each transect (i.e., there were four means for each transect). The breeding population for each habitat quality class was estimated as the mean density across all transects in that habitat grade multiplied by the respective area (Francis & Bell 2010). Combined estimates across all habitat types were obtained for the four surveys and fitted within demographic models developed by this study.

Mark-recapture observations

During each visit to the study area, a series of study burrows (see Figure 1) were inspected several times during three visits in November/December, January/February, and April/May, corresponding with the early-incubation, late-incubation/early-chick rearing and late-chick rearing phases of the black petrel breeding season, respectively. During each visit, each study burrow was visited between one and ten times to determine the breeding status (i.e., breeder or non-breeder) and breeding outcome (i.e., successful or unsuccessful) for each burrow, and to record the adult occupants of each burrow so that breeding status could be attributed to individual band ID. Multiple visits were also required to identify partner birds and non-breeding birds using burrows. All non-banded birds encountered were banded.

2.2 Demographic assessment methodology

Model structure

All demographic assessment models were developed using NIWA’s SeaBird demographic assessment software (Francis & Sagar 2012), which provides a flexible modelling platform for trialling variation in model structure and parameterisation. The starting model structure for this assessment (Model 1, “previous base”) was the same as the black petrel model of Francis and Bell (2010), referred to as BPET7, updated by Bell et al. (2014) (both also developed using SeaBird). Model run 1 (previous base model) partitioned the population into 15 states (Table 2) and estimated 18 parameters (Table 3), including 9 states and 4 transition probabilities (Table 4). Some of these parameters were year-varying. Briefly, Model 1 estimated:

- Separate annual survival probabilities of juveniles, non-breeders (which include some pre-breeders) and breeders (non-breeder and breeder survival probabilities were also combined for reporting purposes and referred to as *adult* survival);
- Annual breeding probabilities that were constant with respect to year, with separate estimates contingent on breeding status in the previous year;
- Age at first breeding, also constant with respect to year;
- Separate annual resighting probabilities for different states, that were allowed to vary by year; and
- The breeding population size in 1996, i.e., the first year of mark-recapture data collection.

Table 2: The 15 states in the partition of the population model (in each year every modelled bird is in exactly one of these states).

State label	State number	Description
chick	1	Fledgling chicks in the season of their birth
age 1 – age 9	2 – 10	Juveniles aged 1–9 that have not returned to the breeding area*
pbr	11	Pre-breeders: juveniles which have appeared in the study area but have not yet bred
nbr	12	Adults (birds that have previously bred) in the study area which did not breed in the current year
fbr	13	Adults that bred unsuccessfully in the study area in the current year
sbr	14	Adults that bred successfully in the study area in the current year
oth	15	Adults breeding outside the study area

* In this study “juvenile” is used to identify all individuals that have not yet returned to the study area, though Bell et al. (2016b) specifies juveniles to be all individuals age 1–4 (i.e. prior to first breeding by an individual).

Table 3: Estimated parameters of Model 1. Resighting probabilities were assumed to be zero for juveniles and for adults in state oth. Most parameters were treated as year-invariant, but annual values were estimated for all resighting parameters as well as those for adult survival (nbrsurv, brsurv), except that survival rates for the last year (which are confounded with the resighting rates for the same year) were assumed equal to those for the previous year. Details of how each component of the transition matrix was calculated from the model parameters are given by Francis & Bell (2010).

Parameter	Description
N_0	Initial (1996) size of the adult population in the study area
$P1stapp6$	Probability a bird first appears as an adult in a breeding colony at age 6, given that it survives to that age
oddsmult	The slope of linear relation between $\text{logit}(P1stappa)$ and age a
$Pappstd$	Probability, for a chick, banded in the study area and surviving, that its 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
$Tpbrbr/Tnbrbr/Tfbrbr/Tsbrbr$	The probability that a pre-breeder, non-breeder, failed breeder, or successful breeder in the study area in one year will breed the next year, given that it survives
$Psuccess$	The probability that a bird that breeds is successful (produces a fledgling)
$jursurv/nbrsurv/brsurv$	Annual probability of survival for juveniles and pre-breeders, non-breeders, or breeders
$Prpbr/Prnbr/Prfbr/Prsbr$	The probability of resighting a pre-breeder, non-breeder, failed breeder, or successful breeder

Table 4: Transition matrix for model 1.

	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	P_{jv4}	...	0	P_{br4}	0	P_{fbr4}	P_{sbr4}	P_{oth4}
...
age8	0	0	0	0	0	...	P_{jv9}	P_{pbr9}	0	P_{fbr9}	P_{sbr9}	P_{oth9}
age9	0	0	0	0	0	...	0	0	P_{fbr10}	P_{sbr10}	P_{oth10}	0
pbr	0	0	0	0	0	...	0	T_{prbpbr}	0	T_{pbrfbr}	T_{pbrsbr}	T_{pbroth}
nbr	0	0	0	0	0	...	0	0	T_{nbrnbr}	T_{nbrfbr}	T_{nbrsbr}	0
fbr	0	0	0	0	0	...	0	0	T_{fbrnbr}	T_{fbrfbr}	T_{fbrsbr}	0
sbr	0	0	0	0	0	...	0	0	T_{sbrnbr}	T_{sbrfbr}	T_{sbrsbr}	0
oth	0	0	0	0	0	...	0	0	0	0	0	1

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 determined by parameters $P1stapp6$ and $oddsmult$, and the appearance in the study colony, with probability $Pappstd$, or elsewhere (i.e., state oth) with probability $1-Pappstd$.

This first appearance of the adult 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	$P_{oth10} = 1 - P_{appstd}$
study	adult	fbr	$P_{fbr10} = P_{appstd}(1 - P_{success})$
study	adult	sbr	$P_{sbr10} = P_{appstd} \times P_{success}$

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 P_{brstd}) or elsewhere (with probability $1 - P_{brstd}$). 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	$T_{pbrfbr} = T_{pbrbr} \times P_{brstd}(1 - P_{success})$
study	sbr	$T_{pbrsbr} = T_{pbrbr} \times P_{brstd} \times P_{success}$
other	oth	$T_{pbroth} = T_{pbrbr} \times (1 - P_{brstd})$

Once a bird starts breeding in the study area it moves between states nbr, fbr, and sbr in the same way (and controlled by the same parameters). The model assumes that individuals moving to state oth never leave it. Individuals are rarely observed moving from a study burrow to outside the study area and will tend to return back to the same or another burrow within the study area.

Observations

Only mark-recapture observations and transect survey population estimates were fitted to by demographic assessment models developed by this study. These observations are summarised in Table 5).

Table 5: Summary of observations fit to by GBI population models developed by Francis & Bell (2010), Bell et al. (2014), and developed by this study.

Data type	Francis & Bell (2010)	additional in Bell et al. (2014)	additional in the present report
Mark-recapture			
Year covered	1996–2009	2010–2014	2015–2017
Birds banded as chicks	1 798	862	604
Birds banded as adults	1 507	445	252
Abundance estimation (and CVs)			
No. of breeders in 2005	1 964 (0.10)		
No. of breeders in 2010		1 525 (0.11)	
No. of breeders in 2013		3 248 (0.10)	
No. of breeders in 2016			3 989 (0.11)

Model development process

In addition to Model 1 (the previous base), a number of alternative model parameterisations were trialled in consultation with the Aquatic Environment Working Group; these differ with respect to the parameterisation of: survival of pre-breeders, and whether annual resighting or breeding probabilities were constant or allowed to vary with respect to year. To test whether the year-varying pattern of successful breeders resighting probabilities of Model 1 was driven by the transition between different breeding status. Model 3 fixed the resighting probabilities of the successful breeder to 1. In Model 4, the working group's suggestion to re-assign the annual survival probability of pre-breeders from the non-breeder class to the juvenile class was followed. In addition, a greatly simplified parameterisation ignored observations of individuals prior to first breeding as in Model 2 (Table 6).

Table 6: Model run labels and descriptions for the model runs.

Model type	Model	Description
Base case	1	Base case model, uses the same structure as BPET7 by Francis & Bell (2010) and Bell et al. (2014) with the updated data
Simple model	2	Presence/absence of banded birds only
Fixed resight probability	3	Resight probability fixed at 1 for success breeders
Sensitivity of Model 3	3.1	Model 3, but with combined resight probability of successful and failed breeders
	3.2	Model 3.1, but with a combined survival rate of breeders and non-breeders
	3.3	Model 3.2, but with combined resight probability of prebreeders and non-breeders
Re-classify pre-breeder survival	4	Model 1, but with a re-classified survival rate of pre-breeders into juvenile class.

Candidate models were constructed and fitted to the mark-recapture data, and the most parsimonious model was selected using Akaike's Information Criterion (AIC) (Burnham & Anderson 2004). However, the AIC favours over-parameterisation, which might lead to some implausible model structures. In this assessment, both AIC scores and the biological plausibility of assumptions made by model structures were considered.

Parameter estimation

Survival S_{iy} , is the proportion of black petrels in the i^{th} partition class that survive natural mortality to the end of year y . An observation in time step t in year y can be specified as part-way through the mortality that occurred in that time step. Thus, if p is the proportion of that mortality that had occurred before the observation $n_{ity:p}$ is defined as the number of individuals in the i^{th} class at the time of the observation. Here $n_{ity:p}$ was calculated as the weighted sum:

$$n_{ity:p} = (1-p) n_{ity} + pn'_{ity} = (1-p + pT_{ity})n_{ity}$$

Where n_{ity} and $n'_{ity} (=S_{ity}n_{ity})$ are the numbers before and after the mortality in this year.

Age at first breeding is a function of the probability $P_{br,a}$ of a bird breeding at age a , multiplied by the proportion of the age group P_a .

$$A = \sum_{a=4}^{11} P_{br,a} P_a$$

$$P_{br,6} = cP_{1stbr}(6)$$

$$P_{br,a} = P_{br,a-1} P_{surv,juv} P_{1stbr}(a) (1 - P_{1stbr}(a-1)) / P_{1stbr}(a-1)$$

Where the constant c is adjusted so that $\sum_{a=4}^{11} P_{br,a} = 1$.

Markov chain Monte Carlo (MCMC) model runs

The Metropolis–Hastings algorithm was used. Three independent chains were then run for 200 000 iterations, keeping every 1000th sample. As a preliminary step to improve mixing, the covariance matrix (used to generate the proposal distribution) was recalculated empirically from the first 100 000 iterations, which were then discarded. This step was undertaken twice.

3. RESULTS

3.1 Field observations and relative population estimates

Census grid burrow counts

Figure 2 shows the annual counts of all burrows and breeding burrows in the census and the percentage of burrows used for breeding with the additional data added since the last analysis (from 2011 to 2017), and some revision of the earlier data. Burrow counts (detailed in Appendix 1) were consistently higher in some grids than in others, indicating spatial heterogeneity in burrow density. There was a strong upward trend in the total number of burrows since 2000, which reached a plateau around 2010 (Figure 2). The number of breeding burrows shifted from a lower plateau (at about 78) before 2005 to a higher plateau (at about 92) from 2006 up to 2013. From 2014 to 2017, the number of breeding burrows continued to increase from 91 to 103, which was partially caused by the use of detector dogs in later years. The percentage of burrows used for breeding fluctuated between 56% and 71% across the study period with a mean of $61.89\% \pm 1.0\%$ (1SE) over the study period and no obvious trend.

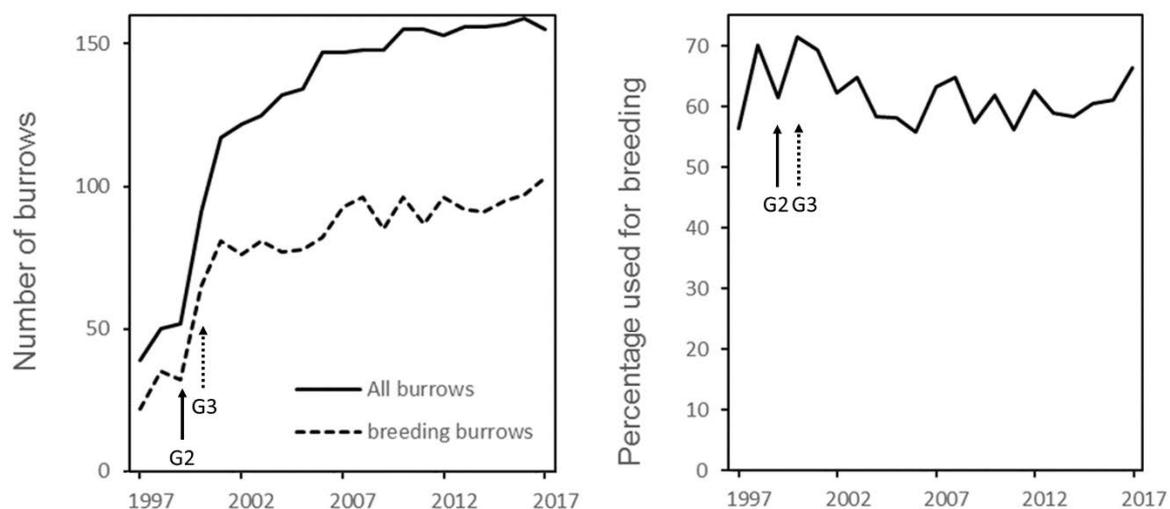


Figure 2: Annual counts of all burrows and breeding burrows in the census (left) and the percentage of burrows used for breeding (right). See Appendix 1 for counts by grid. The arrows marked with G2 and G3 indicate when the 2nd and 3rd set of grids were added to the census burrow count.

Transect survey population estimates

The individual line transect spatial locations and counts for the 2016 survey are detailed in Appendix 2. The total breeding population estimate from the transect survey increased from 3248 individuals (CV = 0.10) in 2013 to 3989 individuals (CV = 0.12) in 2016 (Table 5). However, the increase was much more pronounced in medium-quality habitat, increasing from 1555 individuals (CV = 0.13) in 2013 to 1949 individuals (CV = 0.16) in 2016, compared with 747 individuals (c.v. = 0.06) in 2013 to 1125 individuals (CV = 0.25) in 2016 for high grade habitat (where most mark-recapture study burrows were located) and 945 individuals (CV = 0.22) in 2013 to 915 individuals (CV = 0.21) in 2016 for low grade habitat (Figure 3).

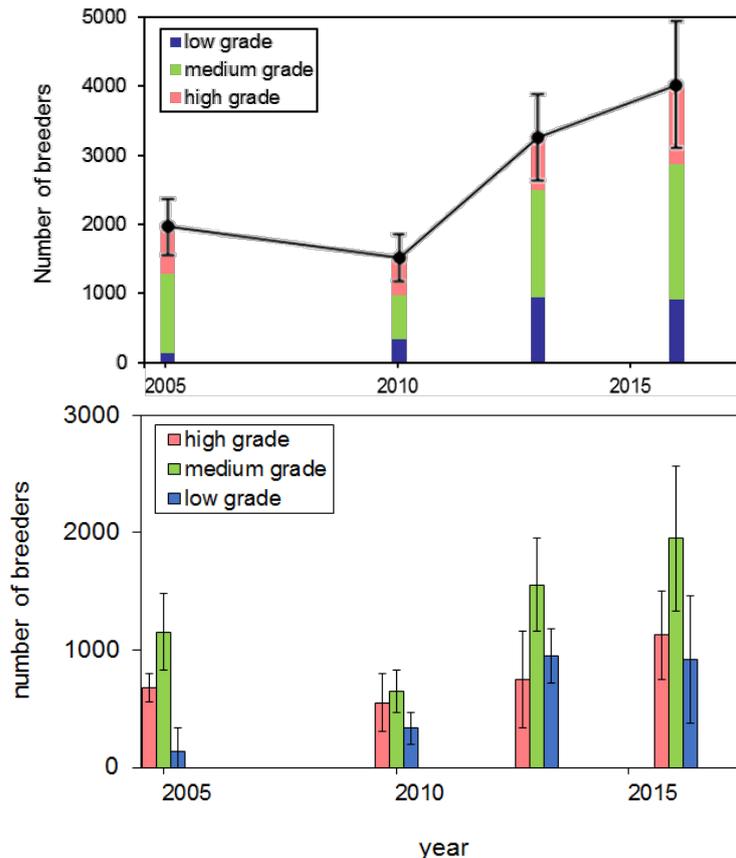


Figure 3: Top panel: total population estimation from the four transect surveys (2005, 2010, 2013, and 2016) for the study area. Bottom panel: population estimation by habitat quality grades. The error bars represent 95% CI of and relative estimations.

Mark-recapture observations

Mark-recapture data were collected from study burrows (see Figure 4) and comprised the resighting histories of 5456 individuals. Eighty-eight birds were banded prior to 1996 (the first resighting season used in this assessment), including individuals banded since 1964. Of these, 83 birds were resighted during the study period (1996 to 2017) and, so, were included in this assessment. Banded birds were either banded as a chick (known age, cumulative $n = 3300$ individuals), or as an adult (unknown age, cumulative $n = 2150$ individuals). An average of 96 ± 8 adults were banded each year. The annual frequency of unknown age bandings has been relatively consistent through time and annual resightings of these birds has increased steadily since 1996 (Figure 5A). By comparison, the frequency of known age (chick) bandings increased around 2005 and subsequent resightings of these birds increased markedly after 2013. (Figure 5B).

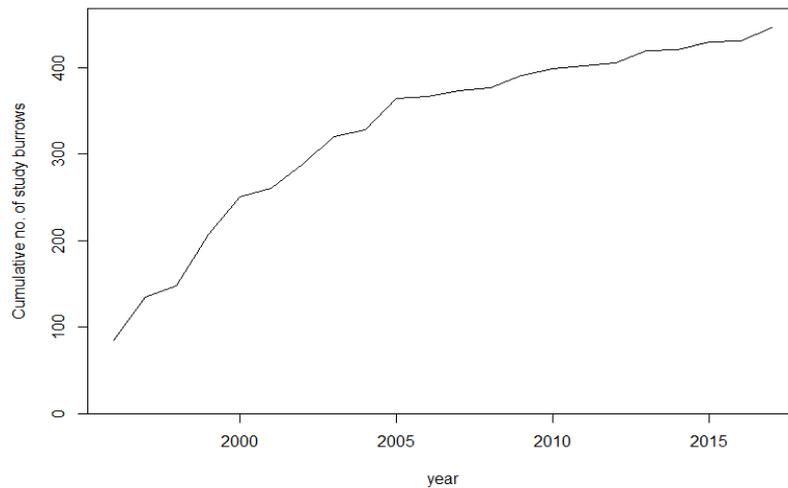


Figure 4: Cumulative number of study burrows.

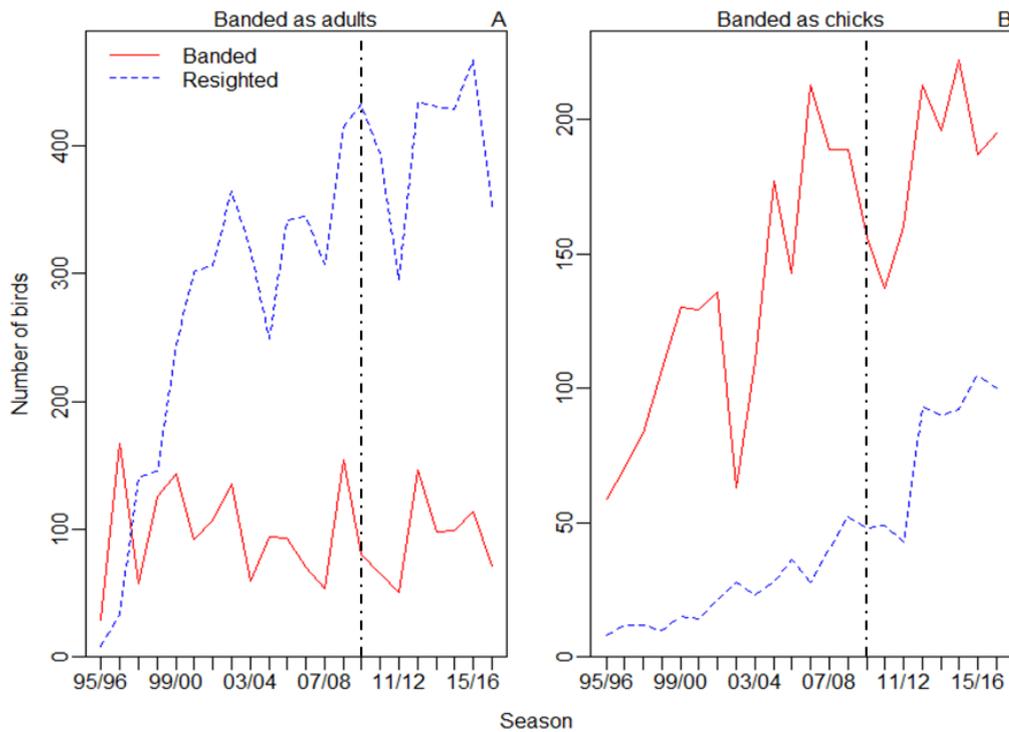


Figure 5: The total number of birds banded and resighted by year: A, birds banded as adults (unknown age); B, birds banded as chicks (known age).

Age at first breeding of known-age birds

Of the 2219 chicks banded prior to 2013, only 161 (7.3%) birds have subsequently been observed breeding (Table 7). Excluding cohorts born prior to 1992 (for which there was not consistent resighting effort at early ages), the earliest and latest observed first breeding was at age 4 and 16, respectively (the most common age when first observed breeding was age 6).

Table 7: For study birds (i.e., birds banded in study areas) banded as chick before 2013, the age they were first observed breeding and the number not yet observed breeding, by year of banding (birds that were observed dead or with uncertain breeding status before seen breeding were excluded from this table). ‘-’ denotes impossible combination. (Observations of birds banded before 1992 were excluded from summary calculations, because these birds could well have bred before the sampling programme that started in 1996.)

Year banded	Age when first observed breeding															Any age	Not observed breeding yet
	4	5	6	7	8	9	10	11	12	13	14	15	16	18	25		
1978	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	0
1986	-	-	-	-	-	-	0	0	1	0	0	2	0	0	0	3	0
1987	-	-	-	-	-	0	0	0	0	1	0	0	0	0	0	1	2
1988	-	-	-	-	1	0	1	0	1	0	0	1	0	1	1	6	0
1989	-	-	-	0	1	0	0	1	0	0	0	0	0	0	0	2	1
1990	-	-	2	3	1	0	0	0	0	0	0	0	0	0	0	6	1
1992	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
1996	0	1	1	0	0	0	0	0	0	0	0	0	0	0	-	2	57
1997	0	1	0	1	2	1	0	0	0	0	0	0	0	0	-	5	64
1998	0	1	2	0	0	0	0	0	0	0	0	0	0	0	-	3	74
1999	0	0	2	2	2	0	1	0	1	0	0	0	0	0	-	8	96
2000	0	2	3	3	2	2	0	0	0	0	0	0	0	-	-	12	115
2001	0	1	0	0	2	1	0	0	0	0	0	0	1	-	-	5	122
2002	0	0	4	2	1	0	0	5	0	0	1	0	-	-	-	13	119
2003	0	2	1	1	0	0	2	0	0	0	0	-	-	-	-	6	56
2004	1	1	0	3	1	1	0	0	0	1	-	-	-	-	-	8	101
2005	0	2	4	5	2	1	0	0	0	-	-	-	-	-	-	14	160
2006	0	2	3	5	1	0	1	0	-	-	-	-	-	-	-	12	128
2007	0	2	3	2	0	4	2	-	-	-	-	-	-	-	-	13	190
2008	2	0	3	3	1	2	-	-	-	-	-	-	-	-	-	11	174
2009	1	2	6	4	1	-	-	-	-	-	-	-	-	-	-	14	170
2010	1	1	5	2	-	-	-	-	-	-	-	-	-	-	-	9	143
2011	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	4	129
2012	0	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	156
All years	6	23	40	36	18	12	7	6	3	2	1	3	1	2	1	161	2 058

Observations of pre-breeders

Of known age birds in their first resighting year, only 35.9% were confirmed to be breeding (Table 8). The mean age of a known age individual returning to the colony as a non-breeding bird (i.e. pre-breeder) was 5.6 years, whereas first-time breeders had a mean age of 7.0. The mean duration of the pre-breeding period across all known age individuals was 0.6 years, and did not exceed 4 years, with a single exception (7 years) (Table 9). Since only half (50.6%) of the petrels banded as adults were known to be breeders when banded (Table 10), it is likely that some of those adult birds were banded as pre-breeders in addition to older birds.

Table 8: 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	1	0
4	30	7	8
5	45	8	14
6	22	3	21
7	14	2	17
8	4	2	8
9	3	3	10
10	1	5	3
11	0	0	4
12	0	2	0
13	0	0	1
14	1	0	1
15	0	0	0
16	0	1	1
17	0	1	0
18	1	0	0
All	122	35	88

Table 9: Number of years between first resighting and first resighting as a breeder for the 143 birds that were banded as chicks and subsequently seen breeding.

Age at first resighting	No. of years before seen breeding (after first resighting)					
	0	1	2	3	4	7
3	0	0	0	1	0	0
4	8	8	1	2	0	1
5	14	15	4	3	1	0
6	21	10	1	0	2	0
7	17	3	1	0	0	0
8	8	0	1	0	0	0
9	10	0	0	0	0	0
10	3	0	1	0	0	0
11	4	0	0	0	0	0
13	1	0	0	0	0	0
14	1	0	0	0	0	0
16	1	0	0	0	0	0
All	88	36	9	6	3	1

Table 10: Breeding state of birds banded as adults.

Breeder	Non-breeder	Unknown
1091	951	113

Breeding success

Across all seasons, 67.4% ($\pm 0.9\%$ 1SE) of all observed study birds were confirmed as breeding. Of these, 50.6% ($\pm 1.4\%$) bred successfully (i.e., produced a fledged chick). The most frequently identified reason for breeding failure was egg disappearance 3.4 ($\pm 0.6\%$), followed by embryo death 3.1 ($\pm 0.4\%$). None of these or the other identified causes of death displayed a clear temporal pattern with respect to relative importance (Figure 6).

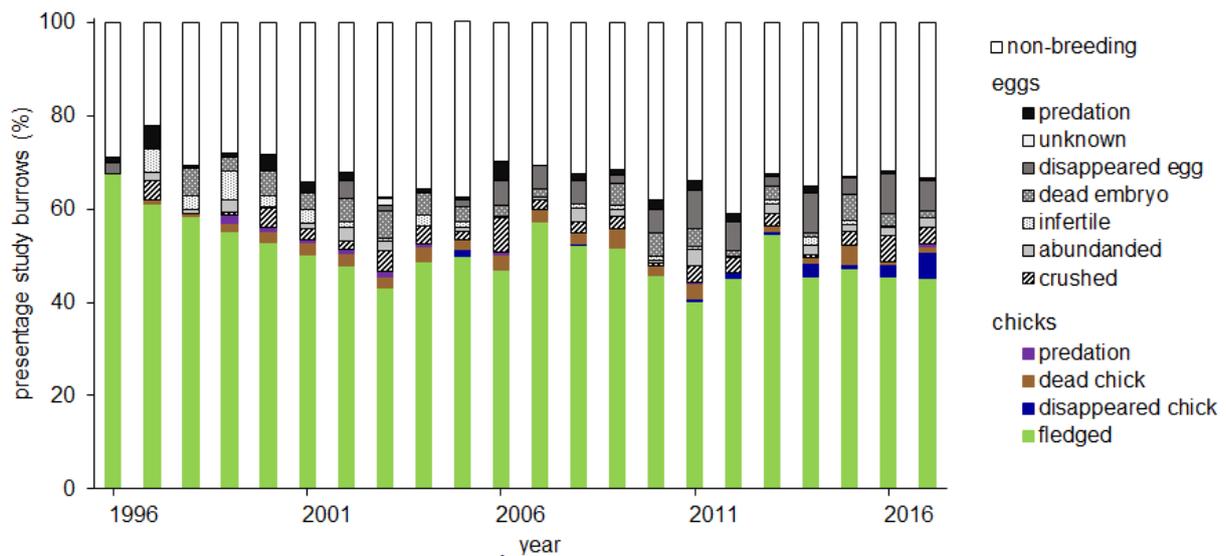


Figure 6: Breeding status or outcome of study burrows by year.

3.2 Mode of the Posterior Distribution (MPD) model runs

Model fits

Model fits to annual resightings of banded birds and to line transect population size estimates are shown for Models 1, 3, and 4 (i.e., all models including pre-breeder classes) (Figure 7). Fits to annual observed resighted birds were very good for all of these model runs. Model 3 gave the best fits to both non-breeders and successful breeders, confirmed by best model fit in terms of log-likelihood contribution (Table 11). Model fits to line transect population size estimates were good for all years except 2010, for which all models estimated much greater numbers than observed (Figure 7). In addition, all three models produced lower estimates than observed in 2016.

Estimated parameters

Model estimates of all demographic rates for the four model runs at MPD are shown in Table 12. These are compared with the previous base case model run estimates from Bell et al. (2014). The results for each model run are described in more detail below.

Model 1

This model run was parameterised as the previous base case described by Bell et al. (2014) (see Table 6). The annual survival probabilities of successful and unsuccessful breeders (Figure 8) were broadly consistent with the previous assessments by (Bell et al. 2014). Survival estimates were generally greater for successful breeders than failed breeders. The mean survival probabilities across all adults (regardless of breeding state) was 0.87. The annual resighting estimates of pre-breeders and non-breeders were comparable with those of Bell et al. (2014) (not shown here). The estimated mean age at first breeding (7.2 years) (Figure 9), was slightly older than the previous assessment estimate of 6.8 years (Bell et al. 2014). The juvenile annual survival estimate for this model run of 1.00 was biologically implausible, indicating confounding with other model parameters.

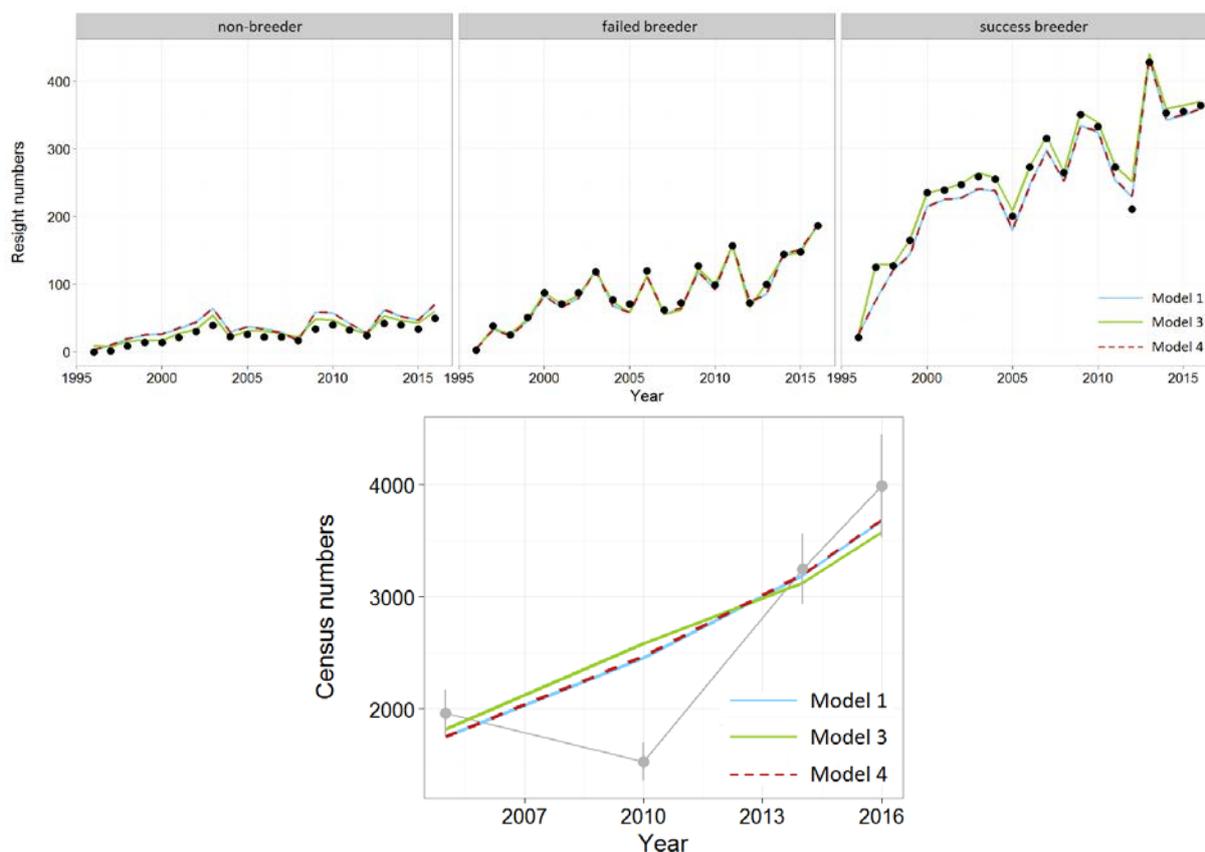


Figure 7: Model MPD run fits to mark-recapture observations (top) and line transect population estimates (bottom). Empirical data are shown as black or grey dots, with the model estimated values as coloured lines, error bars in the population estimation plots indicate ranges of 95 % CI.

Table 11: Summary of model run total number of parameters, log-likelihood, and AIC scores.

Model	No. of parameters	-ln(L) for mark-recapture data	-ln(L) for census data	AIC
1	144	16721.1	30.6	33791.4
2	44	8909	–	17906
3	144	16423.2	31.7	33197.8
4	144	16722.5	30.7	33794.4

Table 12: Estimates of selected key black petrel demographic parameters (calculated from model parameter estimates) of Bell et al. (2014), and models of this assessment.

Parameter	(2014)	Model 1	Model 2	Model 3	Model 4
Initial (1996) size of the adult population in the study area	–	1 545	–	2 048	2 129
Mean age of first breeding	6.9	7.2	–	6.9	6.8
Percentage of birds that skip the pre-breeder stage Of birds that appear in the study area and survive to breed, the percentage that breeds the study area	3.10	3.10	–	5.00	3.20
Average annual survival rates:	0.92	1.00	–	0.95	0.93
non-breeding adults	0.86	0.86	–	0.86	0.86
breeding adults	0.89	0.88	–	0.89	0.88
all adults	0.89	0.87	0.86	0.86	0.87
Percentage of adults breeding in any year	77	80	–	72	79
Percentage of breeding attempts that are successful	76	73	–	71	73

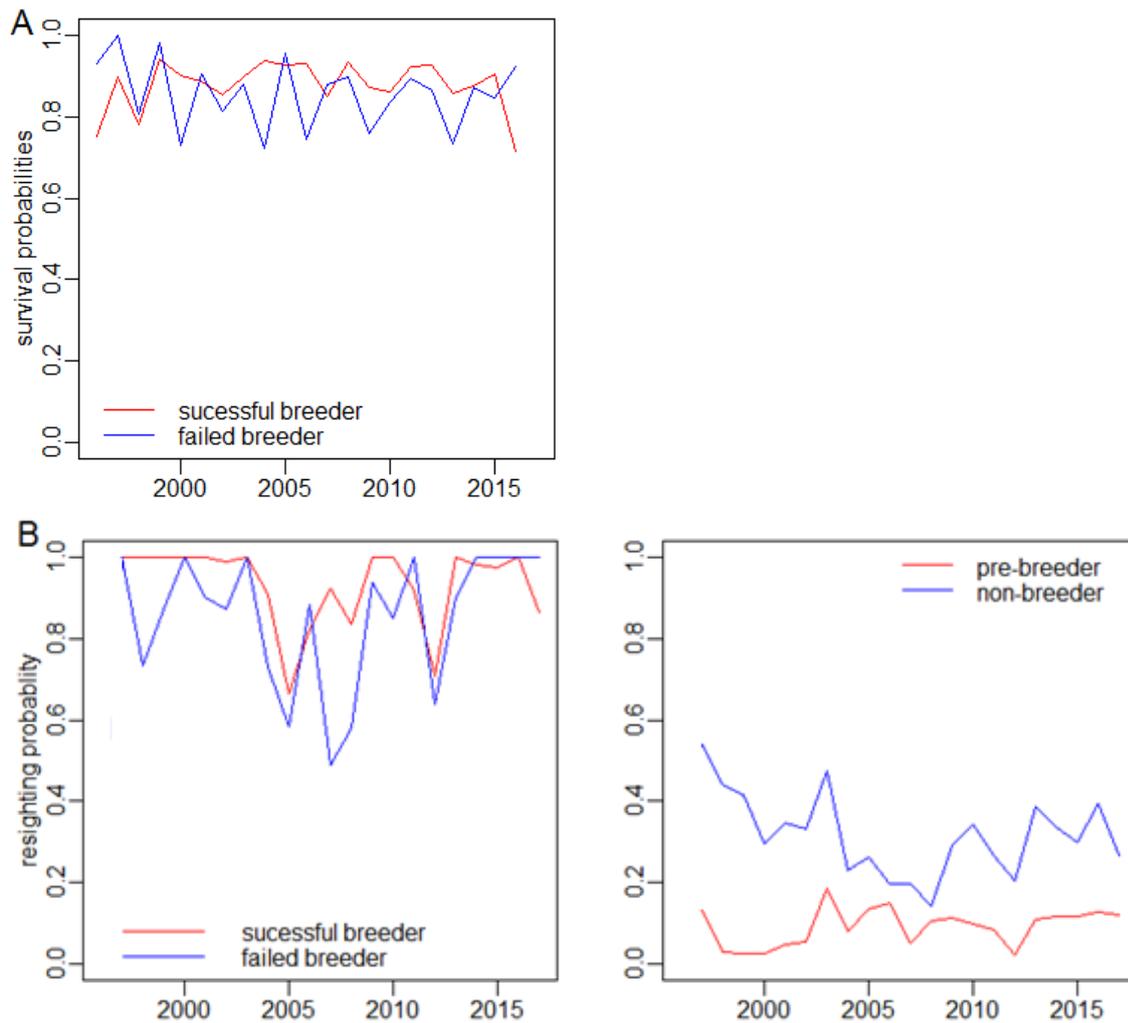


Figure 8: Estimated probabilities of (A) survival and (B) resighting probabilities of Model 1.

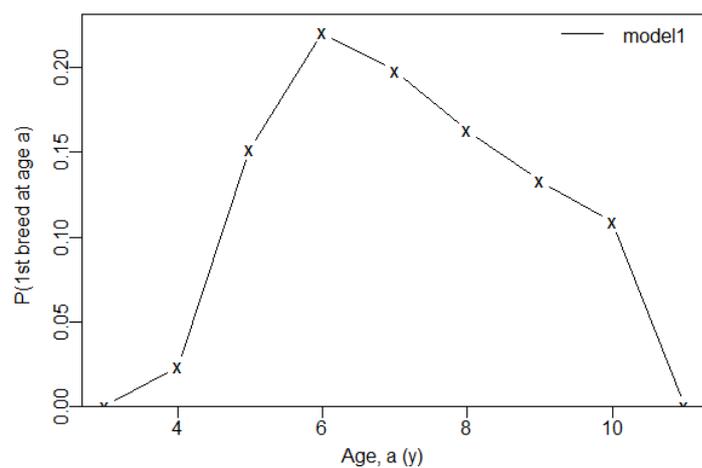


Figure 9: The estimated distribution of age at first breeding recomposed from maturation parameters estimated by Model 1.

Model 2

Model 2 had the same simplified structure and parameterisation as BPET1 by Francis and Bell (2010) and ignored an individual's observations prior to first observed breeding. The estimated adult survival probability across all years was ~ 0.87 (see Table 12) and annual resighting probabilities varied between 0.5 and 0.84 with no obvious year trend (Figure 10).

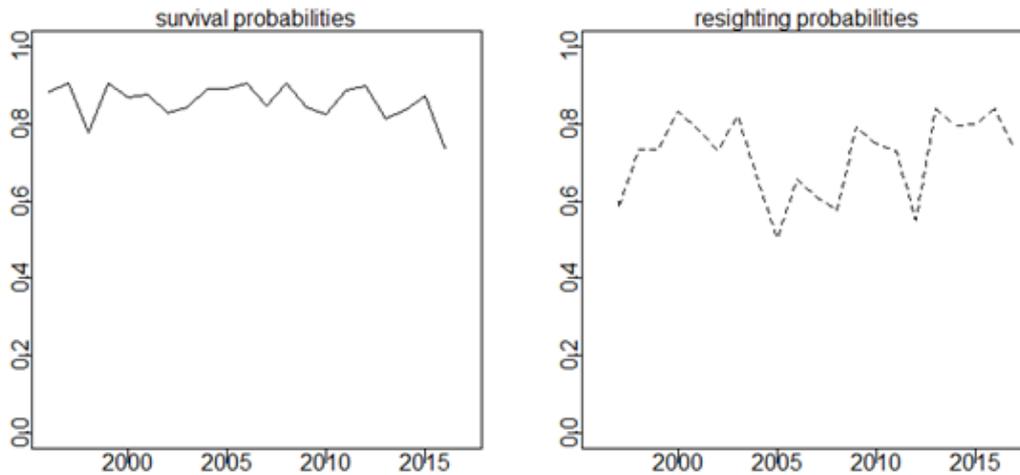


Figure 10: Estimated probabilities of survival probabilities (left) and resighting probabilities (right) of Model 2.

Model 3

Model 3 was parameterised as Model 1, though it assumed that the annual resighting probability of breeders was 1 (i.e., all breeders were seen) and annual breeding rates for successful and failed breeders were allowed to be time-varying. The year trend in annual breeding probabilities followed a similar pattern to that of year-varying resighting probabilities estimated by Model 1 and 2 (Figure 12), i.e. low estimates were obtained for corresponding years in the mid-2000s. The juvenile survival estimate for this model run of 0.95 was much more plausible relative to that for Model 1. However, annual adult survival estimates were essentially unchanged from model run 1 (compare Figure 8 and Figure 11; also see Table 12).

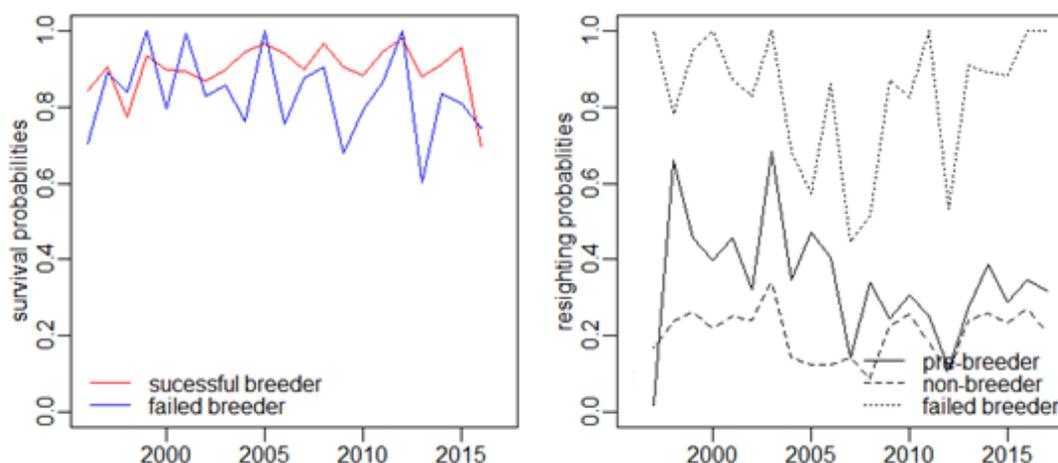


Figure 11: Estimated probabilities of survival probabilities (left) and resighting probabilities (right) of Model 3.

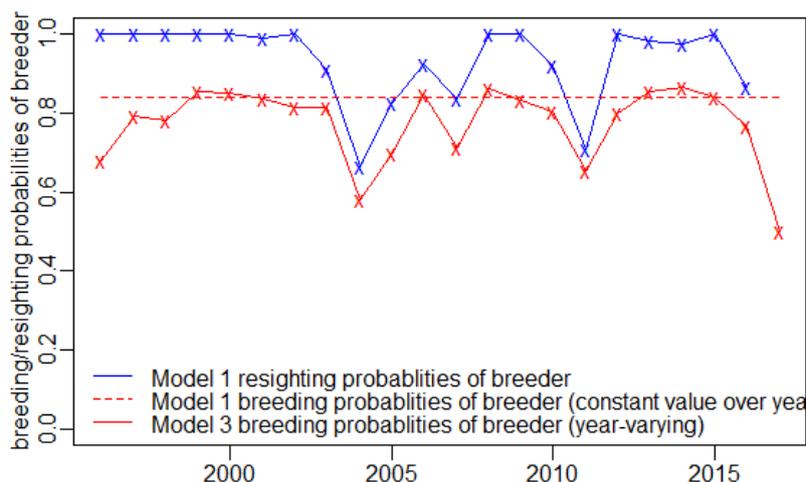


Figure 12: Resighting probabilities (year-varying) and breeding probabilities of successful breeder (constant value over years) of Model 1, compared with the breeding probabilities of successful breeders in Model 3.

An exploratory set of sensitivity runs to model run 3 were conducted to examine the best parameterisation of survival and resighting parameters (Table 13) for Model 3. Model 3.3 had the lowest AIC and fewest number of parameters. This model run assumed the same annual resighting probability for successful and failed breeders and also combined the survival rate of breeders and non-breeders into a single adult survival rate. Despite the improvements to model AIC, this model was not considered for MCMC because too many changes were made relative to the old base case model structure, although this more parsimonious structure could be considered for future model development.

Table 13: The parameterisation and model AIC (Akaike Information Criterion) of sensitivity runs to Model 3. All models were fit to the same observations. Interpretation: e.g., for model 3.1 there were three vectors of survival parameters, one for pbr, one for nbr, and one for both fbr and sbr.

Model run	Survival parameters			Resighting parameters				No. of parameters	AIC - min(AIC)
	pbr	nbr	br	pbr	nbr	fbr	sbr		
3.1	1	2	3	1	2	3	4	39	12.48
3.2	1	2	3	1	2	3	3	38	2.92
3.3	1	2	2	1	2	3	3	37	0

Model 4

Model 4 was as Model 3, though combined pre-breeder survival with juvenile survival instead of adult survival. The mean adult survival estimate from Model 4 was similar to the other runs (see Table 12) and year-varying demographic rates were very similar to those of Model 1 (compare Figure 8 and Figure 13). With respect to juvenile survival, the estimate from Model 4 (0.93) was more plausible than from Model 1 (1.00) and produced a decreased percentage of individuals returning to breed in the study area (61% from Model 4, compared with 100% from Model 1).

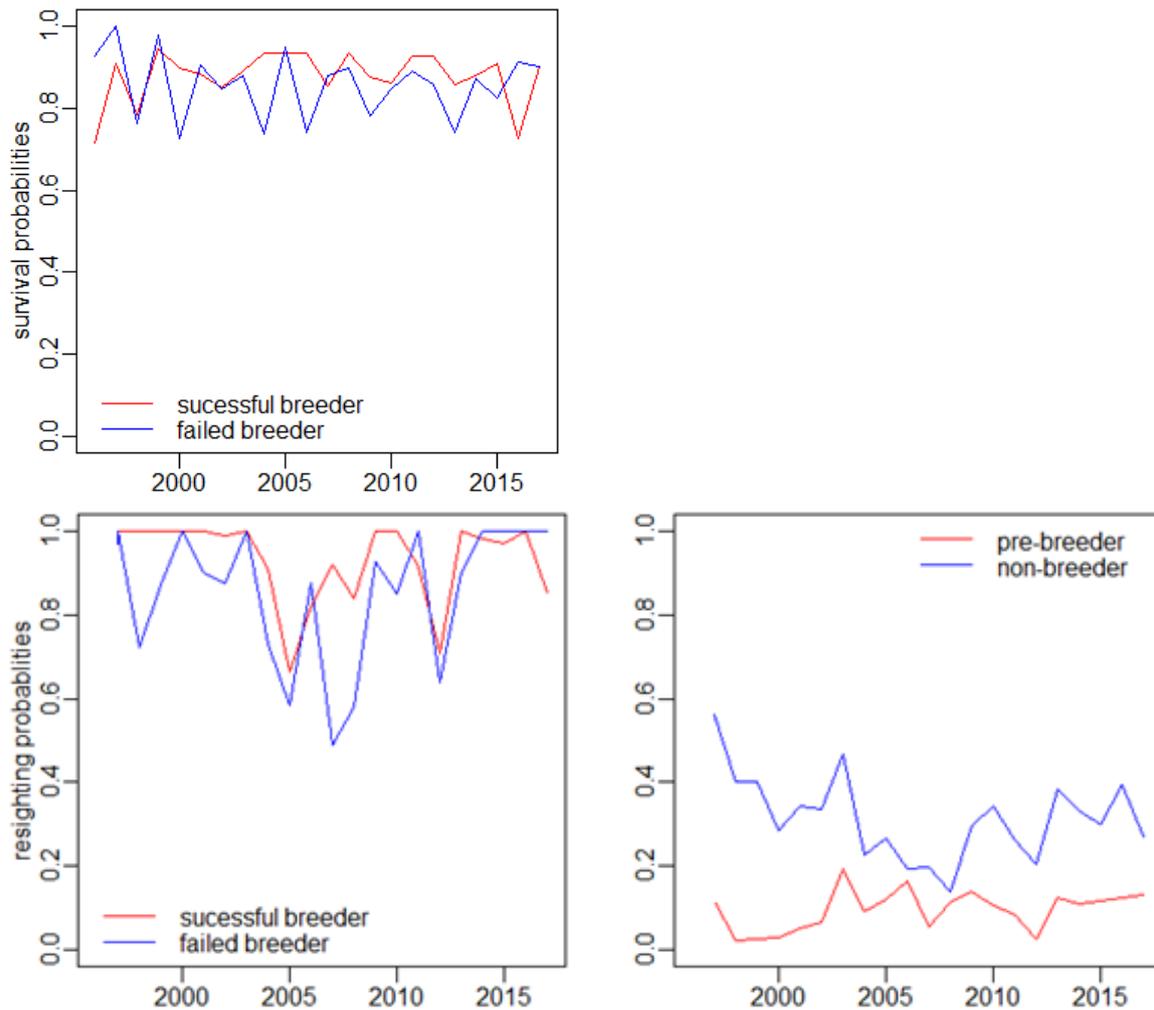


Figure 13: Estimated probabilities of survival (top) and resighting (bottom) probabilities of Model 4.

Likelihood profile of juvenile survival

A likelihood profile on juvenile survival for Model 4 indicated that the optimal juvenile survival rate was between 0.85 and 0.875 (Figure 14A). However, juvenile survival within this range produced poor model fits to line transect population size estimates. This indicated contradictory information from mark-recapture observations and population size estimates: the population size estimates indicate that the breeding population decreased between 2005 and 2010, and then increased rapidly between 2010 and 2016. Model 4 estimated a breeding population growth rate between 0.88% y^{-1} (if $juvsurv = 0.85$) and 0.33% y^{-1} (if $juvsurv = 0.875$) (Figure 14B).

Altering juvenile survival within the optimal range had little effect on other parameter estimates, such as the adult survival rate (Figure 15A, B) and the age at first breeding (Figure 15C).

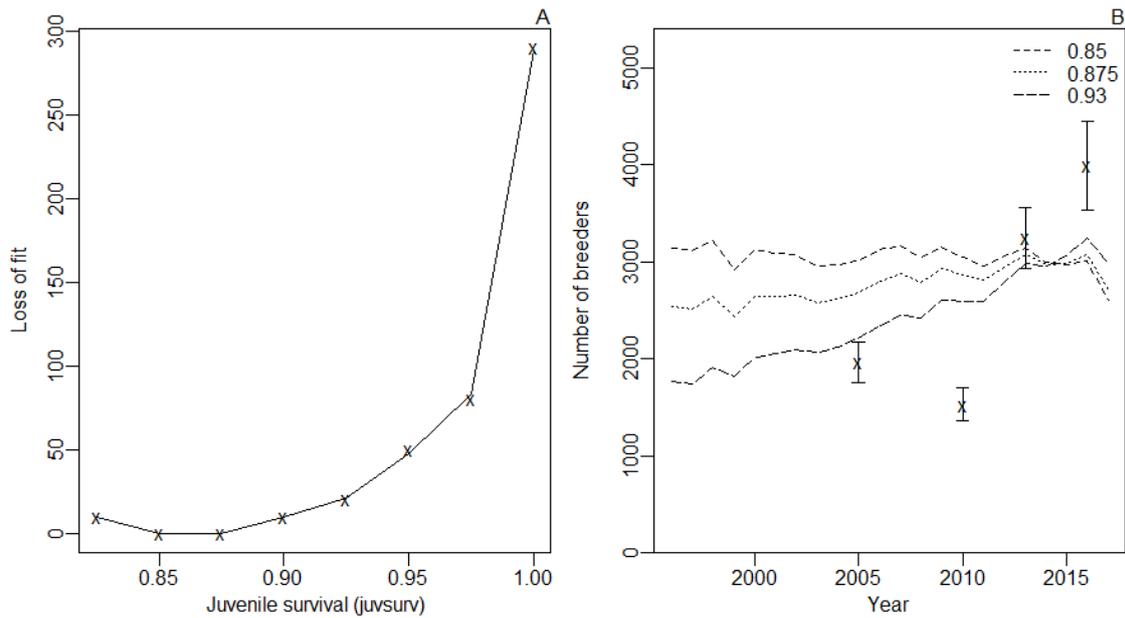


Figure 14: Results of a posterior profile on juvenile survival rate for Model 4: A, the loss of fit; and B, population trajectories associated with alternative values of juvenile survival.

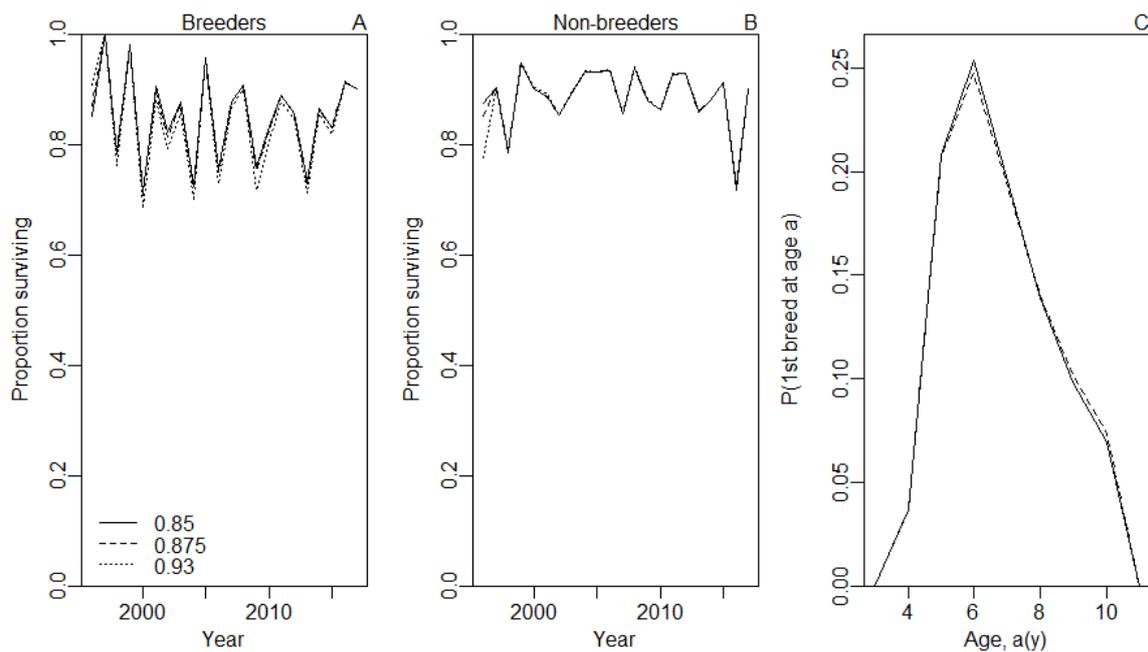


Figure 15: The effect of assuming alternative values of juvenile survival (0.85, 0.875, or 0.93) on other key demographic rates including: A – estimated survival for breeder and non-breeders; B – estimated distribution of ages at first breeding for the same three values of juvsurv; and C – estimated age at first breeding.

3.3 MCMC model runs

MCMC model runs were undertaken for Models 1, 2, 3, and 4. A visual inspection of the trace plots for Model 1, Model 3, and Model 4 indicated that the method of empirically recalculating the covariance matrix to generate the MCMC proposal distribution was effective in giving an acceptable degree of mixing for estimated parameters. There was a good agreement in the distribution of estimates obtained from different chains (Appendix 3).

Parameter estimates

The MCMC posteriors of year-varying annual adult survival and resighting probability are displayed in Figure 16 to Figure 19 and all parameter estimates are tabulated in Table 14. Estimates of adult survival for the last ten years (2007 to 2016) were derived from the MCMC samples and reproduced in Table 15. The adult survival rates estimated by MCMC range between 0.86 and 0.89 across Model 1, Model 3, and Model 4, and the MPD estimate for these models were within the ranges of 95% c.i. from the model MCMC results. For juvenile survival, Model 3 and Model 4 estimate lower means compared with Model 1, and the MCMC results indicate that the overall estimates for this parameter are still unrealistically high with large uncertainty around this parameter. Model 3 estimated lower values for the percentage of breeding attempts that were successful.

Table 14: Mean estimates of selected key black petrel demographic parameters (calculated from model parameter estimates) from MCMC results of Model 1 to Model 4. The upper and lower bounds 95% credible intervals are included in the parentheses.

Parameter	Model 1	Model 2	Model 3	Model 4
Initial (1996) size of the adult population in the study area	1133 (1009–1271)	–	2299 (1306–3812)	1072 (1001–1185)
Mean age of first breeding	6.86 (6.51–7.13)	–	6.89 (6.59–7.16)	6.86 (6.60–7.12)
Percentage of birds that skip the pre-breeder stage	7.5 (3.6–13.3)	–	6.8 (3.1–12.6)	3.9 (1.8–7.0)
Of birds that appear in the study area and survive to breed, the percentage that breeds the study area	68.6 (62.2–75.0)	–	68.7 (61.7–76.3)	58.8 (50.4–67.4)
Average annual survival rates:				
juveniles	0.986 (0.953–0.999)	–	0.967 (0.922–0.997)	0.957 (0.921–0.994)
non-breeding adults	0.860 (0.835–0.884)	–	0.853 (0.830–0.875)	0.814 (0.784–0.852)
breeding adults	0.889 (0.876–0.902)	–	0.890 (0.877–0.903)	0.879 (0.866–0.892)
all adults	0.883 (0.872–0.893)	0.857 (0.832–0.872)	0.880 (0.871–0.888)	0.867 (0.857–0.878)
Percentage of adults breeding in any year	77.7 (76.1–79.3)	–	71.9 (69.0–74.2)	81.8 (80.1–83.4)
Percentage of breeding attempts that are successful	73.2 (71.7–74.7)	–	69.6 (68.1–71.1)	73.1 (71.7–74.4)

Table 15: Mean estimates of selected key black petrel adult survival from 2007–2016 (calculated from model parameter estimates) from MCMC results of Model 1 to Model 4. The upper and lower bounds 95% credible intervals are included in the parentheses.

Parameter	Model 1	Model 2	Model 3	Model 4
non-breeding adults	0.839 (0.806–0.872)	–	0.831 (0.802–0.860)	0.830 (0.791–0.865)
breeding adults	0.884 (0.866–0.903)	–	0.883 (0.866–0.900)	0.872 (0.856–0.889)
all adults	0.874 (0.859–0.890)	0.852 (0.832–0.875)	0.870 (0.857–0.880)	0.864 (0.850–0.879)

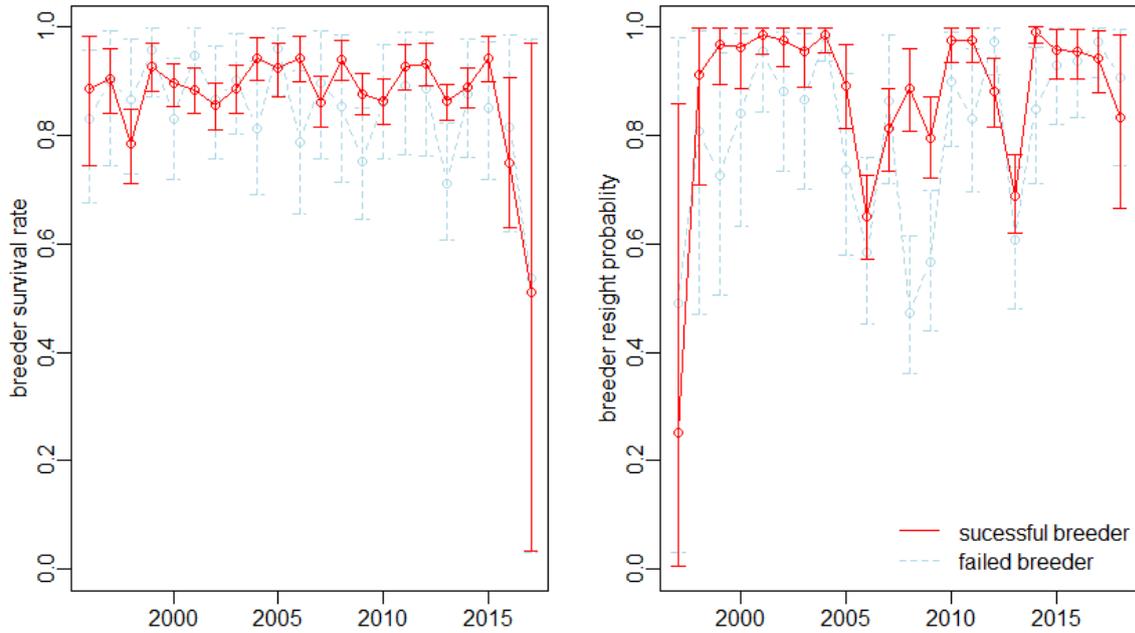


Figure 16: Model 1 MCMC estimates of annual breeder survival rates and annual breeder resight probabilities of black petrel. Points are median estimates, bars are 95% confidence intervals.

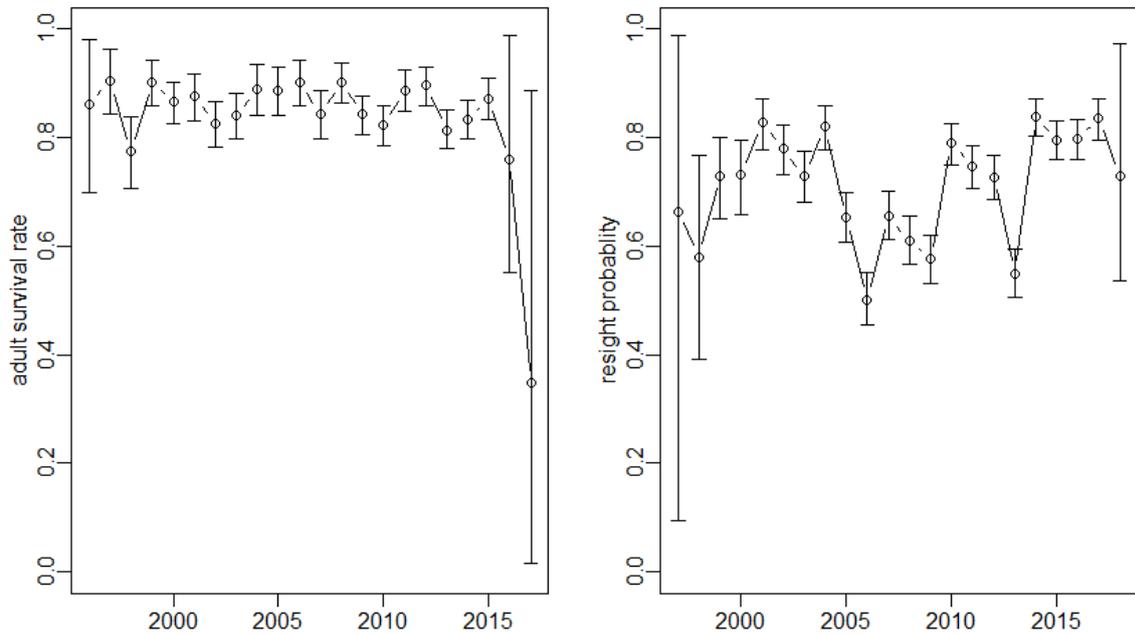


Figure 17: Model 2 MCMC estimates of annual adult survival rates and annual resight probabilities of black petrel. Points are median estimates, bars are 95% confidence intervals.

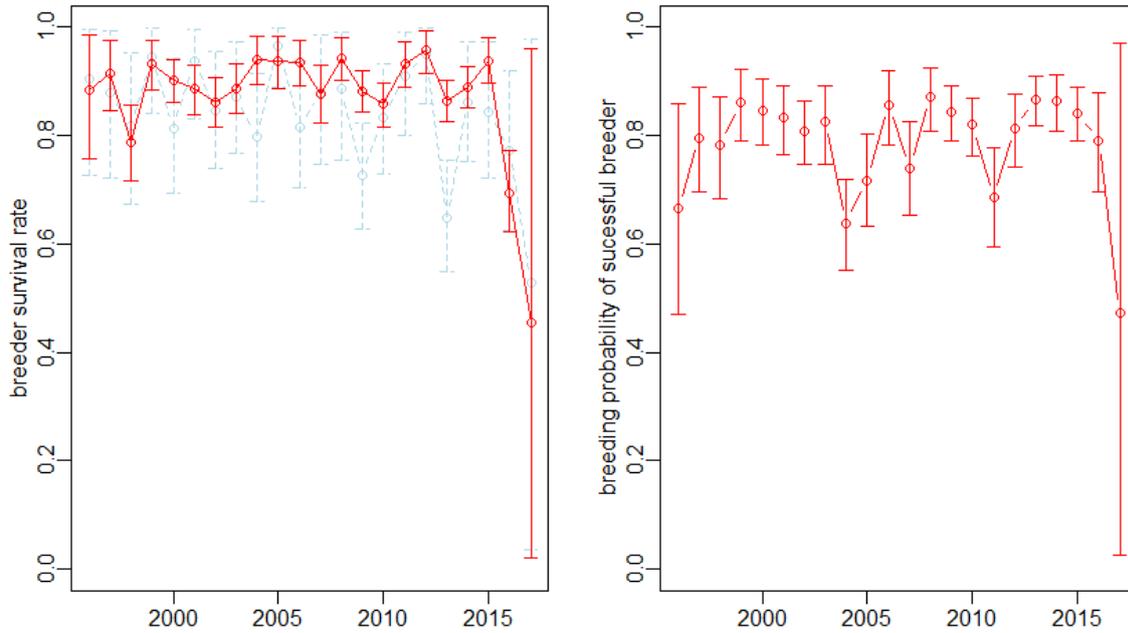


Figure 18: Model 3 MCMC estimates of annual breeder survival rates and annual breeding probability of successful breeders. Points are median estimates, bars are 95% confidence intervals.

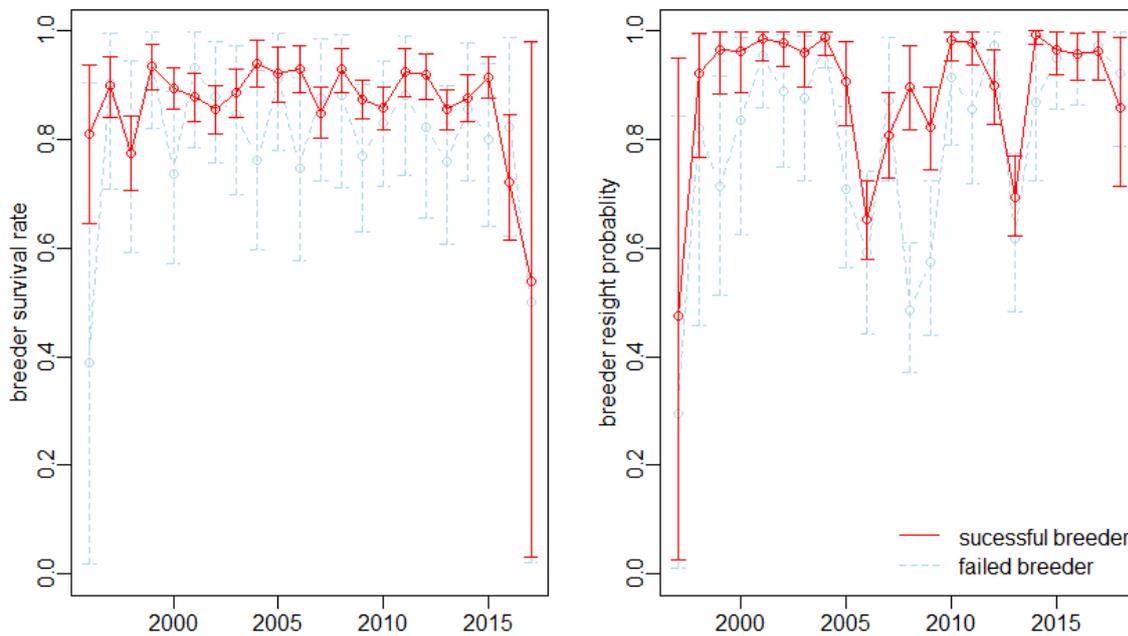


Figure 19: Model 4 MCMC estimates of annual breeder survival rates and annual breeder resight probabilities of black petrel. Points are median estimates, bars are 95% confidence intervals.

4. DISCUSSION

4.1 Adult survival

This work updates the quantitative modelling of the GBI study population of the black petrel, using mark-recapture data from 1996 and four census estimates from transect surveys. Models developed by Francis & Bell (2010) and Bell et al. (2014) were updated. All models produced very good fits to mark-recapture observations and reasonable fits to population size estimates (see Figure 7). When the previous base case model (Bell et al. 2014) was updated with new observations, very similar demographic rate estimates were obtained, though adult survival estimates were slightly reduced; Bell et al. (2014) estimated an adult survival of 0.89 at MPD, which was updated to 0.86 or 0.87 in this assessment, depending on model run. However, MCMC runs (not undertaken by Bell et al. 2014) of models including pre-breeders produced comparable adult survival estimates ranging from 0.87 (95% CI = 0.86–0.88) to 0.88 (95% CI = 0.87–0.89). Adult survival estimates in recent years (2007–2016) were slightly lower compared with the means of the entire study period (see Table 15).

4.2 Breeder resighting probability

The updated previous base case model (Model 1) estimated year-varying resighting probabilities ranging from 0.66 to 1.00 (see Figure 8). However, in the field, ecologists believe that the resighting rate for successful breeders is higher than this (closer to 80–90% on average) and unlikely to be lower than 0.70 in any year during the study period. A more likely explanation for these birds not being observed in these years was that they did not breed in that year. Hence Model 3, which assumed that all breeders were observed and the resighting probability of breeders was allowed to vary by year, is a more realistic model and the authors propose this is considered as the new base case model for this population. Note that the estimated annual probabilities of breeding from Model 3 mirrored the pattern of resighting probabilities of successful breeders in Model 1 (compare Figure 8 and Figure 11), indicating that these parameters were confounded given the observations. However, despite these substantial changes to model parameterisation and improved fit to mark-recapture observations (see Figure 7), Model 3 produced highly comparable estimates of adult survival to Model 1, the previous base case model structure (see Table 14).

4.3 Juvenile survival

The annual juvenile survival rate was estimated to be 1.00 (100%) by Model 1, which updated the previous base case. The probable reason for obtaining this unrealistically high value was the confounding of juvenile survival probability and the probability of a bird hatched in the study area returning to produce a burrow in the study area. Birds have been observed relocating between GBI and LBI, but in what seems to be very low numbers — only 2 LBI-born birds have been recorded on GBI and only one GBI-born bird has been recaptured on LBI. Furthermore, an unknown proportion of breeding birds may move in or out of the study area on GBI. To obtain robust estimates of juvenile survival, information for estimating the emigration rate would be required. However, field-based data collection has not been designed to provide the information requirements for estimating the rate of emigration.

Model 4 followed the working group's suggestion by re-assigning the survival probability of pre-breeders from the non-breeder class (as assumed by Model 1 and Model 3) to the juvenile class. This was justified on the basis that pre-breeders would be biologically most comparable to other juveniles that had not yet bred. This parameterisation also increased the number of observations for estimating juvenile survival and slightly reduced the estimate of juveniles returning to the study area to 59% (95% CI = 50–67%) from 69% (95% CI = 62–75%) from Model 1, as well as producing a more plausible, though still high juvenile survival estimate of 0.96 (0.92–0.99), compared with 0.99 (95% CI = 0.96–1.00) from Model 1. Note that this estimate is higher than those considered for the estimation of population trajectory (see Figure 15) and may have produced improved fits to population size estimates

than were obtained from that assessment. However, with respect to adult survival the Model 4 parameterisation produced very similar estimates compared with Model 1 (see Table 14 and Table 15).

4.4 Age at first breeding

The estimates of age at first breeding are similar across Model 1 (6.86, 95% CI = 6.51–7.13), Model 3 (6.89, 95% CI = 6.59–7.16) and Model 4 (6.86, 95% CI = 6.60–7.12), and these results are similar to the value estimated in the previous assessment (6.9) (see Table 14). The uncertainty around the estimate of age at first breeding, is associated with few banded chicks returning to the study area providing relatively few observations for the estimation of survival of the known-age birds prior to first breeding.

4.5 Exploration of parsimonious models

Both Model 1 and Model 3 have 144 parameters, which provided a challenge for parameter estimation and model convergence. Several variants of Model 3 were considered to search for the best parameterisation of survival and resighting parameters based on model AIC. The optimal model, Model 3.3, had the fewest number of parameters, achieved by combining the resighting probabilities of successful breeders and failed breeders and by combining the survival rate of breeders and non-breeders. All parameters were constant with respect to year, except for the breeding probability of breeders. The outputs of Model 3 indicated that the resighting probability of breeders was not contingent on breeding success in the preceding year and that survival rate was not different for breeders and non-breeders. Loglikelihood scores for the mark-recapture data remained the same over Model 3.1 to Model 3.3. This suggests that simplification of model structure and parameterisation is possible, with no or little cost of fitting to the mark-recapture data. These models were not carried forward to MCMC by this assessment because they were developed late in the assessment process. The authors suggest that future assessments consider simpler model parameterisations, which appear to be more parsimonious and should improve mixing at MCMC.

4.6 Fits to population size estimates

The population trend predicted by the model produced a relatively poor fit to the line transect population size estimates (as found by previous assessments) compared with mark-recapture fits, which indicates a conflict between the information from the two sets of observations (see Figure 7). Most mark-recapture study burrows were located in the high-quality habitat, where the population growth rate indicated by the line transect survey was lower than medium- and low-grade habitat (see Figure 3). To explain the apparent conflicting information from mark-recapture and population size estimates, future assessments could re-weight the mark-recapture data by the habitat type to see if the fits to population size estimates are improved. To estimate adult survival that is more representative of the wider study area (i.e., covered by the line transect survey area), more mark-recapture study burrows will need to be established in low- and medium-grade habitat areas. This would allow an assessment of whether variable population growth from the line transect survey is caused by variable adult survival or variation in other demographic rates, such as spatial heterogeneity in the rate of breeding site selection by pre-breeders.

4.7 Accounting for emigration

The demographic assessment model assumed that the demographic parameters of the study area are representative of the GBI population. The current model structure assumes that each individual decides whether to breed inside or outside the study area at first breeding and remains faithful to this decision throughout their lives. Emigration rates could be estimated from observations of marked individuals made outside the study site. To provide the information requirements for estimating emigration rate, it is recommended that, where possible, birds from random burrows on transect surveys and random area surveys are checked for bands, and that unidentified birds are banded.

5. CONCLUSIONS

This assessment has made some improvements to model parameterisation though produced similar estimates of key demographic rates to previous assessments, i.e., with respect to adult survival and age at first breeding — the key outputs of this assessment. Another advance made in this assessment was the estimation of credible intervals (and MCMC posteriors) for all estimated parameters that can be used by other research. Future assessments may consider including updated observations of individuals sighted outside the study area and may account for the distance of these observations from the study area in some way. This will be necessary to account for a potential downward bias in adult survival estimates caused by unaccounted for emigration of breeders from the study area. The apparent conflict between mark-recapture and line transect population size estimates could be addressed by re-weighting the transect data based on the habitat quality of the study burrows from which the mark-recapture data were collected (to test whether the two data sources now agree). Ideally, future field research will collect a greater proportion of mark-recapture information from low- and medium-grade habitat to assess whether adult survival is different in these faster-growing populations, or if this is likely to be caused by variation in other demographic rates, such as spatial heterogeneity in the rate of breeding site selection by pre-breeders.

6. ACKNOWLEDGMENTS

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Appendix 1: Census grids count data for 1996 to 2017

Table A1.1: Census grid burrow counts for field seasons from 1996 to 2017, by the grid, type (br, breeding; nbr, non-breeding; emp, empty), and year.

Grid	Year	Kauri dam			Palmers track			South forks		
		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
G1	2010	4	15	7	2	19	9	7	8	5
G1	2011	5	16	4	3	20	5	8	9	3
G1	2012	7	18	1	2	17	9	5	7	8
G1	2013	4	13	8	3	21	7	3	11	7
G1	2014	3	16	6	4	21	7	5	9	7
G1	2015	2	15	9	5	21	5	3	16	3
G1	2016	5	16	4	4	23	3	5	10	8
G1	2017	5	17	5	6	21	7	4	13	8
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
G2	2010	3	18	5	2	8	4	2	3	5
G2	2011	3	19	4	1	11	2	4	8	0
G2	2012	2	19	5	1	8	5	3	7	3
G2	2013	0	18	7	1	7	6	0	7	6
G2	2014	1	18	6	3	9	2	4	6	3
G2	2015	1	17	6	1	6	8	2	9	3
G2	2016	4	19	2	2	11	1	1	10	2
G2	2017	1	25	3	3	7	6	1	10	4

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
G3	2010	2	4	1	4	7	4	0	5	1
G3	2011	2	4	1	7	5	3	1	4	1
G3	2012	0	4	4	5	8	5	0	4	2
G3	2013	2	3	2	4	7	4	0	4	1
G3	2014	1	4	2	3	8	4	1	4	0
G3	2015	1	3	3	5	7	2	0	3	3
G3	2016	1	2	3	4	9	0	2	3	1
G3	2017	2	3	1	6	4	5	2	4	2

Appendix 2: Line transect survey data for 2016

Table A2.1: Breakdown of transect lengths and borrow counts by stratum for 2016 (non, non-petrel habitat; lo, poor grade; med, medium grade; hi, high grade) and burrow type (br, breeding; nbr, non-breeding; emp, empty)

transect	Transect length					Number of burrows								
	total	no	lo	med	hi	lo			med			hi		
						br	nbr	emp	br	nbr	emp	br	nbr	emp
LT3	246	0	0	81	165	0	0	0	6	0	1	6	1	2
LT4	400	50	272	64	14	4	2	3	1	0	2	1	0	0
LT7	400	0	30	255	115	2	1	0	13	1	3	2	1	2
LT11	400	0	175	183	42	4	1	1	0	6	2	0	2	0
LT14	400	34	169	147	50	2	3	4	1	2	1	2	0	0
LT15	420	0	91	148	181	2	2	2	3	1	3	4	0	1
LT18	240	30	157	53	0	2	1	1	2	0	1	0	0	0
LT22	400	20	160	220	0	4	1	0	7	3	4	0	0	0
LT30	90	0	0	90	0	0	0	0	6	1	2	0	0	0
LT34	120	0	0	0	120	0	0	0	0	0	0	5	1	0
LT36	400	0	28	226	146	0	0	0	7	4	3	18	0	2
LT39	289	0	0	0	289	0	0	0	0	0	0	21	4	7
LT40	400	22	140	238	0	1	1	2	10	3	3	0	0	0
LT42	400	21	178	201	0	4	1	1	4	1	0	0	0	0
LT43	400	0	95	273	32	0	0	2	4	4	1	0	1	0
LT45	240	0	161	79	0	1	0	0	2	0	0	0	0	0
LT49	142	0	0	71	71	0	0	0	2	0	2	1	0	2
LT53	320	0	0	231	79	0	0	0	8	0	1	3	1	2
LTGT1	400	18	147	128	107	0	0	0	1	0	0	5	1	3
LTGT3	400	0	0	400	0	0	0	0	4	3	3	0	0	0

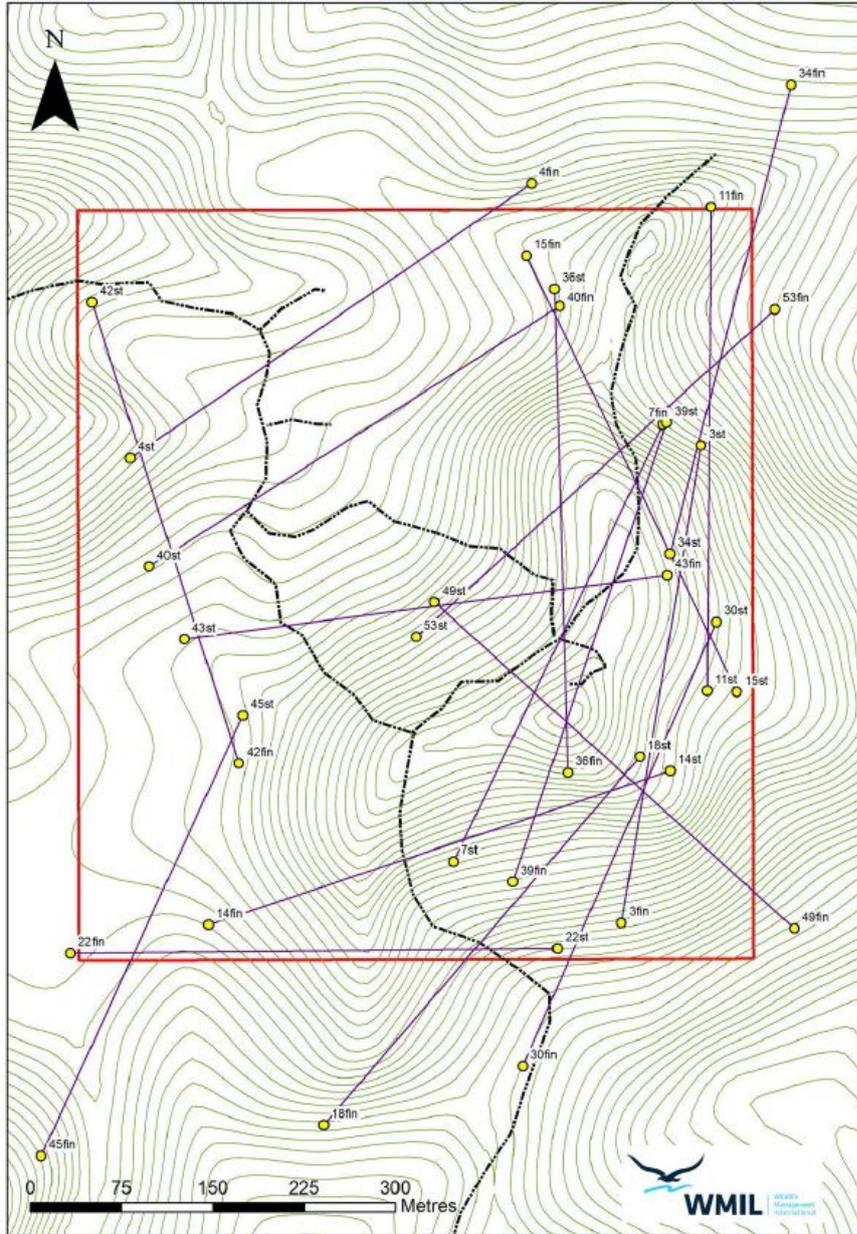


Figure A2.1: Locations of line transects for the 2016 survey.

Appendix 3: MCMC diagnostic plots

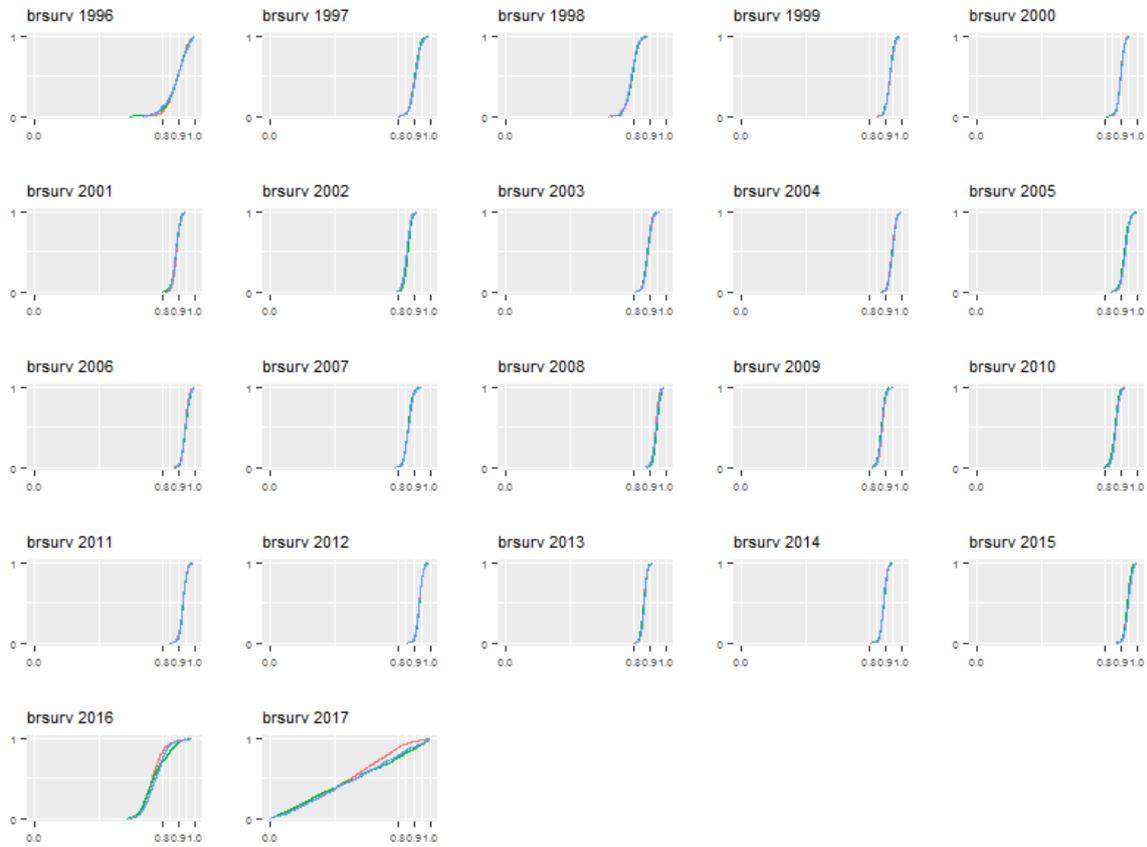


Figure A3.1: The accumulated frequency of Model1 MCMC estimates of breeder survival rates of black petrel. Colours represent different MCMC chains.

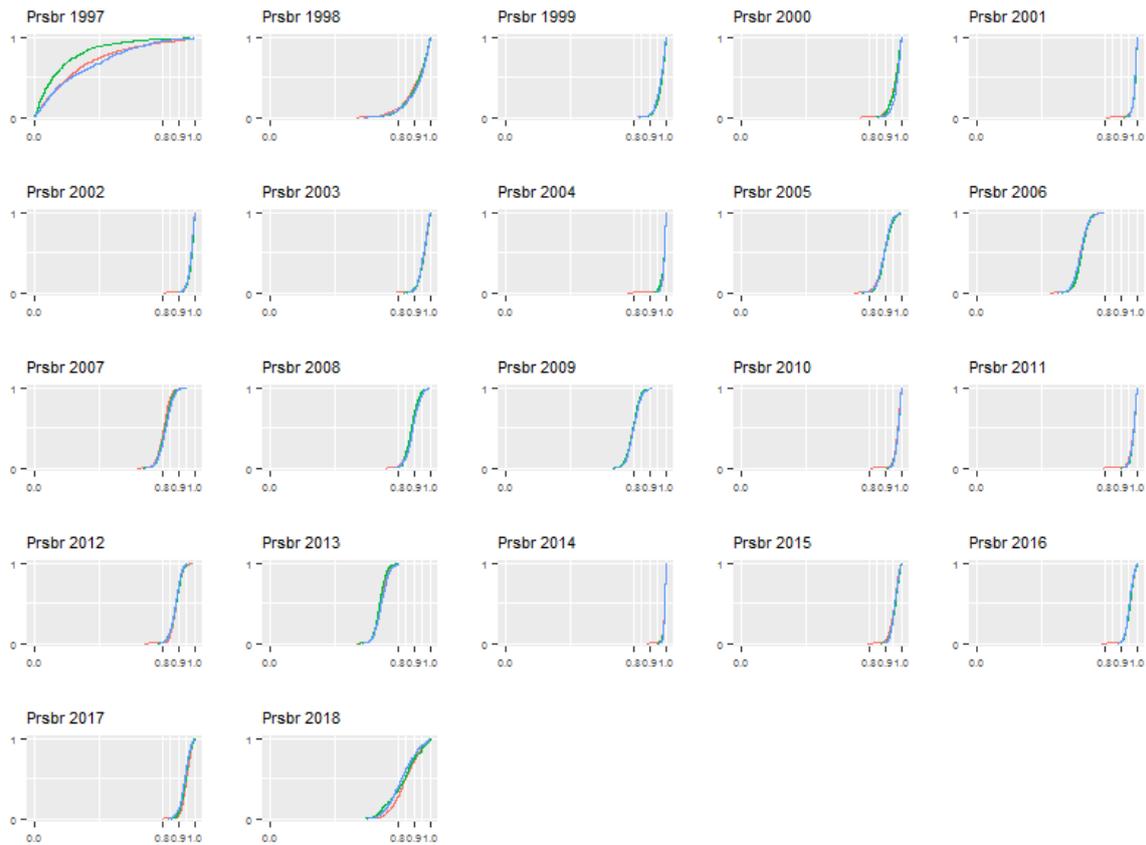


Figure A3.2: The accumulated frequency of Model 1 MCMC estimates of the resight probabilities of successful breeders. Colours represent different MCMC chains.

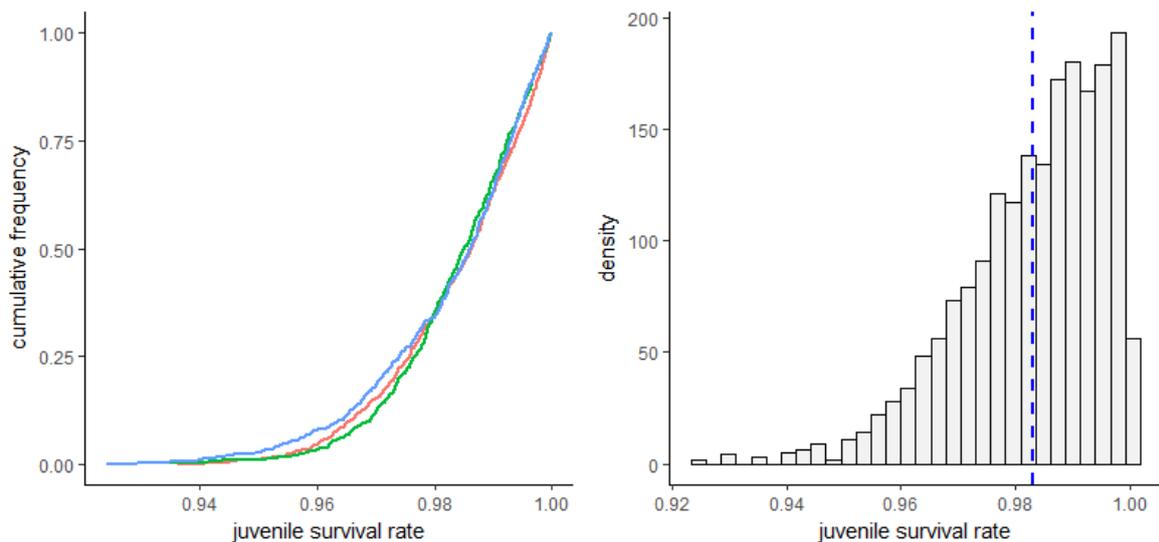


Figure A3.3: Accumulated frequency (left) and posterior distribution (right) of the juvenile survival rate of Model 1. The different colours in the accumulated frequency plot denote the different chain, and the dashed line in the posterior distribution represents the mean.

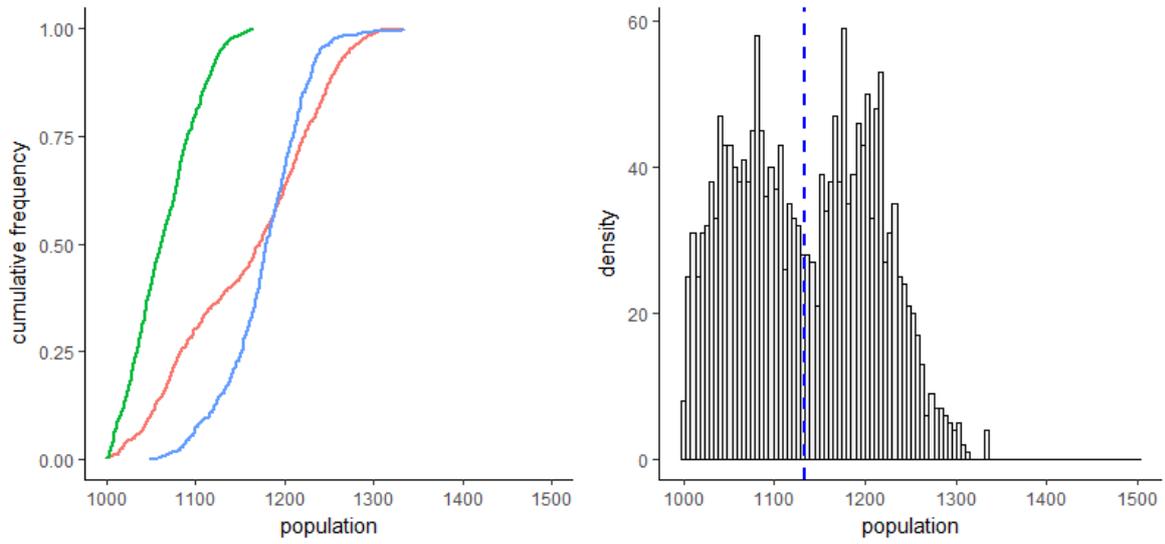


Figure A3.4. Accumulated frequency (left) and posterior distribution (right) of the initial population of Model 1. The different colours in the accumulated frequency plot denote the different chain, and the dashed line in the posterior distribution represents the mean.

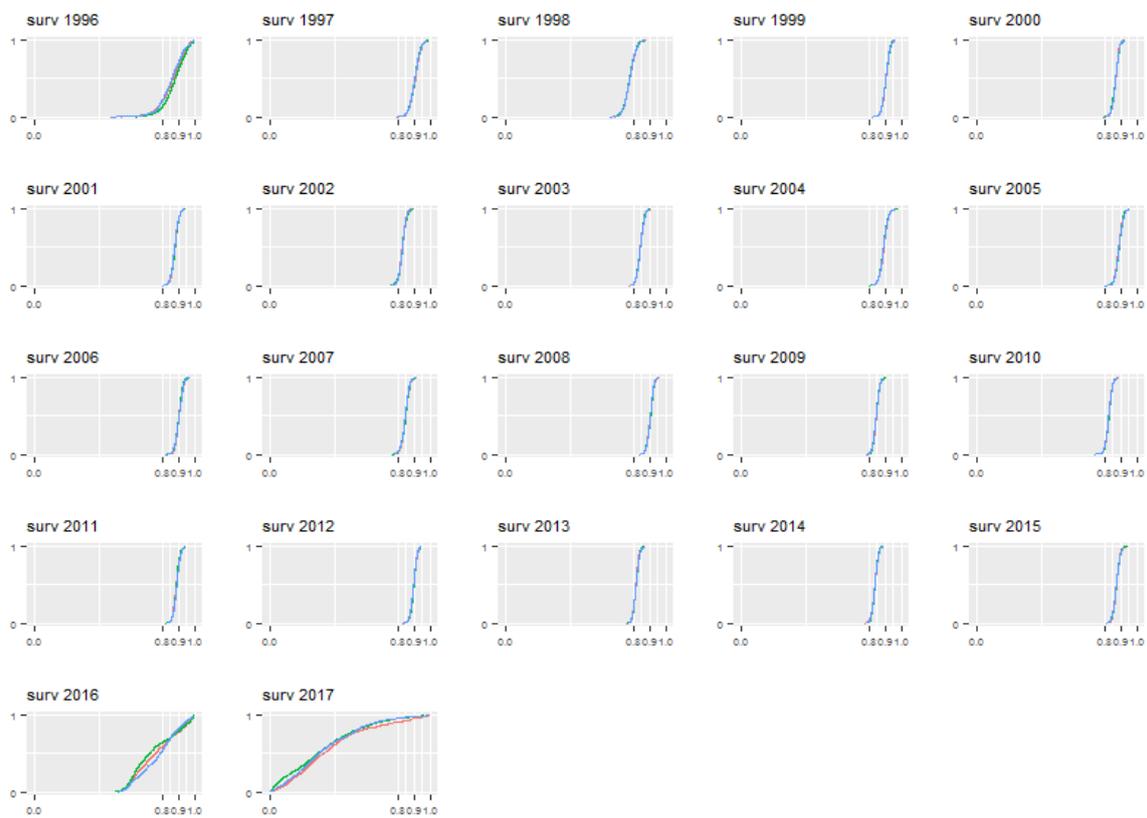


Figure A3.5: The accumulated frequency of Model 2 MCMC estimates of survival rates of adult black petrel. Colours represent different MCMC chains.

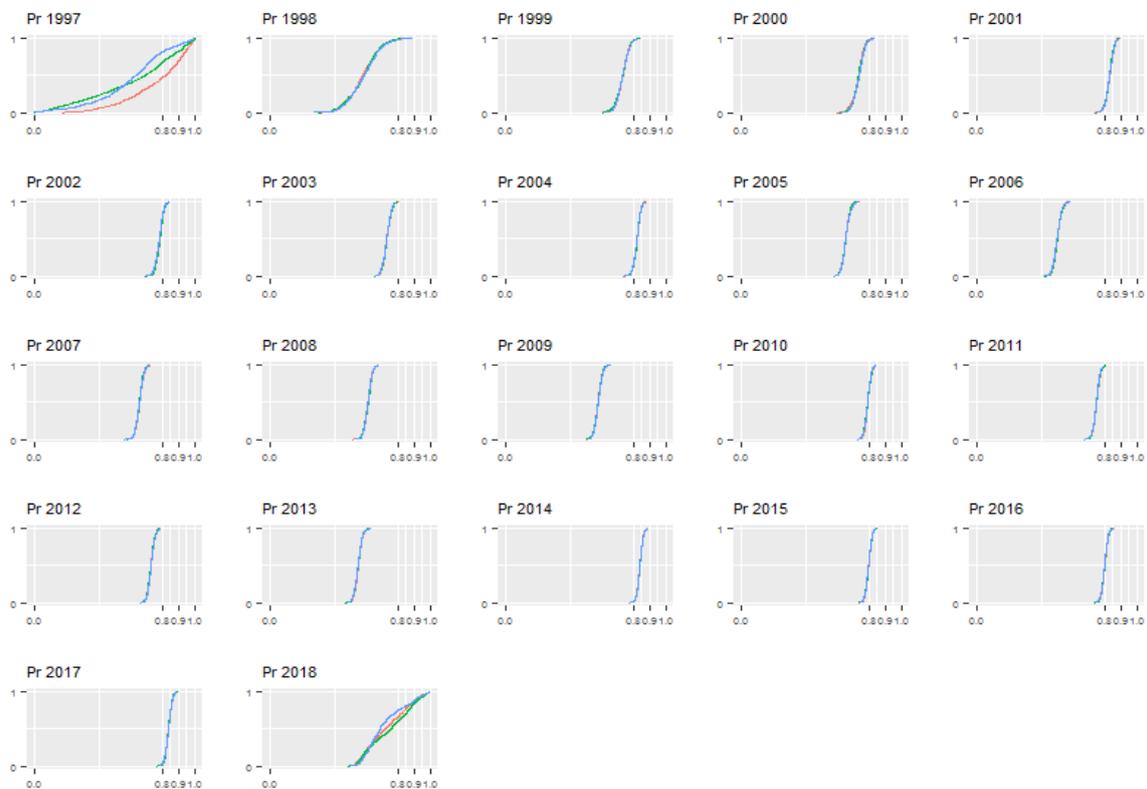


Figure A3.6: The accumulated frequency of Model 2 MCMC estimates of the resight probabilities of adult black petrels. Colours represent different MCMC chains.



Figure A3.7: The accumulated frequency of Model3 MCMC estimates of survival rates of adult black petrel. Colour represents different MCMC chains.

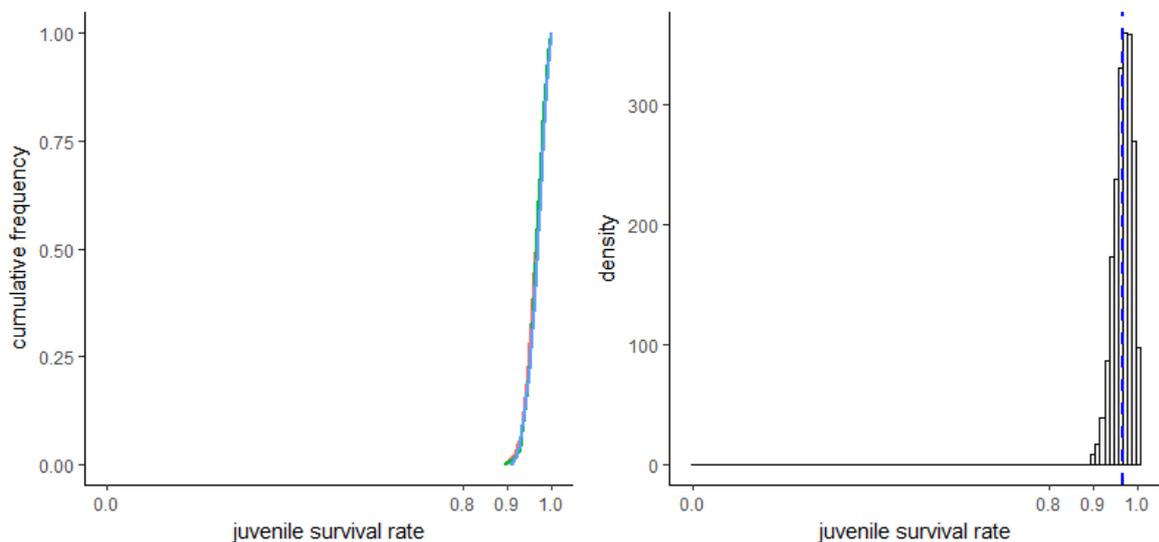


Figure A3.8: Accumulated frequency (left) and posterior distribution (right) of the juvenile survival rate of Model 3. The different colours in the accumulated frequency plot denote the different chain, and the dashed line in the posterior distribution represents the mean.

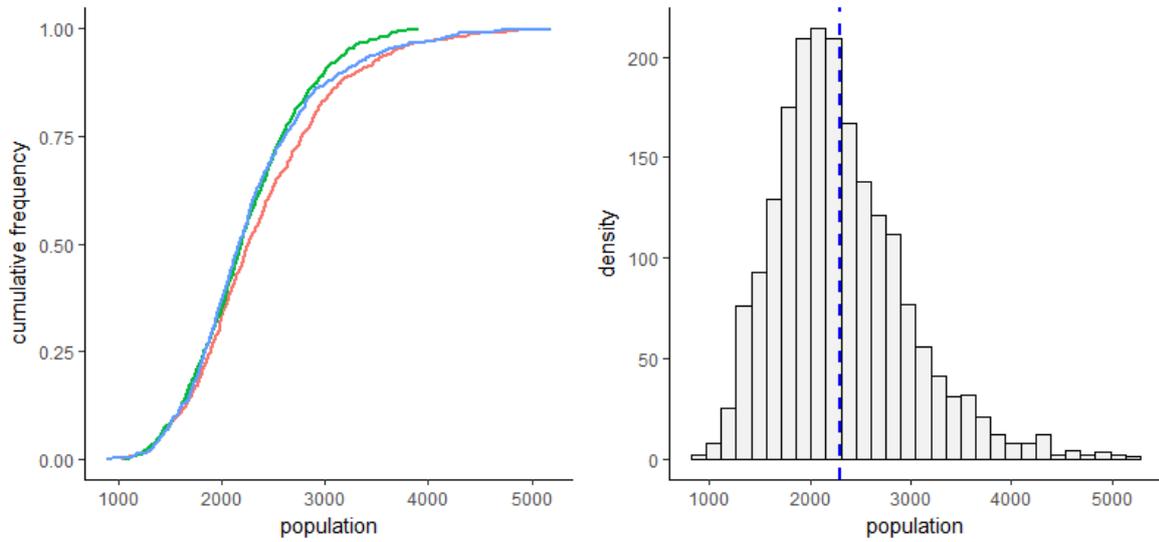


Figure A3.9: Accumulated frequency (left) and posterior distribution (right) of the initial population of Model 3. The different colours in the accumulated frequency plot denote the different chain, and the dashed line in the posterior distribution represents the mean.

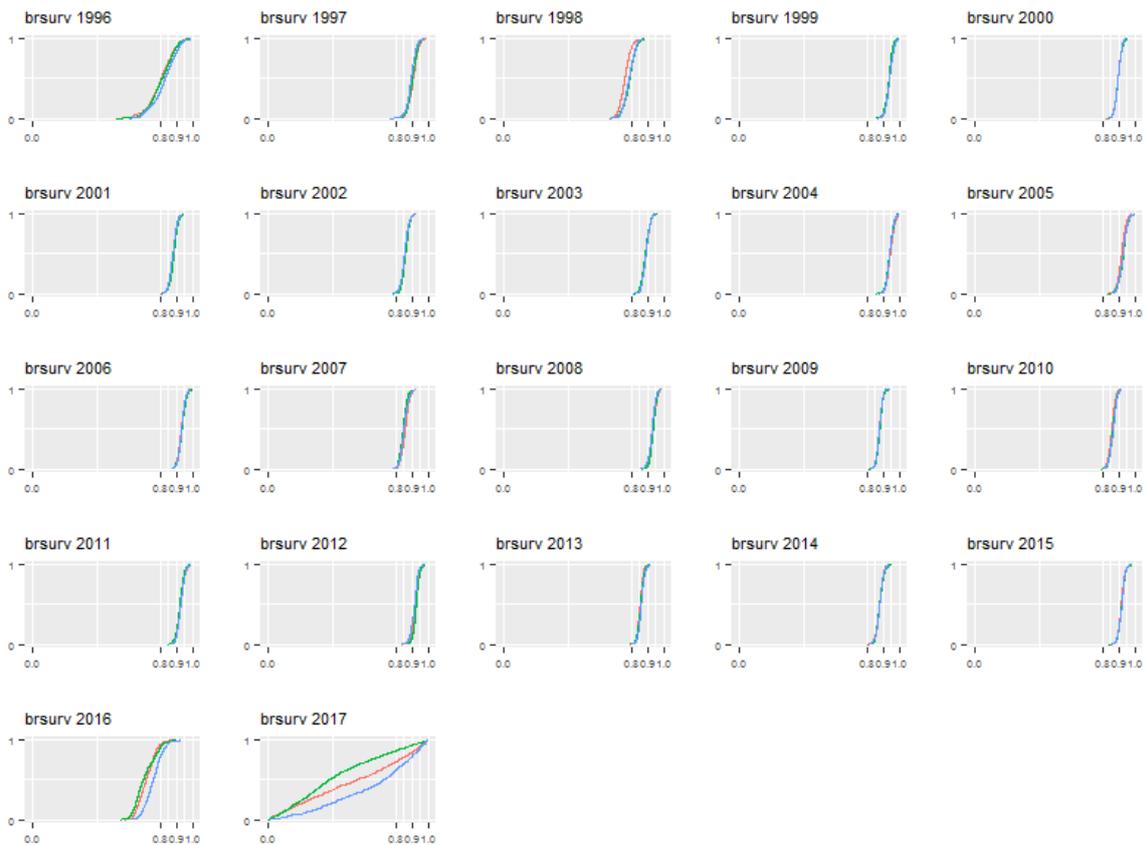


Figure A3.10: The accumulated frequency of Model 4 MCMC estimates of breeder survival rates of black petrel. Colours represent different MCMC chains.

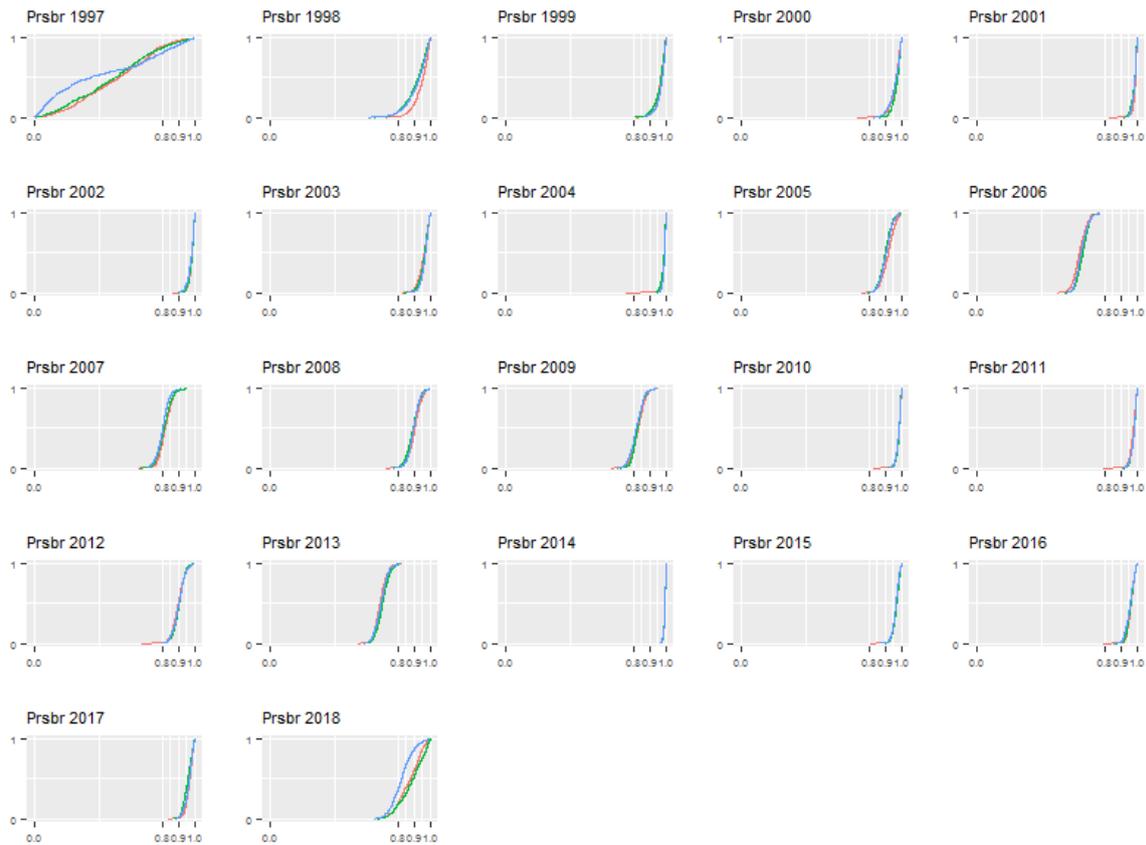


Figure A3.10: continued. The accumulated frequency of Model 4 MCMC estimates of the resight probabilities of successful breeders. Colours represent different MCMC chains.

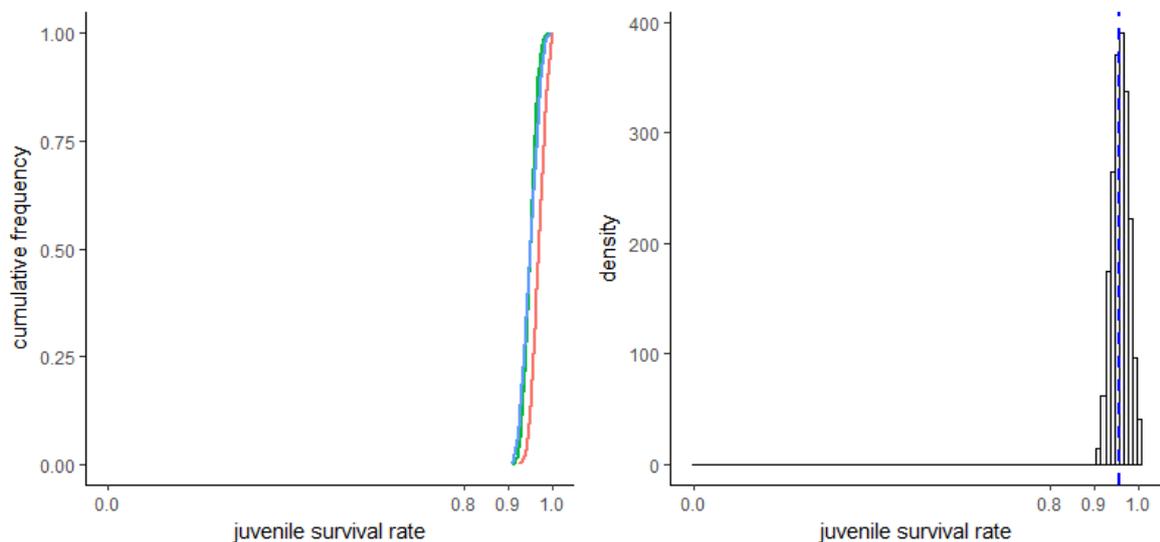


Figure A3.11: Accumulated frequency (left) and posterior distribution (right) of the juvenile survival rate of Model 4. The different colours in the accumulated frequency plot denote the different chain, and the dashed line in the posterior distribution represents the mean.

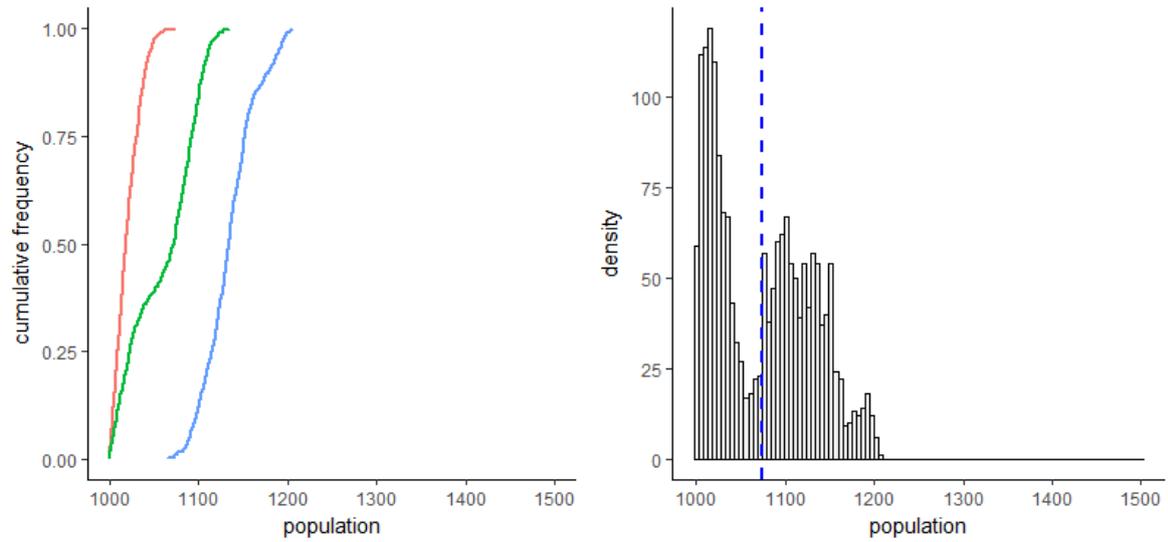


Figure A3.12: Accumulated frequency (left) and posterior distribution (right) of the initial population of Model 4. The different colours in the accumulated frequency plot denote the different chain, and the dashed line in the posterior distribution represents the mean.


```

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@base_parameter
name nbrsurv
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0.9 0.9 0.9 0.9
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2010 2011 2012 2013 2014 2015 2016 2017

@base_parameter
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0.9 0.9 0.9 0.9
year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
2010 2011 2012 2013 2014 2015 2016 2017

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@base_parameter
name oddsmult
values 3

@base_parameter
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@base_parameter
name Pbrstd
values 0.5

@base_parameter
name Tfbrbr
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name Tsbrbr
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@base_parameter
name Tnbrbr
values 0.5

@base_parameter
name Tpbrbr
values 0.5

@base_parameter
name Prjuv
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@base_parameter
name Proth
values 0

@base_parameter
name Prpbr
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0.9 0.9 0.9 0.9

```

year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
2010 2011 2012 2013 2014 2015 2016 2017

@base_parameter

name Prnbr

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0.9 0.9 0.9 0.9

year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
2010 2011 2012 2013 2014 2015 2016 2017

@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 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 2008 2009
2010 2011 2012 2013 2014 2015 2016 2017

@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 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 2008 2009
2010 2011 2012 2013 2014 2015 2016 2017

@derived_parameter

name Nrec

step 1

formula $0.5 * Nsbr * (1 + Noth / (Nnbr + Nfbr + Nsbr))$

@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 $P1stapp9 * Pappstd * (1 - Pbr1st)$

@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)

@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

@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

```

```

@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

@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)

@derived_parameter
name Tnbrnbr
formula 1-Tnbrbr

@derived_parameter
name Tnbrfbr
formula Tnbrbr*(1-Psuccess)

@derived_parameter
name Tnbrsbr
formula Tnbrbr*Psuccess

@derived_parameter
name Tfbrnbr
formula 1-Tfbrbr

@derived_parameter
name Tfbrfbr
formula Tfbrbr*(1-Psuccess)

@derived_parameter
name Tfbrsbr
formula Tfbrbr*Psuccess

@derived_parameter
name Tsbrnbr
formula 1-Tsbrbr

```

```

@derived_parameter
name Tsbrfbr
formula Tsbrbr*(1-Psuccess)

@derived_parameter
name Tsbrsbr
formula Tsbrbr*Psuccess

@derived_parameter
name Plstapp4
formula 1/(1+(1-Plstapp5)*oddsmult/Plstapp5)

@derived_parameter
name Plstapp5
formula 1/(1+(1-Plstapp6)*oddsmult/Plstapp6)

@derived_parameter
name Plstapp7
formula 1/(1+(1-Plstapp6)/(oddsmult*Plstapp6))

@derived_parameter
name Plstapp8
formula 1/(1+(1-Plstapp7)/(oddsmult*Plstapp7))

@derived_parameter
name Plstapp9
formula 1/(1+(1-Plstapp8)/(oddsmult*Plstapp8))

```

Population file for Model 4

This file was exactly the same as for Model 1 except that the following two command block was changed

```

@base_parameter
name Prsbr
values 1

@base_parameter
name Tsbrbr
values 0.5
year_blocks 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
2010 2011 2012 2013 2014 2015 2016 2017

```

Population file for Model 4

This file was exactly the same as for Model 1 except that the @survival command block was changed to the following

```

@survival
parameter_map 1 1 1 1 1 1 1 1 1 1 1 2 3 3 3
parameter_names juvsurv nbrsurv brsurv

```

Estimation file for Model 1 and Model 4

The estimation files of Model 1 and Model 4 are the same.

```

@estimator Bayes
@max_iters 2500
@max_evals 4000
@grad_tol 0.000001
@profile

parameter juvsurv
n 16
l 0.7
u 1.0

@abundance census
years 2005 2010 2014 2016

```

```

step 1
proportion_mortality 0
selectivity selbr
2005 1964
2010 1530
2014 3248
2016 3989
dist normal
cv 0.1

```

[mark-recapture observations removed to conserve space]

```

@estimate
parameter initialisation.NO
prior uniform
lower_bound 1000
upper_bound 15000

```

```

@estimate
parameter juvsurv
lower_bound 0
upper_bound 1
prior uniform

```

```

@estimate
parameter nbrsurv
lower_bound 0 0 0 0 0 0 0 0 0 0 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 1 1 1 1 1 1 1 1 1 1
prior uniform

```

```

@estimate
parameter brsurv
lower_bound 0 0 0 0 0 0 0 0 0 0 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 1 1 1 1 1 1 1 1 1 1
prior uniform

```

```

@estimate
parameter Prpbr
lower_bound 0 0 0 0 0 0 0 0 0 0 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 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 0 0 0 0 0 0 0 0 0 0
upper_bound 1 1 1 1 1 1 1 1 1 1 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 0 0 0 0 0 0 0 0 0 0
upper_bound 1 1 1 1 1 1 1 1 1 1 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 0 0 0 0 0 0 0 0 0 0
upper_bound 1 1 1 1 1 1 1 1 1 1 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
prior uniform

@estimate
parameter Pbr1st
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

```

Estimation file for Model 3

This file was exactly the same as for Model 1 except for the following two command blocks:
The following block in Model 1 is not presented in Model 3

```

@estimate
parameter Prsbr
lower_bound 0 0 0 0 0 0 0 0 0 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 1 1 1 1 1 1 1 1 1
prior uniform

and

@estimate
parameter PrsbrTbrbr
lower_bound 0 0 0 0 0 0 0 0 0 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 1 1 1 1 1 1 1 1 1
prior uniform

```

Parameter estimates for Model 1

initialisation.NO juvsurv 1 nbrsurv 22 brsurv 22 Prpbr 22 Prnbr 22 Prfbr 22 Prsbr 22
Plstapp6 1 oddsmult 1 Pappstd 1 Pbrlst 1 Pbrstd 1 Tfbrbr 1 Tsbrbr 1 Tnbrbr 1 Tpbrbr
1 Psuccess 1
1545 1 0.9295 1 0.806 0.9814 0.7312 0.9038 0.8121 0.8781 0.722 0.9568 0.7449 0.8772
0.8975 0.7577 0.8357 0.8938 0.8653 0.7325 0.8701 0.8456 0.9209 0.9 0.7511 0.8989
0.7793 0.9427 0.9001 0.887 0.8545 0.8955 0.9362 0.9267 0.9311 0.8507 0.935 0.8733
0.8596 0.9239 0.9265 0.8562 0.8741 0.906 0.7158 0.9 0.9996 0.1365 0.02957 0.02628
0.02473 0.04659 0.05516 0.1879 0.08239 0.1337 0.1513 0.0534 0.1067 0.115 0.09984
0.08396 0.02113 0.111 0.1158 0.1187 0.1269 0.1199 0.3515 0.5393 0.4434 0.4143 0.2959
0.3476 0.3322 0.4746 0.229 0.2646 0.198 0.1972 0.1417 0.2936 0.3428 0.2664 0.2044
0.3858 0.3354 0.3004 0.3954 0.2657 7.78e-006 1 0.7348 0.8722 1 0.9011 0.8724 1 0.7312
0.5855 0.8839 0.4889 0.5807 0.9386 0.8508 1 0.6395 0.8991 1 1 1 1 1.302e-005 1 1 1
1 0.9877 1 0.9091 0.6656 0.823 0.9219 0.8361 1 1 0.9178 0.7082 1 0.9802 0.9726 0.9985
0.865 0.9624 5 0.1923 0.03103 1 0.753 0.8391 0.5224 0.1818 0.7325

Parameter estimates for Model 3

initialisation.NO juvsurv 1 nbrsurv 22 brsurv 22 Prpbr 22 Prnbr 22 Prfbr 22 Prsbr 1
Plstapp6 1 oddsmult 1 Pappstd 1 Pbrlst 1 Pbrstd 1 Tfbrbr 1 Tsbrbr 22 Tnbrbr 1 Tpbrbr
1 Psuccess 1
2048 0.9489 0.871 0.8451 0.8158 1 0.786 0.9898 0.8398 0.8749 0.7948 1 0.7972 0.8886
0.9237 0.723 0.8253 0.9082 1 0.6245 0.8676 0.8347 0.7972 0.9 0.9237 0.9146 0.7862
0.9388 0.8974 0.8913 0.8635 0.8884 0.9326 0.943 0.9308 0.8715 0.9471 0.884 0.856
0.925 0.9626 0.8646 0.8897 0.9303 0.6793 0.9 8.044e-008 0.03807 0.6747 0.495 0.4133
0.4642 0.3318 0.6865 0.3316 0.4383 0.3605 0.1486 0.3095 0.2723 0.3175 0.2421 0.104
0.2829 0.3809 0.313 0.347 0.2935 1 0.1371 0.2331 0.251 0.2119 0.2581 0.2411 0.3481
0.1472 0.1316 0.13 0.1481 0.09123 0.2411 0.2662 0.1916 0.1096 0.2596 0.2726 0.237
0.2998 0.2343 1.152e-005 1 0.7816 0.9506 1 0.8733 0.8261 1 0.6746 0.5339 0.854 0.4354
0.5006 0.8711 0.8087 1 0.5176 0.9074 0.8896 0.8889 1 1 1 0.3619 1.25 0.2239 0.04953
0.6775 0.726 0.6751 0.7876 0.7814 0.8511 0.8494 0.8352 0.8137 0.8238 0.6255 0.7122
0.8578 0.7349 0.872 0.8467 0.8103 0.6715 0.8063 0.8601 0.8637 0.8352 0.7888 0.5 0.4098
0.5944 0.7061

Parameter estimates for Model 4

initialisation.NO juvsurv 1 nbrsurv 22 brsurv 22 Prpbr 22 Prnbr 22 Prfbr 22 Prsbr 22
Plstapp6 1 oddsmult 1 Pappstd 1 Pbrlst 1 Pbrstd 1 Tfbrbr 1 Tsbrbr 1 Tnbrbr 1 Tpbrbr
1 Psuccess 1
2129 0.9341 0.9278 1 0.7627 0.9768 0.7256 0.906 0.8462 0.8778 0.7386 0.9498 0.7399
0.8776 0.8983 0.78 0.8452 0.8909 0.8562 0.7415 0.8716 0.8258 0.9128 0.9 0.7152 0.9095
0.7836 0.9449 0.8984 0.8824 0.851 0.8917 0.9319 0.9335 0.9323 0.8551 0.9322 0.877
0.8611 0.9256 0.9259 0.8561 0.8782 0.9088 0.7246 0.9 0.9996 0.1158 0.02068 0.02558
0.02961 0.05002 0.06682 0.1931 0.09016 0.1206 0.1638 0.05377 0.1141 0.1378 0.1046
0.08276 0.02446 0.1247 0.1103 0.1162 0.126 0.1327 0.3709 0.5624 0.3997 0.4016 0.2859
0.3429 0.3368 0.4664 0.2283 0.2655 0.1945 0.1962 0.139 0.2957 0.3423 0.2645 0.2029
0.3849 0.3322 0.2977 0.3955 0.2691 1.835e-005 1 0.7214 0.87 1 0.8995 0.8743 1 0.7301
0.5827 0.876 0.488 0.581 0.9273 0.8484 1 0.6396 0.9011 1 1 1 1 0.001598 1 1 1 1
0.9888 1 0.9096 0.6648 0.8213 0.918 0.8371 1 1 0.9161 0.7062 1 0.9814 0.9719 0.9985
0.8521 0.9584 5 0.2608 0.03188 0.6087 0.7481 0.84 0.5226 0.2691 0.733