ORIGINAL ARTICLE

Estimating survival and reproduction in a quasi-biennially breeding seabird with uncertain and unobservable states

Christophe Barbraud · Henri Weimerskirch

Abstract Estimating the effects of environmental factors on the population dynamics of albatrosses is necessary for their conservation. This requires estimation of demographic parameters, long-time series of capture–recapture data, and knowledge of their at-sea distribution. For biennial albatrosses, multistate mark–recapture models (MSMR) considering individuals during their sabbatical year as unobservable could provide reliable estimates. However, this requires that state assignment is determined with certainty which may not be the case in historical data. We applied multievent mark–recapture models (MEMR) to data on adult Wandering Albatross (*Diomedea exulans*) at Possession Island collected between 1966 and 2006. The models accounted for state uncertainty for those breeding states where the breeding outcome was uncertain. Survival estimates obtained from models not accounting for temporary emigration were higher than those obtained from models accounting for temporary emigration. For males and females, survival estimates from the MEMR models were higher than those from CJS and MSMR models. Annual survival probability was 0.924 (SE = 0.034) for breeding females, 0.971 (SE = 0.038) for non-breeding females, 0.954 (SE = 0.018) for breeding males, and 0.938 (SE = 0.017) for non-breeding males. Whereas Wandering Albatrosses are generally considered as obligate biennial breeders, we found that the probability that successful breeders attempted to breed in a subsequent year was 0.069 for females and 0.048 for males, although their probability of success was 44–62% lower than that of individuals that skipped breeding.

Keywords Capture–recapture · Multievent · Multistate · Temporary emigration · Wandering Albatross

Introduction

Albatrosses are among the most highly threatened birds of the world, with 18 of 22 species considered as threatened and the remaining 4 species considered as near threatened (IUCN 2009). Their large body size (from 1.8 to nearly 12 kg), small clutch size (one egg per breeding attempt), and longevity (up to 64 years) make albatrosses particularly prone to extinction when environmental factors disrupt the fecundity–dispersal–mortality balance (Bennett and Owens 2002). Several tens of thousands of albatrosses are killed accidentally every year in longline fisheries when they attempt to remove bait from hooks during setting and hauling operations, and get caught and consequently drown (Brothers 1991; Weimerskirch et al. 1997a, b). This is because albatrosses are wide-ranging, highly migratory, species whose foraging ranges overlap oceanic habitats favoured by many longline fisheries, and are attracted to fishing vessels as a potential source of food (bait, discharge of waste, offal). This bycatch is thought to be the major cause of declines (Gales 1998), although climate change has also been recently proposed as a potential additional cause of decline (Rolland et al. 2009). Demographic information is needed to help infer the causes of decline. However, the population-level effects of bycatch and climate change are difficult to quantify for several reasons. First, imperfect knowledge on the at-sea distribution of the different classes of the populations (breeders, non-breeders) complicates our

C. Barbraud (✉) · H. Weimerskirch
Centre d'Etudes Biologiques de Chizé, CNRS (UPR 1934),
79360 Villiers en Bois, France
e-mail: barbraud@cebc.cnrs.fr

understanding of the covariations between demographic parameters and the spatial distribution of fisheries or climate anomalies. Recently, innovative bio-logging techniques have helped reveal the at-sea distribution of albatross populations (Jouventin and Weimerskirch 1990; Weimerskirch et al. 2002; Phillips et al. 2004). Second, the shortage of reliable statistics on the level of bycatch per population per fishery makes it difficult to estimate the proportion of individuals killed. However, the impact of longline fisheries on demographic parameters can be quantified using the theory for the dynamics of exploited populations (Burnham and Anderson 1979; Lebreton 2005; Véran et al. 2007). Finally, the paucity of sufficiently detailed demographic data and the particular breeding strategies of albatrosses with variable proportions of individuals that skip breeding events and stay at sea where they remain unavailable for capture, which constitutes temporary emigration (Kendall et al. 1997; Fujiwara and Caswell 2002; Kendall and Nichols 2002), complicate the estimation of demographic parameters. Temporary emigration may bias survival estimates and, therefore, the relationships between survival and fishery related covariates.

The multistate mark–recapture models (MSMR; Schwarz et al. 1993; Brownie et al. 1993), incorporating observable and unobservable states appear as a powerful approach to estimate demographic parameters while explicitly accounting for temporary emigration (Fujiwara and Caswell 2002; Kendall and Nichols 2002; Schaub et al. 2004; Converse et al. 2009). These models have been successfully developed and used for albatrosses, and permit estimation of survival, breeding and success probabilities (Hunter and Caswell 2009), conditional on breeding state (successful or failed) being correctly assigned. Observable birds are those that attempt to breed (successfully or not), while unobservable birds are non-breeders that remain at sea.

An increasing number of long-term studies are providing data needed to estimate demographic parameters of albatrosses with MSMR models, but information on breeding status may be uncertain, particularly for the early part of the longer studies or for those where infrequent visits to the colony do not allow breeding state assignment. Typically, individuals are recorded as breeders, but the breeding outcome is not recorded with certainty. Multievent mark–recapture models (MEMR; Pradel 2005) decoupling the observation event from the state assessment may be a solution to estimate demographic parameters in the presence of state uncertainty. Capture histories are coded with the particular type of observation that was made when the individual was encountered or the fact that the animal was not observed (events). Observed events are assumed to depend only on the underlying states which remain unobserved.

In this paper, we analysed capture–recapture data of a population of Wandering Albatross *Diomedea exulans* to obtain sex-specific estimates of survival, breeding and success probabilities for this population using MEMR models, to take adequately into account breeding state uncertainty during the earlier part of a long-term study. Survival estimates are then compared with those obtained from MSMR and Cormack-Jolly-Seber (CJS) models. Finally, we tested for temporal trends in survival probabilities.

Methods

Study site and capture–recapture data

Monitoring of the Wandering Albatross (*Diomedea exulans*) was carried out at Possession Island (46°S, 52°E), Crozet, southwestern Indian Ocean. Numbers remained relatively stable during the 1960s, before a marked decline beginning in the early 1970s until 1986, followed by a slight increase until 2003. Since 2003, the breeding population is again declining (Delord et al. 2008). Between 1965 and 2005, the overall estimated number of total pairs breeding declined from ∼850 to ∼580, with ∼500 to ∼380 pairs breeding annually (Delord et al. 2008). Since 1966, a capture–mark–recapture program has been undertaken annually between December and April. Most rings of breeding birds were checked in January and February (3–4 visits per nest), just after egg-laying, and all chicks were ringed with stainless steel rings in September and October before fledging. At fledging, breeding performance was determined. Each year, new individuals found in the colony were ringed. Adults were sexed from plumage characteristics and size. We used data on breeding adults identified from the 1966 through 2006 breeding seasons, which were either ringed as chicks or as adults. This yielded a total of 1,792 female and 1,902 male life histories.

Wandering Albatrosses are considered as biennial breeders (Tickell 1968). Breeding adults that successfully raise a fledgling in year t will generally take one sabbatical year in year $t + 1$ during which they stay at sea. Those that failed to raise a fledgling in year t return to breed in varying proportions from year $t + 1$. After close examination of our dataset, we found that 6.4% of males and 7.8% of females were observed breeding in the year consecutive to a successful breeding event. A total of 163 events concerned birds that bred successfully during two consecutive years, of which ∼74% were with the same partner and ∼15.3% with a different partner. A total of 149 events concerned birds that failed during their breeding attempt following a successful breeding attempt, of which ∼58% bred with the same partner, and ∼4% with a different partner. Waugh et al. (1997) reported a similar pattern in the closely related Southern Royal Albatross (*Diomedea epomophora*).

Modelling survival, breeding and success probabilities
with uncertainty

Our starting point was the MSMR model developed by
Hunter and Caswell (2009) for biennial breeders. This
model distinguishes with four states; two observable
states consisting of failed breeder (FB) and successful
breeder (SB), and two unobservable states consisting of
non-breeders whose previous breeding attempt failed
(PFB) and non-breeders whose previous breeding attempt
was successful (PSB). The unobservable states account
for temporary absence corresponding to birds that skip
breeding after breeding unsuccessfully or successfully.
This MSMR model requires that states are assessed with
certainty. However, at Possession Island, the breeding
state (failed or successful) was assessed systematically
for all breeding individuals only since 1987. Between
1966 and 1986, state assessment was uncertain for a
number of individuals (some individuals were classified
as breeders but the success or failure was not always
ascertained), and consequently the MSMR model could
not be used. We therefore used MEMR models which are
a generalisation of MSMR models (Pradel 2005). In
MEMR models, observations do not necessarily corre-
spond to states, which allows the handling of state
uncertainty, and the state "dead" is explicitly included.
The state dead is an absorbing state representing death or
permanent emigration from the study area. We thus
considered five states (FB, SB, PFB, PSB and dead).
States occupied are not directly observed; rather at each
occasion t, an event happens and is recorded leading to
an observed encounter history. In our case, we thus
considered four events; 0 = "not observed", 1 = "seen
as a failed breeder", 2 = "seen as a successful breeder",
3 = "seen as a breeder but status not ascertained", which
were used to build capture histories. Events and states are
considered as random variables, and it is assumed that an
event at occasion t depends only on an underlying state
(which is not observed) of the individual at the moment,
and that successive states obey a Markov chain. Models
were parameterised in terms of the probability of sur-
vival, the probability of breeding given survival, and
the probability of success given breeding. Transition

probabilities between states were thus modelled with a
three-step procedure where survival, breeding and success
are considered as three successive steps in transition
matrices. Figure 1 presents a multinomial tree diagram
describing the probability structure for multistate obser-
vations, and parameters of the model are defined in
Table 1.

Several constraints were made to ensure that the model
reflected the life cycle of the Wandering Albatross and did
not contain redundant parameters. The state dead being
explicitly included in the model but being never encoun-
tered implied several constraints (initial encounter proba-
bility was fixed to 0, transition probabilities from the state
dead to the other states were fixed to 0, and capture
probability was fixed to 0; see Pradel 2005 and Choquet
et al. 2009a). The probability of seeing individuals in
unobservable states and transitions between unobservable
states were constrained to zero. Since some individuals
were observed breeding in the year consecutive to a suc-
cessful breeding event, we did not constrain β_{SB} to 0. To
limit redundancy in survival parameters, we did not con-
sider models where survival probabilities all varied sepa-
rately (Hunter and Caswell 2009). Earlier studies have
demonstrated that MSMR models with unobservable states
can cope with Markovian temporary emigration, and that
most parameters are identifiable unless survival, immigra-
tion and emigration are all time dependent (Kendall and
Nichols 2002; Schaub et al. 2004). We thus tested models
where at least one parameter type (survival, breeding or
success probability) was held constant. Finally, since for
the Wandering Albatross breeding at South Georgia,
Hunter and Caswell (2009) found strong evidence for state-
dependent breeding and success probabilities (their
Table 7), we only considered models where breeding and
success probabilities were entirely state dependent, and we
constrained time-varying parameters to be equal at $t = 1$
and $t = 2$, and $t = K-2$ and $t = K-1$, where K is the
number of capture occasions (see also Cole and Morgan
2011). This MEMR model is parameterised by the initial
state probabilities vector:

$$\Pi^t = \begin{pmatrix} \pi_{FB}^t & \pi_{SB}^t & 0 & 1-\pi_{FB}^t-\pi_{SB}^t & 0 \end{pmatrix},$$

the survival–transition probabilities matrix:

$$
\Phi^t = \begin{pmatrix}
s_{FB}^t\beta_{FB}^t(1-\gamma_{FB}^t) & s_{FB}^t\beta_{FB}^t\gamma_{FB}^t & s_{FB}^t(1-\beta_{FB}^t) & 0 & 1-s_{FB}^t \\
s_{SB}^t\beta_{SB}^t(1-\gamma_{SB}^t) & s_{SB}^t\beta_{SB}^t\gamma_{SB}^t & 0 & s_{SB}^t(1-\beta_{SB}^t) & 1-s_{SB}^t \\
s_{PFB}^t\beta_{PFB}^t(1-\gamma_{PFB}^t) & s_{PFB}^t\beta_{PFB}^t\gamma_{PFB}^t & s_{PFB}^t(1-\beta_{PFB}^t) & 0 & 1-s_{PFB}^t \\
s_{PSB}^t\beta_{PSB}^t(1-\gamma_{PSB}^t) & s_{PSB}^t\beta_{PSB}^t\gamma_{PSB}^t & 0 & s_{PSB}^t(1-\beta_{PSB}^t) & 1-s_{PSB}^t \\
0 & 0 & 0 & 0 & 1
\end{pmatrix}
\begin{matrix} FB \\ SB \\ PFB \\ PSB \\ Dead \end{matrix},
$$

with column headers: FB, SB, PFB, PSB, Dead

Fig. 1 A multinomial tree diagram describing the probability structure for multistate observations when state is not always observed, adapted from Conn and Cooch (2009). *Solid boxes* marked *FB*, *SB*, *PSB*, *PSB* and † indicate possible states (alive in state *FB*, *SB*, *PFB*, *PSB*; dead), while *dashed boxes* represent possible observations following initial release. Possible observations include *FB* (encountered in state failed breeder), *SB* (encountered in state successful breeder), *B* (encountered in a breeding state but failure or success not ascertained), and *0* (not encountered). State transition probabilities were decomposed in a three-step process as the product of probabilities of survival (s), breeding given survival (β) and success given breeding (γ). The state transition and event probabilities are more rigorously defined in Table 1

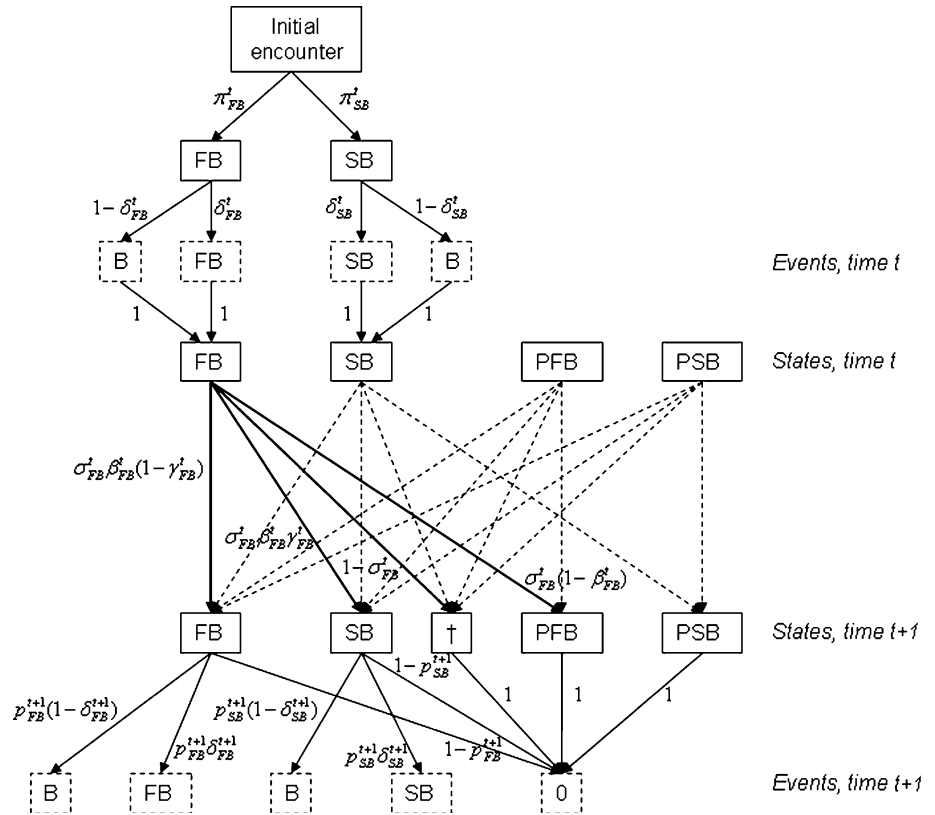**Table 1** Definition of parameters used in the multievent mark–recapture model incorporating unknown states

Parameter	Definition
π_s^t	Probability that an individual is in state s when first encountered at time t
s_s^t	Probability that an individual in state s at time t survives to time $t + 1$ and does not permanently emigrate from the study area
β_s^t	Probability that an individual in state s at time t breeds at time $t + 1$ given that it survives to $t + 1$
γ_s^t	Probability that an individual in state s at time t breeds successfully at time $t + 1$ given that it survives to and breeds at time $t + 1$
p_s^t	Probability that an individual in state s at time t is encountered at time t
δ_s^t	Probability that the state of an individual is observed given that it is in state s at time t and encountered at time t

and the event probabilities matrix:

$$B^t = \begin{pmatrix} 1-p_{FB}^t & p_{FB}^t\delta_{FB}^t & 0 & p_{FB}^t(1-\delta_{FB}^t) \\ 1-p_{SB}^t & 0 & p_{SB}^t\delta_{SB}^t & p_{SB}^t(1-\delta_{SB}^t) \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{pmatrix} \begin{matrix} \text{FB} \\ \text{SB} \\ \text{PFB} \\ \text{PSB} \\ \text{Dead} \end{matrix}$$

with columns headed: not encountered, FB ascertained, SB ascertained, not ascertained.

We tested several hypotheses by considering constrained models for each parameter type, except p and δ which were kept time varying and state dependent. We tested for time variation in survival, breeding and success probabilities. We tested for equality in survival between breeders and non-breeders, between successful and failed breeders (currently or previously), and for all states. Males and females were analysed separately, and sex-specific estimates were compared with the program Contrast (Hines and Sauer 1989).

The assessment of goodness-of-fit (GOF) remains an open question with MEMR models (Kendall 2009) and there is no GOF test for MSMR models with unobservable states (Pradel 2005). We therefore performed several GOF tests. First, we examined a GOF test for presence–absence data only (CJS model). Second, we examined the GOF tests of MSMR models with two states (FB and SB) in which individuals with an uncertain state were arbitrarily assigned to the FB or the SB state. Finally, we performed approximate GOF tests for MEMR models following Viallefont et al. (1995) and Rivalan et al. (2005) by

discounting the change of deviance (Δdev) between models that accounted for reproductive skipping (i.e. multistate models with two observable and two unobservable states) and models that did not account for reproductive skipping (models with two observable states). In this case, the GOF tests were approximated as:

$$GOF = testWBWA + test3G.Sr + test3G.Sm \\ + testM.ITEC + testM.LTEC - \Delta dev$$

with

$$df = df_{testWBWA} + df_{test3G.Sr} + df_{test3G.Sm} + df_{testM.ITEC} \\ + df_{testM.LTEC} - 1$$

GOF tests were performed with the program U-CARE 2.5 (Choquet et al. 2009b), and were run for males and females separately.

We first based inference on information-theoretic model selection, using AIC (Burnham and Anderson 2002) for model selection between models without trends. We tested for effects of linear and quadratic trends using likelihood-ratio tests and analyses of deviance following Grosbois et al. (2008). Data analyses were completed in program E-SURGE 1.4.6 (Choquet et al. 2009a).

Modelling survival with MSMR and CJS models

We compared survival estimates obtained from the MEMR models with those obtained with MSMR and CJS models. Because the breeding state of individuals was not ascertained for all individuals prior to 1987, for the MSMR analyses we decided to assign the uncertain state to be the successful breeding state (see "Results"). We then built three types of MSMR models. MSMR-1 was a model with two observable states (FB and SB). MSMR-2 was a model with one observable state (individual seen) and one unobservable state. MSMR-3 was a model with two observables states and two unobservable states. MSMR-4 was a model identical to MSMR-3 but where changes were made within the life histories assuming obligate biennial breeding. Breeding events consecutive to a successful breeding attempt were censored and replaced by zero corresponding to a temporary emigration of the bird (i.e. the transitions SB to SB and SB to FB were not allowed). Finally, we estimated adult survival probabilities with a CJS model. For all models, we used the same model structure, i.e. all transition probabilities were constrained to be constant, capture probabilities to be time dependent, and survival to be constant and equal for all states. Data analyses were completed in program M-SURGE 1.8.5 (Choquet et al. 2006) and MARK 5.0 (White and Burnham 1999). Because MSMR and MEMR models are prone to local minima during the likelihood maximisation routine, we ran the same models

10 times (sometimes 20 times) to ensure that they converged to the lowest deviance. Estimates are given $\pm 1SE$.

Results

Goodness-of-fit

There was a clear lack of fit of the CJS model for males $\left(\chi^2_{353} = 4306.68, P < 0.001 \right)$ and females $\left(\chi^2_{301} = 4441.89, P < 0.001 \right)$. Tests 2, and particularly subtest 2.Ct accounted for a large part of the overall GOF tests (Table 2). The z statistic associated with subtest 2.Ct was positive (males: $z = 48.42$, females: $z = 53.71$), indicating trap-shyness. Among individuals alive at two successive occasions, those encountered on the first occasion were less reencountered at the second occasion. This reflected biennial breeding in the Wandering Albatross. There was a lack of fit of MSMR models with two observable states (Table 2). Tests WBWA were significant and indicated a memory effect, i.e. individuals tended to return to previously occupied states. Tests M accounted for a large part of the overall GOF tests, indicating trap-shyness. However, compared to the CJS models MSMR models better fitted the data. Overdispersion factors ($\hat{c}$) decreased from 12.20–14.76 to 1.35–1.96. The best fit was obtained for MSMR models where the uncertain state was assigned to be the SB state and where reproductive skipping was accounted for ($\hat{c}$ between 1 and 1.19). These approximate GOF tests therefore indicated that the MEMR model fitted to the data. Given the high breeding success of Wandering Albatrosses ($\sim$73%) and the capture history patterns including the uncertain state typical of successful breeders' capture histories (e.g. year t in uncertain state, year $t + 1$ unobserved, year $t + 2$ in uncertain state, year $t + 3$ unobserved...), it is likely that the uncertain state mostly corresponded to the SB state.

Survival, breeding and success probabilities

For females, the favoured model indicated that survival of successful and failed breeders was similar but different from survival of non-breeders, either post-successful or post-failed, and that survival, breeding and success probabilities were constant (Table 3). Non-breeding females had a higher survival than breeding females (Table 4). Although, the difference in AIC with a model where survival of females was not state dependent was small (2.118), we retained the lowest AIC model since the difference in survival estimates was 4.7%, which can strongly impact population growth rate for such a long-lived species. Females that failed in their breeding attempt and those whose previous breeding attempt was successful had very

Table 2 Goodness-of-fit statistics for CJS and MSMR models with two observable states for male and female Wandering Albatrosses (*Diomedea exulans*) at Possession Island, Crozet, 1966–2006

	Subtest	χ^2	df	P	$\hat{c}$
Female CJS	3.Sr	65.72	35	0.003	14.76
	3.Sm	133.38	98	0.010	
	2.Ct	3,502.72	38	<0.001	
	2.Cl	740.06	127	<0.001	
	Total	4,441.89	301	<0.001	
Male CJS	3.Sr	37.29	38	0.502	12.20
	3.Sm	136.13	101	0.011	
	2.Ct	2,902.26	38	<0.001	
	2.Cl	1,230.99	176	<0.001	
	Total	4,306.68	353	<0.001	
Female MSMR (B = FB)	WBWA	147.43	66	<0.001	1.96
	3G.Sr	98.11	72	0.022	
	3G.Sm	414.187	387	0.164	
	M.ITEC	551.07	108	<0.001	
	M.LTEC	245.42	110	<0.001	
	Total	1,456.21	743	<0.001	
Male MSMR (B = FB)	WBWA	140.88	66	<0.001	1.95
	3G.Sr	63.78	72	0.744	
	3G.Sm	476.59	421	0.031	
	M.ITEC	534.76	112	<0.001	
	M.LTEC	391.72	155	<0.001	
	Total	1,607.74	826	<0.001	
Female MSMR (B = SB)	WBWA	121.39	65	<0.001	1.47
	3G.Sr	90.99	67	0.027	
	3G.Sm	329.12	358	0.861	
	M.ITEC	282.91	85	<0.001	
	M.LTEC	90.75	46	<0.001	
	Total	915.16	621	<0.001	
Male MSMR (B = SB)	WBWA	132.92	73	<0.001	1.35
	3G.Sr	55.90	74	0.941	
	3G.Sm	422.38	418	0.431	
	M.ITEC	230.33	98	<0.001	
	M.LTEC	164.41	83	<0.001	
	Total	1,006.64	746	<0.001	

FB Failed breeder, *SB* successful breeder, *B* unascertained breeding state. $\hat{c}$ is the overdispersion coefficient calculated as χ^2/df. MSMR-3 is a model with two observable states (*FB* and *SB*) and two unobservable states (*PFB* and *PSB*) following Hunter and Caswell (2009)

high probabilities of breeding, contrary to females whose breeding attempt was successful and those whose previous breeding attempt failed (Table 4). The success probability of females that failed in their breeding attempt and of those whose previous breeding attempt was successful was more than twice the success probability of females that were successful in their breeding attempt and of those whose previous breeding attempt failed (Table 4). The estimated probabilities that a breeding female was detected were,

respectively 0.401 ± 0.013 and 0.884 ± 0.010 for females that failed and succeeded in their breeding attempt. Given that a breeding female was detected, the estimated probability that its state was assigned was $\delta = 0.840 \pm 0.004$.

For males, the favoured model had a similar structure as for females, with the exception of breeding probabilities which were best modelled as time varying (Table 3). Breeding males tended to have a higher survival than non-breeding males (Table 4). Similarly to females, males that failed in their breeding attempt and those whose previous breeding attempt was successful had very high probabilities of breeding, contrary to males whose breeding attempt was successful and those whose previous breeding attempt failed (Table 4). The lowest success probability was for successful breeding males and the highest was for males whose previous breeding attempt was successful (Table 4). The estimated probabilities that a breeding male was detected were, respectively, 0.551 ± 0.018 and 0.881 ± 0.009 for males that failed and succeeded in their breeding attempt. Given that a breeding male was detected, the estimated probability that its state was assigned was $\delta = 0.828 \pm 0.004$. For both males and females, the probability to ascertain the breeding state increased with time-varying and was ~1 from 1987.

Breeding males tended to have higher survival probabilities than breeding females and non-breeding males tended to have lower survival probabilities than females, but the differences were not significant (Table 4). Among failed breeders, males were less likely to breed than females, and the reverse was observed among successful breeders (Table 4). Probability of success conditional on breeding was higher for males than for females, except for failed breeders (Table 4).

For non-breeding females, we found support for a quadratic trend in survival probability ($LRT_{constant/trend+trend^2}$: $\chi^2_1 = 4.602$, $P = 0.032$). Slope estimates indicate that survival decreased slightly from the late 1960s to the mid-1990s and has increased since. For non-breeding males, there was evidence for a linear trend in survival (ANODEV: F test$_{constant/trend/time}$ = 8.347, $P = 0.006$), indicating that survival increased during the study period. No statistically significant trend was detected for breeding females (ANODEV: F test$_{constant/trend/time}$ = 1.564, $P = 0.218$; F test$_{constant/trend+trend^2/time}$ = 0.985, $P = 0.383$) and for breeding males (ANODEV: F test$_{constant/trend/time}$ = 0.568, $P = 0.456$; ANODEV: F test$_{constant/trend+trend^2/time}$ = 1.644, $P = 0.207$).

Comparing estimates between MEMR, MSMR, and CJS models

Assuming the estimates from the MEMR models are correct, comparison of survival estimates for equivalent

Table 3 ΔAIC values for multievent models for the Wandering Albatross on Possession Island, Crozet

In all cases, π is constant, p and δ are time-dependent, and π, p, δ, β and γ are estimated separately for each state. Numbers in parentheses indicate rank-deficiency according to rank calculations in E-SURGE (Rouan et al. 2009)

Time constraint model	Survival constraint model		
	$s_1 = s_2 = s_3 = s_4$	$s_1 = s_2, s_3 = s_4$	$s_1 = s_3, s_2 = s_4$
Female			
s, β, γ	2.118 (0)	0 (0)	3.126 (0)
s, β, γ_t	88.438 (2)	88.652 (2)	89.273 (2)
s, β_t, γ	41.551 (1)	39.594 (1)	55.602 (1)
s_t, β, γ	20.756 (0)	70.604 (0)	66.689 (0)
Male			
s, β, γ	28.570 (0)	30.015 (0)	30.015 (0)
s, β, γ_t	85.234 (4)	74.955 (4)	72.938 (4)
s, β_t, γ	17.234 (2)	0 (2)	18.511 (2)
s_t, β, γ	29.400 (0)	78.500 (1)	66.961 (0)

Table 4 Pooled survival, breeding and success probabilities for male and female Wandering Albatrosses for Possession Island, Crozet, 1966–2006

Parameter	Males	Females	P value
s_B	0.954 (0.017)	0.924 (0.034)	0.430
s_{NB}	0.938 (0.017)	0.971 (0.038)	0.428
β_{FB}	0.857 (0.018)	0.956 (0.035)	0.012
β_{SB}	0.045 (0.004)	0.069 (0.006)	0.001
β_{PFB}	0.080 (0.015)	0.047 (0.038)	0.419
β_{PSB}	0.999 (0.001)	0.997 (0.011)	0.827
γ_{FB}	0.573 (0.013)	0.549 (0.013)	0.192
γ_{SB}	0.406 (0.039)	0.265 (0.029)	0.004
γ_{PFB}	0.624 (0.049)	0.260 (0.109)	0.002
γ_{PSB}	0.726 (0.010)	0.692 (0.012)	0.029

Sex-specific estimates were compared with program Contrast (Hines and Sauer 1989) and the P values are shown

Table 5 Pooled survival estimates obtained from MEMR, MSMR and CJS models for male and female Wandering Albatrosses at Possession Island, Crozet, 1966–2006

Model	Males	Bias	Females	Bias
MEMR	0.948 (0.0019)		0.946 (0.0025)	
MSMR-1	0.948 (0.0017)	−0.02	0.943 (0.0018)	−0.40
MSMR-2	0.943 (0.0017)	−0.56	0.937 (0.0019)	−1.01
MSMR-3	0.947 (0.0019)	−0.08	0.946 (0.0025)	−0.07
MSMR-4	0.947 (0.0019)	−0.07	0.946 (0.0025)	−0.07
CJS	0.947 (0.0017)	−0.05	0.942 (0.0018)	−0.42

MEMR estimates are from models where survival was constrained to be constant and equal for all states. MSMR-1 estimates are from a model with two observable states, MSMR-2 estimates are from a model with one observable state and one unobservable state, MSMR-3 estimates are from a model with two observable states and two unobservable states following Hunter and Caswell (2009), MSMR-4 estimates are from a MSMR-3 model where the life histories were modified assuming obligate biennial breeding

parameterisations (i.e., constant survival, constant and state dependent transitions, time and state dependent capture probabilities) indicate that the MSMR and CJS models provided survival estimates that are negatively biased (Table 5). However, the percent relative bias was small, ranging from −0.07 to −1.01%. Bias was more severe for transition probabilities, being positively or negatively biased in the MSMR-3 model (Table 6) and in the MSMR-4 model (results not shown).

Discussion

In a species such as the Wandering Albatross with complex breeding events including biennial breeding, the MEMR model selection results gave greatest support to a parameterisation with different survival probabilities for breeders and non-breeders in both males and females. In males,

breeders had a higher survival than non-breeders. In contrast, breeding females had a lower survival probability than non-breeding females.

These results may be interpreted in the light of the differences in foraging areas and parental investment between males and females. Regarding foraging areas, the main foraging areas for breeding males are oceanic waters around and west of Possession Island (Weimerskirch et al. 1997a, b). In these waters, managed by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), albatross bycatch has been reduced to almost zero during the last two decades following mitigation measures implemented on fishing vessels. Non-breeding males mainly forage in oceanic waters situated north of 45°S (Weimerskirch and Wilson 2000; Weimerskirch et al., unpublished data), which are not managed by CCAMLR or any other convention, and bycatch of

Table 6 Mean transition estimates obtained from MEMR and MSMR-3 models for male and female Wandering Albatrosses at Possession Island, Crozet, 1966–2006

Parameter	Female			Male		
	MEMR	MSMR-3	Bias	MEMR	MSMR-3	Bias
$\psi_{FB \to SB}$	0.525 (0.023)	0.545 (0.015)	+3.81	0.491 (0.015)	0.535 (0.014)	+8.96
$\psi_{FB \to PFB}$	0.044 (0.035)	0.032 (0.007)	−27.27	0.143 (0.018)	0.034 (0.006)	−76.22
$\psi_{PFB \to FB}$	0.035 (0.029)	0.025 (0.009)	−28.57	0.030 (0.007)	0.051 (0.016)	+70
$\psi_{PFB \to SB}$	0.012 (0.011)	0.000 (0.000)	−100	0.050 (0.010)	0.000 (0.000)	−100
$\psi_{PSB \to FB}$	0.307 (0.012)	0.092 (0.017)	−70.03	0.274 (0.010)	0.113 (0.016)	−58.76
$\psi_{PSB \to SB}$	0.700 (0.014)	0.908 (0.017)	+29.71	0.725 (0.010)	0.887 (0.016)	+22.34

Standard errors for the MEMR model estimates were obtained using the delta method (Seber 1982)

albatrosses is known to occur, mainly in fisheries targeting tuna species. These contrasted situations may partly explain the lower survival of non-breeding males, which are probably more exposed to fisheries without bycatch mitigation measures than are breeding males. The positive trend found for survival of non-breeding males may partly reflect the implementation of mitigation measures within the CCAMLR area since the 1990s. Non-breeding females exploit a similar geographic area to non-breeding males (Weimerskirch and Wilson 2000; Weimerskirch et al., unpublished data), and breeding females also forage in waters north of Possession Island, although within a more restricted area than non-breeding birds. Therefore, both breeding and non-breeding females are potentially exposed to fisheries without mitigation measures. The lower survival of breeding females may reflect the higher costs of reproduction in females than in males. Indeed, parental investment in rearing chicks is on average higher in males than in females, but the associated costs are higher in females than in males (Weimerskirch et al. 2000). This hypothesis is further supported by our success probability estimates, indicating that on average breeding males had a higher probability of success than breeding females, particularly for males breeding consecutively to a successful breeding attempt. However, the lower survival of breeding females may also result from an additional extrinsic source of mortality during breeding. An earlier demographic study of this population reported a lower adult survival in females than in males during the period 1966–1985 (estimated from a CJS model) possibly linked to an increase in long-line fishing effort for tuna species within the foraging range of breeding females (Weimerskirch et al. 1997a, b). As for non-breeding males, the increase in survival of non-breeding females since the mid-1990s may partly reflect the implementation of bycatch mitigation measure within the CCAMLR area since the 1990s. Note that, when testing for trend effects, local minima were commonly found, and therefore, these temporal trends must be interpreted with caution. Overall, males and females had similar survival probabilities (males: 0.947 ± 0.002; females: 0.942 ± 0.002).

Breeding females had higher probabilities of breeding during a consecutive year than breeding males. This might be partly caused by the slightly (3%) lower survival of breeding females. Indeed, the male partners of those females that died during or just after the breeding season will attempt breeding the following year but will need to find a new partner, which requires 2–3 years (Jouventin et al. 1999). Therefore, their breeding probability will be lower than those of surviving females which will tend to re-pair with the same male. Additionally, the breeding probability estimates may suggest that females are pairing with failed or post-failed males.

The MEMR model selection results suggested that in both sexes breeding probability was influenced by previous breeding performance: individuals that failed and those that succeeded in year $t - 2$ were ~ 10 to ~ 20 times more likely to breed than those that were successful or failed in year $t - 1$. These breeding probabilities reflect the biennial breeding strategy of the Wandering Albatross and agree well with the results found by Hunter and Caswell (2009) on the Wandering Albatross at South Georgia using a similar modelling approach. However, we note two interesting results in addition to the sex-specific differences discussed above: (1) probabilities of consecutive breeding attempts following successful breeding differed from zero, and (2) breeding probabilities for individuals that failed during their previous breeding attempt were very low. Consecutive breeding following a successful breeding attempt have been recorded for a few other albatross species previously viewed as obligate biennial breeders: Wandering Albatross at Marion Island (Vincent 2008), Southern Royal Albatross in New Zealand (Waugh et al. 1997). Grey headed Albatrosses (*Thalassarche chrysostoma*) are in an intermediate state with biennial and annual breeding since biennial breeding represents up to 19% of breeding attempts after successful breeding at Marion Island (Ryan et al. 2007; Converse et al. 2009), although

estimates seem lower for other populations (Prince et al. 1994; Waugh et al. 1999). According to our estimates, the probability of performing two consecutive successful breeding attempts was ~0.018 for males and females. Consecutive breeding after a successful breeding attempt in assumed obligate biennial breeding albatrosses might, therefore, be more widespread than previously thought, although large sample sizes and long-term studies are needed to detect this behaviour given its low probability. Individuals that failed during their previous breeding attempt had low breeding probabilities. This result is surprising since those birds should have time to recover sufficient body condition to attempt breeding the following year. This pattern suggests that individual quality, age or breeding experience result in some individuals consistently having greater breeding success, as shown in the Wandering Albatross (Weimerskirch 1992).

Temporary emigration causes problems in the analysis of CMR data, leading to biased estimates of survival (Kendall and Bjorkland 2001). When Markovian emigration occurs, as in biennially breeding species, Kendall and Bjorkland (2001) found that, when the probability of remaining in the unobservable state is lower than the probability of moving into an unobservable state, then survival probability estimates are positively biased when the unobservable state is not accounted for. Our findings agree with the results of Kendall and Bjorkland (2001) and Converse et al. (2009): survival estimates from CJS models were higher than those from MSMR-2 models, and male survival estimates from MSMR-1 models were higher than those from MSMR-3 models. Although the survival estimates from the MEMR models tended to be slightly higher than those from all other models, the estimates were very close, particularly with those from the CJS models. It is, therefore, difficult to draw strong conclusions. With respect to survival, ignoring state uncertainty should produce state-dependent estimates that are too close together, because each apparent state is a mixture of both states. Using MEMR models should produce survival estimates that are more distinct, not necessarily higher. In Table 5, we evaluated models that have no state structure and survival. Therefore, we would expect MEMR models to produce the same survival estimates as MSMR models, which they essentially do. Accordingly, MSMR-3 models produced survival estimates for breeding and non-breeding females that were less distinct (0.946 and 0.979, respectively) than those produced by the MEMR model (0.924 and 0.971, respectively). Differences in survival estimates between MEMR and MSMR or CJS models have been noted in a few other studies when sex or disease status of individuals are not ascertained. Nichols et al. (2004) evaluated a CJS model where sex identification was backdated to first capture and found higher survival estimates with the CJS model than with a model taking into account sex uncertainty. Conn and Cooch (2009) found a substantial decrease in precision in survival estimates if encounters of individuals whose state cannot be determined are censored prior to analysis.

Although we imposed some constraints to limit rank deficiency, some of the MEMR models were rank deficient according to rank calculations implemented in E-SURGE (Rouan et al. 2009). All models with constant parameters were full rank, and most models with time-varying survival probabilities were full rank. Rank deficiency was most severe for models where the success probability was time-varying. We suspect this was mainly caused by a lack of data, since those individuals attempting to breed following a successful breeding attempt or after a sabbatical year consecutive to a failed breeding attempt were very few. This lack of data may also explain the rank deficiency in models where breeding probabilities were time-varying. Structural redundancy is another possibility causing rank deficiency and this requires further analyses.

Local minima were a recurrent problem when maximising the likelihood function. Among the available options in E-SURGE and M-SURGE to ensure convergence to the lowest deviance, we found running several times the model with random initial values the most efficient. Using initial values from the last model often ended with local minima. Adding age effects or additional states to such MEMR models will probably enhance the problem as well as computation time (Gauthier et al. 2011).

To conclude, MEMR models allowed us to properly assign state, and thus to use all the data without censoring, to estimate survival, breeding and success probabilities of male and female Wandering Albatrosses. Parameter estimates suggest quasi-biennially breeding in this previously assumed strict biennial breeding species, as well as sex- and state-specific differences in survival, breeding and success probabilities. These differences may partly result from spatially distinct foraging areas between sexes and states, and/or sex-specific differences in reproductive effort.

References

Bennett PM, Owens IPF (2002) Evolutionary ecology of birds. Oxford University Press, Oxford

Brothers N (1991) Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. Biol Conserv 55:255–268

Brownie C, Hines JE, Nichols JD, Pollock KH, Hestbeck JB (1993) Capture-recapture studies for multiple strata including non-Markovian transition probabilities. Biometrics 49:1173–1187

Burnham KP, Anderson DR (1979) The composite-dynamic method as evidence for age-specific waterfowl mortality. J Wildl Manag 43:356–366

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Choquet R, Reboulet A-M, Pradel R, Gimenez O, Lebreton J-D (2006) M-SURGE 1.8 user's manual. CEFE, Montpellier

Choquet R, Rouan L, Pradel R (2009a) Program E-SURGE: a software application for fitting multievent models. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, New York, pp 845–865

Choquet R, Lebreton J-D, Gimenez O, Reboulet A-M, Pradel R (2009b) U-CARE: Utilities for performing goodness of fit tests and manipulating capture-recapture data. Ecography 32:1071–1074

Cole DJ, Morgan BJT (2011) Determining parameter redundancy of multistate mark-recapture models for seabirds. J Ornithol (in press)

Conn PB, Cooch EG (2009) Multistate capture-recapture analysis under imperfect state observation: an application to disease models. J Appl Ecol 46:486–492

Converse SJ, Kendall WL, Doherty PF Jr, Ryan PG, Johnson DH (2009) Multistate models for estimation of survival and reproduction in the grey-headed albatross (*Thalassarche chrysostoma*). Auk 126:77–88

Delord K, Besson D, Barbraud C, Weimerskirch H (2008) Population trends in a community of large Procellariiforms of Indian Ocean: potential effects of environment and fisheries interactions. Biol Conserv 141:1840–1856

Fujiwara M, Caswell H (2002) A general approach to temporary emigration in mark-recapture analysis. Ecology 83:3266–3275

Gales R (1998) Albatross populations: status and threats. In: Robertson G, Gales R (eds) Albatross biology and conservation. Surrey Beatty, Chipping Norton, pp 20–45

Gauthier G, Millot E, Weimerskirch H (2011) Estimating dispersal, recruitment and survival in a biennal species, the wandering albatross. J Ornithol (in press)

Grosbois V, Gimenez O, Gaillard J-M, Pradel R, Barbraud C, Clobert J, Møller AP, Weimerskirch H (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biol Rev 83:357–399

Hines JE, Sauer JR (1989) Program CONTRAST—a general program for the analysis of several survival or recovery rate estimates. Fish Wild Tech Rep 24:1–7

Hunter CM, Caswell H (2009) Rank and redundancy of multistate mark-recapture models for seabird populations with unobservable states. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, New York, pp 797–825

IUCN (2009) 2009 IUCN Red List of threatened species. http://www.iucnredlist.org/

Jouventin P, Weimerskirch H (1990) Satellite tracking of wandering albatrosses. Nature 343:478–746

Jouventin P, Lequette B, Dobson FS (1999) Age-related mate choice in the wandering albatross. Anim Behav 57:1099–1106

Kendall WL (2009) One size does not fit all: adapting mark-recapture and occupancy models for state uncertainty. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, New York, pp 765–780

Kendall WL, Bjorkland R (2001) Using open robust design models to estimate temporary emigration from capture-recapture data. Biometrics 57:1113–1122

Kendall WL, Nichols JD (2002) Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. Ecology 83:3276–3284

Kendall WL, Nichols JD, Hines JE (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578

Lebreton JD (2005) Dynamical and statistical models for exploited populations. Aust NZ J Stat 47:49–63

Nichols JD, Kendall WL, Hines JE, Spendelow JA (2004) Estimation of sex-specific survival from capture-recapture data when sex is not always known. Ecology 85:3192–3201

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Prog Ser 266:265–272

Pradel R (2005) Multievent: an extension of multistate capture-recapture models to uncertain states. Biometrics 61:442–447

Prince P, Rothery P, Croxall J, Wood A (1994) Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. Ibis 136:50–71

Rivalan P, Prévot-Juillard AC, Choquet R, Pradel R, Jacquemin B, Girondot M (2005) Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. Oecologia 145:564–574

Rolland V, Nevoux M, Barbraud C, Weimerskirch H (2009) Respective impact of climate and fisheries on the growth of an albatross population. Ecol Appl 19:1336–1346

Rouan L, Choquet R, Pradel R (2009) A general framework for modelling memory in capture-recapture data. J Agric Biol Environ Stat 14:338–355

Ryan P, Phillips R, Nel D, Wood AG (2007) Breeding frequency in grey-headed albatrosses (*Thalassarche chrysostoma*). Ibis 149:45–52

Schaub M, Gimenez O, Schmidt BR, Pradel R (2004) Estimating survival and temporary emigration in the multistate capture-recapture framework. Ecology 85:2107–2113

Schwarz CJ, Schweigert JF, Arnason AN (1993) Estimating migration rates using tag-recovery data. Biometrics 49:177–193

Seber GAF (1982) The estimation of animal abundance and related parameters. MacMillan, New York

Tickell WLN (1968) The biology of the great albatrosses *Diomedea exulans* and *Diomedea epomophora*. Antarct Res Ser 12:1–55

Véran S, Gimenez O, Flint E, Kendall WL, Doherty PF Jr, Lebreton JD (2007) Quantifying the impact of longline fisheries on adult survival in the black-footed albatross. J Appl Ecol 44:942–952

Viallefont A, Cooke F, Lebreton JD (1995) Age-specific cost of first-time breeding. Auk 112:67–76

Vincent ZD (2008) Survival and reproduction in a biennially-breeding seabird, the Wandering Albatross. Master thesis, University of Cape Town

Waugh SM, Sagar PM, Paull D (1997) Laying dates, breeding success and annual breeding of southern royal albatrosses *Diomedea epomophora epomophora* at Campbell Island during 1964–69. Emu 97:194–199

Waugh S, Weimerskirch H, Moore P, Sagar P (1999) Population dynamics of black-browed and grey-headed albatrosses

Diomedea melanophrys and *D. chrysostoma* at Campbell Island, New Zealand, 1942–96. Ibis 141:216–225

Weimerskirch H (1992) Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. Oikos 64:464–473

Weimerskirch H, Wilson RP (2000) Oceanic respite for wandering albatrosses. Nature 406:955–956

Weimerskirch H, Brothers N, Jouventin P (1997a) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationship with long-line fisheries: conservation implications. Biol Conserv 79:257–270

Weimerskirch H, Cherel Y, Cuénot-Chaillet F, Ridoux V (1997b) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. Ecology 78:2051–2063

Weimerskirch H, Barbraud C, Lys P (2000) Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. Ecology 81:309–318

Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G, Lipp HP (2002) GPS tracking of foraging albatrosses. Science 295:1259

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139