EURING PROCEEDINGS

Estimating dispersal, recruitment and survival in a biennially breeding species, the Wandering Albatross

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Abstract The study of dispersal or recruitment in long-lived birds using capture–recapture methods is challenging because temporary emigration is often a source of heterogeneity in detection probabilities. To deal with this problem, we introduced unobservable states in the multistate, spatial recruitment model of Lebreton et al. (Oikos 101:253–264, 2003) to study dispersal, recruitment and survival in the Wandering Albatross (*Diomedea exulans*), a species with a biennial reproduction (individuals skip breeding following a successful reproduction). We highlight some of the limitations and challenges encountered in using this approach. Our dataset came from a 36-year capture–recapture study conducted at three colonies of the Crozet archipelago. The model had five reproductive stages: pre-breeders, successful breeders, failed breeders, and birds in the year after a successful or a failed breeding attempt, which are unobservable. In adults, movements between colonies (i.e. breeding dispersal) were nested within reproductive stages. Several models with different constraints on survival equally fitted the data but had some rank deficiencies (i.e. non-identifiable parameters). Survival estimates were most biologically realistic (from 0.91 to 0.95) when survival was set equal between observable/unobservable states but free to vary between successful/failed breeders and among colonies. Age-specific recruitment probabilities peaked at 9–10 years and appeared well estimated despite limitations in setting the age of constant recruitment probability. Modelling natal dispersal and recruitment required a simplification of the structure of the model due to computer limitations. When applying the complete and reduced versions of the model to the same dataset, we found that survival was well estimated in both cases. Some transition probability estimates were also similar, but transitions from unobservable to observable states were poorly estimated in the simplified version. We conclude that the simplified version of the model should be limited to the estimation of natal dispersal and that the model with a full structure should be used to estimate breeding dispersal.

Introduction

Dispersal is a population process difficult to properly estimate in animals (Clobert et al. 2001). This process is often divided in two components, natal and breeding dispersal. Natal dispersal is defined as movement from the site of birth to the site of first reproduction, whereas breeding dispersal is defined as movement between sites during consecutive breeding attempts by adults. Multistate capture–recapture models provide a natural framework to study movements of marked animals (Lebreton and Pradel

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2002; Cam et al. 2004) and have been used extensively since they were first introduced in the landmark paper of Hestbeck et al. (1991).

The spatial recruitment model developed by Lebreton et al. (2003) was a significant advance in the study of dispersal using marked animals. This multistate capture–recapture model allows for simultaneous estimation of natal dispersal, breeding dispersal and age-dependent recruitment, while controlling for detection probability. Indeed, in many iteroparous species, young animals not only face the decision of where to settle when breeding for the first time but also when they should do so. Individuals that breed too early in life may face increased costs in terms of reproduction or survival (Viallefont et al. 1995; Tavecchia et al. 2001), which may favour deferred maturity. Lebreton et al.'s (2003) model is especially suited for long-lived animals such as seabirds where the process of accession to reproduction is spread over several years (Oro and Pradel 2000; Crespin et al. 2006; Henaux et al. 2007; Jenouvrier et al. 2008).

A problem encountered when using capture–recapture models in long-lived birds is that marked individuals may not be observable at some stages of the life cycle. For instance, several (though not all) colonial seabirds marked as chicks remain at sea during their immature years and thus are not observable before they return to a colony to start breeding (Crespin et al. 2006; Jenouvrier et al. 2008). During their immature years, these individuals can prospect several potential sites before settling at a specific one for their first reproduction. Another problem arises when adults skip a breeding event and remain at sea, thereby also becoming temporarily unobservable. An example of that is provided by the Wandering Albatross (*Diomedea exulans*), a biennially breeding species. Because of their lengthy breeding cycle, which lasts almost a full year, adults skip breeding the year following a successful breeding attempt, and sometimes also following a failed attempt. Failure to account for this temporary emigration may lead to biased estimates of movement or survival parameters (Converse et al. 2009). One way to account for these sources of heterogeneity is to introduce unobservable states in a multistate model (Fujiwara and Caswell 2002; Hunter and Caswell 2009).

In the Wandering Albatross, fidelity to the natal site is believed to be high and fidelity to the breeding site very high (Weimerskirch et al. 1997; Inchausti and Weimerskirch 2002), but even low dispersal rates may have a significant impact on the population structure of long-lived species such as albatrosses (Milot 2009). However, dispersal rates have never been properly estimated before in this species using adequate capture–recapture methods. Our objective was therefore to study natal and breeding dispersal, as well as recruitment, in three colonies

of Wandering Albatrosses located in the Crozet archipelago using the spatial recruitment model of Lebreton et al. (2003). Because of the biennial reproduction of the Wandering Albatross, we introduced unobservable states (Hunter and Caswell 2009) into the model of Lebreton et al. (2003). We used two unobservable states to take into account that probability of being absent at the breeding colony may differ depending if the previous breeding attempt was successful or not.

In this paper, we first describe in detail the model used to estimate breeding and natal dispersal and age-specific recruitment probabilities. Second, we examine the consequences on parameter estimates of imposing various constraints on survival probabilities, a requirement of these models to solve identifiability problems. Third, we consider practical difficulties linked with the estimation of natal dispersal and recruitment probabilities. Finally, we examine the limitations associated with using a model with a simplified structure to estimate dispersal. The estimation and analysis of dispersal per se are reported elsewhere (Gauthier et al. 2010).

Methods

Study area and species

The study focuses on three discrete colonies of Wandering Albatrosses located along the coast of Ile de la Possession in the Crozet archipelago, Southern Indian Ocean: Pointe Basse, Baie du Marin, and North-east Coast, which included several loose aggregations. The colonies Baie du Marin and North-east Coast were separated by <1 km but Pointe Basse was 8 km from the nearest colony. Adults return to the breeding grounds in December, females typically lay a single egg in January and most young fledge in November. Therefore, individuals that successfully rear a chick do not attempt to breed 2 years in a row, but individuals that lose their egg or chick may either skip or attempt breeding in the following year. After fledging, young remain at sea for several years and thus are unobservable until they return to a colony to breed, from age 5 years onward.

Data collection

Adult and young albatrosses were marked with metal leg rings at the nest every year for the period 1969–2004 (36 years; see Weimerskirch et al. 1997 for details). Observations of marked individuals at the nest occurred annually by systematically walking each colony at least twice, and breeding attempts were classified as either successful (a young fledged), unsuccessful or unknown

success. During the last 20 years of the program, individuals with unknown success were rare (<5%) but were more common in earlier years (up to 50% in some years). For analysis, unknown were pooled with unsuccessful attempts, which means that the latter category was heterogeneous because it was a mixture of successful and unsuccessful attempts, especially in earlier years. The sex was unknown for several individuals, and thus was ignored in the analyses.

The model

Our multistate model is an extension of the spatial recruitment model of Lebreton et al. (2003). Because of the size of the dataset and the very large number of parameters to estimate, we proceeded in two steps for the analysis. First, we used only adults to model adult breeding dispersal. Second, we included young to model natal dispersal and recruitment.

Adult model

Following Hunter and Caswell (2009), we summarised the life cycle of adult Wandering Albatrosses in four stages: (1) successful breeders (SB): individuals that fledged a young in the current year; (2) failed breeders (FB): individuals that attempted to breed but failed to fledge a young; (3) previous successful breeders (PSB): non-observable individuals that were successful at their last breeding
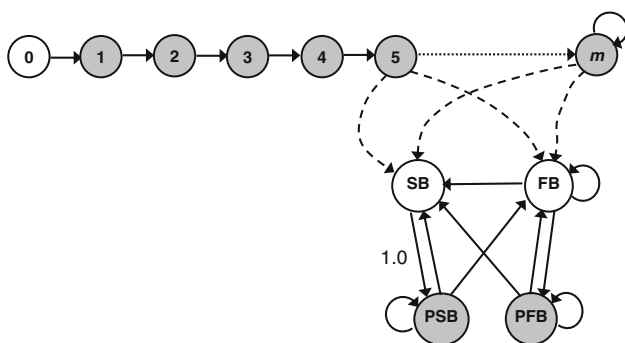

Fig. 1 Stage-based model of the life cycle of the Wandering Albatross (*Diomedea exulans*). Numbers refer to age classes among pre-breeders and recruitment (*dashed line*) can occur at any age between 5 and *m* years (*m* = age at which recruitment probability becomes constant). Only stage transitions within a single colony are presented but the same formulation applies to each colony, with added transitions between stages SB and FB among colonies (breeding dispersal) and from pre-breeders of age 5 to *m* to stages SB or FB among colonies (natal dispersal). *White circles* are observable stages and *grey circles* are unobservable stages. *SB* Successful breeders, *FB* failed breeders, *PSB* previous successful breeders, *PFB* previous failed breeders.

attempt; and (4) previous failed breeders (PFB): non-observable individuals that failed at their last breeding attempt (Fig. 1). These four breeding stages were replicated at each of the three colonies and thus a "state" was a combination of a breeding stage (SB, FB, PSB or PFB) and a colony (denoted A, B and C). The full transition matrix was composed of a series of sub-matrices (movements among sites) for each breeding stage, and had a total of 12 states (Table 1). The model included parameters S, the probability of apparent survival, p, the probability of capture and ψ, the probability of transition among states. Several ψ could be fixed. Because individuals do not breed in the year following a successful breeding attempt, the transition from SB to PSB was fixed to 1. Also, by definition of the model, transitions from the state FB to PSB, PFB to PSB and PSB to PFB were impossible, and were fixed to 0. Because individuals stay at sea during a skip year and are thus unobservable, they retained their colony of origin during those years, but could change colony when they subsequently returned to breed. Probabilities of capture of unobservable states (PSB and PFB) were fixed to 0.

Young-adult model

When young were included in the model, we added one additional state at each colony, pre-breeding, PB, and *m* age classes among pre-breeders (Fig. 1). We defined two ages, *c*, the minimum age at which recruitment can occur, and *m*, the age at which recruitment probability can be considered constant for all subsequent ages (the latter option is preferable to fixing recruitment to 0 beyond age *m* to account for the occasional recruitment of older individuals). We fixed *c* at 5 because inspection of the database revealed the first breeding attempts at this age; the value of *m* was formally tested in the model. However, this model was too complex (see "Results" for details) and we were forced to simplify it by pooling colonies within the states PSB and PFB (Table 2). We will refer to this version as the model with the simplified structure.

As in Lebreton et al. (2003), the lower right 3×3 transition sub-matrix between age 0 and 1 represents natal dispersal (Table 2). Although natal dispersal can take place any time prior to first reproduction, for convenience we forced it to occur between age 0 and 1 because individuals are not observable between marking at birth and their first reproduction. Between age 1–4, as no individuals recruit and dispersal was forced to occur at the first age, transitions of individuals within the PB state were fixed at 1 in the lower-right 3×3 sub-matrix (Table 3). From age 5 to *m*, individuals start to recruit and thus individuals in the PB state may either recruit as a breeder (states SB or FB) with

Table 1 Transition matrix of the adult model (full structure)

From: \ To:	SB(1) A	B	C	FB(2) A	B	C	PSB(3) A	B	C	PFB(4) A	B	C
SB A	0	0	0	0	0	0	1	0	0	0	0	0
SB B	0	0	0	0	0	0	0	1	0	0	0	0
SB (1) C	0	0	0	0	0	0	0	0	1	0	0	0
FB A	ψ_{21}^{AA}	ψ_{21}^{AB}	ψ_{21}^{AC}	ψ_{22}^{AA}	ψ_{22}^{AB}	ψ_{22}^{AC}	0	0	0	ψ_{24}^{AA}	0	0
FB B	ψ_{21}^{BA}	ψ_{21}^{BB}	ψ_{21}^{BC}	ψ_{22}^{BA}	ψ_{22}^{BB}	ψ_{22}^{BC}	0	0	0	0	ψ_{24}^{BB}	0
FB (2) C	ψ_{21}^{CA}	ψ_{21}^{CB}	ψ_{21}^{CC}	ψ_{22}^{CA}	ψ_{22}^{CB}	ψ_{22}^{CC}	0	0	0	0	0	ψ_{24}^{CC}
PSB A	ψ_{31}^{AA}	ψ_{31}^{AB}	ψ_{31}^{AC}	ψ_{32}^{AA}	ψ_{32}^{AB}	ψ_{32}^{AC}	ψ_{33}^{AA}	0	0	0	0	0
PSB B	ψ_{31}^{BA}	ψ_{31}^{BB}	ψ_{31}^{BC}	ψ_{32}^{BA}	ψ_{32}^{BB}	ψ_{32}^{BC}	0	ψ_{33}^{BB}	0	0	0	0
PSB (3) C	ψ_{31}^{CA}	ψ_{31}^{CB}	ψ_{31}^{CC}	ψ_{32}^{CA}	ψ_{32}^{CB}	ψ_{32}^{CC}	0	0	ψ_{33}^{CC}	0	0	0
PFB A	ψ_{41}^{AA}	ψ_{41}^{AB}	ψ_{41}^{AC}	ψ_{42}^{AA}	ψ_{42}^{AB}	ψ_{42}^{AC}	0	0	0	ψ_{44}^{AA}	0	0
PFB B	ψ_{41}^{BA}	ψ_{41}^{BB}	ψ_{41}^{BC}	ψ_{42}^{BA}	ψ_{42}^{BB}	ψ_{42}^{BC}	0	0	0	0	ψ_{44}^{BB}	0
PFB (4) C	ψ_{41}^{CA}	ψ_{41}^{CB}	ψ_{41}^{CC}	ψ_{42}^{CA}	ψ_{42}^{CB}	ψ_{42}^{CC}	0	0	0	0	0	ψ_{44}^{CC}

SB successful breeders, *FB* failed breeders, *PSB* previous successful breeders, *PFB* previous failed breeders. The superscripts refer to transition among colonies (A, B and C) and the subscripts to transition among breeding stages (1, 2, 3 or 4)

Table 2 Transition matrix of the young-adult model (simplified structure) between age 0 and 1 when natal dispersal takes place

From: \ To:	SB(1) A	B	C	FB(2) A	B	C	PSB(3) A-C	PFB(4) A-C	PB(5) A	B	C
SB A	0	0	0	0	0	0	1	0	0	0	0
SB B	0	0	0	0	0	0	1	0	0	0	0
SB (1) C	0	0	0	0	0	0	1	0	0	0	0
FB A	ψ_{21}^{AA}	ψ_{21}^{AB}	ψ_{21}^{AC}	ψ_{22}^{AA}	ψ_{22}^{AB}	ψ_{22}^{AC}	0	$\psi_{24}^{A\bullet}$	0	0	0
FB B	ψ_{21}^{BA}	ψ_{21}^{BB}	ψ_{21}^{BC}	ψ_{22}^{BA}	ψ_{22}^{BB}	ψ_{22}^{BC}	0	$\psi_{24}^{B\bullet}$	0	0	0
FB (2) C	ψ_{21}^{CA}	ψ_{21}^{CB}	ψ_{21}^{CC}	ψ_{22}^{CA}	ψ_{22}^{CB}	ψ_{22}^{CC}	0	$\psi_{24}^{C\bullet}$	0	0	0
PSB(3) A-C	$\psi_{31}^{\bullet A}$	$\psi_{31}^{\bullet B}$	$\psi_{31}^{\bullet C}$	$\psi_{32}^{\bullet A}$	$\psi_{32}^{\bullet B}$	$\psi_{32}^{\bullet C}$	$\psi_{33}^{\bullet\bullet}$	0	0	0	0
PFB(4) A-C	$\psi_{41}^{\bullet A}$	$\psi_{41}^{\bullet B}$	$\psi_{41}^{\bullet C}$	$\psi_{42}^{\bullet A}$	$\psi_{42}^{\bullet B}$	$\psi_{42}^{\bullet C}$	0	$\psi_{44}^{\bullet\bullet}$	0	0	0
PB A	0	0	0	0	0	0	0	0	ψ_{55}^{AA}	ψ_{55}^{AB}	ψ_{55}^{AC}
PB B	0	0	0	0	0	0	0	0	ψ_{55}^{BA}	ψ_{55}^{BB}	ψ_{55}^{BC}
PB (5) C	0	0	0	0	0	0	0	0	ψ_{55}^{CA}	ψ_{55}^{CB}	ψ_{55}^{CC}

SB successful breeders, *FB* failed breeders, *PSB* previous successful breeders, *PFB* previous failed breeders, *PB* pre-breeder. The superscripts refer to transition among colonies (A, B and C) and the subscripts to transition among breeding stages (1, 2, 3, 4 or 5). A dot superscript means pooled across colonies. The upper-left 8 × 8 sub-matrix applies to breeders of unknown age captured at the same occasion than non-breeders of age 0

a specific probability, or remain as a pre-breeder (these probabilities appear on the diagonal of the sub-matrices in the bottom 3 rows of the matrix; Table 4). Finally, the upper-left 8 × 8 sub-matrix in Tables 2, 3 and 4 applies to adults, i.e. individuals initially marked as adults (unknown age) and individuals marked as young once they have recruited into the breeding population.

Because immature individuals are non-observable, their annual survival cannot be estimated between age 0 and 5, only their overall survival during this 5-year period. From age 5 onward, we assumed that the survival of all individuals was identical to that of adults of unknown age, whether they had recruited or not because individuals that had not yet recruited were unobservable.

Data analysis

We performed goodness-of-fit tests for multistate models (Pradel et al. 2003) using the software U-CARE 2.2.1 (Choquet et al. 2009a). We ran the test on the observable stages (SB and FB) of the full adult plus young dataset at the three colonies, excluding the initial marking of young in the nest because individuals were never re-observed in the state pre-breeder, and thus contributed no information to the test (Crespin et al. 2006). We calculated a variance inflation factor ($\hat{c}$) by dividing the sum of the χ^2 statistic of the relevant contingency tables by their degree of freedom.

Our first analysis concentrated on the adults only, and combined individuals that were marked as adults or marked

Table 3 Transition matrix of the young-adult model (simplified structure) between ages 1 and 4, before any recruitment in the breeding population has taken place

From \ To:	SB(1) A	SB(1) B	SB(1) C	FB(2) A	FB(2) B	FB(2) C	PSB(3) A-C	PFB(4) A-C	PB(5) A	PB(5) B	PB(5) C
SB(1) A	0	0	0	0	0	0	1	0	0	0	0
SB(1) B	0	0	0	0	0	0	1	0	0	0	0
SB(1) C	0	0	0	0	0	0	1	0	0	0	0
FB(2) A	ψ_{21}^{AA}	ψ_{21}^{AB}	ψ_{21}^{AC}	ψ_{22}^{AA}	ψ_{22}^{AB}	ψ_{22}^{AC}	0	$\psi_{24}^{A\bullet}$	0	0	0
FB(2) B	ψ_{21}^{BA}	ψ_{21}^{BB}	ψ_{21}^{BC}	ψ_{22}^{BA}	ψ_{22}^{BB}	ψ_{22}^{BC}	0	$\psi_{24}^{B\bullet}$	0	0	0
FB(2) C	ψ_{21}^{CA}	ψ_{21}^{CB}	ψ_{21}^{CC}	ψ_{22}^{CA}	ψ_{22}^{CB}	ψ_{22}^{CC}	0	$\psi_{24}^{C\bullet}$	0	0	0
PSB(3) A-C	$\psi_{31}^{\bullet A}$	$\psi_{31}^{\bullet B}$	$\psi_{31}^{\bullet C}$	$\psi_{32}^{\bullet A}$	$\psi_{32}^{\bullet B}$	$\psi_{32}^{\bullet C}$	$\psi_{33}^{\bullet\bullet}$	0	0	0	0
PFB(4) A-C	$\psi_{41}^{\bullet A}$	$\psi_{41}^{\bullet B}$	$\psi_{41}^{\bullet C}$	$\psi_{42}^{\bullet A}$	$\psi_{42}^{\bullet B}$	$\psi_{42}^{\bullet C}$	0	$\psi_{44}^{\bullet\bullet}$	0	0	0
PB(5) A	0	0	0	0	0	0	0	0	1	0	0
PB(5) B	0	0	0	0	0	0	0	0	0	1	0
PB(5) C	0	0	0	0	0	0	0	0	0	0	1

Notation as in Table 2

Table 4 Transition matrix of the young-adult model (simplified structure) between ages 5 to m, when recruitment in the breeding population (transition from state PB to SB or FB) takes place

From \ To:	SB(1) A	SB(1) B	SB(1) C	FB(2) A	FB(2) B	FB(2) C	PSB(3) A-C	PFB(4) A-C	PB(5) A	PB(5) B	PB(5) C
SB(1) A	0	0	0	0	0	0	1	0	0	0	0
SB(1) B	0	0	0	0	0	0	1	0	0	0	0
SB(1) C	0	0	0	0	0	0	1	0	0	0	0
FB(2) A	ψ_{21}^{AA}	ψ_{21}^{AB}	ψ_{21}^{AC}	ψ_{22}^{AA}	ψ_{22}^{AB}	ψ_{22}^{AC}	0	$\psi_{24}^{A\bullet}$	0	0	0
FB(2) B	ψ_{21}^{BA}	ψ_{21}^{BB}	ψ_{21}^{BC}	ψ_{22}^{BA}	ψ_{22}^{BB}	ψ_{22}^{BC}	0	$\psi_{24}^{B\bullet}$	0	0	0
FB(2) C	ψ_{21}^{CA}	ψ_{21}^{CB}	ψ_{21}^{CC}	ψ_{22}^{CA}	ψ_{22}^{CB}	ψ_{22}^{CC}	0	$\psi_{24}^{C\bullet}$	0	0	0
PSB(3) A-C	$\psi_{31}^{\bullet A}$	$\psi_{31}^{\bullet B}$	$\psi_{31}^{\bullet C}$	$\psi_{32}^{\bullet A}$	$\psi_{32}^{\bullet B}$	$\psi_{32}^{\bullet C}$	$\psi_{33}^{\bullet\bullet}$	0	0	0	0
PFB(4) A-C	$\psi_{41}^{\bullet A}$	$\psi_{41}^{\bullet B}$	$\psi_{41}^{\bullet C}$	$\psi_{42}^{\bullet A}$	$\psi_{42}^{\bullet B}$	$\psi_{42}^{\bullet C}$	0	$\psi_{44}^{\bullet\bullet}$	0	0	0
PB(5) A	ψ_{51}^{AA}	0	0	ψ_{52}^{AA}	0	0	0	0	ψ_{55}^{AA}	0	0
PB(5) B	0	ψ_{51}^{BB}	0	0	ψ_{52}^{BB}	0	0	0	0	ψ_{55}^{BB}	0
PB(5) C	0	0	ψ_{51}^{CC}	0	0	ψ_{52}^{CC}	0	0	0	0	ψ_{55}^{CC}

Notation as in Table 2

as young but had recruited in the population (in the latter case, the first time that the individual was recorded breeding became the first encounter). This dataset included 4,090 individuals (2,035 ringed at Pointe Basse, 470 at Baie du Marin and 1,585 at North-east Coast) spanning 36 occasions of capture. In our most general model, capture probabilities varied among colonies, breeding success (i.e. between successful and failed breeders) and over time; survival varied among colonies, breeding success and breeding status (i.e. presence/absence at the colony); finally, transition probabilities differed among all states (i.e. colonies and breeding stages). All effects on capture, survival and transition probabilities were interactive.

Fully parameterised models with unobservable states typically lead to identifiability problems (Lebreton et al. 2003; Hunter and Caswell 2009), and reduced models have to be used to estimate parameters properly. We constrained parameters sequentially, starting with capture and then proceeding with survival. All models with constraints on capture probability (e.g. equal probabilities among colonies or successful/failed breeders) were strongly rejected, and thus the preferred model retained full time, colony and breeding success effects on this parameter. For survival, we constrained parameters to be equal among colonies ($S_A = S_B = S_C$), breeding success ($S_{SB} = S_{FB}$ and $S_{PSB} = S_{PFB}$) or breeding status ($S_{SB} = S_{PSB}$ and $S_{FB} = S_{PFB}$). We

examined how imposing any of these constraints (alone or in combination) affected survival probability estimates. We did not examine any reduced models with respect to transition probabilities because such constraints were associated with biological hypotheses (e.g. asymmetry of dispersal among colonies), a question examined in details in Gauthier et al. (2010).

Our second analysis included all individual ringed as adults and chicks in the nest. This dataset included 8,346 individuals (of which 2,906 were ringed as chicks at Pointe Basse, 899 at Baie du Marin and 2,614 at North-east Coast) over 30 years (1975–2004). In this analysis, we started the modelling process by using one of the preferred models in the analysis with adults only. For young, survival varied among colonies, transitions within the PB stage (natal dispersal) varied according to colony, and transitions from the stage PB to breeding stages SB or FB (recruitment) were age-specific. We examined how changing the value of m (age at which recruitment probability became constant) affected age-specific recruitment probabilities. Since individuals were never recaptured in the pre-breeder stage after initial marking, capture probability of this stage was fixed to zero.

Because the model used to estimate recruitment and dispersal in young was based on a simplified version of the initial model used to estimate transition probabilities in the adult dataset (i.e. colonies were pooled within the unobservable states PSB and PFB), we examined what could be the consequences of that on parameter estimates in the adults. We tested this by running the simplified structure of the adult portion of the model (Table 2) with the adult dataset and we compared survival and transition parameter estimates with those obtained with the full-structure model (Table 1).

All data analyses were conducted with the software M-SURGE 1.8 (Choquet et al. 2004). We relied on the algorithm of M-SURGE for rank calculations, which is based on the formal method of Catchpole and Morgan (1997) and uses the properties of the numerical derivative matrix (Gimenez et al. 2003; Choquet et al. 2005). Because multistate models are prone to local minima during the likelihood maximisation routine, we ran the same models at least three times (and most often more than five times) with different starting values to ensure that they converged to the lowest deviance. We selected models based on their QAIC values because a variance inflation factor was used.

Results

Goodness-of-fit test

Overall, the goodness-of-fit tests indicated a lack of fit of the multistate model to the data ($\chi^2_{1389} = 2{,}369$, $P < 0.001$).

Looking at the test components, we found no evidence for the presence of transient individuals in the population (test 3G.Sr, $\chi^2_{170} = 156$, $P = 0.764$). However, there was a strong trap dependence effect in capture probabilities (test M-ITEC, $\chi^2_{123} = 796$, $P < 0.001$; test M-LTEC, $\chi^2_{79} = 314$, $P < 0.001$; Pradel et al. 2003). Schaub et al (2004) showed that the latter tests were sensitive to non-random temporary emigration in a single state situation, a conclusion that should also apply to the multistate situation. Inspection of the contingency tables revealed that individuals seen at time t were seen again in lower numbers at time $t + 1$ than those not seen at time t, likely a consequence of individuals skipping a breeding year after a successful reproduction event. Because this immediate trap-dependence effect is taken into account in our model by the unobservable states, the component testing for this effect (M-ITEC) can be ignored. However, the residual test components still indicated a lack of fit ($\chi^2_{1266} = 1{,}843$, $P < 0.001$). We corrected for this lack-of-fit by using a $\hat{c} = 1.455$ for all models.

Parameter constraints and survival estimates

Models where adult survival varied among colonies, between successful/failed breeders and/or presence/absence at the colony performed better in terms of QAIC than the model where survival was held constant (adult dataset only; Table 5). However, all these models except the one with a simple colony effect (Model 7) presented rank deficiencies as some survival parameters were not separately identifiable according to M-SURGE. The problem was most severe when all three effects were present in interaction (Model 2). Model selection was also ambiguous since all four top models in Table 5 differed very little in terms of QAIC. Because of that, we compared survival estimates among models presented in Table 5. Models where survival varied according to breeding success (Model 5), colony (Model 7) or both effects in interaction (Model 3) yielded apparent survival estimates that were biologically realistic (values ranging from 0.907 to 0.948; Fig. 2). However, all models where survival differed between individuals present/absent at the colony (Models 1, 2, 4 or 6) presented some unrealistic estimates of survival (as low as 0.745 or as high as 1.0; Weimerskirch et al. 1997; Barbraud and Weimerskirch 2010). Among the four top models in Table 5, only the one where survival varied according to colony and breeding success (Model 3) yielded biologically realistic survival estimates (Fig. 2).

The estimation of recruitment

When we included the state pre-breeder (Fig. 1) at the three colonies in the model and used the combined adult

Table 5 Model selection of adult apparent survival (S) in the Wandering Albatross

Model no.	Constraints on survival	Deviance	Parameters in model structure	Rank deficiency	ΔQAIC
1	$S_{SB}^A = S_{FB}^A, S_{PSB}^A = S_{PFB}^A, S_{SB}^B = S_{FB}^B, S_{PSB}^B = S_{PFB}^B, S_{SB}^C = S_{FB}^C, S_{PSB}^C = S_{PFB}^C$	60,064.09	270	3	0.00
2	$S_{SB}^A, S_{FB}^A, S_{PSB}^A, S_{PFB}^A, S_{SB}^B, S_{FB}^B, S_{PSB}^B, S_{PFB}^B, S_{SB}^C, S_{FB}^C, S_{PSB}^C, S_{PFB}^C$	60,064.11	276	9	0.01
3	$S_{SB}^A = S_{PSB}^A, S_{FB}^A = S_{PFB}^A, S_{SB}^B = S_{PSB}^B, S_{FB}^B = S_{PFB}^B, S_{SB}^C = S_{PSB}^C, S_{FB}^C = S_{PFB}^C$	60,064.14	270	3	0.03
4	$S_{SB}^A = S_{SB}^B = S_{SB}^C, S_{FB}^A = S_{FB}^B = S_{FB}^C, S_{PSB}^A = S_{PSB}^B = S_{PSB}^C, S_{PFB}^A = S_{PFB}^B = S_{PFB}^C$	60,069.08	268	2	0.28
5	$S_{SB}^A = S_{SB}^B = S_{SB}^C = S_{PSB}^A = S_{PSB}^B = S_{PSB}^C, S_{FB}^A = S_{FB}^B = S_{FB}^C = S_{PFB}^A = S_{PFB}^B = S_{PFB}^C$	60,072.48	266	1	1.43
6	$S_{SB}^A = S_{SB}^B = S_{SB}^C = S_{FB}^A = S_{FB}^B = S_{FB}^C, S_{PSB}^A = S_{PSB}^B = S_{PSB}^C = S_{PFB}^A = S_{PFB}^B = S_{PFB}^C$	60,074.58	266	1	1.76
7	$S_{SB}^A = S_{FB}^A = S_{PSB}^A = S_{PFB}^A, S_{SB}^B = S_{FB}^B = S_{PSB}^B = S_{PFB}^B, S_{SB}^C = S_{FB}^C = S_{PSB}^C = S_{PFB}^C$	60,098.13	267	0	3.20
8	Constant	60,107.43	265	0	23.39

For all models, capture probabilities depend upon time, colony and reproductive success and movement probabilities depend upon colony and reproductive state. Rank deficiency was identified by the software M-SURGE

SB Successful breeders, *FB* failed breeders, *PSB* previous successful breeders, *PFB* previous failed breeders, *A, B, C* colonies

and young dataset, the model could not run because of lack of computer memory. The problem arose because the model now had 15 states with up to m age classes to account for the protracted recruitment of young in the breeding population (in albatrosses, recruitment may be spread over 10 years or more). This is why we simplified the structure of the adult portion of the model by pooling colonies within the non-observable states PSB and PFB (Tables 2, 3 and 4). This reduced the number of states in the model from 15 to 11, which freed enough memory to allow the model to run.

When we varied the age at which recruitment probability could be considered constant (m), the preferred model was with $m = 11$ years but the difference in QAIC with a model where $m = 10$ was small (Table 6). We could not test for values of $m > 11$ because these models would not run due to lack of computer memory. To determine if this inability introduced serious biases, we compared recruitment probabilities when m changed from 9 to 11 years. When $m = 11$, recruitment was negligible at 5 years (~ 0.01); it then increased steadily with age to reach 0.45 at 9 and 10 years and decreased at 11+ years (Fig. 3). By 11 years, 87% of the individuals that would eventually recruit had done so. When $m = 10$, recruitment probabilities were almost identical until 9 years, and at 10 and 11 years, the probability was in between those obtained in the model where $m = 11$. The same pattern was found in the model with $m = 9$. Variations in the proportion of recruits that bred successfully or failed at their first attempt (transition from PB to SB vs PB to FB) were also similar between models where m varied from 9 to 11 years (Fig. 3). Individuals that recruited at a young age failed more often at their first breeding attempt than those that recruited at a later age (0.72 at 5 and 6 years vs 0.34 at 11+ years).

Comparison of models with full versus simplified structure

To make this comparison, we ran the adult portion of the model with a simplified structure on the adult dataset (Table 2) using the same constraints as in Model 2 of Table 5. We found that survival estimates for failed and successful breeders at each colony were virtually identical with either the simplified or the full structure of the model. For state transition probabilities, results were more equivocal. Whereas some transition parameter estimates were similar in both versions of the models (e.g. ψ_{FB-SB} and $\psi_{PSB-PSB}$ for all colonies; ψ_{FB-FB}, ψ_{PFB-SB}, ψ_{FB-PFB} and ψ_{PFB-FB} for colony A), others were not (e.g. ψ_{PSB-SB} and ψ_{PSB-FB} for all colonies; ψ_{FB-FB}, ψ_{PFB-SB} and ψ_{PFB-FB} for colonies B and C; Fig. 4). Generally, parameter estimates for transitions from unobservable to observable states differed most between models with the simplified versus the full structure.

Discussion

Unobservable states were introduced into multi-state models to control for heterogeneity due to the temporary emigration of individuals, as in the Wandering Albatross. The trap-shyness found in the goodness-of-fit test confirmed that the biennial reproduction of this species was a significant source of heterogeneity in the dataset. Controlling for temporary emigration with unobservable states can improve parameter estimates, as shown by Converse et al. (2009) for survival probabilities in the Grey-headed Albatross (*Thalassarche chrysostoma*). However, unobservable states can also introduce some problems such as rank deficiencies (Kendall and Nichols 2002). The solution to that is usually
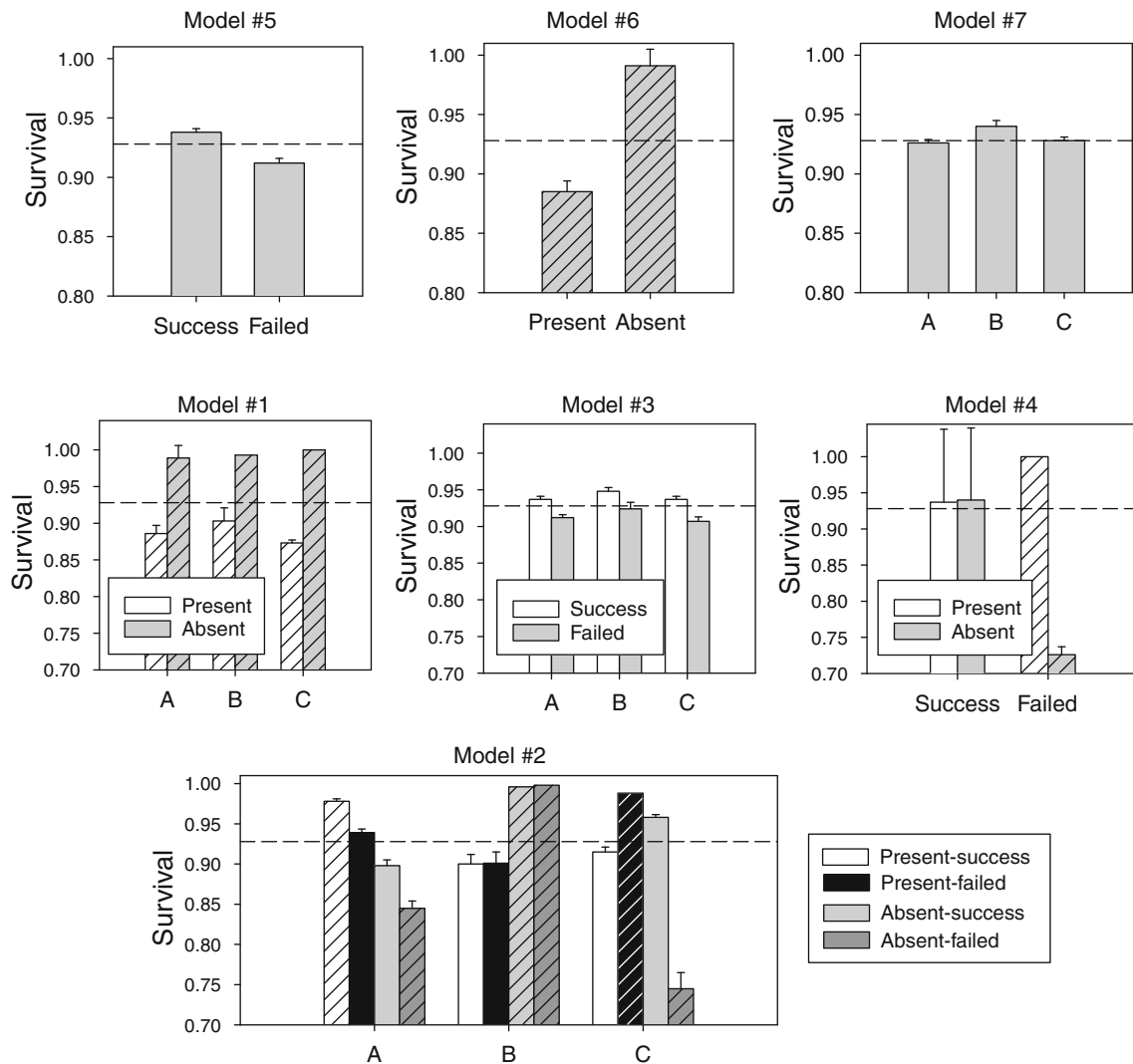
Fig. 2 Estimates of annual apparent survival probability of adult Wandering Albatrosses obtained with the models listed in Table 1. Depending on the model, survival could vary according to the colony (*A* Pointe Basse, *B* Baie du Marin, *C* North-east Coast), the reproductive success (successful or failed), presence/absence at the colony, or a combination of these factors. The *dashed line* is the survival in the constant model (0.928). *Hatched bars* are survival probabilities considered biologically unrealistic. *Error bars* are standard errors

Table 6 Model selection of age of constant recruitment probabilities in the Wandering Albatross

Model no.	Recruitment age	Deviance	Np	ΔQAIC
9	11	79,116.45	141	0.00
10	10	79,125.43	139	2.18
11	9	79,139.52	137	7.68

For all models, capture, survival and movement probabilities of adults vary according to Model 2 in Table 5, and survival and movement probabilities of young vary among colonies

np Number of identifiable parameters

to impose constraints on some parameters, most notably on survival rates. Hunter and Caswell (2009) formally explored this problem in models similar to, though simpler than, the ones that we used and found that a large number of models with a minimum of constraints were actually full rank, which means that all parameters were identifiable despite the presence of unobservable states.

Introducing unobservable states in the spatial recruitment model of Lebreton et al. (2003) resulted in some rank deficiencies for survival in the case of the Wandering Albatross. Converse et al. (2009) showed with simulations that, in a four-state model with two unobservable states, models with different constraints on survival cannot be reliably distinguished on the basis of the QAIC, a result that our Table 5 also seems to indicate. Examination of survival parameter estimates revealed large discrepancies depending on the constraints imposed on the probability of apparent survival (*S*). Generally, we found that survival

probabilities were most poorly estimated when S differed according to presence/absence at the colony (i.e. between observable/unobservable states). In contrast, survival estimates obtained when S was set equal between individuals present/absent at the colony, but different among colonies and reproductive success, were similar to those obtained in full-rank models such as those with constant survival or colony-specific survival. These apparent survival rate estimates were consistent with previous analyses in this

Fig. 3 Estimates of age-specific probability of recruiting in the breeding population of Wandering Albatrosses according to the age in years (m) at which recruitment probability is set constant. The *hatched area* is individuals that bred successfully at their first breeding attempt and the *unhatched area* those that failed. *Error bars* are standard errors

species (Weimerskirch et al. 1997). We did not examine models with full temporal variation in survival rate because this would have resulted in an overparameterised model where rank deficiency problems would have likely been more severe (Hunter and Caswell 2009). Moreover, long-lived species with high survival like albatrosses typically show little year to year variation in survival rate (Saether and Bakke 2000; Saether et al. 2004).

The greatest problem encountered when we included individuals marked as chicks in the model was that it was too large to run in M-SURGE on any computer. The problem arose because we now had 15 states, at least 10 age classes and up to 35 capture occasions, which resulted in a model with >300 parameters that far exceeded the memory capacity. This is why we were forced to simplify the model to 11 states and to reduce the dataset to 30 years. Although such a model would run, it was very slow even on a fast computer (>24 h). Another issue is that multistate models are prone to local minima during the likelihood maximisation routine, a problem that increases with the complexity of the model. A solution to this problem is to run the same model several times using different starting values (Choquet et al. 2005), but this further exacerbates the problem of computing time and limits the total number of candidate models that can be tested.

We could not test for age-specific recruitment probabilities beyond 11 years of age, again due to computer limitations. Despite this, results suggest that this was not a
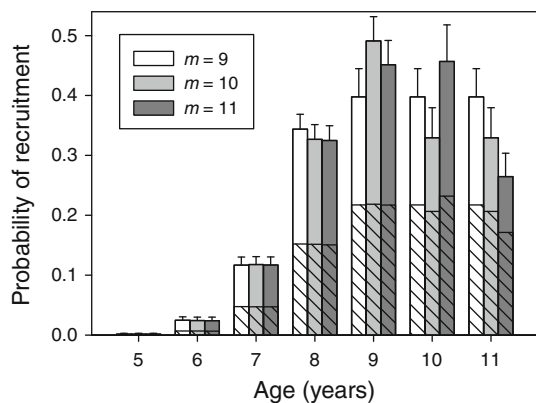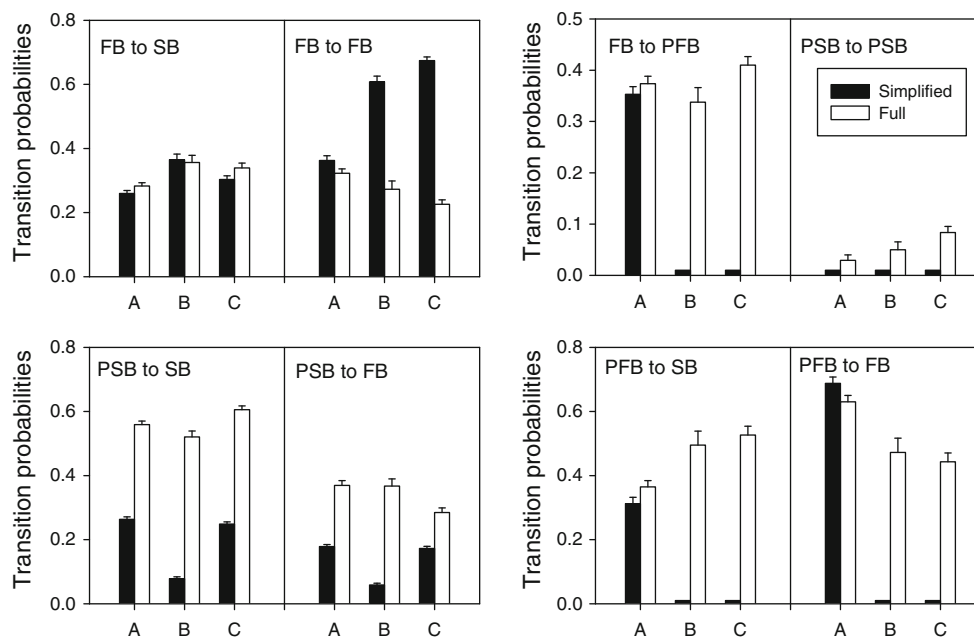

Fig. 4 Estimates of annual movement probabilities of adult Wandering Albatrosses among breeding stages (*SB* successful breeders, *FB* failed breeders, *PSB* previous successful breeders, *PFB* previous failed breeders) and colonies (*A* Pointe Basse, *B* Baie du Marin, *C* North-east Coast) obtained from models with either the full (Table 1) or the simplified structure on the adult portion of the matrix (colonies pooled within the breeding stages PSB and PFB; Table 2). *Error bars* are standard errors

serious bias in our analysis because recruitment probabilities apparently peaked around 9–10 years of age. Furthermore, reducing the age at which recruitment probabilities become constant did not markedly change our estimates. The median age at first reproduction estimated here (9–10 years) is similar to previous estimates (Weimerskirch et al. 1997). Over the period 1966–1975, age at first reproduction tended to decrease in this population from 11–12 years to 9–10 years. Weimerskirch and Jouventin (1987) attributed this decrease to the abrupt decline (up to 50%) experienced by the population on the Île de la Possession during the 1970s, which was followed by a stabilisation and a slow recovery (Weimerskirch et al. 1997). We found evidence that the probability of successful breeding increased with the age at first breeding. A possible cost for individuals that recruit too early in life has been reported before in long-lived birds, both in terms of reduced breeding success and subsequent survival (Viallefont et al. 1995; Tavecchia et al. 2001; Reid et al. 2003). Because albatrosses forage in an environment where productivity is low and food distribution is spatially and temporally unpredictable, slow improvements in foraging skills with age could explain the observed increase in breeding success with recruitment age (Weimerskirch et al. 2005).

A weakness of our model with the simplified structure was the pooling of colonies in unobservable states (PSB and PFB). A consequence of this was that we could no longer track the colony of origin of adults when they returned to breed after a sabbatical year. When we compared parameter estimates from models with either the simplified or full structure applied to the adult dataset with the same constraints, we found no difference in survival estimates but substantial differences in the estimation of some adult transition probabilities, especially those from unobservable to observable states. It is not possible to determine the consequence of that on transition probabilities of young because the full model would not run with the pre-breeder state. However, because individuals in the pre-breeder state first move into one of the two breeder states (BS or FB) where the full colony structure was retained, natal dispersal and recruitment probabilities may still be well estimated in the model with a simplified structure. Nonetheless, estimates of adult dispersal should be based on a model retaining the full structure. Using these models, Gauthier et al. (2010) successfully estimated breeding and natal dispersal in the Wandering Albatross with the current dataset and examined various hypotheses that could explain the observed patterns.

Future directions

One source of heterogeneity that was ignored in our dataset is the uncertainty on the reproductive success of some individuals. Uncertainty in state assignment can be taken into account with the multi-event model developed by Pradel (2005) (see Barbraud and Weimerskirch 2010 for an example). Such models can now be implemented in the user-friendly software E-SURGE specifically developed for the multi-event situation (Choquet et al. 2009b). A further advantage of this software is that transitions can be decomposed in several elementary steps. In our model, the ψ were modelled as the product of two processes: the probability of moving across breeding stages and, conditional upon breeding, the probability of staying or moving to a new colony. In theory, these two processes could be decomposed and these probabilities estimated separately. However, in doing so, one implicitly assumes that these two processes are independent, which may not be the case. For instance, the probabilities of breeding again the year after a failure or of breeding successfully following a sabbatical year may not be the same at all colonies, or else the probability of staying or moving from a colony may not be the same after a breeding success or a failure. Combining these two processes into a single ψ as we did allows for such interactions. Finally, one has to consider the added complexity of running the model that we used for the Wandering Albatross in a multi-event framework.

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