Research

Recruitment processes in long-lived species with delayed maturity: estimating key demographic parameters

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Long-lived species show delayed maturity and generally skip breeding sites on a given year, causing difficulties in estimating demographic parameters. A novel multi-state capture – recapture model (model G for general) is proposed to estimate survival and recruitment. Model G considers long and short periods of non-attendance at the breeding site. Model G is compared against a reduced model (model R) to test if pre-breeders skip the studied site a given year, potentially prospecting other breeding habitats.

This model is applied to the vulnerable Cory's shearwaters seabird species. As for many species, natal philopatry, pre-breeding attendance and prospecting play an important role for recruitment into the breeding population. Model G shows that all Cory's shearwaters come back to their natal colony, and attend the colony before recruiting into the breeding population. Moreover, model G is preferred against model R, highlighting that prospecting plays a potentially role in the recruitment processes. Return and recruitment probabilities show similar time variation, suggesting an environmental forcing. The maximum probability of the first breeding is reached at the age of seven years. During the first year the annual survival rate is 0.52 (IC$_{95\%}$ = [0.40, 0.64]) and pre-breeders and adult annual survival rates do not differ, being respectively 0.88, IC$_{95\%}$ = [0.83, 0.92] and 0.89, IC$_{95\%}$ = [0.88, 0.9].

Model G provides an improvement to estimate demographic parameters for long-lived species life cycle and an adequate framework to test the influence of covariates. Model G is structured by age and breeding status categories, allowing easy further population models.

Recruitment to a breeding population is a gradual, complex process for long-lived species with delayed maturity. For those species, recruitment parameters are especially difficult to estimate due to the high mobility and low detectability during the pre-breeding period. Animals that have not yet start to breed, i.e. pre-breeders, are often detected at the breeding site before the first breeding attempt (Cadiou et al. 1994) and their attendance potentially plays an important role for mate, habitat selection and recruitment probability (Danchin et al. 1998). To optimize their future fitness it is believed that pre-breeders that attend the breeding colony before maturity gather information on habitat quality (Boulinier et al. 1996, Schjorring et al. 1999, Frederiksen and Bregnballe 2001). This prospecting behavior, involves the temporary movement in and out the studying breeding site (Fujiwara and Caswell 2002a) generating different problems in the estimation of demographic parameters (Barker 1999), The temporary absence from a study site is confounded with detection failure and unbiased estimates may only be obtained within a probabilistic framework that allows the estimation of detection probabilities

(capture-mark-recapture techniques(CMR); Lebreton et al. 1992, Williams et al. 2002). Temporal absence from the study site is in part 'absorbed' into the detection probability (Pradel and Lebreton 1999). In contrast, long absence from the study site seriously impairs estimates of pre-recruitment parameters. The recent extension of multisite CMR models (Brownie et al. 1993, Schwarz et al. 1993) to unobservable states (Pradel and Lebreton 1999) partially overcomes this problem (Fujiwara and Caswell 2002a).

Crespin et al. (2006) studied the impact of environmental conditions on return probabilities of pre-breeders by applying a CMR model with an unobservable state on the common guillemot *Uria aalge*. Their model (model C, hereafter) distinguished three breeding states: 'breeding at the colony', 'non-breeding at the colony' and 'non-breeding and not at the colony'. The last state cannot be observable, i.e. unobservable state. Although this extends the analytical framework for recruitment studies, it also includes a series of assumptions that limit its application. First, in Model C pre-breeders older than one year, non-breeders and adults survival probabilities are assumed to be equal. Secondly, an

animal that prospected once will either prospect or breed as no return to the unobservable state is allowed. Finally, the non-breeding state comprises both pre-breeders and previous breeders skipping breeding a given year. As a result, the model does not allow estimating specific annual survival rate for pre-breeders, breeders and non-breeders, nor the frequency of attendance or the frequency of first breeding at a given age (see Table 1 for parameters definition).

To avoid these assumptions, we propose a more general model, Model G, hereafter (Fig. 1). Model G distinguishes two pre-breeder states structured by age and three adult states. The two pre-breeders states depend on the presence or absence of individuals at the studied site. Adults comprise breeders, and non-breeders that are or are not present at the colony. Compared to model C, model G explicitly introduces unobservable states for each age-by- pre-breeding states, and allows transitions between them. Therefore, Model G can estimate the parameters underlying (1) pre-breeding attendance, (2) recruitment, and (3) breeding frequency (see Table 1 for a detailed description). To test the role of movement in and out the breeding site, occurring with prospecting behavior, model G is compared against a reduced model (model R). Model R does not consider explicitly the absence of pre-breeders from the studied breeding site in a given year (i.e. unobservable pre-breeder states of model G are removed). If pre-breeders leave the studied site in a given year for potentially prospecting model G should be preferred against model R.

We use these new models to investigate recruitment processes in a vulnerable species, the Cory's shearwater *Calonectris diomedea*. The Cory's shearwater is a long-lived seabird with delayed maturity, low fertility and intermittent breeding (Thibault et al. 1997). Cory's shearwaters tend to spend their first winter in sub-tropical areas (Ristow et al. 2000) and gradually return to the breeding grounds where they begin to visit breeding colonies before recruiting. The population study site is located on Lavezzi Island. It consists of several sub-colonies, with a total size of approximately 350–400 breeding pairs. Since 1978, on a yearly basis five sub-colonies have been closely monitored (104–133 nests). Here, the data from the five sub-colonies are pooled in order to estimate all the parameters. In this case, birds that do not attend the studied colony, may be (1) at sea, or (2) prospecting other colonies. There were only three birds marked at Lavezzi that were resighted in islet close to Lavezzi (a few hundred meters). Most of the Cory's shearwater marked at Lavezzi Island since 1978 were never observed in others archipelagoes, although a spread capture-recapture network exist across the Mediterranean Sea (Jenouvrier et al. unpubl.). Available data on movements of the Cory's shearwater include mainly few recoveries of beached birds, or birds trapped in the nets or the trawl lines of fisheries. Therefore, as for many other seabirds (for e.g. the kittiwake, Danchin et al. 1998; and the great cormorant, Frederiksen and Bregnballe 2001), we expect that pre-breeding attendance and prospecting among nearby colonies may play an important role in recruitment, indicating the benefit of Model G against model R.

Methods

Study area and data collection

Data was collected at Lavezzi Island (Corsica, France) in the Mediterranean Sea. Since 1978, adults are ringed and recaptured annually near and/or in their nests, mainly during the pre-laying stage (April-early May). Birds captured in an active nest, i.e. with an egg, are classified as breeders. Birds captured in the vicinity of the colony but never in an active nest are classified as (1) pre-breeder if they have never attempted to breed before, or as (2) non-breeders if they have reproduced at least once before. From late September to early October, chicks are marked before fledging. Among the 1451 birds marked as chicks, about 18% (n = 261) returned to the colony as pre-breeders and/or breeders. The minimum age of first return and first breeding are three and four years old, respectively.

Life-cycle

The life cycle is described in Fig. 1. Here, a newborn chick (state denoted 'CH') leaves the breeding site and moves to a pre-breeding unobservable state (denoted 'PU', Fig. 1). The pre-breeders begin to return to the natal colony at the age of three (observable pre-breeding state, denoted 'PB' Fig. 1). We consider 11 age classes, as almost all shearwaters that return to the colony do so before the age of 11 years (92% of females and 95% for males). Birds enter the adult phase of their life cycle (denoted 'A'; Fig. 1) after their first reproduction. In this study we focus on the pre-breeding part of the life cycle, where the potential of the model G is better illustrated. The adult phase analysis is described in Appendix A in the Supplementary material, and is independent from the one presented here.

Table 1. Demographic parameters estimated by model G.

| Life cycle phases	Annual survival	Recruitment/fecundity
Pre-breeding	Pre-breeders survival according to age	frequency of attendance according to age (proportion of pre-breeders that attend to the colony a given year) frequency of skipping breeding site according to age (proportion of pre-breeders that do not attend to the colony a given year)
Recruitment		frequency of first breeding attempt according to age (proportion of individuals that breed for their first time to the colony a given year)
Breeding	Breeder and non-breeder survival	frequency of breeding (proportion of adults that breed to the colony a given year, given that they have breed at least once previously) frequency of skipping breeding site (proportion of adult that do not attend to the colony a given year)
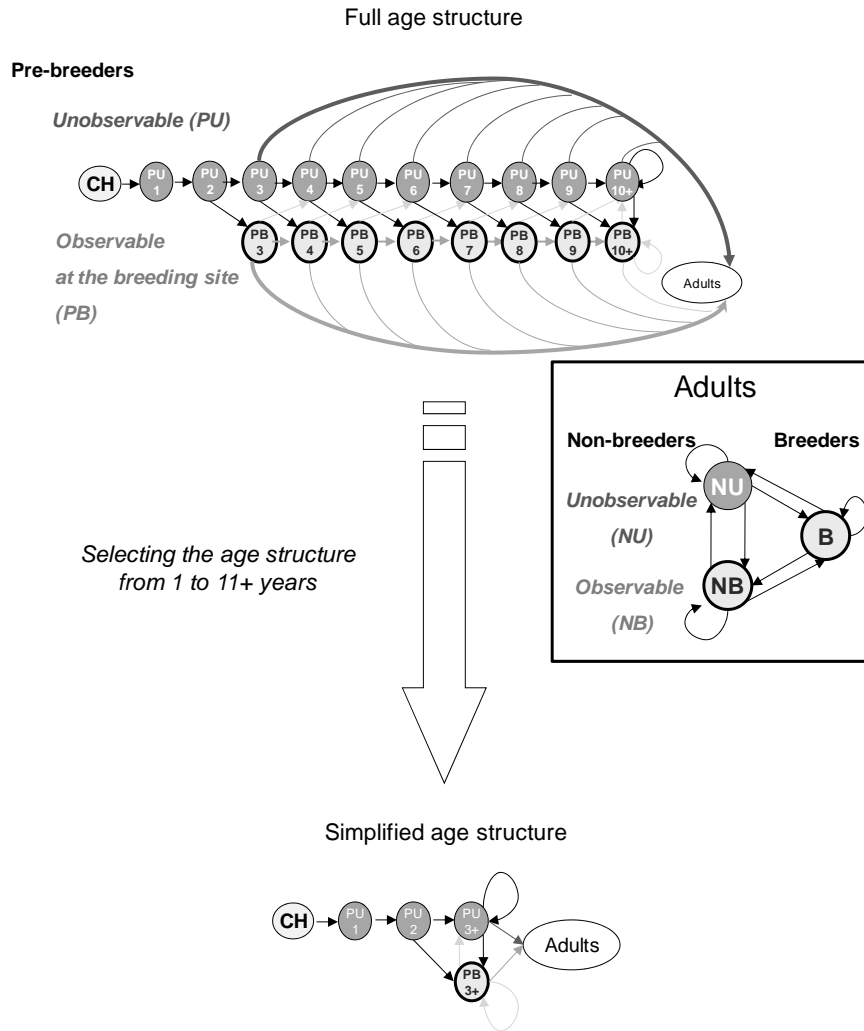
Fig. 1. Description of the life cycle underlying model G. Model G is structured by age and breeding states, and the adult part of the life cycle is highlighted in the box. To select the appropriate age structure, the model selection goes from a model with a full age structure to a model with a simplified one (arrow). Chicks (CH) that survived the first year become pre-breeder unobservable next year (PU). As long as a bird does not breed, it could be present at the colony as a pre-breeder observable (PB), or it could stay at sea or prospecting other colonies as a pre-breeder unobservable in the studied colony. Once a bird had started to breed, it becomes an adult (Box). Breeders (B) could skip reproduction as a non-breeder observable at the colony (NB) or not (NU). Dark grey indicates an unobservable state, whereas bright grey indicates an observable state.

Model G

Multi-state capture – recapture models include three kinds of state-specific parameters (Brownie et al. 1993, Schwarz et al. 1993): the detection probability P_{t+1}^s (probability that an individual is captured or re-sighted at time $t+1$ in state s given that it is alive and present at time t), the survival probability S_t^r (probability that an individual in state r at time t survives until time $t+1$), and the conditional transition probability ψ_t^{rs} (probability that an individual in state r at time t is in state s at time $t+1$, given that the individual has survived from time t to time $t+1$). In our analysis, s is 'CH', 'PB', 'PU' and 'A' and t vary from 1978 to 2004. Complex models contain parameters that are not estimable, either due to a lack of data or because of structural redundancy (Gimenez et al. 2004). For this reason we double checked parameter redundancy using a numerical version of the method (Catchpole et al. 1997, Choquet et al.

2005) and by drawing profile likelihood of suspected parameters (Choquet et al. 2004, Gimenez et al. 2004).

To solve structural redundancy we added specific constraints to the parameters based on biologically reasonable assumptions (Fujiwara and Caswell 2002a). Firstly, survival of birds in the unobservable state and the observable state are constrained to be equal. Secondly, survival and transition probabilities are set constant over the first ten years to take into account the progressive return of the birds marked at the colony at the beginning of the study. Finally, variations in the survival of birds over time are assumed to be similar, regardless of the state considered (noted S^{r+}). Finally, transition probabilities do not change over time (noted ψ^{rs}.). Further in the selection procedure, this last assumption has been relaxed in simpler models, i.e. models with few parameters. Model selection began with model G1 $\{S^{r+}{}_t\ p^s{}_t\ \psi^{a11*rs}.\}$ considering 11 age classes (noted a11).

Selection procedure

A first step in model selection is to assess the goodness-of-fit (GOF) of the model that assumes independent fate between past and present history of individual. A direct goodness of fit test of Model G cannot be calculated but, as in Crespin et al. (2006), an approximate fit test can be derived from the GOF test of a more general model, the JMV model (Jolly MoVe or JMV; Pradel et al. 2003) with two age classes. The test consists of two components: 1) dependence on the previous capture history (Test3G) and 2) the dependence on current capture (TestM; Pradel et al. 2003). The tests are computed using the program U-CARE (Choquet et al. 2005). In our case, the GOF indicated that the JMV model provided a good description of the data (Table 1, global test: $p = 0.345$).

Model selection follows the parsimonious principle based on the Akaike information criterion (AIC). The AIC is calculated as model deviance plus twice the number of estimable parameters in the model. Models with the lowest AIC values must be viewed as the best model (Burnham and Anderson 2002). All models are computed with program M-SURGE (Choquet et al. 2004). Some of the model specifications in the M-SURGE command language are provided in the Supplementary material, Appendix B. Single parameter estimates are presented with 95% confidence limits, whereas estimates averaged over time or age are presented with their standard errors.

Testing the existence of prospecting

Prospecting behaviors involve (1) pre-breeder attendance at the colony before first breeding attempts, and (2) temporary absence from the studied colony. To test the second consequence of prospecting behaviors, model G is confronted to a reduced model (Model R, for 'reduced') where the unobservable pre-breeder states are removed (Fig. 1). In model R, the absence of pre-breeders is not specifically modeled by unobservable states, thus it is absorbed into the detection probability P (Viallefont et al. 1995). To consider that pre-breeders attendance to the colony varied according to age, an age effect is incorporated on detection probabilities in model R. Note that this age effect on detection probabilities is not present in model G as this models has specific parameter to account for temporary absence, i.e. the unobservable state. The starting model of the R-group models is R1 $\{S^{r+}_t, p^{a11*PB+}_t, p^A_t, \psi^{a11*r}\}$. To validate the comparison of G- against R-models fitted to real data, we simulated a set of stratified capture-recapture data with similar features of the real data set (i.e. 27 occasions and 55 newly marked individuals released at each occasion). The simulated data are generated under the hypothesis of constant survival, constant detection probability and age varying transition probabilities, according to values similar to those of Cory's shearwater. Each individual at each occasion has a Bernouilli distribution to survive, to prospect at the colony, or to breed given that it survives, and is detected given that it survives. The data set is simulated using program Matlab (MATLAB 2006a).

Results

Model G1, provides a better starting point for model selection than the JMV model ($\Delta AIC = 129.07$, Fig. 2 Box 1).

Model age structure and detection probabilities

The age structure for transition probabilities is modeled in two steps. The selection procedure began on age-dependent recruitment parameters (i.e. age-effect on transitions from states PU or PB to A), and subsequently focused on the probabilities to skip attendance of the breeding site during the pre-breeding phase (i.e. age-effect on transitions from states PU or PB to PU). The appropriate age structure is identified by grouping classes with similar values of transitions (Fig. 2 Box 2). Model G9 with a three age classes for recruitment probabilities, followed by model G13 assuming seven age classes for the probabilities to leave the breeding site during the pre-breeding phase (transitions from PU/PB to PU) have lower AIC than the model G1. Then, follows model G18 with an age effect on transitions from PB to A, without an age effect on transitions from PU to A. Finally, the best model G20 assumes a quadratic effect of age (Fig. 3a). An age effect on pre-breeders detection probability do not improve the AIC value (Supplementary material, Appendix B, Table 2a, model G20 vs models G21-G24). Detection probabilities vary over time (Fig. 3b).

Survival probabilities

The best model G28, assumes age-dependent, but constant survival probabilities over time and state (Fig. 2 Box 3). Annual survival rate estimates are 0.52 ($IC_{95\%} = [0.40, 0.64]$)) during the first year at sea, 0.88 ($IC_{95\%} = [0.83, 0.92]$) for pre-breeders and 0.85 ($IC_{95\%} = [0.81, 0.88]$) for adults. The more detailed adult analysis (Supplementary material, Appendix A) shows similar adult survival rates (0.89, $IC_{95\%} = [0.88; 0.90]$, Fig. 5a).

Transitions probabilities

Model G31 (Fig. 2 Box 4), assuming parallel time variations for all transition probabilities, is the selected model (Fig. 3a). The probability that pre-breeders return to the natal colony increases over time from 0.03 ($IC_{95\%} = [0.02, 0.05]$) at three years old, to 0.49 ($IC_{95\%} = [0.37, 0.62]$) at five years olds (Fig. 3a). The probability for pre-breeders to remain at the colony, decreased over age, varying from 0.93 ($IC_{95\%} = [0.87, 0.97]$) at four years old to 0.46 ($IC_{95\%} = [0.36, 0.57]$) at seven years old. The probability that pre-breeders skip the colony, given their attendance the year before, is 0.15 ($IC_{95\%} = [0.05, 0.38]$) at six years old and 0.32 ($IC_{95\%} = [0.24, 0.43]$) at seven years or more and for younger birds it is virtually zero. Recruitment probabilities from the unobservable pre-breeding state are null (0.00, $IC_{95\%} = [0.00, 0.02]$). Birds that recruited in the breeding colony always return first as pre-breeders. Recruitment varies according to age, with its maximum at 7+ years old (0.21, $IC_{95\%} = [0.16, 0.28]$,
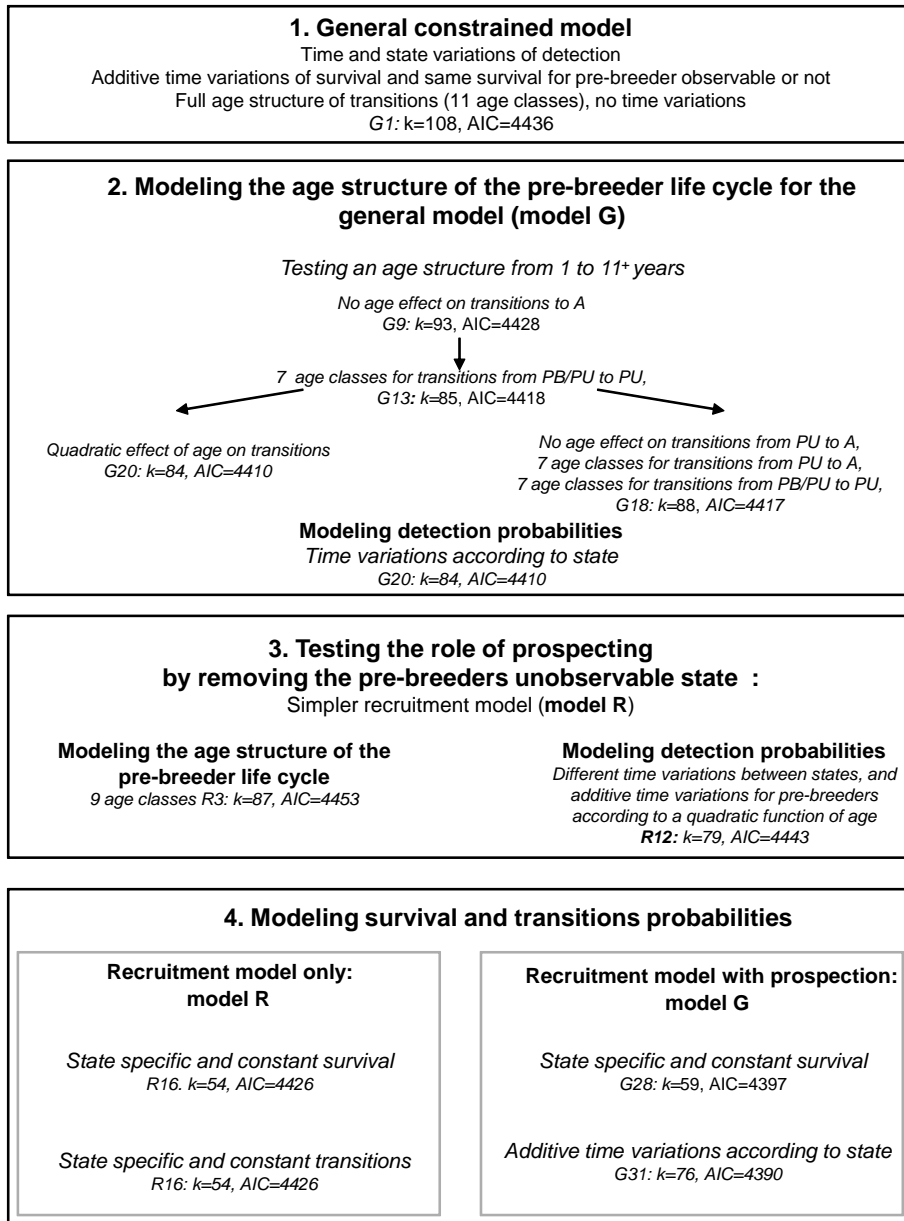
Fig. 2. Different steps of the model selection procedure (Results and Supplementary material Appendix B Table 2 for more details).

Fig. 3a). The average probability to breed at the natal colony, i.e. the philopatry, is 0.14 ± 0.06.

Model G vs model R

Model G is strongly preferred against model R for the simulated data (AIC values: 7837.5 and 8453.2 for models G and R respectively). This result validates the comparison of model G against model R in the following selection procedure. The model R group are different from model G group, especially for detection probabilities (Methods). Another model selection is conducted to identify the best R model for the Cory's shearwater data (Fig. 2 Box 5). Model R16 takes into account nine age classes, with a quadratic effect of age on transitions and detection probabilities selected. As expected, an age effect is retained on detection probability in R-models (Fig. 4a) but not in

G-models (Fig. 3b). Detection probabilities are high for six year-old birds (average value 0.29 ± 0.17) varying over time (Fig. 4) in a similar manner as the recruitment parameters highlighted in G-models. G-models have lower AIC values than R-models, and the AIC difference between the best model (G31 and R16) of each type is large (ΔAIC = 36.82).

Discussion

A new analytical framework

In seabirds, settlement and habitat decisions are known to be affected by prospecting colonies during the pre-breeding period (Boulinier et al. 1996). Indeed, breeding habitat quality is the primary determinant of breeding success (Danchin et al 1998). First habitat selection involves that
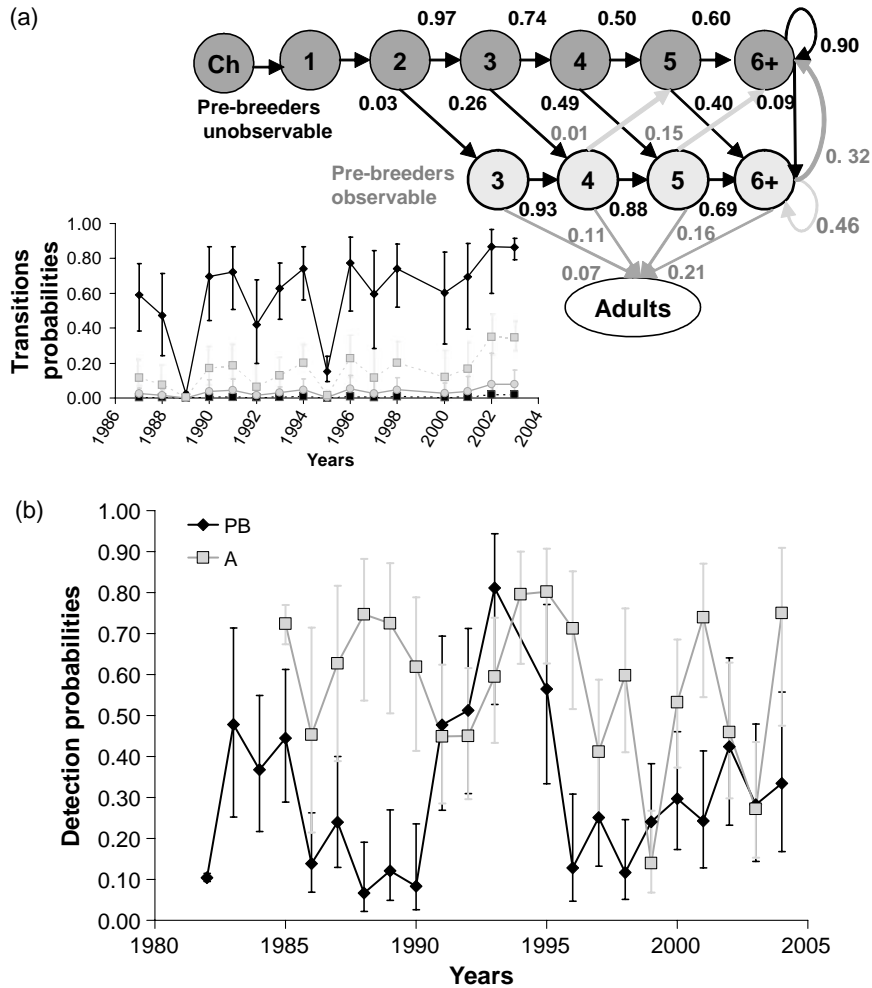
Fig. 3. (a) Transitions and (b) detection probabilities of the Cory's shearwater from the best model G31. Probabilities fluctuated over time between (a) 1987 and 2003 and (b) 1982 and 2004. Only transitions probabilities varied according to age. Error bars represent the 95% CI. (a) Transitions probabilities are at the boundary 0 for time 1999. The black line and fill black diamond stand for the probabilities to return at the colony as a pre-breeder (Ψ from PU to PB), the black dotted line and fill black square for probabilities of first breeding for birds that never return to the colony as pre-breeders (Ψ from PU to A), grey line and fill grey circle for probabilities to skipping breeding site for pre-breeders that were observable the previous year (Ψ from PB to PU), and finally the grey dotted line and fill grey square for probabilities of first breeding for birds that were pre-breeders the previous year at the colony (Ψ from PB to A). (b) Adult detection probabilities are not estimable for time 1983 and 1984, as pre-breeders detection probability at time 1994.

Table 2. Goodness-Of-Fit (GOF) tests of the JollyMove (JMV). The JMV GOF test involves several components detailed below in (a) (see Pradel et al. 2003 for more details) that led to testing models detailed below in (b). JMV assumes that survival, transitions and detection probabilities are solely time and state dependent. Additionally, transient models allow survival to differ between newly marked and previously marked animals. Trap dependent models assume that detection probabilities may differ for animals that were caught or not during the previous occasion.

(a)

3GSM			MITEC			MLTEC		
DF	χ^2	p	DF	χ^2	p	DF	χ^2	p
58	35.1	0.993	24	46.2	0.004	16	21.7	0.153

(b)

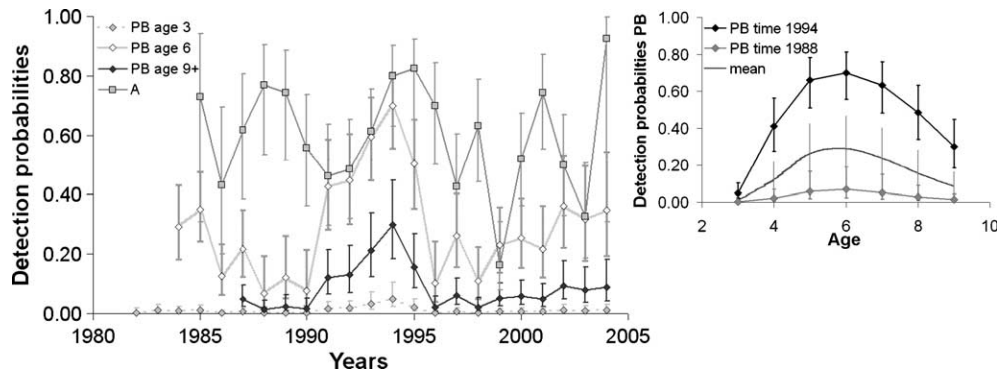| JMV			Trap dependent		
DF	χ^2	p	DF	χ^2	p
98	103	0.345	74	56.8	0.931

Fig. 4. Detection probabilities of the Cory's shearwater from the model R. Detection probabilities varied with age and fluctuated over time between 1982 and 2004.

pre-breeders attend at the colony before their first breeding attempts. Indeed, for long-lived species with delayed maturity, it would not be valuable for first time breeders to have assessed the quality of their natal site when they were chicks (Danchin et al. 1998). Second, prospecting behaviors involve that pre-breeders leave the studied colony temporarily to prospect other breeding sites. To date, the multi-state G-model is the first attempt to model these sequential processes from birth to recruitment for long-lived species with delayed maturity. It includes age-dependent, key demographic parameters to measure the pattern and magnitude of attendance at the colony and skipping breeding sites. Pre-breeding attendance is estimated with model G and the comparison of model G against model R allows to test if pre-breeders skip breeding sites a given year.

Model assumptions

Model G assumes that birds first sighted at the colony have not bred elsewhere. As age increases, so does the probability that a bird first seen at the colony has bred elsewhere. These movements may occur with a higher probability in inexperienced breeders settling in low-quality patches that return to their natal colony at older ages (Serrano et al. 2005). Taking this into account, the estimate of age of first return to the colony and the one of the first breeding attempt would be positively biased. However, Cory's shearwaters are extremely philopatric (Rabouam et al. 1998), and resightings of birds marked at the Lavezzi elsewhere have rarely occurred (J. C. Thibault unpubl.). Our assumption that Cory's shearwaters that return to Lavezzi colony have not attempted to breed elsewhere is robust.

Another assumption that implies a similar bias is the misclassification of birds between breeders, and pre-breeders/non breeders. In Lavezzi the capture – recapture started very early in the breeding season (Methods). The potential misclassification of early failed breeders into the pre-breeder/non-breeder categories is thus unlikely.

Recruitment processes

Our study highlights that Cory's shearwater always return to their natal colony as pre-breeders before attempting to breed at the colony. Most of the birds return to the colony at five and six years old (probabilities of 0.49 and 0.40

respectively). Once pre-breeders have attended to their natal colony, the probability for their return is very high, although it decreases with age (0.93, 0.88, 0.69, 0.46 from age four to seven and older years). Indeed, for those birds the accession to reproduction increases gradually with age. The probabilities of first breeding at ages of four, five, six and older are 0.07, 0.11, 0.16 and 0.21, respectively. During the pre-breeding phase at the natal colony several non-exclusive processes may occur. For example, the potential higher breeding cost for young birds, related to their lower foraging ability, may delay the first reproduction (Machetti and Price 1989). Young birds are also constrained by their inferiority as competitors (Wooller and Coulson 1977), especially in dense populations that may limit their access to mates and vacant sites.

Model G is strongly preferred against model R, suggesting that birds temporally leave the studied colonies to potentially prospect actively other breeding habitats. Temporary absence from the focal colony occurs for birds that are mostly older than six years old. This suggests that birds that did not recruit to their natal breeding colony have higher probability to prospect other colonies as they grow older. Potentially they recruit later in other breeding sites. Indeed, immigrants recruit later compared to philopatric birds (Frederiksen and Bregnballe 2001). The temporal and spatial scale of the study must be kept in mind when interpreting these results where the temporary absence from the studied colonies (five among the eight colonies of Lavezzi Island population) is estimated a given year. The observation of pre-breeders on the studied site on a given year does not exclude the possibility that birds will not prospect other non-monitored colonies nearby.

The probabilities to return and recruit to Lavezzi colony show strong year to year variations regardless of the age considered. Several factors may affect the attendance and the reproduction at a given colony in a given year; such as intraspecific competition for mate and site, predation, parasitism, density of introduced species and food resources. However, for pre-breeders the temporal variations appear similar whether they are present or absent from the colony the previous year, suggesting a common environmental forcing. Several studies highlighted that during a poor year, few birds return or attempt to breed in the colony (Reed et al. 2003). Crespin et al. (2006) showed that the probabilities of returning to the colony for common guillemots Uria aalge, are positively correlated with a large

spatial scale climatic oscillation, the winter North Atlantic Oscillation.

Survival probabilities

Cory's shearwater survival probabilities during the first year at sea, and during the pre-breeder phase are 0.52, $IC_{95\%} = [0.40; 0.64]$ and 0.85, $IC_{95\%} = [0.81; 0.88]$, respectively. Using multi-state models provides more reliable estimates than those calculated on return rates of marked chicks, because they account for changes in detection probability. However, adult survival seems underestimated using data of only known-age birds. Crespin et al. (2006) highlighted a similar bias using a comparable modeling approach. Using data on adult birds irrespective of their age and taking into account sabbatical years, gives a higher adult survival probability (Fig. 5a). The lower number of capture histories, the large numbers of years where birds are unobservable and the lower detection probabilities during the pre-breeding periods could be factors that bias adult survival estimations. Studying the factors affecting the bias

and precision of estimates requests a large amount of simulated data that is under the scope of this study. We are aware of the potential bias and suggest to conduct different analyses for the juvenile and adult part of the life cycle. The two separate analyses of the pre-breeding and breeding phase, respectively, suggested a similar estimate of survival: 0.88, $IC_{95\%} = [0.83, 0.92]$ for pre-breeders and 0.89, $IC_{95\%} = [0.88, 0.90]$ for adults, respectively.

Skipping breeding among adults

Once recruited to the colony, the temporary absence from the focal colony is very low (Supplementary material, Appendix A). Breeders skip reproduction, although they stay as non-breeders at the colony. Non-breeding a given year could be related to several factors, such as the absence of a partner (Bried and Jouventin 2002) or individual quality component (Cam et al. 1998). In agreement with our findings (Fig. 5b), Cam et al. (1998) highlighted a higher probability of breeding the following year for breeders than for non-breeders. Moreover, as for Cory's shearwater (Fig. 5a), adult survival rates are lower for non-breeders compared to those of breeders for kittiwakes (Cam et al. 1998). These results support the hypothesis that non-breeders tend to be individuals of lower quality.

Conclusion

Model G provides a significant improvement on estimating demographic parameters for many long-lived species with delayed maturity and skipping breeding sites. The model gives an adequate framework to test the influence of factors affecting patterns and magnitude of pre-breeding attendance at the natal colony, recruitment and breeding processes. Ultimately, the step between model G and structured population models is straightforward (Fujiwara and Caswell 2002b), allowing easy projections for population dynamics.
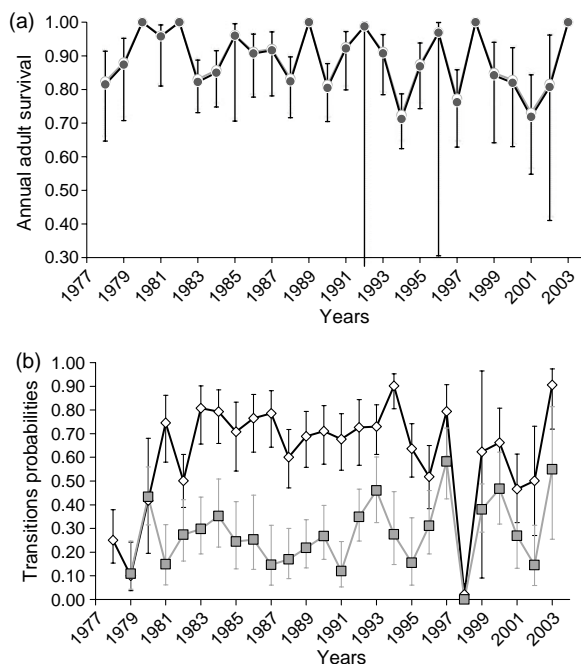
Fig. 5. (a) Annual survival probabilities (b) and probability of breeding the following year given birds where breeding or not the previous years, for adult Cory's shearwater breeding at Lavezzi Island between 1978 and 2004. (a) The black line and fill black dot stands for adult survival of non-breeders, whereas grey line and white dot for breeders. Adult survival probabilities in years 1980, 1982, 1989, 1998, and 2003 are all identifiable, but near the boundary value of one (Fig. 2, Supplementary material Appendix A). (b) The probability of breeding the following year is represented respectively by the black line and white diamonds for breeders, and by the grey line and fill grey squares for non-breeders. The transition from non-breeders to breeders is not identifiable in years 1978, and is estimated at a boundary in years 1998 (Fig. 2). The averaging estimations come from the two best models $\{S^{a2+r}_t, p^{NB+m}_t, p^B, \psi^{rs}_t\}$ and $\{S^{a2+}_t, p^{NB+m}_t, p^B, \psi^{rs}_t\}$ and error bar represented the 95% CI.

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