Oikos

O17882
Péron, G., Crochet, P.-A., Choquet, R., Pradel, R., Lebreton, J.-D. and Gimenez, O. 2010. Capture-recapture models with heterogeneity to study survival senescence in the wild. – Oikos 119: 524–532.

Appendix 1

Model description

Individual heterogeneity in multievent models

There were 2^k observable states (k being the number of parameters types affected by heterogeneity in the model), plus one or two AE–states depending on the presence of survival heterogeneity in the model, and the state dead. We describe in this appendix two of the considered models: (1) the model $\{S_H; E_0; D_0\}$ including heterogeneity in survival probabilities only ($2^1+2+1=5$ states; part 3) and (2) the model $\{S_H; E_H; D_H\}$ including the three kinds of heterogeneity (survival, detection and emigration: $2^3+2+1=11$ states; part 4).

When considering detection heterogeneity, we did not allow individuals to move between high- and low-detection classes, based on the finding that individuals tend to be site-faithful on a small scale when breeding in LR (Prévot-Julliard et al. 1998b). However, when a bird emigrated, the model did not keep memory of its previous classes of detection and emigration, letting it free to change either of these classes upon return. The model permitted returning individuals to settle in a different zone of the pond or to change of dispersal behaviour.

Parameterisation

The complex model structure rendered necessary the use of some constraints on the parameters. These and the effects that were considered in the model selection procedure are presented below.

Initial proportions
The Π-vector represents the probability of being in the different classes of heterogeneity at first detection. We assumed that Π was constant over time, hence assuming that the proportions of the different classes of heterogeneity did not vary over time.

Preliminary results (not shown) indicated a poor fit of a model in which Π varied with age, probably because the small number of individuals entering the dataset after age 14 (onset of senescence) rendered some Π-parameters non-estimable. Moreover, when Π varied with age, there might have been identifiabilities issues because high-survival individuals entering the dataset at old age do have a low survival indeed.

Dispersal probabilities
Dispersal probabilities were modelled as constant over time, for parsimony and because parameter identifiability required that the probability of returning from the unobservable state to the study colony was kept constant over time and that the survival probabilities were the same in the states AE and in the states available for detection (Fujiwara and Caswell 2002). Heterogeneity in emigration probability was modelled in a fashion similar to 'mover–stayer models' that consider a class with high site–tenacity and a 'volatile' class (Goodman 1961). Once in the state AE, individual lost their classification as low/high detection and low/high emigration. Therefore, after emigration, they could become more detectable, or more site-faithful, and reversely (Table A3)

Detection probabilities
The matrix of the probabilities of being detected when alive and present on the study site (P) was modelled as time–dependent to fit with the known variation in resighting effort over years (Prévot-Julliard et al. 1998a). Heterogeneity was modelled in a fashion additive to time. Given the high small-scale site fidelity exhibited by breeders within the study colony (Prévot-Julliard et al. 1998b), exchanges between detection classes were expected to be low and we chose not to allow for direct transitions between heterogeneity classes. Indirect transitions were possible after temporary emigration.

Breeding status confirmation probabilities
They were modelled as constant over time in order to keep parsimonious. Indeed, if detection probabilities varied with time because of between-year variation in detection effort, breeding status confirmation probabilities were supposedly more related to the configuration

of the colony (distribution of the roost sites, density of the vegetation), and could be considered time-invariant in a first approach. If there was heterogeneity in detection probabilities in the model considered, breeding status confirmation probability was modelled as depending on detectability.

Survival probabilities: modelling age-effect

We considered the age-effect on survival as being additive (on a logit scale) to the heterogeneity level, if any.

Models with a complete age-effect (age or TFC treated as categorical variables: 29 levels in our case) are the straightforward way to model age-dependency on survival because they make no hypothesis on the shape of that dependency. However, studying the strength of senescence requires the estimation of a slope describing the decrease in survival probabilities with age (Jones et al. 2008), something that can be computed using age or TFC as a continuous variable in a constrained log–linear relationship that moreover reduces the number of parameters in the model (Loison et al. 1999, Nichols et al. 1997).

However, the sparseness of data at old ages (only 14 individuals were observed at an age ≥ 22, of which none was seen after age 25) renders maximum likelihood estimators unstable, and produces boundary survival estimates (boundary estimates are age-specific survival probabilities that are estimated at 0 or 1 because of low sample size). For example, the occasional individual who will survive 1 year after the others will induce a survival probability of 1 at that age. These boundary estimates are likely to hamper the accurate detection and estimation of the strength of survival senescence, particularly when using constrained regressions (Jones et al. 2008). We first ran a model with complete age-effect, and it appeared that the age–threshold after which boundary estimates were an issue was 22. Boundary estimates were excluded from the constrained relationship presented below.

From age 1 to 22, age–dependency was modelled using a threeparameter piecewise relationship. Age one had a separate survival estimate (because we expected it to be lower; Pugesek et al. 1995 in a related species). Then, we modelled a plateau that lasted up to an age-threshold (which is species-specific: Jones et al. 2008). It was estimated to be 14-year old in black-headed gull by mean of life-history comparisons (Péron et al. unpubl.); in other Larid species, the threshold was found around 14 years in *Larus californicus* (Pugesek et al. 1995) and between 13 and 16 in *Rissa tridactyla* (Aebischer and Coulson 1990, Frederiksen et al. 2004). Afterwards we modelled a logit-linear decline in survival probabilities (Loison et al. 1999).

Implementation of true age in CMR models when first capture occurs at a varying age

True age (as opposed to TFC, see main text) was implemented with a computer intensive procedure. E-SURGE uses the GEMACO syntax to constrain the parameters. The phrase required for modelling the dependency of CMR parameters on true age, when individuals enter the dataset at various ages, was based upon the use of groups. Individuals entering the dataset at age A were in the Ath group. In the Ath group at the tth session after their first observation, individuals had the age A+t. The syntax for this relationship, to be entered in GEMACO, is started below:

```
{g(1).a(1)       +         g(1).a(2)&g(2).a(1)          +         g(1).a(3)&g(2).a(2)&g(3).a(1)+…
age1                       age2                                   age3                          …
```

Further details can be found in (Choquet 2008). We provide below a short and flexible R-program (R Project Core Team 2008) that generates this syntax for any number of age classes:

```
RES<-""
#maximum age at first entry in the dataset:
Amax=23
for (A in 2:Amax) {
     for (i in 2:A) {
        RES=paste(RES,"g(",as.character(i-1),").a(",as.character(A+1-i),")&",sep  =
     "")
     }
     RES=paste(RES,"+",sep="")
}
#maximum potential age:
Apot=29
for (A in (Amax+1):Apot) {
     for (i in 2:Amax) {
        RES=paste(RES,"g(",as.character(i-1),").a(",as.character(A+1-i),")&",sep  =
     "")
     }
     RES=paste(RES,"+",sep="")
}
RES<- gsub("(\\+) (\\})"," }", paste("{",gsub("(\\)&(\\+)",")+",RES),"}")
)
RES
```

With the values 23 and 29 for Amax and Apot (these values correspond to the black-headed gull dataset), we obtained the following sentence to be entered as a shortcut for True Age in GEMACO:

{g(1).a(1)+g(1).a(2)&g(2).a(1)+g(1).a(3)&g(2).a(2)&g(3).a(1)+g(1).a(4)&g(2).a(3)&g(3).a(2)&g(4).a(1)+g(1).a(5)&g(2).a(4)&g(3).a(3)&g(4).a(2)&g(5).a(1)+g(1).a(6)&g(2).a(5)&g(3).a(4)&g(4).a(3)&g(5).a(2)&g(6).a(1)+g(1).a(7)&g(2).a(6)&g(3).a(5)&g(4).a(4)&g(5).a(3)&g(6).a(2)&g(7).a(1)+g(1).a(8)&g(2).a(7)&g(3).a(6)&g(4).a(5)&g(5).a(4)&g(6).a(3)&g(7).a(2)&g(8).a(1)+g(1).a(9)&g(2).a(8)&g(3).a(7)&g(4).a(6)&g(5).a(5)&g(6).a(4)&g(7).a(3)&g(8).a(2)&g(9).a(1)+g(1).a(10)&g(2).a(9)&g(3).a(8)&g(4).a(7)&g(5).a(6)&g(6).a(5)&g(7).a(4)&g(8).a(3)&g(9).a(2)&g(10).a(1)+g(1).a(11)&g(2).a(10)&g(3).a(9)&g(4).a(8)&g(5).a(7)&g(6).a(6)&g(7).a(5)&g(8).a(4)&g(9).a(3)&g(10).a(2)&g(11).a(1)+g(1).a(12)&g(2).a(11)&g(3).a(10)&g(4).a(9)&g(5).a(8)&g(6).a(7)&g(7).a(6)&g(8).a(5)&g(9).a(4)&g(10).a(3)&g(11).a(2)&g(12).a(1)+g(1).a(13)&g(2).a(12)&g(3).a(11)&g(4).a(10)&g(5).a(9)&g(6).a(8)&g(7).a(7)&g(8).a(6)&g(9).a(5)&g(10).a(4)&g(11).a(3)&g(12).a(2)&g(13).a(1)+g(1).a(14)&g(2).a(13)&g(3).a(12)&g(4).a(11)&g(5).a(10)&g(6).a(9)&g(7).a(8)&g(8).a(7)&g(9).a(6)&g(10).a(5)&g(11).a(4)&g(12).a(3)&g(13).a(2)&g(14).a(1)+g(1).a(15)&g(2).a(14)&g(3).a(13)&g(4).a(12)&g(5).a(11)&g(6).a(10)&g(7).a(9)&g(8).a(8)&g(9).a(7)&g(10).a(6)&g(11).a(5)&g(12).a(4)&g(13).a(3)&g(14).a(2)&g(15).a(1)+g(1).a(16)&g(2).a(15)&g(3).a(14)&g(4).a(13)&g(5).a(12)&g(6).a(11)&g(7).a(10)&g(8).a(9)&g(9).a(8)&g(10).a(7)&g(11).a(6)&g(12).a(5)&g(13).a(4)&g(14).a(3)&g(15).a(2)&g(16).a(1)+g(1).a(17)&g(2).a(16)&g(3).a(15)&g(4).a(14)&g(5).a(13)&g(6).a(12)&g(7).a(11)&g(8).a(10)&g(9).a(9)&g(10).a(8)&g(11).a(7)&g(12).a(6)&g(13).a(5)&g(14).a(4)&g(15).a(3)&g(16).a(2)&g(17).a(1)+g(1).a(18)&g(2).a(17)&g(3).a(16)&g(4).a(15)&g(5).a(14)&g(6).a(13)&g(7).a(12)&g(8).a(11)&g(9).a(10)&g(10).a(9)&g(11).a(8)&g(12).a(7)&g(13).a(6)&g(14).a(5)&g(15).a(4)&g(16).a(3)&g(17).a(2)&g(18).a(1)+g(1).a(19)&g(2).a(18)&g(3).a(17)&g(4).a(16)&g(5).a(15)&g(6).a(14)&g(7).a(13)&g(8).a(12)&g(9).a(11)&g(10).a(10)&g(11).a(9)&g(12).a(8)&g(13).a(7)&g(14).a(6)&g(15).a(5)&g(16).a(4)&g(17).a(3)&g(18).a(2)&g(19).a(1)+g(1).a(20)&g(2).a(19)&g(3).a(18)&g(4).a(17)&g(5).a(16)&g(6).a(15)&g(7).a(14)&g(8).a(13)&g(9).a(12)&g(10).a(11)&g(11).a(10)&g(12).a(9)&g(13).a(8)&g(14).a(7)&g(15).a(6)&g(16).a(5)&g(17).a(4)&g(18).a(3)&g(19).a(2)&g(20).a(1)+g(1).a(21)&g(2).a(20)&g(3).a(19)&g(4).a(18)&g(5).a(17)&g(6).a(16)&g(7).a(15)&g(8).a(14)&g(9).a(13)&g(10).a(12)&g(11).a(11)&g(12).a(10)&g(13).a(9)&g(14).a(8)&g(15).a(7)&g(16).a(6)&g(17).a(5)&g(18).a(4)&g(19).a(3)&g(20).a(2)&g(21).a(1)+g(1).a(22)&g(2).a(21)&g(3).a(20)&g(4).a(19)&g(5).a(18)&g(6).a(17)&g(7).a(16)&g(8).a(15)&g(9).a(14)&g(10).a(13)&g(11).a(12)&g(12).a(11)&g(13).a(10)&g(14).a(9)&g(15).a(8)&g(16).a(7)&g(17).a(6)&g(18).a(5)&g(19).a(4)&g(20).a(3)&g(21).a(2)&g(22).a(1)+g(1).a(23)&g(2).a(22)&g(3).a(21)&g(4).a(20)&g(5).a(19)&g(6).a(18)&g(7).a(17)&g(8).a(16)&g(9).a(15)&g(10).a(14)&g(11).a(13)&g(12).a(12)&g(13).a(11)&g(14).a(10)&g(15).a(9)&g(16).a(8)&g(17).a(7)&g(18).a(6)&g(19).a(5)&g(20).a(4)&g(21).a(3)&g(22).a(2)+g(1).a(24)&g(2).a(23)&g(3).a(22)&g(4).a(21)&g(5).a(20)&g(6).a(19)&g(7).a(18)&g(8).a(17)&g(9).a(16)&g(10).a(15)&g(11).a(14)&g(12).a(13)&g(13).a(12)&g(14).a(11)&g(15).a(10)&g(16).a(9)&g(17).a(8)&g(18).a(7)&g(19).a(6)&g(20).a(5)&g(21).a(4)&g(22).a(3)+g(1).a(25)&g(2).a(24)&g(3).a(23)&g(4).a(22)&g(5).a(21)&g(6).a(20)&g(7).a(19)&g(8).a(18)&g(9).a(17)&g(10).a(16)&g(11).a(15)&g(12).a(14)&g(13).a(13)&g(14).a(12)&g(15).a(11)&g(16).a(10)&g(17).a(9)&g(18).a(8)&g(19).a(7)&g(20).a(6)&g(21).a(5)&g(22).a(4)+g(1).a(26)&g(2).a(25)&g(3).a(24)&g(4).a(23)&g(5).a(22)&g(6).a(21)&g(7).a(20)&g(8).a(19)&g(9).a(18)&g(10).a(17)&g(11).a(16)&g(12).a(15)&g(13).a(14)&g(14).a(13)&g(15).a(12)&g(16).a(11)&g(17).a(10)&g(18).a(9)&g(19).a(8)&g(20).a(7)&g(21).a(6)&g(22).a(5)+g(1).a(27)&g(2).a(26)&g(3).a(25)&g(4).a(24)&g(5).a(23)&g(6).a(22)&g(7).a(21)&g(8).a(20)&g(9).a(19)&g(10).a(18)&g(11).a(17)&g(12).a(16)&g(13).a(15)&g(14).a(14)&g(15).a(13)&g(16).a(12)&g(17).a(11)&g(18).a(10)&g(19).a(9)&g(20).a(8)&g(21).a(7)&g(22).a(6)+g(1).a(28)&g(2).a(27)&g(3).a(26)&g(4).a(25)&g(5).a(24)&g(6).a(23)&g(7).a(22)&g(8).a(21)&g(9).a(20)&g(10).a(19)&g(11).a(18)&g(12).a(17)&g(13).a(16)&g(14).a(15)&g(15).a(14)&g(16).a(13)&g(17).a(12)&g(18).a(11)&g(19).a(10)&g(20).a(9)&g(21).a(8)&g(22).a(7)}

EXAMPLE 1. Matrix description of one of the simplest heterogeneity model

The 5-state model with heterogeneity in survival only (Fig. 2 in the main text) is described in Table A1. As all models considered in this study, it includes the possibility to emigrate temporarily, and also to record information on the breeding status; otherwise it reduces to Pledger et al.'s (2003) two-class finite mixture model $\{\Phi(h_2), p(t)\}$ (Pradel 2009). If the two survival-classes and the two 'status confirmation events' are merged together this model becomes the temporary emigration model of Fujiwara and Caswell (2002).

Table A1.Matrix description of a multievent model accounting for survival heterogeneity using two classes, while allowing for temporary emigration and detailed observation structure. (a) survival probabilities (S-matrix): ϕ_1 and ϕ_2 are the two survival probabilities (high and low). (b) Transition probabilities (Ψ–matrix): ψ and ψ' are the emigration and return transition probabilities respectively. The product $\Phi = S \times \Psi$ constitutes the survival/transition matrix that is common to multistate and multievent models. (c) Event probabilities (B-matrix): p and r are respectively detection and breeding status assignment probabilities. There is no heterogeneity in detection in this example model. States S1 and S2 code for the two survival classes in the study site, while AE1 and AE2 code for them in the 'Alive Elsewhere' site. There were three possible observations following initial release (0: not seen, 1: seen and breeding status confirmed; 2: seen but breeding status not confirmed), which correspond to the three columns of the B-matrix.

(a) S

	S1	S2	AE1	AE2	Dead
S1	ϕ_1	0	0	0	$1-\phi_1$
S2	0	ϕ_2	0	0	$1-\phi_2$
AE1	0	0	ϕ_1	0	$1-\phi_1$
AE2	0	0	0	ϕ_2	$1-\phi_2$
dead	0	0	0	0	1

(b) Ψ

	S1	S2	AE1	AE2	Dead
S1	$1-\psi$	0	ψ	0	0
S2	0	$1-\psi$	0	ψ	0
AE1	ψ'	0	$1-\psi$'	0	0
AE2	0	ψ'	0	$1-\psi$'	0
dead	0	0	0	0	1

(c) $B=P\times R$

	0	1	2
S1	1–p	$p\times r$	$p\times (1-r)$
S2	1–p	$p\times r$	$p\times (1-r)$
AE1	1	0	0
AE2	1	0	0
dead	1	0	0

EXAMPLE 2: Matrix description of the most complex model

The multievent model $S_H;D_H;E_H$ has three kinds of heterogeneity. As all models considered in this study, it includes the possibility to emigrate temporarily, and also to record information on the breeding status; otherwise it reduces to Pledger et al.'s (2003) two-class finite mixture model {$\Phi(h_2)$, $p(h_2+t)$} (Pradel, 2008). If the eight heterogeneity classes and the two "status confirmation events" are merged together this model becomes the temporary emigration model of Fujiwara and Caswell (2002).

There are 11 states in this model which is the most detailed we considered. A bird breeding in LR can be in one of the eight states denoted $S_iD_jE_k$, where i, j, k can be 'low' or 'high'. An individual in state $S_{low}D_{high}E_{high}$ for example has low survival, high capture and high emigration probabilities. Alternatively, the bird can be 'Alive elsewhere' in states AES_{low} and AES_{high}, or it can be dead, a state that is explicitly included in the model. The recorded events are '0' for "not seen", '1' for 'seen as confirmed breeder', and '2' for 'seen as unconfirmed breeder'.

In addition to the matrix description we provide for this model more detail of the practical implementation, in the form of the GEPAT/GEMACO instructions. These are the interfaces of E-SURGE that are used to constrain multievent models (Choquet et al. 2009a).

Table A2. Survival probabilities (S-matrix) of multievent model accounting for survival, detection and emigration heterogeneity using two classes, while allowing for temporary emigration and detailed observation structure. ϕ_1 and ϕ_2 are the two survival probabilities. States denominations are described above.

		State at time t										
	To\from	$S_{low}D_{low}E_{low}$	$S_{low}D_{high}E_{low}$	$S_{low}D_{low}E_{high}$	$S_{low}D_{high}E_{high}$	$S_{high}D_{ow}E_{low}$	$S_{high}D_{high}E_{low}$	$S_{high}D_{low}E_{high}$	$S_{high}D_{high}E_{high}$	AES_{low}	AES_{high}	dead
State before dispersal	$S_{low}D_{low}E_{low}$	ϕ_1	0	0	0	0	0	0	0	0	0	1-ϕ_1
	$S_{low}D_{high}E_{low}$	0	ϕ_1	0	0	0	0	0	0	0	0	1-ϕ_1
	$S_{low}D_{low}E_{high}$	0	0	ϕ_1	0	0	0	0	0	0	0	1-ϕ_1
	$S_{low}D_{high}E_{high}$	0	0	0	ϕ_1	0	0	0	0	0	0	1-ϕ_1
	$S_{high}D_{low}E_{low}$	0	0	0	0	ϕ_2	0	0	0	0	0	1-ϕ_2
	$S_{high}D_{high}E_{low}$	0	0	0	0	0	ϕ_2	0	0	0	0	1-ϕ_2
	$S_{high}D_{low}E_{high}$	0	0	0	0	0	0	ϕ_2	0	0	0	1-ϕ_2
	$S_{high}D_{high}E_{high}$	0	0	0	0	0	0	0	ϕ_2	0	0	1-ϕ_2
	AES_{low}	0	0	0	0	0	0	0	0	ϕ_1	0	1-ϕ_1
	AES_{high}	0	0	0	0	0	0	0	0	0	ϕ_2	1-ϕ_2
	dead	0	0	0	0	0	0	0	0	0	0	1

The modelling of survival as in Table A2 is done through GEPAT and GEMACO as follow:
GEPAT instruction:

$$\begin{array}{ccccccccccc}
\phi & - & - & - & - & - & - & - & - & - & * \\
- & \phi & - & - & - & - & - & - & - & - & * \\
- & - & \phi & - & - & - & - & - & - & - & * \\
- & - & - & \phi & - & - & - & - & - & - & * \\
- & - & - & - & \phi & - & - & - & - & - & * \\
- & - & - & - & - & \phi & - & - & - & - & * \\
- & - & - & - & - & - & \phi & - & - & - & * \\
- & - & - & - & - & - & - & \phi & - & - & * \\
- & - & - & - & - & - & - & - & \phi & - & * \\
- & - & - & - & - & - & - & - & - & \phi & * \\
- & - & - & - & - & - & - & - & - & - &
\end{array}$$

GEMACO instruction (for the TFC-effect):
f(1:4;9,5:8;10).a(1,2:24)+a(14_24)*x(1)+a(20:24)+others

A .txt file is to be entered as an external covariable and codes for the linear effect of age varying between 14 and 24 (11 age classes):

```
1
11
0.090909091 0.181818182 0.272727273 0.363636364 0.454545455 0.545454545 0.636363636
0.727272727 0.818181818 0.909090909 1
```

Table A3. Dispersal probabilities (Ψ-matrix) of multievent model accounting for survival, detection and emigration heterogeneity using two classes, while allowing for temporary emigration and detailed observation structure. The product $\Phi = S \times \Psi$ constitutes the survival/transition matrix that is common to multistate and multievent models. ψ_1 and ψ_2 are the two probabilities of transition from the study site to states 'Alive elsewhere', corresponding to high and low emigration rates. After a temporary emigration, gulls could completely change the location of their nest, thus change of detectability class. Similarly, after an emigration event, gulls could be more site-faithful (if emigration aims at sparing energy for subsequent breeding) or less site faithful (if the first emigration event is the symptom of a decrease in health status). Therefore our model did not constraint the way individual behaved after a temporary emigration: four different probabilities to return to the study site were implemented. The probabilities of coming back to the study colony are four: ψ_3, ψ_4, ψ_5, ψ_6 respectively the transitions, from the corresponding 'Alive elsewhere' states, to states $S_{low}D_{low}E_{low}$ and $S_{high}D_{low}E_{low}$, $S_{low}D_{high}E_{low}$ and $S_{high}D_{high}E_{low}$, $S_{low}D_{low}E_{high}$ and $S_{high}D_{low}E_{high}$, $S_{low}D_{high}E_{high}$ and $S_{high}D_{high}E_{high}$. $\Sigma\psi$ stands for $\psi_3 + \psi_4 + \psi_5 + \psi_6$.States denominations are described above.

		State before dispersal										
	To\from	$S_{low}D_{low}E_{low}$	$S_{low}D_{high}E_{low}$	$S_{low}D_{low}E_{high}$	$S_{low}D_{high}E_{high}$	$S_{high}D_{ow}E_{low}$	$S_{high}D_{high}E_{low}$	$S_{high}D_{low}E_{high}$	$S_{high}D_{high}E_{high}$	AES_{low}	AES_{high}	**dead**
State at time *t+1*	$S_{low}D_{low}E_{low}$	$1-\psi_1$	0	0	0	0	0	0	0	ψ_1	0	0
	$S_{low}D_{high}E_{low}$	0	$1-\psi_1$	0	0	0	0	0	0	ψ_1	0	0
	$S_{low}D_{low}E_{high}$	0	0	$1-\psi_2$	0	0	0	0	0	ψ_2	0	0
	$S_{low}D_{high}E_{high}$	0	0	0	$1-\psi_2$	0	0	0	0	ψ_2	0	0
	$S_{high}D_{low}E_{low}$	0	0	0	0	$1-\psi_1$	0	0	0	0	ψ_1	0
	$S_{high}D_{high}E_{low}$	0	0	0	0	0	$1-\psi_1$	0	0	0	ψ_1	0
	$S_{high}D_{low}E_{high}$	0	0	0	0	0	0	$1-\psi_2$	0	0	ψ_2	0
	$S_{high}D_{high}E_{high}$	0	0	0	0	0	0	0	$1-\psi_2$	0	ψ_2	0
	AES_{low}	ψ_3	ψ_4	ψ_5	ψ_6	0	0	0	0	$1-\Sigma\psi$	0	0
	AES_{high}	0	0	0	0	ψ_3	ψ_4	ψ_5	ψ_6	0	$1-\Sigma\psi$	0
	dead	0	0	0	0	0	0	0	0	0	0	1

The modelling of dispersal as in Table A3 is done through GEPAT and GEMACO as follow:
GEPAT instruction:

*	0	0	0	0	0	0	0	ψ	0	0
0	*	0	0	0	0	0	0	ψ	0	0
0	0	*	0	0	0	0	0	ψ	0	0
0	0	0	*	0	0	0	0	ψ	0	0
0	0	0	0	*	0	0	0	0	ψ	0
0	0	0	0	0	*	0	0	0	ψ	0
0	0	0	0	0	0	*	0	0	ψ	0
0	0	0	0	0	0	0	*	0	ψ	0
ψ	ψ	ψ	ψ	0	0	0	0	*	0	0
0	0	0	0	ψ	ψ	ψ	ψ	0	*	0
0	0	0	0	0	0	0	0	0	0	*

GEMACO instruction:

f(1 3 5 7,2 4 6 8)+f(9 10).to

Table A4. Detection probabilities (P-matrix) and breeding status confirmation probabilities (R-matrix) of multievent model accounting for survival, detection and emigration heterogeneity using two classes, while allowing for temporary emigration and detailed observation structure. Product P × R constitutes the matrix of event probabilities (B-matrix), which represents the probabilities of recording the events conditional on the occupied state. The 'observation status' ['not seen', 'seen 1' (seen with a high detection probability), 'seen 2' (seen with a low detection probability)] corresponds to transitory states. Then there were three possible events (0: not seen, 1: seen and breeding status confirmed; 2: seen but breeding status not confirmed), which correspond to the three columns of R. p_{low} and p_{high} are the two detection probabilities; r_{low} and r_{high} are the corresponding probabilities of confirming breeding status. States denominations are described above.

(a) P		Observation status		
		not seen	Seen1	Seen2
State at time t+1	$S_{low}D_{low}E_{low}$	$1-p_{low}$	p_{low}	0
	$S_{low}D_{high}E_{low}$	$1-p_{high}$	0	p_{high}
	$S_{low}D_{low}E_{high}$	$1-p_{low}$	p_{low}	0
	$S_{low}D_{high}E_{high}$	$1-p_{high}$	0	p_{high}
	$S_{high}D_{low}E_{low}$	$1-p_{low}$	p_{low}	0
	$S_{high}D_{high}E_{low}$	$1-p_{high}$	0	p_{high}
	$S_{high}D_{low}E_{high}$	$1-p_{low}$	p_{low}	0
	$S_{high}D_{high}E_{high}$	$1-p_{high}$	0	p_{high}
	AES_{low}	1	0	0
	AES_{high}	1	0	0
	dead	1	0	0

(b) R		Event recorded		
		0	1	2
Obser-vation status	not seen	1	0	0
	Seen1	0	r_{low}	$1-r_{low}$
	Seen2	0	r_{high}	$1-r_{high}$

The modelling of event recording as in Table A4 is done through GEPAT and GEMACO as follow:
GEPAT instruction for detection:

```
*  β  –
*  –  β
*  β  –
*  –  β
*  β  –
*  –  β
*  β  –
*  –  β
*  –  –
*  –  –
*  –  –
```

GEPAT instruction for breeding status confirmation:

```
*  –  –
–  β  *
–  β  *
```

GEMACO instruction for detection (modelling time-dependence):
a(1)+a(2:29).[to+t]

GEMACO instruction for breeding status confirmation:
from

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Appendix 2

Simulation study

Because the performances of multievent CMR models have never been formally tested in the presence of several sources of heterogeneity, we carried out three simulation studies.

– The first simulated situation was the absence of senescence and the presence of three kinds of heterogeneity (survival, detection, emigration). It aimed at evaluating the performance of our information-theoretic approach concerning type II errors (i.e. the probability to falsely detect the presence of senescence).

– The second simulated case was the presence of senescence and of the three kinds of heterogeneity, but without the detailed information on detectability, i.e. there was only two events possible ('seen' / 'not seen'). It aimed at illustrating potential issues related to the mixing of detection and emigration heterogeneity.

– The third simulated case was the presence of senescence, three sources of heterogeneity, and detailed data structure (i.e. the frequency of the observed events depended on the detection probability). There were three events possible ('seen 1', 'seen 2', 'not seen').

Data simulation

The simulation studies were based on 30 simulated datasets (except for case no. 2 where we used 60 datasets). The time needed to perform each of these exercises exceeded 10 days each with an Intel Pentium 4HT, 2.6GHz (3.25 × 800) processor with 512 Mb of system memory.

Datasets were simulated as follows. At each of 20 capture sessions, 50 newly marked individuals were released in each of the eight classes of heterogeneity, forming an overall sample size of 8000 individuals. Between each session, individuals were allowed to move to or from a site where detection was impossible. The eight classes had different values of demographic parameters: probability of survival (at age 1 before senescence) was 0.8 or 0.5; of detection 0.5 or 0.1; and of changing site 0.4 or 0.1.

When present in the simulated case, the detailed observation structure was simulated as follows. In the high-detectability class, at each session 80% of the detected individuals produced the event 'seen1' and 20% the event 'seen2'. In the low-detectability class the frequency of 'seen1' was 20% and the frequency of 'seen2' was 80%.

When present in the simulated case, senescence was simulated as a linear decrease in survival with age starting at age 1 and with a slope of –0.033 and –0.021 year^{-1} in the high and low survival classes respectively (Fig. A1), i.e. survival probability was zero at age 25. We deliberately chose to simulate a linear effect (and not a logit-linear effect), so that, as is supposedly the case in real datasets, the logit-linear relationship between age and survival that was used in the CMR model was only approximating the underlying process.

Data analysis

Ten models were fitted on each simulated datasets: $\{S_{0+\bar{a}};D_0;E_0\}$, $\{S_{0+a};D_0;E_0\}$, $\{S_{0+\bar{a}};D_H;E_H\}$, $\{S_{0+a};D_H;E_H\}$, $\{S_{H+\bar{a}};D_0;E_H\}$, $\{S_{H+a};D_0;E_H\}$, $\{S_{H+\bar{a}};D_H;E_0\}$, $\{S_{H+a};D_H;E_0\}$, $\{S_{H+\bar{a}};D_H;E_H\}$ and $\{S_{H+a};D_H;E_H\}$. See main text for the meaning of the symbols. For each dataset-model, we computed the AIC, AIC-weights, and parameter estimates, and for each dataset we computed the importance value of the four considered effects (age-effect on survival, heterogeneity in survival, detection and emigration probabilities; see method in main text). To spare computer time we did not estimate the rank of the models and therefore did not formally detect identifiability problems if they occurred (Rouan et al. 2009, Choquet et al. 2009a), nor did we compute standard errors on the estimates.

Results

Case no.1: Absence of senescence, detailed dataModel selection

The three kinds of heterogeneity were unambiguously selected. Their importance values were 1. Among the 30 datasets, and using the 2-point AIC threshold, model $\{S_{H+a};D_H;E_H\}$ was selected 18 times and model $\{S_{H+\bar{a}};D_H;E_H\}$ (i.e. the model used to simulate the data) 16 times. Thus, despite its absence, the age-effect on survival was selected in more than half the cases.

Slope of the age-effect where it should have been absent

We computed the average estimated slope of the age-effect (on a logit scale) over the 30 models $\{S_{H+a};D_H;E_H\}$. In the low-survival class, the slope estimate was always very positive (average ± SD over the 30 datasets: +0.26 ± 0.05), i.e. not compatible with senescence. Why the models included this strong increase from a low survival at age 1 to a high survival at old age in the low-survival class is not known, but supposedly stems from the quick decrease with age in sample size of low-survival individuals.

In the high-survival class, the estimated slope was on average positive and closer to zero (average ± SD over the 30 datasets: +0.042 ± 0.059). Type II errors for senescence (i.e. negative slopes) occurred in 9 out of 30 cases. Over these 9 cases, the slope was still on average close to zero (–0.027 ± 0.022 on a logit scale, compared to the value obtained in the gull application: –0.16). In short, even if the age effect was selected in more than half of the datasets, the estimated slope in the high-survival class was small and most of the time positive and thus did not provide strong evidence for senescence.

Case no#2: Presence of senescence, non-detailed data

Model selection
Among the 60 datasets, and using the 2-point AIC threshold, model $\{S_{H+a};D_0;E_H\}$ was selected 50 times, model $\{S_{H+a};D_H;E_H\}$ (i.e. the model used to simulate the data) 20 times only, model $\{S_{H+a};D_H;E_0\}$ 11 times, and model $\{S_{0+\bar{a}};D_H;E_H\}$ once. Thus, the age-effect and the survival heterogeneity were generally selected. The two other kinds of heterogeneity proved harder to detect. Importance values of the considered effects were high (Table A5), with the only exception of heterogeneity in detection probability. This issue is discussed under 'potential identifiability issues'.

When neglecting heterogeneity in survival, in 45 out of 60 cases the age-effect was discarded (by AIC); this confirmed the strong bias due to neglecting survival heterogeneity. When neglecting heterogeneity in detection or emigration the age-effect was always selected except for three cases. Therefore, under the simulated scenario, these sources of heterogeneity had a reduced impact on the detection of survival senescence.

Slope of senescence
In the high-survival class the estimated slope of -0.11 ± 0.02 on a logit scale (average ± SD over the 60 datasets) translated into a -0.023 year^{-1} (expected value: -0.033 year^{-1}).

The slope was of slightly lower magnitude in the model without emigration heterogeneity than in the model with it (it was the case in 49 cases out of 60; average slope -0.09 ± 0.02 instead of -0.11 ± 0.02). Therefore, the impact of emigration heterogeneity on the estimation of senescence received some support.

Case no. 3: Presence of senescence, detailed data (three events)

Model selection
Among the 30 datasets, and using the 2-point AIC threshold, model $\{S_{H+a};D_H;E_H\}$ (i.e. the model used to simulate the data) was selected 26 times, model $\{S_{H+a};D_H;E_0\}$ 11 times, model $\{S_{0+a};D_H;E_H\}$ twice, and model $\{S_{H+\bar{a}};D_H;E_H\}$ three times. The age-effect, the survival heterogeneity, and the detection heterogeneity (contrary to Case #2) were unambiguously selected when relying on importance values (Table S5). Emigration heterogeneity was slightly less frequently detected. The three preferred models often ended up very close to one another.

Slope of senescence
In the high-survival class the estimated slope of -0.16 ± 0.02 (average ± SD over the 30 datasets) on a logit scale translated into -0.0329 year^{-1} on a linear scale (expected value: -0.033 year^{-1}).

The slope was not of lower magnitude in the model without emigration heterogeneity than in the model with it (all cases), and discarding emigration heterogeneity did not prevent to detect senescence (all cases). Therefore, the impact of emigration heterogeneity on senescence was not supported in case no. 3.

Discussion

Type-II errors

In case no. 1 the selection of an age-effect when there was none in the data was quite frequent. However, in most cases the estimated slope of the age-effect in the high-survival class was small and positive; if we had computed confidence intervals (not performed due to computer time constraints), we believe these slopes would moreover have appeared non-significantly different from zero. The risk of type-II errors for senescence per se therefore appeared low. Further investigation concerning the surprising find that the low-survival class was impacted by a strong increase in estimated survival probability is required; for low-survival individuals the interval between the sessions might have been too short to study age effects on survival.

Potential identifiability issues
In case no. 2, emigration and detection heterogeneity proved difficult to detect. Moreover when the importance value of emigration heterogeneity was low, it tended to be negatively correlated to the importance value of detection heterogeneity (Fig. A2). Identifiability problems might thus have occurred in some of the simulated cases, between heterogeneity in detection and in emigration. In other words, the model might have difficulties separating individuals not seen because emigrated from those not seen because not detected, hence the large SD on the corresponding importance values in Table A5.

Case no. 3 however illustrated how the use of detailed observation data (three events instead of two, the frequency of each event depending on detectability) made the separation between detection and emigration processes possible. We thereby suggest that in the study we present in the main text, our use of the information about breeding status confirmation did overcome the issue of parameter identifiability raised by case no. 2. Furthermore the tool implemented in E-SURGE did not detect any problem of parameter redundancy in the gull study (see main text).

Table A5. Importance value (IV; see method in main text) of the four considered effects in three simulation studies. See 'data simulation' for the description of the considered cases. Mean and SD were computed on 30 (case no. 1 and 3) or 60 (case no. 2) simulated datasets.

	Case 1		Case 2		Case 3	
Effect considered	Mean	SD	Mean	SD	Mean	SD
Age-effect on survival	0.536	0.410	0.987	0.081	0.910	0.137
Heterogeneity in survival	1.000	0.000	0.987	0.083	0.932	0.088
Heterogeneity in emigration	1.000	0.000	0.874	0.224	0.759	0.228
Heterogeneity in detection	1.000	0.000	0.335	0.307	1.000	0.000

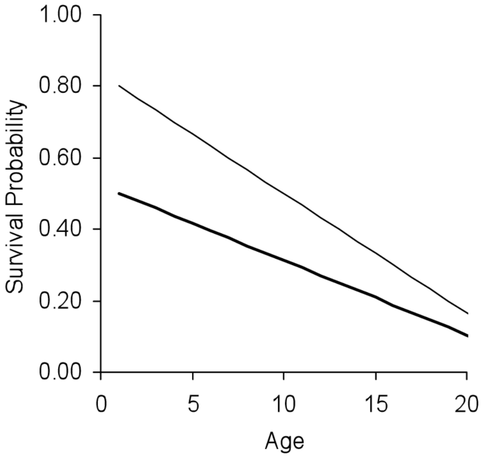

Figure A1. Simulated variation in survival rate with age in the low- (starting at 0.5) and high- (starting at 0.8) survival classes.

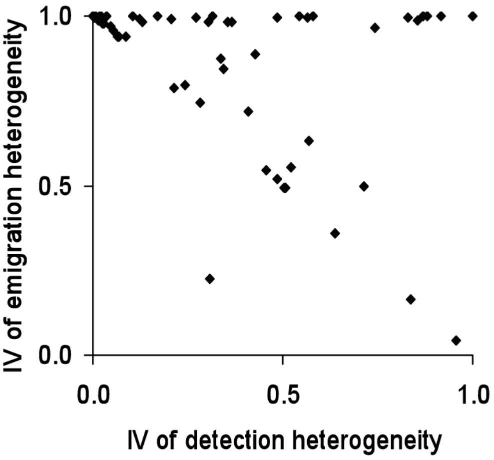

Figure A2. Importance values (IV; see methods in main text) of detection and emigration heterogeneity computed from the 60 datasets in case 2 where the detailed information on detectability was not used.