Appendix C: Individual heterogeneity in capture-recapture models - Frequentist approach using E-SURGE

Introduction

In this appendix, we introduce three methods to cope with individual heterogeneity in capture-recapture models, which we implement in a frequentist framework using maximum likelihood methods. First, we present multistate models in which heterogeneity is measured on individuals using states. Then, we illustrate models with individual random effects and finite mixtures that can help in dealing with hidden heterogeneity. We refer to the paper for a formal presentation of these models and a list of references using them. Throughout this appendix, we use R to simulate data and program E-SURGE is used to fit models. We refer to the relevant literature for an introduction to the use of this program. Note that the frequentist approach can also be implemented with program Mark (appendix A). We refer to this section for comparison of the results we obtain below. Alternatively, the Bayesian approach can be employed (appendix B).

Multistate models

In this section, we aim at illustrating how not accounting for individual heterogeneity may obscure the detection of life-history tradeoffs. In details, we consider two states for the individuals of our fake population, non-breeding (NB) and breeding (B). To mimic individual heterogeneity, we simulate a bunch of good individuals with survival $\phi_{NB} = 0.7$ and $\phi_B = 0.8$ and a bunch of bad individuals with survival $\phi_{NB} = 0.7$ and $\phi_B = 0.6$. Overall, the cost of breeding on survival should be detected only in bad individuals after accounting for individual heterogeneity through quality. For each group of bad vs. good individuals, we consider the same detection probability $p = 0.9$, the same transition probabilities between breeding states $\psi_{NB,B} = 0.8$ and $\psi_{B,NB} = 0.3$, and 100 newly marked individuals for each group in each year of the 6-year study.

Data simulation

Using R code from Kéry and Schaub (2012) book (chapter 9), we first define a function to simulate multistate capture-recapture data:

```r
# Define function to simulate multistate capture-recapture data
simul.ms <- function(PSI.STATE, PSI.OBS, marked, unobservable = NA){
  # Unobservable: number of state that is unobservable
  n.occasions <- dim(PSI.STATE)[4] + 1
  CH <- CH.TRUE <- matrix(NA, ncol = n.occasions, nrow = sum(marked))
  # Define a vector with the occasion of marking
  mark.occ <- matrix(0, ncol = dim(PSI.STATE)[1], nrow = sum(marked))
  g <- colSums(marked)
  for (s in 1:dim(PSI.STATE)[1]){
    if (g[s]==0) next # To avoid error message if nothing to replace
    mark.occ[(cumsum(g[1:s])-g[s]+1)[s]:cumsum(g[1:s])[s],s] <-
    rep(1:n.occasions, marked[1:n.occasions,s])
  } #s
  for (i in 1:sum(marked)){
    for (s in 1:dim(PSI.STATE)[1]){
      if (mark.occ[i,s]==0) next
      first <- mark.occ[i,s]
      CH[i,first] <- s
      CH.TRUE[i,first] <- s
    } #s
    for (t in (first+1):n.occasions){
      # Multinomial trials for state transitions
      if (first==n.occasions) next
      state <- which(rmultinom(1, 1, PSI.STATE[CH.TRUE[i,t-1],,i,t-1])==1)
      CH.TRUE[i,t] <- state
      # Multinomial trials for observation process
      event <- which(rmultinom(1, 1, PSI.OBS[CH.TRUE[i,t],,i,t-1])==1)
      CH[i,t] <- event
    } #t
  } #i
  # Replace the NA and the highest state number (dead) in the file by 0
  CH[is.na(CH)] <- 0
  CH[CH==dim(PSI.STATE)[1]] <- 0
  CH[CH==unobservable] <- 0
  id <- numeric(0)
  for (i in 1:dim(CH)[1]){
    z <- min(which(CH[i,]!=0))
    ifelse(z==dim(CH)[2], id <- c(id,i), id <- c(id))
  }
  return(list(CH=CH[-id,], CH.TRUE=CH.TRUE[-id,]))
# CH: capture histories to be used
# CH.TRUE: capture histories with perfect observation
}
```

Second, we use this function to simulate the two datasets of good and bad individuals:

```
set.seed(1) # for reproducibility
p = 0.9
R = 100
#-----------------------------
#---- good quality individuals
#-----------------------------
# Define mean survival, transitions, recapture, as well as number of occasion
s, states, observations and released individuals
phiA <- 0.7
phiB <- 0.8
psiAB <- 0.8
psiBA <- 0.3
pA <- p
pB <- p
```

```r
n.occasions <- 6
n.states <- 3
n.obs <- 3
marked <- matrix(NA, ncol = n.states, nrow = n.occasions)
marked[,1] <- rep(R, n.occasions)
marked[,2] <- rep(R, n.occasions)
marked[,3] <- rep(0, n.occasions)
# Define matrices with survival, transition and recapture probabilities
# 1. State process matrix
totrel <- sum(marked)*(n.occasions-1)
PSI.STATE <- array(NA, dim=c(n.states, n.states, totrel, n.occasions-1))
for (i in 1:totrel){
  for (t in 1:(n.occasions-1)){
    PSI.STATE[,,i,t] <- matrix(c(
      phiA*(1-psiAB), phiA*psiAB, 1-phiA,
      phiB*psiBA, phiB*(1-psiBA), 1-phiB,
      0, 0, 1 ), nrow = n.states, byrow = TRUE)
  } #t
} #i
# 2.Observation process matrix
PSI.OBS <- array(NA, dim=c(n.states, n.obs, totrel, n.occasions-1))
for (i in 1:totrel){
  for (t in 1:(n.occasions-1)){
    PSI.OBS[,,i,t] <- matrix(c(
      pA, 0, 1-pA,
      0, pB, 1-pB,
      0, 0, 1 ), nrow = n.states, byrow = TRUE)
  } #t
} #i

# Execute function
sim <- simul.ms(PSI.STATE, PSI.OBS, marked)
CH <- sim$CH
his1 = CH[!apply(CH,1,sum)==0,] # remove lines of 0s

#------------------------------
#---- bad quality individuals
#------------------------------
# Define mean survival, transitions, recapture, as well as number of occasion
s, states, observations and released individuals
phiA <- 0.7
phiB <- 0.6
psiAB <- 0.8
psiBA <- 0.3
pA <- p
pB <- p
n.occasions <- 6
n.states <- 3
n.obs <- 3
marked <- matrix(NA, ncol = n.states, nrow = n.occasions)
```

```
marked[,1] <- rep(R, n.occasions)
marked[,2] <- rep(R, n.occasions)
marked[,3] <- rep(0, n.occasions)
# Define matrices with survival, transition and recapture probabilities
# 1. State process matrix
totrel <- sum(marked)*(n.occasions-1)
PSI.STATE <- array(NA, dim=c(n.states, n.states, totrel, n.occasions-1))
for (i in 1:totrel){
  for (t in 1:(n.occasions-1)){
    PSI.STATE[,,i,t] <- matrix(c(
    phiA*(1-psiAB), phiA*psiAB, 1-phiA,
    phiB*psiBA, phiB*(1-psiBA), 1-phiB,
    0, 0, 1 ), nrow = n.states, byrow = TRUE)
  } #t
} #i
# 2.Observation process matrix
PSI.OBS <- array(NA, dim=c(n.states, n.obs, totrel, n.occasions-1))
for (i in 1:totrel){
  for (t in 1:(n.occasions-1)){
    PSI.OBS[,,i,t] <- matrix(c(
    pA, 0, 1-pA,
    0, pB, 1-pB,
    0, 0, 1 ), nrow = n.states, byrow = TRUE)
  } #t
} #i

# Execute function
sim <- simul.ms(PSI.STATE, PSI.OBS, marked)
CH <- sim$CH
his2 = CH[!apply(CH,1,sum)==0,] # remove lines of 0s
```

Last, we pool these two datasets together:

```
his = rbind(his1,his2)
```

Format the data for analysis in E-SURGE. We use RMark to get a file in the inp format (check out these notes by Mike Conroy for more details):

```
k = ncol(his) # nb of capture occasions
n = nrow(his) # nb of individuals
out = array(dim=n)
for (i in 1:n){
    y = (his[i,] > 0) * his[i,]
    out[i] = paste(y,collapse="")
}
capt.hist = data.frame(ch = out)

# export
library(RMark)

## This is RMark 2.2.0
```

```
mstrata.processed=process.data(capt.hist,model="Multistrata")
export.MARK(mstrata.processed, "multistate")

## NULL
```

Model fitting

Now we fit a multistate model using the dataset *multistate.inp*: we assume that survival depends on the breeding states, transition probabilities are constant over time, as well as the detection probability. The states are alive in state A, alive in state B, and dead, and the events are non-detected, seen in state A, seen in state B. We use 1 age class. Transition between successive states can be viewed as involving two distinct processes: survival S followed by transition conditional on survival ψ.

We now present the model components in mathematical terms.

First survival, with in rows the states at time t, in columns the states at time t+1:

$$S = \begin{bmatrix} \phi_A & 0 & 1-\phi_A \\ 0 & \phi_B & 1-\phi_B \\ 0 & 0 & 1 \end{bmatrix}$$

Now the transitions, with among survivors, transitions between states:

$$\psi = \begin{bmatrix} 1-\psi^{A\to B} & \psi^{A\to B} & 0 \\ \psi^{B\to A} & 1-\psi^{B\to A} & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

The observation process is driven by:

$$B_2 = \begin{bmatrix} 1-p & p & 0 \\ 1-p & 0 & p \\ 1 & 0 & 0 \end{bmatrix}$$

where the states are in rows, the observations in columns. At initial capture:

$$B_1 = \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{bmatrix}$$

Initial states are:

$$\Pi = \begin{bmatrix} \pi_A & 1-\pi_A = \pi_B & 0 \end{bmatrix}$$

In GEPAT, we have:

Transitions:

Step1 (survival)

$$S = \begin{bmatrix} y & - & * \\ - & y & * \\ - & - & * \end{bmatrix}$$

Step2 (transition)

$$\psi = \begin{bmatrix} * & y & - \\ y & * & - \\ - & - & * \end{bmatrix}$$

Event: $B = \begin{bmatrix} * & b & - \\ * & - & b \\ * & - & - \end{bmatrix}$

Initial state: $\Pi = \begin{bmatrix} p & * \end{bmatrix}$

In GEMACO, the syntax is:

For Initial State: IS = i

For Transition: S (i.e. step 1) = f T (i.e. step 2) = f.to

For Event: E = firste+nexte

The results are:

```
piA
Par#    1# IS(  1,  1)(  1,  1)(  1   1) | 0.500000000 0.478100968 0.521899032 0.011180128
SA
Par#   13# S(  1,  1)(  1,  1)(  1   1) | 0.692093902 0.666444442 0.716609698 0.012805506
SB
Par#   14# S(  2,  2)(  1,  1)(  1   1) | 0.699862036 0.679730248 0.719251037 0.010085710
Psi(B->A)
Par#   39# T(  2,  1)(  1,  1)(  1   2) | 0.308345294 0.285689496 0.331962784 0.011810894
Psi(A->B)
Par#   40# T(  1,  2)(  1,  1)(  1   2) | 0.777655122 0.750027275 0.803031347 0.013523467
p
Par#   96# E(  1,  2)(  2,  2)(  1   1) | 0.900413342 0.883776245 0.914898215 0.007921038

AIC = 11615.1
```

Now we run the same model without a state effect on survival. We just need to amend the GEMACO syntax as follows:

For Initial State: IS = i

For Transition: S (i.e. step 1) = i T (i.e. step 2) = f.to

For Event: E = firste+nexte

The results are:

```
piA

Par#    1# IS(  1,  1)(  1,  1)(  1   1) | 0.500000000 0.478100968 0.521899032 0.011180128

S

Par#   13# S(  1,  1)(  1,  1)(  1   1) | 0.696844560 0.681337562 0.711916010 0.007802448

Psi(B->A)

Par#   39# T(  2,  1)(  1,  1)(  1   2) | 0.308357742 0.285694711 0.331983005 0.011814729

Psi(A->B)

Par#   40# T(  1,  2)(  1,  1)(  1   2) | 0.777651731 0.750026841 0.803025509 0.013522089

p

Par#   96# E(  1,  2)(  2,  2)(  1   1) | 0.900374454 0.883729698 0.914865964 0.007924680


AIC = 11613.3
```

Let's add individual heterogeneity through an individual covariate for bad vs. good individuals:

```
quality=c(rep(0,nrow(his1)),rep(1,nrow(his2))) # 0 for good, 1 for bad

capt.hist$quality=c(rep('good',nrow(his1)),rep('bad',nrow(his2)))
mstrata.processed=process.data(capt.hist,model="Multistrata",groups = 'qualit
y')

## Warning in process.data(capt.hist, model = "Multistrata", groups = "qualit
y"):
##   quality  is not a factor variable. Coercing to factor.

export.MARK(mstrata.processed, "multistate_cov")

## NULL
```

Now we fit again the two models from above, including the effect of individual heterogeneity. You first need to read the file *multistate_cov.inp* with an individual covariate for quality (group here).

In GEMACO:

For Initial State: IS = i

For Transition: S (i.e. step 1) = f.g T (i.e. step 2) = f.to

For Event: E = firste+nexte

The results are:

```
piA
Par#    1# IS(  1,  1)(  1,  1)(  1   1) | 0.500000000 0.478104493 0.521895507 0.011178326
SA bad
Par#   25# S(  1,  1)(  1,  1)(  1   1) | 0.698644472 0.660832631 0.733938084 0.018674111
SB bad
Par#   26# S(  2,  2)(  1,  1)(  1   1) | 0.578269957 0.547097745 0.608830677 0.015767719
SA good
Par#   50# S(  1,  1)(  1,  1)(  2   1) | 0.687400734 0.652286741 0.720488223 0.017419531
SB good
Par#   51# S(  2,  2)(  1,  1)(  2   1) | 0.800245625 0.775338044 0.823022099 0.012162493
Psi(B->A)
Par#   76# T(  2,  1)(  1,  1)(  1   2) | 0.308126327 0.285494396 0.331719420 0.011798555
Psi(A->B)
Par#   77# T(  1,  2)(  1,  1)(  1   2) | 0.777683687 0.750048031 0.803066097 0.013527034
p
Par#  158# E(  1,  2)(  2,  2)(  1   1) | 0.900017665 0.883411800 0.914487274 0.007909458
```

AIC = 11494.7

Let us fit the same model without a state effect on survival.

In GEMACO:

For Initial State: IS = i

For Transition: S (i.e. step 1) = g T (i.e. step 2) = f.to

For Event: E = firste+nexte

The results are:

```
piA
Par#    1# IS(  1,  1)(  1,  1)(  1   1) | 0.500000000 0.478104493 0.521895507 0.011178326
Sbad
Par#   25# S(  1,  1)(  1,  1)(  1   1) | 0.626213649 0.602717237 0.649129396 0.011847691
Sgood
Par#   50# S(  1,  1)(  1,  1)(  2   1) | 0.757126606 0.737215797 0.775987212 0.009892566
Psi(B->A)
Par#   76# T(  2,  1)(  1,  1)(  1   2) | 0.308357754 0.285699775 0.331977526 0.011812035
Psi(A->B)
Par#   77# T(  1,  2)(  1,  1)(  1   2) | 0.777651734 0.750035176 0.803018483 0.013518169
p
Par#  158# E(  1,  2)(  2,  2)(  1   1) | 0.899885314 0.883231523 0.914394116 0.007931599
```

AIC = 11541.1

Clearly, the inclusion of quality improves the AIC. Also, the model with a difference in survival between breeders and non-breeders is better supported by the data when individual heterogeneity is accounted for.

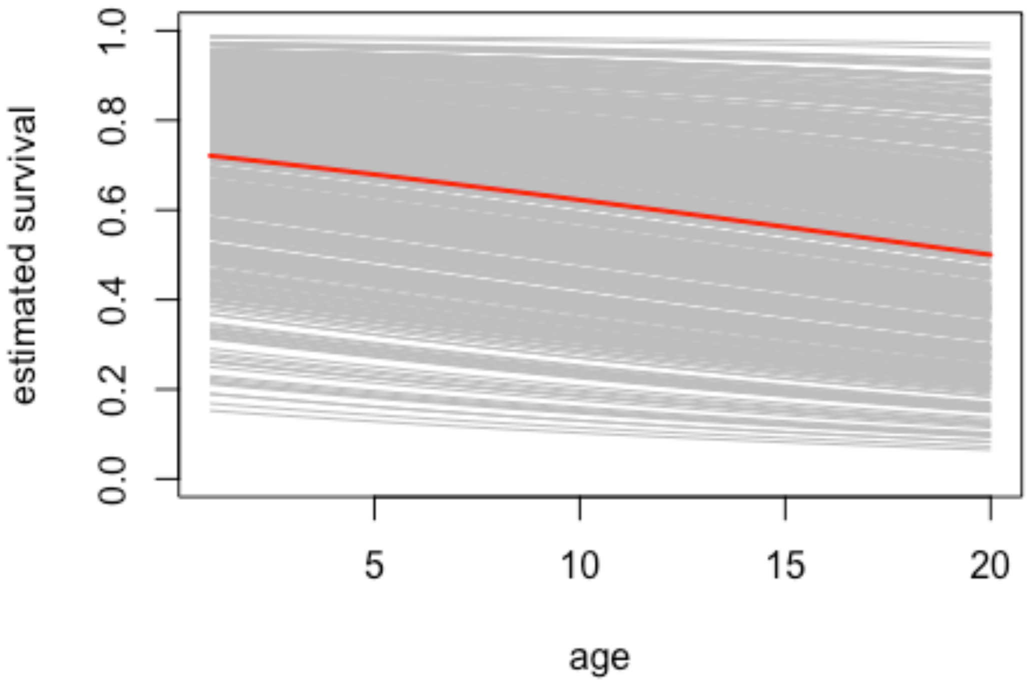
Models with individual random effects

Here, we aim at illustrating how not accounting for individual heterogeneity may obscure the detection of senescence in survival. More specifically, we consider a single cohort of 500 individuals with survival decreasing as they age over a 20-year study. We also add a frailty for each individual under the form of a normal distribution. Specifically, we specify $logit(\phi_i(a)) = \beta_0 + \beta_1 a + \varepsilon_i$ where $\varepsilon_i \sim N(0, \sigma^2)$. We use $\beta_0 = 1$, $\beta_1 = -0.05$ and $\sigma = 1$. If we condition upon the random effect, survival is decreasing as age increases. Note that we consider the same detection probability $p = 0.5$ for all individuals.

Data simulation

First, we simulate survival for each individual then plot the individual trajectories (in grey) as well as survival conditional on the random effect (in red):

```
rm(list=ls())
r = set.seed(3) # for reproducibility
p = 0.5 # detection
intercept_phi = 1
slope_phi = -0.05
sigmaphi = 1
nind = 500 # nb of individuals
nyear = 20 # duration of the study
expit<-function(x){exp(x)/(1+exp(x))} # reciprocal logit function
z<-data<-x<-matrix(NA,nrow=nind,ncol=nyear)
first<-rep(1,nind)
age = matrix(NA,nind,nyear)
phi = matrix(NA,nind,nyear)
# simulate age-varying survival for each individual
for (i in 1:nind){
  mask <- first[i]:nyear
  age[i,mask] <- mask - first[i] + 1
  phi[i,mask] <- expit(intercept_phi + slope_phi * age[i,mask] + rnorm(1,0,si
gmaphi))
}
plot(age[1,],phi[1,],type='l',col='grey',ylim=c(0,1),xlab='age',ylab='estimat
ed survival')
for (i in 2:nind){
  lines(age[i,],phi[i,],type='l',col='grey')
}
lines(1:nyear,expit(intercept_phi + slope_phi * 1:nyear),col='red',lwd=2)
```



Now simulate the encounter histories:

```
for(i in 1:nind){
  z[i,first[i]] <- x[i,first[i]] <- 1
  for(j in (first[i]+1):nyear){
    z[i,j]<-rbinom(1,1,phi[i,j-1]*z[i,j-1])
    x[i,j]<-rbinom(1,1,z[i,j]*p)
  }
}
his = x
his[is.na(his)]=0 # remove lines with 0's
```

Format data

```
k = ncol(his) # nb of capture occasions
n = nrow(his) # nb of individuals
out = array(dim=n)
for (i in 1:n){
    y = (his[i,] > 0) * his[i,]
    out[i] = paste(y,collapse="")
}
capt.hist = data.frame(ch = out)

# export
```

```
library(RMark)
cjs.processed=process.data(capt.hist,model="CJS")
export.MARK(cjs.processed, "random")

## NULL
```

Model fitting

We fit the model with an age effect but no individual heterogeneity to the simulated dataset.

The states are alive and dead. The events are non-detected (0) or detected (1). Therefore 2 states and 2 events.

In mathematical notation:

$$\Phi = \begin{bmatrix} \phi & 1-\phi \\ 0 & 1 \end{bmatrix}$$

$$B_1 = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$$

$$B_2 = \begin{bmatrix} 1-p & p \\ 1 & 0 \end{bmatrix}$$

$$\Pi = \begin{bmatrix} 1 & 0 \end{bmatrix}$$

- In GEPAT:

Transitions: $\Phi = \begin{bmatrix} y & * \\ - & * \end{bmatrix}$

Event: $\begin{bmatrix} * & b \\ * & - \end{bmatrix}$

Initial state: $[*]$

- In GEMACO:

For Initial State: i

For Transition: i+a*x(1)

For Event: firste+nexte

Age-varying survival

```
Par#   21# T(  1,  1)(  1,  1)(  1   1) | 0.723806618 0.692784709 0.752813691 0.015325031
Par#   78# T(  1,  1)(  2,  2)(  1   1) | 0.740054200 0.714396361 0.764167931 0.012702308
Par#  132# T(  1,  1)(  3,  3)(  1   1) | 0.755668630 0.733968241 0.776138790 0.010760322
Par#  183# T(  1,  1)(  4,  4)(  1   1) | 0.770635823 0.751157005 0.789018153 0.009659580
Par#  231# T(  1,  1)(  5,  5)(  1   1) | 0.784947084 0.765859458 0.802879155 0.009444050
Par#  276# T(  1,  1)(  6,  6)(  1   1) | 0.798598758 0.778390232 0.817396781 0.009949811
Par#  318# T(  1,  1)(  7,  7)(  1   1) | 0.811591827 0.789302718 0.832024827 0.010895601
Par#  357# T(  1,  1)(  8,  8)(  1   1) | 0.823931475 0.799091944 0.846290673 0.012033680
Par#  393# T(  1,  1)(  9,  9)(  1   1) | 0.835626629 0.808091272 0.859896148 0.013201915
Par#  426# T(  1,  1)( 10, 10)(  1   1) | 0.846689493 0.816503330 0.872684179 0.014307462
Par#  456# T(  1,  1)( 11, 11)(  1   1) | 0.857135087 0.824449835 0.884586663 0.015300853
Par#  483# T(  1,  1)( 12, 12)(  1   1) | 0.866980796 0.832005993 0.895587945 0.016157986
Par#  507# T(  1,  1)( 13, 13)(  1   1) | 0.876245942 0.839220375 0.905703041 0.016869562
Par#  528# T(  1,  1)( 14, 14)(  1   1) | 0.884951384 0.846125970 0.914964922 0.017435065
Par#  546# T(  1,  1)( 15, 15)(  1   1) | 0.893119139 0.852746379 0.923416921 0.017859263
Par#  561# T(  1,  1)( 16, 16)(  1   1) | 0.900772053 0.859099381 0.931108003 0.018150095
Par#  573# T(  1,  1)( 17, 17)(  1   1) | 0.907933486 0.865199038 0.938089724 0.018317340
```

```
Par#   582# T(  1,  1)( 18, 18)(  1   1) | 0.914627054 0.871056977 0.944414223 0.018371762
Par#   588# T(  1,  1)( 19, 19)(  1   1) | 0.920876386 0.876683196 0.950132875 0.018324520
p
Par#   653# E(  1,  2)(  2,  2)(  1   1) | 0.496648851 0.468198435 0.525120985 0.014536772

~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
   Index         Beta | Lower & Upper 95 percent CI | S.E.
~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
Intercept of the age effect
Beta#   1# | +0.880595669 +0.705870714 +1.055320625 +0.089145385
Slope of the age effect
Beta#   2# | +0.082827304 +0.050223273 +0.115431335 +0.016634710
###############################################################
p on logit scale
Beta#   3# | -0.013404796 -0.127378210 +0.100568618 +0.058149701
###############################################################
```

Having a look to the parameter estimates, it sounds like the slope of the age effect on survival is estimated positive... Which means that at the population level, whenever individual heterogeneity is ignored, then senescence is completely masked. Even worse, survival is increasing with increasing age.

Now we fit the model with a random effect in the survival process.

- In GEMACO:

```
For Initial State:      i
For Transition:         i+a*x(1) + ind
For Event:              firste+nexte
```

```
~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
```

```
Index        Beta | Lower & Upper 95 percent CI | S.E.

~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

Intercept of the age effect

Beta#   1# | +1.054558008 +0.801511207 +1.307604809 +0.129105511

Slope of the age effect

Beta#   2# | -0.068181499 -0.182575340 +0.046212342 +0.058364205

Beta#   3# | +1.102869039 +0.801536407 +1.404201672 +0.153741139

################### IND.R.E. ESTIMATES UNDER NORM. ASSUMPTIONS

Standard deviation of the random effect

Beta al. ind. #   1# SE | +1.216320118 +0.551659257 +1.880980979 +0.339112684

#################################################################

p on the logit scale

Beta#   4# | +0.016201370 -0.100161997 +0.132564737 +0.059369065

#################################################################
```

The intercept and slope of the age-survival relationship are quite close to the values we used to simulate the data.

Models with finite mixtures

Here, we again aim at illustrating how not accounting for individual heterogeneity may obscure the detection of senescence in survival. In contrast with the previous section, we now use finite mixtures to deal with heterogeneity. More specifically, we consider a cohort of 1000 individuals that are split into a group of robust individuals in proportion π with constant high survival ϕ_R and a group of frail individuals with survival ϕ_F that senesce over the 20 years of the study according to the relationship $logit(\phi_F(a)) = \beta_0 + \beta_1 a$. We use $\pi = 0.3$, $\phi_R = 0.85$, $\beta_0 = 0$ and $\beta_1 = -0.07$. Note that we consider the same detection probability $p = 0.5$ for all individuals.

Data simulation

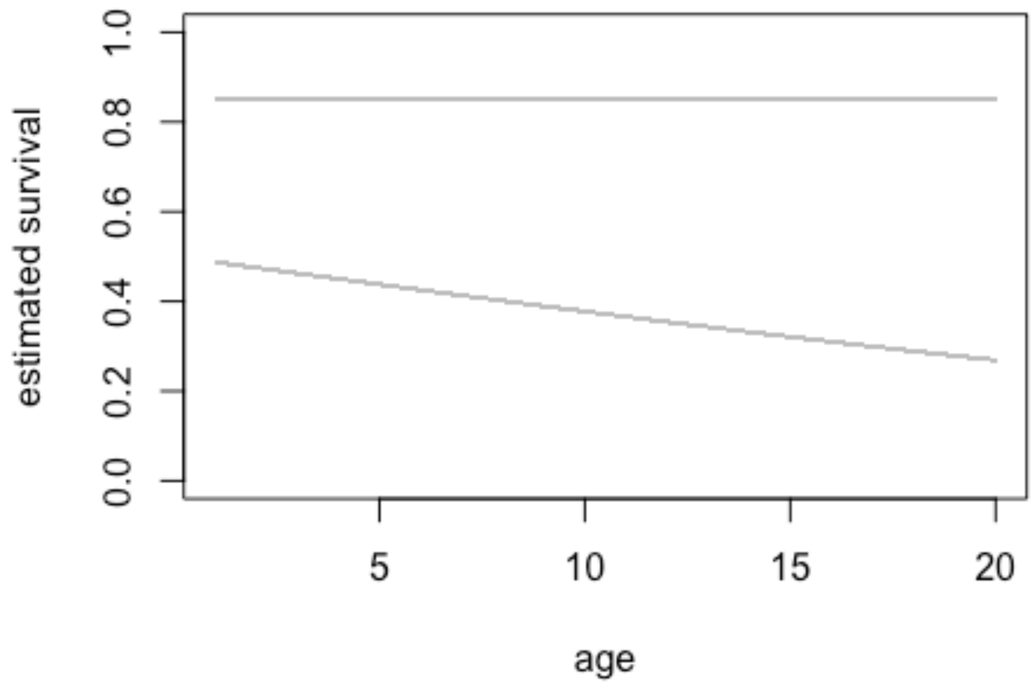
First simulate data

```r
rm(list=ls())
r = set.seed(3) # for reproducibility
p = 0.5 # detection
```

```r
prop_class1 = 0.3 # pi
phi_class1 = 0.85 # survival or robust ind
intercept_phi_class2 = 0 #beta_0
slope_phi_class2 = -0.05 # beta_1
nind = 1000 # nb of ind
nyear = 20 # duration of the study
expit<-function(x){exp(x)/(1+exp(x))} # reciprocal of the logit function
z<-data<-x<-matrix(NA,nrow=nind,ncol=nyear)
first<-rep(1,nind)
age = matrix(NA,nind,nyear)
phi = matrix(NA,nind,nyear)
which_mixture = rep(NA,nind)
# simulate age-varying survival for each individual,
# by first assigning them to the robust or frail class, then using the corresponding
# survival
for (i in 1:nind){
  mask <- first[i]:nyear
  age[i,mask] <- mask - first[i] + 1
  which_mixture[i] <- rbinom(1,1,prop_class1) # assign ind i to a class with prob pi
  if (which_mixture[i] == 1){
    phi[i,mask] <- phi_class1 # robust
  } else {
  phi[i,mask] <- expit(intercept_phi_class2 + slope_phi_class2 * age[i,mask])
} # frail
}
```

Represent graphically survival over time in the two classes:

```r
plot(age[1,],phi[1,],type='l',col='grey',ylim=c(0,1),xlab='age',ylab='estimated survival')
for (i in 2:nind){
  lines(age[i,],phi[i,],type='l',col='grey')
}
```



Now simulate the encounter histories:

```
for(i in 1:nind){
  z[i,first[i]] <- x[i,first[i]] <- 1
  for(j in (first[i]+1):nyear){
    z[i,j]<-rbinom(1,1,phi[i,j-1]*z[i,j-1])
    x[i,j]<-rbinom(1,1,z[i,j]*p)
  }
}
his = x
his[is.na(his)]=0
```

Format data

```
k = ncol(his) # nb of capture occasions
n = nrow(his) # nb of individuals
out = array(dim=n)
for (i in 1:n){
    y = (his[i,] > 0) * his[i,]
    out[i] = paste(y,collapse="")
}
capt.hist = data.frame(ch = out)

# export
```

```
library(RMark)
cjs.processed=process.data(capt.hist,model="CJS")
export.MARK(cjs.processed, "mixture")

## NULL
```

Model fitting

Let's fit two models assuming homogeneity: first one with an age effect, second one with constant survival. The mathematical structure of the model is given in the previous section.

In GEMACO:

For Initial State: to

For Transition: i+a*x(1)

For Event: firste+nexte

Age-varying survival estimates

```
Par#    21# T(  1,  1)(  1,  1)(  1   1) | 0.634502002 0.609101468 0.659175569 0.012783734
Par#    78# T(  1,  1)(  2,  2)(  1   1) | 0.664560709 0.643729318 0.684770533 0.010474694
Par#   132# T(  1,  1)(  3,  3)(  1   1) | 0.693342124 0.675555482 0.710571432 0.008935426
Par#   183# T(  1,  1)(  4,  4)(  1   1) | 0.720691941 0.704072792 0.736726761 0.008331994
Par#   231# T(  1,  1)(  5,  5)(  1   1) | 0.746494372 0.729339294 0.762915578 0.008566903
Par#   276# T(  1,  1)(  6,  6)(  1   1) | 0.770671662 0.751918395 0.788406236 0.009309127
Par#   318# T(  1,  1)(  7,  7)(  1   1) | 0.793181957 0.772414467 0.812514367 0.010229179
Par#   357# T(  1,  1)(  8,  8)(  1   1) | 0.814015923 0.791238494 0.834826954 0.011116020
Par#   393# T(  1,  1)(  9,  9)(  1   1) | 0.833192529 0.808633891 0.855163983 0.011860800
Par#   426# T(  1,  1)( 10, 10)(  1   1) | 0.850754381 0.824748161 0.873493398 0.012417022
Par#   456# T(  1,  1)( 11, 11)(  1   1) | 0.866762952 0.839680331 0.889870582 0.012773115
Par#   483# T(  1,  1)( 12, 12)(  1   1) | 0.881293983 0.853505895 0.904401415 0.012936700
Par#   507# T(  1,  1)( 13, 13)(  1   1) | 0.894433255 0.866289150 0.917219527 0.012925645
Par#   528# T(  1,  1)( 14, 14)(  1   1) | 0.906272847 0.878089131 0.928471722 0.012762790
Par#   546# T(  1,  1)( 15, 15)(  1   1) | 0.916907952 0.888962354 0.938308381 0.012472733
Par#   561# T(  1,  1)( 16, 16)(  1   1) | 0.926434262 0.898963963 0.946877123 0.012079847
```

```
Par#   573# T(  1,  1)( 17, 17)(  1   1) | 0.934945891 0.908148071 0.954318713 0.011607075
Par#   582# T(  1,  1)( 18, 18)(  1   1) | 0.942533803 0.916567709 0.960764571 0.011075243
Par#   588# T(  1,  1)( 19, 19)(  1   1) | 0.949284670 0.924274621 0.966335432 0.010502719
p
Par#   653# E(  1,  2)(  2,  2)(  1   1) | 0.498743562 0.474462571 0.523030481 0.012399528

~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
   Index        Beta | Lower & Upper 95 percent CI | S.E.
~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
Intercept of the age effect
Beta#   1# | +0.419474040 +0.291573267 +0.547374812 +0.065255496
Slope of the age effect
Beta#   2# | +0.132105603 +0.104773345 +0.159437860 +0.013945029
##################################################################
p on the logit scale
Beta#   3# | -0.005025762 -0.102238679 +0.092187155 +0.049598427
##################################################################
```

AIC = 5602.4

The parameter estimates of the model with constant survival are:

```
S
Par#    21# T(  1,  1)(  1,  1)(  1   1) | 0.725899443 0.709680514 0.741542274 0.008129685
P
Par#   653# E(  1,  2)(  2,  2)(  1   1) | 0.475812335 0.451522130 0.500217519 0.012432103
```

AIC = 5715.0

Again, as in the previous section, it's striking to see that survival is increasing when age increases if individual heterogeneity is ignored. In other words, senescence is masked.

Now let's fit a model with heterogeneity - two-finite mixture - in the survival probability, with constant parameters over time. The states are alive class 1, alive class 2 and dead. The events are non-detected (0) or detected (1). Therefore 3 states and 2 events.

In mathematical notation,

$$\Phi = \begin{bmatrix} \phi^1 & 0 & 1-\phi^1 \\ 0 & \phi^2 & 1-\phi^2 \\ 0 & 0 & 1 \end{bmatrix}$$

Individuals can be allowed to move from a heterogeneity class to the other through the addition of a transition matrix:

$$\Phi = \begin{bmatrix} \phi^1 & 0 & 1-\phi^1 \\ 0 & \phi^2 & 1-\phi^2 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} 1-\psi^{1\to 2} & \psi^{1\to 2} & 0 \\ \psi^{2\to 1} & 1-\psi^{2\to 1} & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

The observation process:

$$B_1 = \begin{bmatrix} 0 & 1 \\ 0 & 1 \\ 1 & 0 \end{bmatrix}$$

$$B_2 = \begin{bmatrix} 1-p & p \\ 1-p & p \\ 1 & 0 \end{bmatrix}$$

The initial states:

$$\Pi = \begin{bmatrix} \pi & 1-\pi \end{bmatrix};$$

- In GEPAT:

Transitions: $\begin{bmatrix} \psi & - & * \\ - & \psi & * \\ - & - & * \end{bmatrix}$ if no transitions among classes,

and $\begin{bmatrix} \psi & - & * \\ - & \psi & * \\ - & - & * \end{bmatrix}$ (step 1: survival) $\begin{bmatrix} * & \psi & - \\ \psi & * & - \\ - & - & * \end{bmatrix}$ (step 2: transition) otherwise.

Event: $\begin{bmatrix} * & \beta \\ * & \beta \\ * & - \end{bmatrix}$

Initial state: $[\pi *]$

- In GEMACO:

For Initial State: i

For Transition: f if no transitions, f (step 1) and from.to (step 2) otherwise.

For Event: firste + nexte

The results are (model without transition):

```
Pi
Par#    1# IS(  1,  1)(  1,  1)(  1   1) | 0.748543574 0.653145204 0.824744130 0.043980224
S in class 1
Par#   41# T(  1,  1)(  1,  1)(  1   1) | 0.519903016 0.464158678 0.575156158 0.028432652
S in class 2
```

```
Par#   42# T(  2,  2)(  1,  1)(  1   1) | 0.875371408 0.843116523 0.901767410 0.014901018
```

p

```
Par#  1094# E(  1,  2)(  2,  2)(  1   1) | 0.507100506 0.482518751 0.531647978
0.012543062
```

AIC = 5586.7

Obviously, for frail individuals, we miss the age effect to be able to detect senescence. Now let's add age to this model. The syntax in GEMAC needs to be amended as follows:

For Initial State:	i
For Transition:	from.[i+a*x(1)]
For Event:	firste+nexte

```
Pi
Par#    1# IS(  1,  1)(  1,  1)(  1   1) | 0.294256551 0.165112317 0.467812500 0.079027988
S in class 1 age 1
Par#   41# T(  1,  1)(  1,  1)(  1   1) | 0.875054721 0.760952848 0.939055475 0.043984603
S in class 2 age 1
Par#   42# T(  2,  2)(  1,  1)(  1   1) | 0.549419208 0.486878288 0.610436543 0.031680222
S in class 1 age 2
Par#  136# T(  1,  1)(  2,  2)(  1   1) | 0.873680874 0.771445476 0.934092071 0.040395671
S in class 2 age 2... and so on
Par#  137# T(  2,  2)(  2,  2)(  1   1) | 0.457972782 0.359820192 0.559499665 0.051627316
Par#  226# T(  1,  1)(  3,  3)(  1   1) | 0.872294124 0.781485444 0.928803259 0.036775417
Par#  227# T(  2,  2)(  3,  3)(  1   1) | 0.369272919 0.214092346 0.557187982 0.090917607
Par#  311# T(  1,  1)(  4,  4)(  1   1) | 0.870894401 0.791039496 0.923195478 0.033139612
Par#  312# T(  2,  2)(  4,  4)(  1   1) | 0.288605164 0.113920623 0.561430205 0.120373358
Par#  391# T(  1,  1)(  5,  5)(  1   1) | 0.869481631 0.800058733 0.917291656 0.029512714
Par#  392# T(  2,  2)(  5,  5)(  1   1) | 0.219428679 0.056839754 0.567339001 0.134577053
```

```
Par#   466# T(  1,  1)(  6,  6)(  1   1) | 0.868055744 0.808466542 0.911143364 0.025933967
Par#   467# T(  2,  2)(  6,  6)(  1   1) | 0.163033321 0.027401186 0.573886545 0.134612431
Par#   536# T(  1,  1)(  7,  7)(  1   1) | 0.866616669 0.816136245 0.904853295 0.022468726
Par#   537# T(  2,  2)(  7,  7)(  1   1) | 0.118923874 0.012982355 0.580731224 0.124477476
Par#   601# T(  1,  1)(  8,  8)(  1   1) | 0.865164336 0.822849453 0.898617060 0.019229590
Par#   602# T(  2,  2)(  8,  8)(  1   1) | 0.085528922 0.006098728 0.587726599 0.108703766
Par#   661# T(  1,  1)(  9,  9)(  1   1) | 0.863698678 0.828223841 0.892795622 0.016413068
Par#   662# T(  2,  2)(  9,  9)(  1   1) | 0.060863793 0.002853126 0.594798655 0.090993113
Par#   716# T(  1,  1)( 10, 10)(  1   1) | 0.862219624 0.831624921 0.888003767 0.014344226
Par#   717# T(  2,  2)( 10, 10)(  1   1) | 0.042977390 0.001332033 0.601905266 0.073794596
Par#   766# T(  1,  1)( 11, 11)(  1   1) | 0.860727109 0.832208366 0.885068078 0.013454384
Par#   767# T(  2,  2)( 11, 11)(  1   1) | 0.030178460 0.000621246 0.609020147 0.058433586
Par#   811# T(  1,  1)( 12, 12)(  1   1) | 0.859221066 0.829372485 0.884574801 0.014049219
Par#   812# T(  2,  2)( 12, 12)(  1   1) | 0.021107065 0.000289587 0.616125624 0.045433815
Par#   851# T(  1,  1)( 13, 13)(  1   1) | 0.857701429 0.823294953 0.886333504 0.016034341
Par#   852# T(  2,  2)( 13, 13)(  1   1) | 0.014721066 0.000134949 0.623209051 0.034831448
Par#   886# T(  1,  1)( 14, 14)(  1   1) | 0.856168135 0.814690775 0.889619546 0.019039551
Par#   887# T(  2,  2)( 14, 14)(  1   1) | 0.010246943 0.000062876 0.630260898 0.026409477
Par#   916# T(  1,  1)( 15, 15)(  1   1) | 0.854621120 0.804234323 0.893752500 0.022715244
Par#   917# T(  2,  2)( 15, 15)(  1   1) | 0.007122795 0.000029292 0.637273662 0.019848161
Par#   941# T(  1,  1)( 16, 16)(  1   1) | 0.853060321 0.792365477 0.898290509 0.026832541
Par#   942# T(  2,  2)( 16, 16)(  1   1) | 0.004946395 0.000013645 0.644241217 0.014810879
Par#   961# T(  1,  1)( 17, 17)(  1   1) | 0.851485677 0.779341741 0.902978670 0.031257457
Par#   962# T(  2,  2)( 17, 17)(  1   1) | 0.003432704 0.000006356 0.651158420 0.010987269
Par#   976# T(  1,  1)( 18, 18)(  1   1) | 0.849897128 0.765314906 0.907672877 0.035912276
Par#   977# T(  2,  2)( 18, 18)(  1   1) | 0.002381123 0.000002961 0.658020846 0.008110822
Par#   986# T(  1,  1)( 19, 19)(  1   1) | 0.848294615 0.750380525 0.912290836 0.040750672
Par#   987# T(  2,  2)( 19, 19)(  1   1) | 0.001651151 0.000001379 0.664824620 0.005962504
p
Par#  1094# E(  1,  2)(  2,  2)(  1   1) | 0.502494541 0.477418750 0.527557789 0.012801305
```

```
~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
   Index        Beta | Lower & Upper 95 percent CI | S.E.
~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
pi on the logit scale
Beta#   1# | -0.874799776 -1.620671255 -0.128928297 +0.380546673
###############################################################
Intercept of the age effect for class 1
Beta#   2# | +1.958917382 +1.098782490 +2.819052274 +0.438844333
Intercept of the age effect for class 2
Beta#   3# | +0.565155134 +0.040178984 +1.090131285 +0.267844975
Slope of the age effect for class 1
Beta#   4# | -0.012506830 -0.086831557 +0.061817897 +0.037920779
Slope of the age effect for class 2
Beta#   5# | -0.366830798 -0.764287874 +0.030626277 +0.202784222
###############################################################
p on the logit scale
Beta#   6# | +0.009978247 -0.090386484 +0.110342979 +0.051206496
###############################################################

AIC = 5584.4
```

Seems like we've managed to capture the main patterns in the simulated data.