Document 1- R codes for the construction of the stage-structured matrix model for spotted hyenas infected with CDV

S. Benhaiem, L. Marescot

2018-08-02 12:11:50

This code loads the input values for the 3 epidemic periods and builds the matrix model. It is structured as follows:

a) Loading input values (Multi-Event-Capture-Mark-Recapture (MECMR) parameter estimates)
b) Building the submatrices: Survival, State transition (demographic, social, infection) and Fecundity submatrices
c) Assembling the submatrices into the meta-matrix
d) Building the next generation matrix for the estimation of R0

Note that parameter and submatrix names may differ between main text and R codes.

Construction of the matrix model

a) Loading the input values (Multi-Event-Capture-Mark-Recapture (MECMR) parameter estimates)

First, we load the R package popbio (Stubben & Milligan 2007) and the Maximum Likelihood Estimates (MLE) from the MECMR model fitted in E-surge, for each epidemic period. These estimates correspond to the values presented in Table 1 in the main text.

```
library(popbio)
source('Input_90-92(pre-epidem).R')
source('Input_93-94(epidem).R')
source('Input_95-99(post-epidem).R')
```

The Table 1 below shows the probability of surviving (ϕ), becoming infected (β), a breeder (ψ), and of maintaining the current social state (r) in female spotted hyenas during each period, as estimated via the MECMR model. Demographic states were abbreviated as cubs (C), subadults (SA), breeders (B) or non-breeders (NB), social states as high status (H) or low status (L) and infection states as susceptible (S), infected (I) or recovered (R). This table is equivalent to Table 1 in the main text.

Parameter	pre-epidemic	epidemic	post-epidemic
$\phi_{C.L.S}$	0.86	0.78	0.81
$\phi_{C.L.I}$	0.62	0.48	0.54
$\phi_{C.H.S}$	0.90	0.84	0.72
$\phi_{C.H.I}$	0.79	0.67	0.86
$\phi_{SA.L.S}$	0.90	0.83	0.86
$\phi_{SA.LH.IR}$	0.69	0.56	0.61
$\phi_{SA.H.S}$	0.97	0.95	0.96
ϕ_{B}	0.95	0.91	0.93

Parameter	pre-epidemic	epidemic	post-epidemic
ϕ_{NB}	0.86	0.78	0.82
r_{LL}	0.97	0.97	0.97
r_{HH}	0.94	0.94	0.94
$\beta_{C.L}$	0.45	0.99	0.85
$\beta_{C.H}$	0.23	0.96	0.67
$\beta_{SABNB.L}$	0.02	0.66	0.13
$\beta_{SABNB.H}$	0.45	0.90	0.42
$b_{SA.L}$	0.01	0.01	0.01
$b_{B.L}$	0.45	0.45	0.45
b_{NB}	0.60	0.60	0.60
$b_{SA.H}$	0.04	0.04	0.04
$b_{B.H}$	0.60	0.49	0.49
$b_{B.H}$	0.68	0.68	0.68

b) Building the submatrices: Survival, State transition (demographic, social, infection) and Fecundity submatrices

The definitions of the parameters are provided in the input files (see below section 2)a)).

Survival

Below we construct 4 diagonal matrices representing the survival process for cubs, subadults, breeders and non breeders, respectively. For instance, elements in the di agonal of the matrix Surv.C represent the survival probabilites of cubs given their social and infection state.

$$Surv.C = \begin{bmatrix} \phi_{C.L.S} & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_{C.L.I} & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_{C.L.R} & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_{C.H.S} & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_{C.H.I} & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_{C.H.R} \end{bmatrix}$$

```
Surv.C <- diag(c(phiCLS, phiCLI, phiCLR, phiCHS, phiCHI,phiCHR))
Surv.S <- diag(c(phiSLS, phiSLI, phiSLR, phiSHS, phiSHI, phiSHR))
Surv.B <- diag(c(phiBLS, phiBLI, phiBLR, phiBHS, phiBHI, phiBHR))
Surv.NB <- diag(c(phiNBLS, phiNBLI,phiNBLR, phiNBHS, phiNBHI, phiNBHR))
```

State transitions

Each entry in the submatrices described below correspond to the probability of transition (or survival), or the fecundity, from a 'starting' combination of social and infection states to a 'following' combination of social and infection states. The 6 rows and 6 columns in these submatrices correspond to: Low social status - Susceptible, Low social status - Infected, Low social status - Recovered, High social status - Susceptible, High social status - Infected, High social status - Recovered.

Demographic states

We build six demography submatrices (i.e. recruitment and non-recruitment submatrices); three to account for the transition to the breeder state and three others to account for the transition to the non-breeder state. Both states are accessible from subadults, breeders and non-breeders.

```
Rec.S <- diag(c(bSL, bSL, bSL, bSH, bSH,bSH))
Rec.B <- diag(c(bBL, bBL, bBL, bBH, bBH,bBH))
Rec.NB <- diag(c(bNBL, bNBL, bNBL, bNBH, bNBH,bNBH))
NRec.S <- diag(c((1-bSL), (1-bSL), (1-bSL),(1-bSH), (1-bSH),(1-bSH)))
NRec.B <- diag(c((1-bBL), (1-bBL), (1-bBL),(1-bBH), (1-bBH),(1-bBH)))
NRec.NB <- diag(c((1-bNBL), (1-bNBL), (1-bNBL),(1-bNBH), (1-bNBH),(1-bNBH)))
```

Social states

We build a social submatrix to account for the fact that subadults, breeders and non-breeders can either stay within their social state or change it. Cubs had the same social state as their mother.

```
R <- matrix(c(
  rLL.S,       0,           0,          1-rHH.S,    0,          0,
  0,           rLL.I,       0,          0,          1-rHH.I,    0,
  0,           0,           rLL.R,      0,          0,          1-rHH.R,
  1-rLL.S,     0,           0,          rHH.S,      0,          0,
  0,           1-rLL.I,     0,          0,          rHH.I,      0,
  0,           0,           1-rLL.R,    0,          0,          rHH.R)

  ,byrow=T,nrow=6)
```

Infection states

We build three infection submatrices: one for newborns, one for cubs, and one for subadults, breeders and non-breeders. In the matrix of infection for newborns (I.F), we considered that mothers only produced susceptible newborns, irrespective of their own infection status. Indeed, as adults do not excrete the virus actively as young individuals, we considered the transmission of CDV to be strictly horizontal.

```
I.F <- matrix(c(
  1,         1,         1,         0,         0,         0,
  0,         0,         0,         0,         0,         0,
  0,         0,         0,         0,         0,         0,
  0,         0,         0,         1,         1,         1,
  0,         0,         0,         0,         0,         0,
  0,         0,         0,         0,         0,         0)

  ,byrow=T,nrow=6)
```

In the matrix of infection for cubs (I.C), the only possible infection transitions were from a susceptible to a susceptible state or from a susceptible to an infected state. As recovered cubs were absent from our original CMR dataset, we set the columns for recovered cubs to 0.

```
I.C <- matrix(c(

  1-betaCL,  0,         0,         0,         0,         0,
  betaCL,    0,         0,         0,         0,         0,
  0,         1,         0,         0,         0,         0,
  0,         0,         0,         1-betaCH,  0,         0,
  0,         0,         0,         betaCH,    0,         0,
  0,         0,         0,         0,         1,         0)

  ,byrow=T,nrow=6)
```

The structure of the matrices of infection for subadults (I.SA), breeders (I.AD) and non-breeders (I.AD) is similar as the one for cubs (except that the transition from recovered to recovered occurs (3rd column and 3rd row for low-ranking and 6th column and 6th row for high-ranking).

For instance, the possible transitions in the infection matrix of subadults (I.SA) are: from suceptible (first (for low-ranking) and fourth (for high-ranking) columns) to susceptible (first (for low-ranking) and fourth (for high-ranking) rows) with probability $1-\beta_{SA.L.S}$ or $1-\beta_{SA.H.S}$, from susceptible to infected (second and fifth rows) with probability $\beta_{SA.L.S}$ or $\beta_{SA.H.S}$, and from infected (second and fifth columns)to recovered (third and sixth rows) with probabilities equal to 1 for the transitions I->R and R->R.

$$I.SA = \begin{bmatrix} 1-\beta_{SA.L} & 0 & 0 & 0 & 0 & 0 \\ \beta_{SA.L} & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-\beta_{SA.H} & 0 & 0 \\ 0 & 0 & 0 & \beta_{SA.H} & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 \end{bmatrix}$$

```
I.SA <- matrix(c(

  1-betaSL,   0,         0,          0,          0,          0,
  betaSL,     0,         0,          0,          0,          0,
  0,          1,         1,          0,          0,          0,
  0,          0,         0,          1-betaSH,   0,          0,
  0,          0,         0,          betaSH,     0,          0,
  0,          0,         0,          0,          1,          1)

  ,byrow=T,nrow=6)

I.AD <- matrix(c(

  1-betaADL,   0,         0,          0,          0,          0,
  betaADL,     0,         0,          0,          0,          0,
  0,          1,         1,          0,          0,          0,
  0,          0,         0,          1-betaADH,  0,          0,
  0,          0,         0,          betaADH,    0,          0,
  0,          0,         0,          0,          1,          1)

  ,byrow=T,nrow=6)
```

Fecundity

We construct the fecundity matrix for breeder females which is a diagonal matrix of 1, as all females which are in a breeder state a given year produce offspring with a probability of 1. The matrix is then multiplied by the litter size and the sex ratio (as the model is female-based), which are constant across social and infection states.

```
fB <- ls* sr * diag(c(fLS, fLI, fLR, fHS, fHI,fHR))
```

c) Assembling the submatrices into the meta-matrix

All these processes described in 1.b) are then combined via multiplications of matrices (%*% in R) to generate successive events within a one year projection interval: 1) change in demographic state, 2) change in social

state, 3) change in infection state and then 4) survival (the matrices below should be read from right to left). We assumed that all births and deaths occurred simultaneously at the end of the projection interval, that is, we modelled the population with a birth pulse reproduction and a pre-breeding census.

```
NetF<-Surv.C%*%I.C%*%I.F%*% fB # Net Fecundity submatrix (called "Fertility" in the manuscript)

CS <- Surv.S%*%I.SA # the survival-transition submatrix to the subadult state from the cub state
SB <- Surv.B%*%I.AD%*%R%*%Rec.S # the survival-transition submatrix to the breeder state from the subad
BB <- Surv.B%*%I.AD%*%R%*%Rec.B  # the survival-transition submatrix to the breeder state from the bree
NBB <- Surv.B%*%I.AD%*%R%*%Rec.NB # the survival-transition submatrix to the breeder state from the non
SNB <- Surv.NB%*%I.AD%*%R%*%NRec.S # the survival-transition submatrix to the non-breeder state from th
BNB <- Surv.NB%*%I.AD%*%R%*%NRec.B # the survival-transition submatrix to the breeder state from the no
NBNB<- Surv.NB%*%I.AD%*%R%*%NRec.NB # the survival-transition submatrix to the non-breeder state from t
```

Finally, we combine these survival-transition submatrices within a single meta-matrix M.final

$$M.final = \begin{bmatrix} Z & Z & NetF & Z \\ CS & Z & Z & Z \\ Z & SB & BB & NB \\ Z & SB & BB & NBB \\ Z & SNB & BNB & NBNB \end{bmatrix}$$

```
Z <- matrix(0,6,6)

M <-  rbind(cbind (Z,       Z,       NetF,   Z),
            cbind (CS,      Z,       Z,      Z),
            cbind (Z,       SB,      BB,     NBB),
            cbind (Z,       SNB,     BNB,    NBNB))


rownames(M)<-  c("CLS","CLI","CLR","CHS","CHI","CHR",
                 "SLS","SLI","SLR","SHS","SHI","SHR",
                 "BLS","BLI","BLR","BHS","BHI","BHR",
                 "NBLS","NBLI","NBLR","NBHS","NBHI","NBHR")

colnames(M)<-  c("CLS","CLI","CLR","CHS","CHI","CHR",
                 "SLS","SLI","SLR","SHS","SHI","SHR",
                 "BLS","BLI","BLR","BHS","BHI","BHR",
                 "NBLS","NBLI","NBLR","NBHS","NBHI","NBHR")

M.final <- M[-c(3,6), -c(3,6)] # We remove the recovered cubs as they do not exist in the data
```

d) Building the next generation matrix for the estimation of R0

```
### -- Building the transition matrix Tr.final:

Tr <-  rbind(cbind (Z,       Z,       Z,      Z),
             cbind (CS,      Z,       Z,      Z),
             cbind (Z,       SB,      BB,     NBB),
             cbind (Z,       SNB,     BNB,    NBNB))

Tr.final <- Tr[-c(3,6), -c(3,6)]
```

```
### -- Building the identity matrix I:

Id <- diag(22)

### --- Building N, the fundamental matrix as N = (Id-Tr.final)-^1:

N <- solve((lambda(M.final)*Id) -Tr.final) # Here we include the population's growth rate

## ---- Building F, the fertility matrix:


F <- matrix(c(

  0, 0,           0, 0,          0, 0,         0, 0, 0,         0, 0, 0,         0, 0, 0,             0
  0, phiCLS*betaCL, 0, phiCHS*betaCL, 0, phiSLS*betaCL, 0, 0, phiSHS*betaCL, 0, 0, phiBLS*betaCL, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,         0, 0, 0,         0, 0, 0,
  0, phiCLS*betaCH, 0, phiCHS*betaCH, 0, phiSLS*betaCH, 0, 0, phiSHS*betaCH, 0, 0, phiBLS*betaCH, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,         0, 0, 0,         0, 0, 0,
  0, phiCLS*betaSL, 0, phiCHS*betaSL, 0, phiSLS*betaSL, 0, 0, phiSHS*betaSL, 0, 0, phiBLS*betaSL, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,         0, 0, 0,         0, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,         0, 0, 0,         0, 0, 0,
  0, phiCLS*betaSH, 0, phiCHS*betaSH, 0, phiSLS*betaSH, 0, 0, phiSHS*betaSH, 0, 0, phiBLS*betaSH, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, phiCLS*betaADL, 0, phiCHS*betaADL, 0, phiSLS*betaADL, 0, 0, phiSHS*betaADL, 0, 0, phiBLS*betaADL, 0
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, phiCLS*betaADH, 0, phiCHS*betaADH, 0, phiSLS*betaADH, 0, 0, phiSHS*betaADH, 0, 0, phiBLS*betaADH, 0
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, phiCLS*betaADL, 0, phiCHS*betaADL, 0, phiSLS*betaADL, 0, 0, phiSHS*betaADL, 0, 0, phiBLS*betaADL, 0
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,
  0, phiCLS*betaADH, 0, phiCHS*betaADH, 0, phiSLS*betaADH, 0, 0, phiSHS*betaADH, 0, 0, phiBLS*betaADH, 0
  0, 0,            0, 0,             0, 0,         0, 0, 0,            0, 0, 0,         0, 0, 0,

  ),byrow=T,nrow=22)


### --- Next generation Matrix NGM:

NGM <- F %*% N

rownames(NGM)<-  c("CLS","CLI","CHS","CHI",
                   "SLS","SLI","SLR","SHS","SHI","SHR",
                   "BLS","BLI","BLR","BHS","BHI","BHR",
                   "NBLS","NBLI","NBLR","NBHS","NBHI","NBHR")

colnames(NGM)<-  c("CLS","CLI","CHS","CHI",
                   "SLS","SLI","SLR","SHS","SHI","SHR",
                   "BLS","BLI","BLR","BHS","BHI","BHR",
                   "NBLS","NBLI","NBLR","NBHS","NBHI","NBHR")
```

Reference

Stubben, C. & Milligan, B. Estimating and analyzing demographic models using the popbio package in R. J. Stat. Softw 22, 1-23 (2007).