

openCR 1.4 Examples

Murray Efford

2019-06-30

Contents

1	Introduction	1
2	Non-spatial analyses	1
2.1	Patuxent meadow voles	1
2.2	Dippers	10
2.3	<i>Gonodontis</i> moths	18
2.4	Orongorongo Valley brushtail possums	20
3	Spatially explicit analyses	27
3.1	Kielder Forest field voles	27
3.2	Patuxent ovenbirds	29
3.3	Orongorongo Valley possums robust design	34
4	References	39

1 Introduction

This vignette applies the functions in the R package **openCR** to various example datasets. Non-spatial analyses are compared to their equivalents in MARK where appropriate.

For clarity, functions and data from other packages are sometimes distinguished using ‘::’ notation, as in `seкр::RMarkInput`. This is not strictly necessary for **seкр** because it is loaded automatically when **openCR** is loaded, making all **seкр** functions and data available. Warnings are often generated during likelihood maximization. These typically relate to nonidentifiable parameters, which are common in open-population models. Warnings are generally suppressed here to keep the output readable.

```
library(openCR)
library(RMark)      # load RMark for MARK comparisons
library(marked)    # load marked for comparisons
MarkPath <- 'c:/MARK' # may need to customise this
testdir <- 'd:/open populations/tests/'
options(digits = 4, width = 90) # for more readable output
```

2 Non-spatial analyses

2.1 Patuxent meadow voles

Meadow voles (*Microtus pennsylvanicus*) were trapped by Nichols et al. (1984) on a 10 × 10 grid at Patuxent Wildlife Research Center, Maryland, USA. The data relate to trapping for 5 nights a month over 6 months in 1983. The data were used by Pollock et al. (1990) and Williams, Nichols and Conroy (2002) to demonstrate capture–recapture methods. The data are provided by **openCR** in several forms; see `?microtusCH` for details and other references.

2.1.1 Data summary

Compare Williams, Nichols and Conroy (2002) Table 17.6 (sex-specific)

```
m.array(microtusFCH) # females
```

```
##   R  2  3  4  5  6 NRecap
## 1 51 40  4  0  0  0      7
## 2 49   34  3  0  0     12
## 3 52    34  1  0     17
## 4 45     31  0     14
## 5 54      45     9
## 6 72              72
```

```
m.array(microtusMCH) # males
```

```
##   R  2  3  4  5  6 NRecap
## 1 53 44  1  0  0  0      8
## 2 69   33  4  0  1     31
## 3 48    32  1  0     15
## 4 56     28  4     24
## 5 45      38     7
## 6 76              76
```

2.1.2 CJS

Fit the models in Williams, Nichols and Conroy (2002) Table 17.8. The predictor ‘t’ refers to a factor with one level for each primary session (a synonym of ‘session’ in **openCR**).

```
args <- list(
  list(microtusFMCH, model = list(phi ~ sex+t, p ~ 1)),
  list(microtusFMCH, model = list(phi ~ t, p ~ 1)),
  list(microtusFMCH, model = list(phi ~ sex+t, p ~ sex)),
  list(microtusFMCH, model = list(phi ~ sex+t, p ~ sex*t)),
  list(microtusFMCH, model = list(phi ~ t, p ~ sex)),
  list(microtusFMCH, model = list(phi ~ sex+t, p ~ t)),
  list(microtusFMCH, model = list(phi ~ sex*t, p ~ 1)),
  list(microtusFMCH, model = list(phi ~ sex*t, p ~ sex)),
  list(microtusFMCH, model = list(phi ~ t, p ~ sex*t)),
  list(microtusFMCH, model = list(phi ~ sex+t, p ~ sex+t)),
  list(microtusFMCH, model = list(phi ~ t, p ~ sex+t)),
  list(microtusFMCH, model = list(phi ~ sex*t, p ~ sex*t)),
  list(microtusFMCH, model = list(phi ~ t, p ~ t)),
  list(microtusFMCH, model = list(phi ~ sex*t, p ~ t)),
  list(microtusFMCH, model = list(phi ~ sex*t, p ~ sex+t)),
  list(microtusFMCH, model = list(phi ~ sex, p ~ sex*t)),
  list(microtusFMCH, model = list(phi ~ 1, p ~ sex*t)),
  list(microtusFMCH, model = list(phi ~ sex, p ~ sex+t)),
  list(microtusFMCH, model = list(phi ~ sex, p ~ t)),
  list(microtusFMCH, model = list(phi ~ 1, p ~ sex+t)),
  list(microtusFMCH, model = list(phi ~ 1, p ~ t)),
  list(microtusFMCH, model = list(phi ~ sex, p ~ 1)),
  list(microtusFMCH, model = list(phi ~ sex, p ~ sex)),
  list(microtusFMCH, model = list(phi ~ 1, p ~ sex)),
  list(microtusFMCH, model = list(phi ~ 1, p ~ 1))
```

```
)
fits <- par.openCR.fit(args, ncores = 6)
```

For comparison we adjust the effective sample size to match that used by the original authors (the default in **openCR** is the number of individuals 308 whereas MARK uses the sum of the release cohort sizes 522)

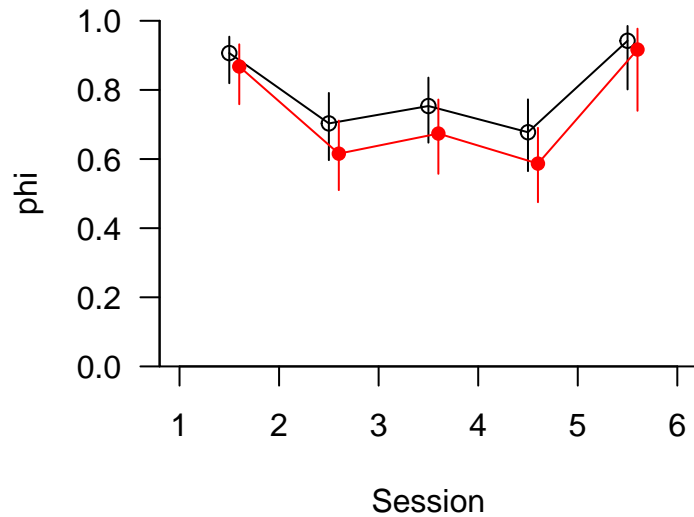
```
ess <- sum(m.array(microtusFMCH, last.session = FALSE)[, 'R'])
AIC(fits, criterion = 'AICc', use.rank = TRUE, n = ess)[, 1:7]
```

##		model	npar	rank	logLik	AIC	AICc	dAICc
## 1	p~1	phi~sex + t	7	7	-368.6	751.3	751.5	0.000
## 2		p~1 phi~t	6	6	-370.3	752.5	752.7	1.229
## 3	p~sex	phi~sex + t	8	8	-368.3	752.5	752.8	1.333
## 5		p~sex phi~t	7	7	-369.6	753.2	753.5	1.979
## 7	p~1	phi~sex * t	11	11	-366.5	754.9	755.4	3.938
## 8	p~sex	phi~sex * t	12	12	-365.5	755.0	755.6	4.144
## 4	p~sex * t	phi~sex + t	16	14	-362.0	752.1	756.9	5.401
## 6	p~t	phi~sex + t	11	10	-367.4	754.9	757.3	5.825
## 9	p~sex * t	phi~t	15	12	-363.6	751.3	757.9	6.394
## 10	p~sex + t	phi~sex + t	12	11	-366.9	755.7	758.3	6.772
## 11	p~sex + t	phi~t	11	10	-368.1	756.2	758.6	7.125
## 13		p~t phi~t	10	9	-369.3	756.5	758.9	7.402
## 14	p~t	phi~sex * t	15	14	-365.4	758.8	761.7	10.172
## 15	p~sex + t	phi~sex * t	16	15	-364.5	759.0	762.0	10.495
## 12	p~sex * t	phi~sex * t	20	18	-360.8	757.5	762.9	11.391
## 16	p~sex * t	phi~sex	12	9	-373.7	765.4	771.7	20.225
## 17	p~sex * t	phi~1	11	8	-375.1	766.3	772.5	21.053
## 18	p~sex + t	phi~sex	8	7	-378.5	770.9	773.2	21.671
## 19	p~t	phi~sex	7	6	-379.7	771.5	773.6	22.134
## 20	p~sex + t	phi~1	7	6	-380.0	772.0	774.1	22.666
## 21	p~t	phi~1	6	5	-381.4	772.8	774.9	23.438
## 22	p~1	phi~sex	3	3	-385.3	776.6	776.6	25.150
## 23	p~sex	phi~sex	4	4	-384.5	777.0	777.1	25.617
## 24	p~sex	phi~1	3	3	-386.1	778.2	778.2	26.735
## 25	p~1	phi~1	2	2	-387.2	778.4	778.4	26.900

Although there is much agreement, AICc values and rankings differ from Williams, Nichols and Conroy (2002) particularly for models such as (ϕ_{s+t}, p_{s*t}) for which MARK counts parameters differently.

Compare Williams, Nichols and Conroy Fig. 17.2:

```
par(mar = c(4,4,2,2))
maledat <- expand.grid(sex = factor('M', levels = c('F','M')), t = factor(1:6))
plot(fits[[1]], ylim=c(0,1), type = 'o')
plot(fits[[1]], newdata = maledat, add = TRUE, xoffset = 0.1, col = 'red', pch = 16,
      type = 'o')
```



2.1.3 CJS by sex

Compare Williams, Nichols and Conroy Table 17.7:

```
fitfm4 <- openCR.fit(microtusFMCH, model = list(p~t*sex, phi~t*sex))
predict(fitfm4, all = TRUE)
```

```
## $p
## session sex estimate SE.estimate lcl ucl
## 1 1 F NA NA NA NA
## 2 2 F 0.8830 0.0548092 7.274e-01 0.9553
## 3 3 F 0.8950 0.0570737 7.216e-01 0.9656
## 4 4 F 0.9623 0.0369813 7.760e-01 0.9947
## 5 5 F 1.0000 0.0002988 3.794e-101 1.0000
## 6 6 F 0.9015 2.7516625 3.776e-26 1.0000
## 7 1 M NA NA NA NA
## 8 2 M 0.9604 0.0386874 7.675e-01 0.9944
## 9 3 M 0.8238 0.0709542 6.420e-01 0.9241
## 10 4 M 0.9113 0.0594247 7.086e-01 0.9775
## 11 5 M 0.8304 0.0690687 6.519e-01 0.9276
## 12 6 M 0.9539 1.1217961 3.868e-21 1.0000
##
## $phi
## session sex estimate SE.estimate lcl ucl
## 1 1 F 0.8882 0.05177 7.409e-01 0.9566
## 2 2 F 0.7819 0.06582 6.272e-01 0.8843
## 3 3 F 0.6811 0.06635 5.399e-01 0.7953
## 4 4 F 0.6889 0.06901 5.409e-01 0.8063
## 5 5 F 0.9243 2.82111 5.740e-34 1.0000
## 6 6 F NA NA NA NA
## 7 1 M 0.8644 0.05246 7.262e-01 0.9388
## 8 2 M 0.5828 0.06554 4.517e-01 0.7032
## 9 3 M 0.7146 0.07239 5.554e-01 0.8339
## 10 4 M 0.5869 0.06852 4.495e-01 0.7120
## 11 5 M 0.8851 1.04161 1.469e-08 1.0000
```

```
## 12      6  M      NA      NA      NA      NA
```

And in MARK:

```
fm <- secr::RMarkInput(microtusFMCH)
markFM <- RMark::mark(fm, model.parameters=list(Phi = list(formula = ~time+sex),
                                                p = list(formula = ~time*sex)),
                    groups = 'sex', invisible = TRUE, output = FALSE, adjust = FALSE)
round(markFM$results$real[,1:4],4)
```

```
##          estimate      se    lcl    ucl
## Phi gF c1 a0 t1  0.9002  0.0334  0.8131  0.9492
## Phi gF c1 a1 t2  0.7224  0.0516  0.6111  0.8117
## Phi gF c1 a2 t3  0.7323  0.0509  0.6218  0.8198
## Phi gF c1 a3 t4  0.6836  0.0533  0.5713  0.7779
## Phi gF c1 a4 t5  0.9353 10.8483  0.0000  1.0000
## Phi gM c1 a0 t1  0.8589  0.0434  0.7510  0.9248
## Phi gM c1 a1 t2  0.6373  0.0562  0.5217  0.7390
## Phi gM c1 a2 t3  0.6487  0.0572  0.5304  0.7513
## Phi gM c1 a3 t4  0.5933  0.0561  0.4805  0.6970
## Phi gM c1 a4 t5  0.9071 15.1106  0.0000  1.0000
## p gF c1 a1 t2   0.8741  0.0562  0.7184  0.9497
## p gF c1 a2 t3   0.9078  0.0501  0.7529  0.9695
## p gF c1 a3 t4   0.9578  0.0408  0.7579  0.9940
## p gF c1 a4 t5   1.0000  0.0000  1.0000  1.0000
## p gF c1 a5 t6   0.8910 10.3341  0.0000  1.0000
## p gM c1 a1 t2   0.9634  0.0354  0.7862  0.9947
## p gM c1 a2 t3   0.7954  0.0778  0.6037  0.9085
## p gM c1 a3 t4   0.9210  0.0526  0.7385  0.9796
## p gM c1 a4 t5   0.8302  0.0688  0.6527  0.9271
## p gM c1 a5 t6   0.9307 15.5045  0.0000  1.0000
```

2.1.4 Combined-sex meadow vole data from JOLLY

Compare Pollock et al. (1990) Table 4.7

```
JS.counts(microtusCH)
```

```
##      n  R  m  r  z
## 1 108 105  0 89 0
## 2 127 121 84 76 5
## 3 102 101 73 68 8
## 4 103 102 73 63 3
## 5 102 100 61 84 5
## 6 149 148 89  0 0
```

[$r_1 = 87$ in the published table, but this is an error]

2.1.5 Pradel models

Using the formulae of Pradel (1996)¹ and the alternative parameterisations in terms of seniority (γ) or population growth rate (λ). The data are for adult male meadow voles at Patuxent.

¹See the help page for `rev.caphist` (`?rev.caphist`) for comment on reverse-time formulations.

```

# gamma parameterisation
fitmpradelg <- openCR.fit(microtusMCH, type = "Pradelg",
                        model = list(p~t, phi~t, gamma~t))
# gamma parameterisation, constant gamma
fitmpradelg1 <- openCR.fit(microtusMCH, type = "Pradelg",
                          model = list(p~t, phi~t, gamma~1))

```

Compare Williams et al. Table 18.4. Manually derived $\lambda_i = \phi_i/\gamma_{i+1}$ (SE not calculated).

```

pg <- predict(fitmpradelg)
pg1 <- predict(fitmpradelg1)
pg$phi[5:6,] <- NA
pg1$phi[5:6,] <- NA
df <- cbind(pg$gamma[,2:3], pg1$gamma[,2:3])
names(df) <- c('gamma', 'segamma', 'gamma1', 'se(gamma1)')
df[2,1:2] <- NA
df$lambda <- pg$phi$estimate / c(df$gamma[-1], NA)
df$lambda1 <- pg1$phi$estimate / c(df$gamma1[-1], NA)
df[,c(1,2,5,3,4,6)]

```

```

##      gamma segamma lambda gamma1 se(gamma1) lambda1
## 1      NA      NA      NA      NA      NA      NA  1.3169
## 2      NA      NA  0.8265  0.6524   0.03039  0.8707
## 3  0.7052  0.06760  1.0694  0.6524   0.03039  1.1014
## 4  0.6682  0.06997  0.9001  0.6524   0.03039  0.9284
## 5  0.6521  0.07513      NA  0.6524   0.03039      NA
## 6  0.5965  0.06334      NA  0.6524   0.03039      NA

```

The Pradel model estimates the same parameters as the conditional-likelihood JSSA models, but deals differently with losses on capture. Estimates of p and ϕ are virtually identical in this example. Estimates of λ differ because the Pradel λ estimates include losses on capture. Pradel (1996) suggested a more elaborate formulation to model losses, but this has not been implemented in **openCR**. The JSSA version is preferred if there are losses on capture.

```

# lambda parameterisation
fitmpradel <- openCR.fit(microtusMCH, type = "Pradel",
                       model = list(p~t, phi~t, lambda~t))
fitmJSSA1CL <- openCR.fit(microtusMCH, type = "JSSA1CL",
                         model = list(p~t, phi~t, lambda~t))
JS <- JS.direct(microtusMCH)
df <- cbind(do.call(rbind, predict(fitmpradel))[2:3],
           do.call(rbind, predict(fitmJSSA1CL))[2:3])
names(df) <- c('Pradel', 'sePradel', 'JSSA', 'seJSSA')
df$JS <- c(JS$p, JS$phi, c(JS$N[-1]/JS$N[-6], NA))
df[c(2:5,7:10,14:16),] # dropping nonidentifiable parameters

```

```

##      Pradel sePradel  JSSA seJSSA  JS
## p.2    0.9604  0.03872  0.9604  0.03872  0.9608
## p.3    0.8238  0.07095  0.8238  0.07095  0.8251
## p.4    0.9114  0.05942  0.9114  0.05941  0.9124
## p.5    0.8304  0.06878  0.8304  0.06878  0.8310
## phi.1  0.8644  0.05246  0.8644  0.05246  0.8641
## phi.2  0.5828  0.06554  0.5828  0.06554  0.5820
## phi.3  0.7146  0.07238  0.7146  0.07238  0.7147
## phi.4  0.5869  0.06852  0.5869  0.06852  0.5870
## lambda.2 0.8265  0.10462  0.8089  0.10027  0.7924

```

```
## lambda.3 1.0694 0.13865 1.0453 0.13193 1.0507
## lambda.4 0.9001 0.12408 0.8808 0.11883 0.8840
```

One would expect the difference to disappear if there are no losses. We construct an artificial dataset that drops these capture histories entirely, and compare estimates across models.

```
tmp <- microtusMCH
tmp <- tmp[apply(tmp,1,min)>=0,,, drop = FALSE]
class(tmp) <- 'caphist'
pradelnoloss <- openCR.fit(tmp, type = "Pradel",
                          model = list(p~t, phi~t, lambda~t))
JSSAnoloss <- openCR.fit(tmp, type = "JSSA1CL",
                        model = list(p~t, phi~t, lambda~t))

df <- cbind(do.call(rbind, predict(pradelnoloss))[2:3],
           do.call(rbind, predict(JSSAnoloss))[2:3])
names(df) <- c('Pradel','sePradel','JSSA','seJSSA')
# also run Pradel model in MARK
captdf <- RMarkInput(tmp, grouped = TRUE, covariates = FALSE)
time <- list(formula = ~time)
mk <- mark(captdf, model = "Pradlambd", model.parameters =
          list(Phi = time, p = time, Lambda = time), invisible = TRUE)
```

```
##
## Note: only 14 parameters counted of 16 specified parameters
## AICc and parameter count have been adjusted upward
##
## Output summary for Pradlambd model
## Name : Phi(~time)p(~time)Lambda(~time)
##
## Npar : 16 (unadjusted=14)
## -2lnL: 935.2
## AICc : 968.9 (unadjusted=964.46615)
##
## Beta
##
## estimate se lcl ucl
## Phi:(Intercept) 1.78861 0.4527 0.90125 2.67596
## Phi:time2 -1.47092 0.5454 -2.53985 -0.40200
## Phi:time3 -0.92284 0.5798 -2.05932 0.21364
## Phi:time4 -1.49868 0.5361 -2.54935 -0.44801
## Phi:time5 0.83191 0.0000 0.83191 0.83191
## p:(Intercept) 0.05291 0.0000 0.05291 0.05291
## p:time2 3.05207 0.0000 3.05207 3.05207
## p:time3 1.43951 0.0000 1.43951 1.43951
## p:time4 2.19252 0.0000 2.19252 2.19252
## p:time5 1.46022 0.0000 1.46022 1.46022
## p:time6 2.16785 0.0000 2.16785 2.16785
## Lambda:(Intercept) -0.31571 0.0000 -0.31571 -0.31571
## Lambda:time2 0.08379 0.0000 0.08379 0.08379
## Lambda:time3 0.37389 0.0000 0.37389 0.37389
## Lambda:time4 0.20930 0.0000 0.20930 0.20930
## Lambda:time5 0.76625 0.0000 0.76625 0.76625
##
##
```

```

## Real Parameter Phi
##      1      2      3      4      5
## 0.8568 0.5788 0.7039 0.572 0.9322
##
##
## Real Parameter p
##      1      2      3      4      5      6
## 0.5132 0.9571 0.8164 0.9043 0.8195 0.9021
##
##
## Real Parameter Lambda
##      1      2      3      4      5
## 0.7293 0.793 1.06 0.8991 1.569
dfmk <- mk$results$real[c(7:10, 1:4, 13:15),1:2]
names(dfmk) <- c('MKPradel', 'seMKPradel')
cbind(df[c(2:5,7:10,14:16),], dfmk) # dropping nonidentifiable parameters

##          Pradel sePradel   JSSA seJSSA MKPradel seMKPradel
## p.2      0.9571  0.04181 0.9571 0.04181  0.9571  0.04181
## p.3      0.8164  0.07355 0.8164 0.07355  0.8164  0.07354
## p.4      0.9043  0.06388 0.9043 0.06388  0.9043  0.06387
## p.5      0.8195  0.07266 0.8195 0.07266  0.8195  0.07266
## phi.1    0.8568  0.05557 0.8568 0.05556  0.8568  0.05556
## phi.2    0.5788  0.06674 0.5788 0.06674  0.5788  0.06674
## phi.3    0.7039  0.07552 0.7039 0.07552  0.7039  0.07551
## phi.4    0.5720  0.07027 0.5720 0.07027  0.5720  0.07027
## lambda.2 0.7930  0.10245 0.7930 0.10245  0.7930  0.10242
## lambda.3 1.0599  0.14327 1.0599 0.14326  1.0599  0.14323
## lambda.4 0.8991  0.13043 0.8991 0.13043  0.8991  0.13041

```

2.1.6 JSSA conditional likelihood with per capita recruitment

This model (JSSAfCL) coincides with the Link and Barker (2005) formulation, as provided in MARK. We compare the two.

```

fitf1 <- openCR.fit(microtusMCH, type= "JSSAfCL", model = list(p~1, phi~1, f~1))
summary(fitf1)

## $versiontime
## [1] "1.4.1, run 10:28:32 30 Jun 2019"
##
## $capthist
##          S1 S2 S3 S4 S5 S6 Total
## Occasions  1  1  1  1  1  1    6
## Detections 56 72 49 57 46 77   357
## Animals    56 72 49 57 46 77   171
##
## $intervals
## [1] 1 1 1 1 1
##
## $modeldetails
##      type fixed distribution
## JSSAfCL none          none
##

```



```

## $AICtable
##      model npar rank logLik  AIC AICc
## p~1 phi~1 f~1    3    3 -507.4 1021 1022
##
## $link
##      p  phi  f
## logit logit log
##
## $coef
##      beta SE.beta    lcl    ucl
## p    2.1434 0.2878  1.5793  2.7075
## phi  0.9351 0.1330  0.6744  1.1958
## f   -1.0797 0.1008 -1.2772 -0.8822
##
## $hessian
## rankH svtol Eigen1 Eigen2 Eigen3
##      3 1e-05      1 0.3432 0.08176
##
## $predicted
## $predicted$p
##      session estimate SE.estimate    lcl    ucl
## 1          1    0.895    0.02704 0.8291 0.9375
## 2          2    0.895    0.02704 0.8291 0.9375
## 3          3    0.895    0.02704 0.8291 0.9375
## 4          4    0.895    0.02704 0.8291 0.9375
## 5          5    0.895    0.02704 0.8291 0.9375
## 6          6    0.895    0.02704 0.8291 0.9375
##
## $predicted$phi
##      session estimate SE.estimate    lcl    ucl
## 1          1    0.7181    0.02693 0.6625 0.7678
## 2          2    0.7181    0.02693 0.6625 0.7678
## 3          3    0.7181    0.02693 0.6625 0.7678
## 4          4    0.7181    0.02693 0.6625 0.7678
## 5          5    0.7181    0.02693 0.6625 0.7678
## 6          6         NA         NA     NA     NA
##
## $predicted$f
##      session estimate SE.estimate    lcl    ucl
## 1          1    0.3397    0.03423 0.2788 0.4139
## 2          2    0.3397    0.03423 0.2788 0.4139
## 3          3    0.3397    0.03423 0.2788 0.4139
## 4          4    0.3397    0.03423 0.2788 0.4139
## 5          5    0.3397    0.03423 0.2788 0.4139
## 6          6         NA         NA     NA     NA

```

And in MARK:

```

df <- RMarkInput(microtusMCH, grouped = TRUE, covariates = FALSE)
null <- list(formula = ~1)
mark(df, model = "LinkBarker", model.parameters = list(Phi = null, p = null, f = null))

```

```

##
## Output summary for LinkBarker model
## Name : Phi(~1)p(~1)f(~1)

```

```

##
## Npar : 3
## -2lnL: 1015
## AICc : 1021
##
## Beta
##           estimate      se      lcl      ucl
## Phi:(Intercept)  0.9351 0.1330  0.6744  1.1958
## p:(Intercept)    2.1434 0.2878  1.5793  2.7074
## f:(Intercept)   -1.0797 0.1008 -1.2772 -0.8822
##
##
## Real Parameter Phi
##      1      2      3      4      5
## 0.7181 0.7181 0.7181 0.7181 0.7181
##
##
## Real Parameter p
##      1      2      3      4      5      6
## 0.895 0.895 0.895 0.895 0.895 0.895
##
##
## Real Parameter f
##      1      2      3      4      5
## 0.3397 0.3397 0.3397 0.3397 0.3397

```

MARK generates files that we don't need, so we call on **RMark** to clean up.

```
RMark::cleanup(ask = FALSE)
```

2.1.7 Direct (closed-form) Jolly-Seber estimates

The Jolly-Seber method in its original form uses sufficient statistics to quickly compute population size, apparent survival and recruitment. Here we use the combined-sex dataset derived from JOLLY. Compare Pollock et al. (1990) Table 4.8:

```
JS.direct(microtusCH)
```

```

##      n   R   m   r   z       p     sep     N   seN   phi   sepHi   covphi   B   seB
## 1 108 105  0 89 0      NA      NA      NA      NA 0.8754 0.03862 -0.001669  NA   NA
## 2 127 121 84 76 5 0.9138 0.03667 138.4 4.145 0.6580 0.04756 -0.001159 30.94 3.563
## 3 102 101 73 68 8 0.8606 0.04545 118.1 4.409 0.6898 0.04881 -0.001226 28.63 2.836
## 4 103 102 73 63 3 0.9380 0.03458 109.4 2.928 0.6266 0.04902      NA 43.30 3.017
## 5 102 100 61 84 5 0.9112 0.03779 111.2 3.126      NA      NA      NA  NA   NA
## 6 149 148 89  0 0      NA      NA      NA      NA      NA      NA      NA  NA   NA

```

2.2 Dippers

Lebreton et al. (1992) demonstrated Cormack-Jolly-Seber methods with a dataset on European Dipper (*Cinclus cinclus*) collected by Marzolin (1988) and the data have been much used since then. Dippers were captured annually over 1981–1987.

2.2.1 Data summary

Compare Lebreton et al. 1992 Table 10:

```
dipperCHM <- subset(dipperCH, covariates(dipperCH)$sex=='Male')
dipperCHF <- subset(dipperCH, covariates(dipperCH)$sex=='Female')
m.array(dipperCHM)
```

```
##      R 1982 1983 1984 1985 1986 1987 NRecap
## 1981 12   6   1   0   0   0   0   5
## 1982 26   11  0   0   0   0   15
## 1983 37   17  1   0   0   0   19
## 1984 39   22  0   1   16
## 1985 45   25  0   20
## 1986 48   28  20
## 1987 46   46
```

```
m.array(dipperCHF)
```

```
##      R 1982 1983 1984 1985 1986 1987 NRecap
## 1981 10   5   1   0   0   0   0   4
## 1982 34   13  1   0   0   0   20
## 1983 41   17  1   0   0   0   23
## 1984 41   23  1   1   16
## 1985 43   26  0   17
## 1986 50   24  26
## 1987 47   47
```

Test 3.SR (Lebreton et al. 1992 p. 86). Lebreton et al. indicate that only component 3SR is meaningful.

```
test3sr <- rbind(
  Male = ucare.cjs(dipperCHM)$test3sr$test3sr,
  Female = ucare.cjs(dipperCHF)$test3sr$test3sr
)[,1:3]
test3sr <- rbind(test3sr, Total = apply(test3sr,2,sum))
test3sr[,3] <- 1 - pchisq(test3sr[,1], test3sr[,2])
test3sr
```

```
##      stat df  p_val
## Male   6.778 5 0.2377
## Female 4.985 5 0.4177
## Total 11.763 10 0.3012
```

2.2.2 CJS models

Compare Lebreton et al. (1992) Table 11

```
dipper.p.t.phi.t <- openCR.fit(dipperCH, model = list(p~t, phi~t))
predict(dipper.p.t.phi.t)
```

```
## $p
##      session estimate SE.estimate    lcl    ucl
## 1981      1      NA           NA      NA      NA
## 1982      2  0.6962    0.16578  0.3303  0.9142
## 1983      3  0.9231    0.07288  0.6161  0.9890
## 1984      4  0.9130    0.05818  0.7140  0.9779
## 1985      5  0.9008    0.05384  0.7360  0.9673
```

```
## 1986      6  0.9324      0.04581 0.7685 0.9829
## 1987      7  0.7435           NA      NA      NA
##
## $phi
##      session estimate SE.estimate      lcl      ucl
## 1981      1  0.7182      0.15556 0.3610 0.9200
## 1982      2  0.4347      0.06883 0.3075 0.5711
## 1983      3  0.4782      0.05971 0.3644 0.5943
## 1984      4  0.6261      0.05927 0.5048 0.7334
## 1985      5  0.5985      0.05605 0.4855 0.7019
## 1986      6  0.7137           NA      NA      NA
## 1987      7      NA           NA      NA      NA
```

The individual covariate 'sex' is a factor with levels 'Female' and 'Male'. We can fit Cormack-Jolly-Seber models directly with `openCR.fit`:

```
dipper.null <- openCR.fit(dipperCH)
dipper.p.sex <- openCR.fit(dipperCH, model = p~sex)
dipper.phi.t <- openCR.fit(dipperCH, model = phi~t)
dipper.phi.sex.p.t.sex <- openCR.fit(dipperCH, model = list(phi~sex, p~t+sex))
```

```
AIC(dipper.null, dipper.p.sex, dipper.phi.sex.p.t.sex)
```

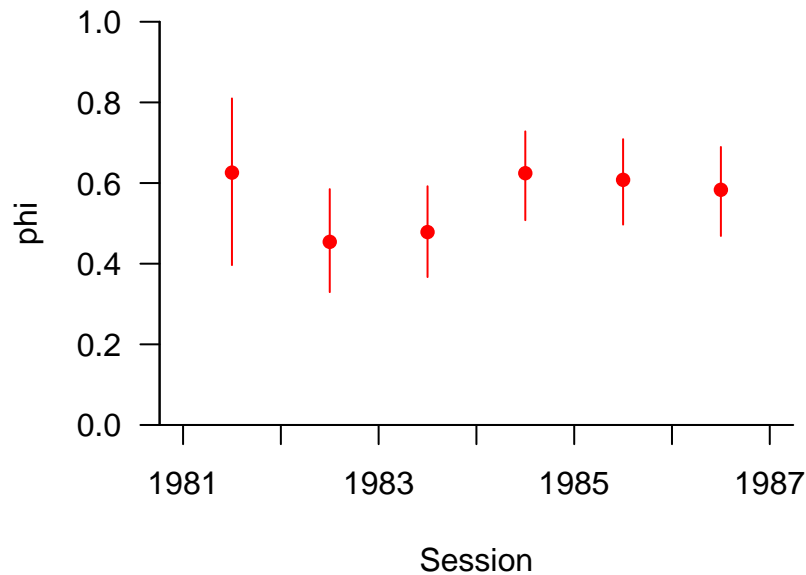
```
##              model npar rank logLik   AIC  AICc   dAIC  AICwt
## dipper.null      p~1 phi~1    2    2 -333.4 670.8 671.1  0.000 0.6632
## dipper.p.sex     p~sex phi~1    3    3 -333.1 672.2 672.7  1.355 0.3368
## dipper.phi.sex.p.t.sex p~t + sex phi~sex    9    9 -331.9 681.9 685.9 11.016 0.0000
```

```
predict(dipper.p.sex, all.levels = TRUE)
```

```
## $p
##      session      sex estimate SE.estimate      lcl      ucl
## 1          1    Male      NA           NA      NA      NA
## 2          2    Male  0.9243      0.03542 0.8191 0.9705
## 3          3    Male  0.9243      0.03542 0.8191 0.9705
## 4          4    Male  0.9243      0.03542 0.8191 0.9705
## 5          5    Male  0.9243      0.03542 0.8191 0.9705
## 6          6    Male  0.9243      0.03542 0.8191 0.9705
## 7          7    Male  0.9243      0.03542 0.8191 0.9705
## 8          1 Female      NA           NA      NA      NA
## 9          2 Female  0.8801      0.04345 0.7661 0.9427
## 10         3 Female  0.8801      0.04345 0.7661 0.9427
## 11         4 Female  0.8801      0.04345 0.7661 0.9427
## 12         5 Female  0.8801      0.04345 0.7661 0.9427
## 13         6 Female  0.8801      0.04345 0.7661 0.9427
## 14         7 Female  0.8801      0.04345 0.7661 0.9427
##
## $phi
##      session      sex estimate SE.estimate      lcl      ucl
## 1          1    Male  0.5607      0.02516 0.5109 0.6093
## 2          2    Male  0.5607      0.02516 0.5109 0.6093
## 3          3    Male  0.5607      0.02516 0.5109 0.6093
## 4          4    Male  0.5607      0.02516 0.5109 0.6093
## 5          5    Male  0.5607      0.02516 0.5109 0.6093
## 6          6    Male  0.5607      0.02516 0.5109 0.6093
## 7          7    Male      NA           NA      NA      NA
```

```
## 8      1 Female  0.5607      0.02516 0.5109 0.6093
## 9      2 Female  0.5607      0.02516 0.5109 0.6093
## 10     3 Female  0.5607      0.02516 0.5109 0.6093
## 11     4 Female  0.5607      0.02516 0.5109 0.6093
## 12     5 Female  0.5607      0.02516 0.5109 0.6093
## 13     6 Female  0.5607      0.02516 0.5109 0.6093
## 14     7 Female      NA          NA     NA     NA
```

```
par(mar = c(4,4,2,2))
plot(dipper.phi.t, par = 'phi', ylim = c(0,1), pch = 16, col = 'red')
```



Comparing to Laake, Johnson and Conn (2013) analysis of dummy ‘dipper’ data in MEE

```
# go to 'marked' to get exact copy of dipper data
# and add a dummy weight field which are random values from 1 to 10
library(marked)
data(dipper)
set.seed(123)
dipper$weight <- round(runif(nrow(dipper),0,9),0)+1
# switch to 'openCR' and fit model
dipperCH2 <- unRMarkInput(dipper) # convert to secr capthist object
sesscov <- data.frame(flood = c(0,1,1,0,0,0,0)) ## extra 0 to complete 7-session vector
fit2 <- openCR.fit(dipperCH2, model = list(p ~ sex + B, phi ~ flood + weight),
                  sessioncov = sesscov)
coef(fit2)[c(4,5,6,1,2,3),]
```

```
##          beta SE.beta    lcl    ucl
## phi      0.34658  0.2696 -0.1818  0.8749
## phi.flood -0.59091  0.2291 -1.0400 -0.1419
## phi.weight  0.03022  0.0391 -0.0464  0.1068
## p        -0.16282  1.1857 -2.4868  2.1612
## p.sexMale  0.47331  0.7221 -0.9421  1.8887
## p.BTRUE   1.96579  0.8877  0.2259  3.7056
```

This does not exactly reproduce Laake, Johnson and Conn (2013) Table 5 because they discount first captures as the basis for trap dependence (without explanation). If their analysis is modified by dropping the line

td[releaseocc]=0 then results agree exactly.

Compare Laake, Johnson and Conn (2013) Table 6 –

```
newdat <- expand.grid(B = c(0,1), sex = c('Female','Male'), weight = 1, flood = 0)
predict(fit2, newdata = newdat)$p
```

```
##   B   sex weight flood estimate SE.estimate   lcl   ucl
## 1 0 Female     1     0  0.4594    0.29448 0.07679 0.8967
## 2 1 Female     1     0  0.8585    0.06524 0.67923 0.9456
## 3 0  Male     1     0  0.5770    0.32151 0.09352 0.9475
## 4 1  Male     1     0  0.9069    0.05827 0.71579 0.9741
```

2.2.3 JSSA models

```
dipper.JSSA <- openCR.fit(dipperCH, type='JSSA1', model = list(phi~t, lambda~t))
predict(dipper.JSSA)$lambda
```

```
##      session estimate SE.estimate   lcl   ucl
## 1981      1      2.792    0.58050 1.8573 4.196
## 1982      2      1.265    0.17102 0.9709 1.649
## 1983      3      1.026    0.12172 0.8132 1.295
## 1984      4      1.104    0.11275 0.9038 1.349
## 1985      5      1.103    0.10876 0.9089 1.338
## 1986      6      0.958    0.09356 0.7911 1.160
## 1987      7      NA         NA      NA      NA
```

2.2.4 Compare JS in openCR and marked

For exact comparison the distribution of n must be changed from Poisson (the default in `openCR.fit`) to binomial (the assumed distribution in MARK and `marked`).

```
## openCR
coef(openCR.fit(dipperCH, type = 'JSSAb', distribution = 'binomial'))
```

```
##      beta SE.beta   lcl   ucl
## p      2.2915  0.3324 1.6399 2.9430
## phi    0.2383  0.1016 0.0391 0.4374
## b      0.6683  0.2233 0.2306 1.1061
## superN 2.7196  0.4295 1.8778 3.5613
```

```
## marked
data(dipper)
crm(dipper, model="js")
```

```
## Starting optimization 4 parameters
##
## Number of evaluations: 100 -2lnl: -958.5951007
## Number of evaluations: 200 -2lnl: -958.7091896
## Elapsed time in minutes: 0.0093
##
## crm Model Summary
##
## Npar : 4
## -2lnL: 705.6
```

```
## AIC : 713.6
##
## Beta
##           Estimate
## Phi.(Intercept) 0.2383
## p.(Intercept)   2.2915
## pent.(Intercept) 0.6683
## N.(Intercept)   2.7196
```

Coefficients are numerically identical. Likelihood and AIC values differ between **openCR** and **marked** because **openCR** omits a constant term.

2.2.5 Compare estimates from different models

```
cjs      <- openCR.fit(dipperCH, type = 'CJS',    model = list(p~t, phi~t))
jssabCL <- openCR.fit(dipperCH, type = 'JSSAbCL', model = list(p~t, phi~t, b~t))
jssafCL <- openCR.fit(dipperCH, type = 'JSSAfCL', model = list(p~t, phi~t, f~t))
jssagCL <- openCR.fit(dipperCH, type = 'JSSAgCL', model = list(p~t, phi~t, gamma~t))
jssalCL <- openCR.fit(dipperCH, type = 'JSSAlCL', model = list(p~t, phi~t, lambda~t),
                      start=jssagCL)
jssab   <- openCR.fit(dipperCH, type = 'JSSAb',   model = list(p~t, phi~t, b~t))
jssaf   <- openCR.fit(dipperCH, type = 'JSSAf',   model = list(p~t, phi~t, f~t))
jssag   <- openCR.fit(dipperCH, type = 'JSSAg',   model = list(p~t, phi~t, gamma~t))
jssal   <- openCR.fit(dipperCH, type = 'JSSAl',   model = list(p~t, phi~t, lambda~t))
jssaN   <- openCR.fit(dipperCH, type = 'JSSAN',   model = list(p~t, phi~t, N~t))
# combine as openCRlist
fits <- openCRlist(cjs, jssabCL, jssafCL, jssagCL, jssalCL, jssab, jssaf, jssag,
                  jssal, jssaN)
```

```
make.table(fits[-1], parm = "p")
```

```
##           session
## model      1981  1982  1983  1984  1985  1986  1987
## fits.jssabCL 0.8477 0.6962 0.9231 0.9130 0.9008 0.9324 0.8196
## fits.jssafCL 0.7597 0.6962 0.9231 0.9130 0.9008 0.9324 0.7230
## fits.jssagCL 0.7771 0.6962 0.9231 0.9130 0.9008 0.9324 0.7777
## fits.jssalCL 0.7368 0.7018 0.9268 0.9133 0.8998 0.9325 0.7323
## fits.jssab   0.8484 0.6962 0.9231 0.9130 0.9008 0.9324 0.8265
## fits.jssaf   0.7602 0.6962 0.9231 0.9130 0.9008 0.9324 0.7193
## fits.jssag   0.7779 0.6962 0.9231 0.9130 0.9008 0.9324 0.7757
## fits.jssal   0.8273 0.6980 0.9296 0.9092 0.9044 0.9291 0.8074
## fits.jssaN   0.7993 0.6962 0.9231 0.9130 0.9008 0.9324 0.8658
```

```
make.table(fits, parm = "phi")
```

```
##           session
## model      1981  1982  1983  1984  1985  1986 1987
## cjs        0.7182 0.4347 0.4782 0.6261 0.5985 0.7137
## jssabCL    0.7182 0.4347 0.4782 0.6261 0.5985 0.6474
## jssafCL    0.7182 0.4347 0.4782 0.6261 0.5985 0.7339
## jssagCL    0.7182 0.4347 0.4782 0.6261 0.5985 0.6823
## jssalCL    0.7101 0.4346 0.4798 0.6255 0.5987 0.7242
## jssab      0.7182 0.4347 0.4782 0.6261 0.5985 0.6420
## jssaf      0.7182 0.4347 0.4782 0.6261 0.5985 0.7376
```

```
## jssag 0.7182 0.4347 0.4782 0.6261 0.5985 0.6841
## jssal 0.7066 0.4331 0.4801 0.6247 0.6006 0.6574
## jssaN 0.7182 0.4347 0.4782 0.6261 0.5985 0.6129
```

Estimates from the models parameterized with lambda (population growth rate) stand out as slightly different. It is not clear whether this is inherent in the parameterization (lambda is the arithmetic sum of the survival and recruitment components) or to an undetected bug in the code. I'm betting on the former.

2.2.6 Compare Schofield and Barker (2016)

Schofield and Barker (2016 supplementary materials) presented an analysis of the dipper data that compared CJS and re-parameterised Jolly-Seber or POPAN models (CMSA models in their terminology). Their favoured parameterisation uses κ (kappa) for recruitment. κ has a complex recursive relationship to p , ϕ and f (their γ). The κ parameterisation enables a revealing factorisation of the likelihood (Link and Barker 2005, Schofield and Barker 2016). It is not so obvious that it has other benefits, and it has not appeared in the applied capture–recapture literature. The kappa parameterisation therefore remains an undocumented feature of **openCR**; we demonstrate it here as a curiosity. For the kappa parameterisation use “k” in the model type (e.g., JSSAk instead of JSSAf) and use the real parameter name “kappa” in model formulae.

We suppress warnings from `openCR.fit` regarding likely confounding - we expect this for ϕ_6 and p_7 .

```
cjs <- openCR.fit(dipperCH, type = 'CJS', model = list(p~t, phi~t))
CMSAn <- openCR.fit(dipperCH, type = 'JSSAkCL', model = list(p~t, phi~t, kappa~t))
CMSA <- openCR.fit(dipperCH, type = 'JSSAk', model = list(p~t, phi~t, kappa~t),
  distribution = "binomial")
CMSApois <- openCR.fit(dipperCH, type = 'JSSAk', model = list(p~t, phi~t, kappa~t),
  distribution = "poisson")
fits <- openCRlist(cjs, CMSAn, CMSA, CMSApois)
AIC(fits)[,1:4] # logLik directly comparable only between CMSA and CMSApois
```

```
##           model npar rank logLik
## cjs           p~t phi~t    12    11 -328.5
## CMSAn        p~t phi~t kappa~t    19    17 -892.7
## CMSA      p~t phi~t kappa~t superN~1    20    18 -895.1
## CMSApois p~t phi~t kappa~t superN~1    20    18 -896.5
```

```
# capture probability
make.table(fits, 'p')
```

```
##           session
## model      1981  1982  1983  1984  1985  1986  1987
## cjs                0.6962 0.9231 0.9130 0.9008 0.9324 0.7435
## CMSAn      0.8598 0.6962 0.9231 0.9130 0.9008 0.9324 0.8571
## CMSA      1.0000 0.7341 0.9270 0.9149 0.9024 0.9338 1.0000
## CMSApois 0.8596 0.6962 0.9231 0.9130 0.9008 0.9324 0.8558
```

```
# survival
make.table(fits, 'phi')
```

```
##           session
## model      1981  1982  1983  1984  1985  1986 1987
## cjs      0.7182 0.4347 0.4782 0.6261 0.5985 0.7137
## CMSAn    0.7182 0.4347 0.4782 0.6261 0.5985 0.6191
## CMSA     0.6983 0.4387 0.4785 0.6262 0.5987 0.5310
## CMSApois 0.7182 0.4347 0.4782 0.6261 0.5985 0.6200
```

```
# kappa (recruitment+)
make.table(fits, 'kappa')
```

```
##           session
## model      1981  1982  1983  1984  1985  1986 1987
## cjs
## CMSAn                2.227 2.364 2.045 1.864 2.091 1.773
## CMSA                2.215 2.361 2.043 1.862 2.089 1.773
## CMSApois            2.227 2.364 2.045 1.864 2.091 1.773
```

```
# superpopulation size
make.table(fits, 'superN')[,1]
```

```
##      cjs      CMSAn      CMSA CMSApois
##      NA       NA     310.4    320.6
```

These estimates (particularly κ_7) differ from those of Schofield and Barker (2016) in part because of a small error in their copy of the dipper data (10 extra individuals in the last release cohort) (M. Schofield pers. comm.).

A derived (H-T) estimate of superpopulation size may be got from the conditional likelihood model:

```
derived(CMSAn)$superN
```

```
## [1] 320.5
```

This is close to the estimate from the full Poisson model, but not identical. More worrying, the superpopulation estimates change when we remaximise the models with different starting values for p and ϕ (for example, those from the CJS model):

```
CMSA2 <- openCR.fit(dipperCH, type = 'JSSAk', model = list(p~t, phi~t, kappa~t),
                  distribution = "binomial", start = cjs)
CMSApois2 <- openCR.fit(dipperCH, type = 'JSSAk', model = list(p~t, phi~t, kappa~t),
                      distribution = "poisson", start = cjs)
fits2 <- openCRlist(CMSA2, CMSApois2)
make.table(fits2, 'superN')[,1]
```

```
##      CMSA2 CMSApois2
##      310.4     331.1
```

It's fairly clear that, despite the reparameterisation, the full model with time variation in all parameters remains unidentifiable. Constraints are needed, as we should have expected!

2.3 *Gonodontis* moths

Male moths (the nonmelanic form of *Gonodontis bidentata*) were trapped, marked and released by Bishop et al. (1978). The data were analysed by Crosbie (1979) and Link and Barker (2005, 2010).

2.3.1 Data summary

```
m.array(gonodontisCH)
```

```
##      R  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 NRecap
## 1  15  8  1  0  0  1  0  0  0  0  0  0  0  0  0  0  5
## 2  52  16  5  1  0  0  0  0  0  0  0  0  0  0  0  0  30
## 3  54  12  2  0  0  0  0  0  0  0  0  0  0  0  0  0  40
## 4  62  12  2  0  0  1  0  0  0  0  0  0  0  0  0  0  47
## 5  29  10  1  1  0  1  0  0  0  0  0  0  0  0  0  0  16
## 6  84  5  3  2  1  0  0  0  0  0  1  0  0  0  0  0  72
## 7  51  15  0  1  0  0  0  0  0  0  0  0  0  0  0  0  35
## 8  74  8  4  0  1  1  3  0  0  0  0  0  0  0  0  0  57
## 9  43  7  1  3  0  1  0  0  0  0  0  0  0  0  0  0  31
## 10 85  2  6  2  2  0  0  0  0  0  0  0  0  0  0  0  73
## 11 15  2  1  0  0  0  0  0  0  0  0  0  0  0  0  0  12
## 12 81  20  3  2  0  0  0  0  0  0  0  0  0  0  0  0  56
```

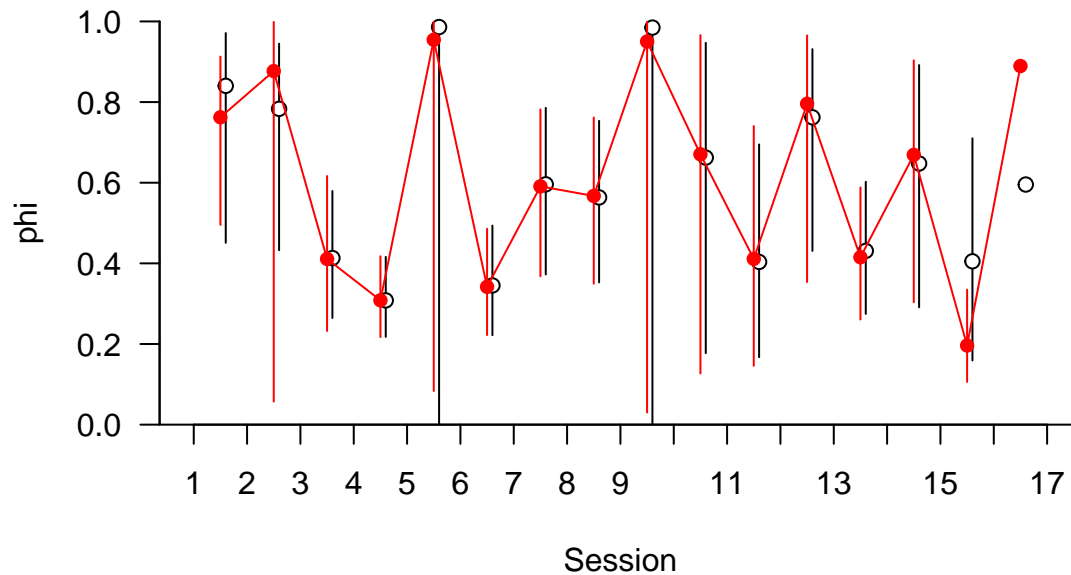
```
## 13 93      8 6 3 0 76
## 14 59      11 1 2 45
## 15 60      5 2 53
## 16 37      4 33
## 17 8      8
```

2.3.2 CJS vs JSSA

```
fitCJS <- openCR.fit(gonodontisCH, model = list(phi~t, p~t))
fitJSSAf<- openCR.fit(gonodontisCH, type = 'JSSAfCL',
  model = list(f~t, phi~t, p~t))
fitJSSAB<- openCR.fit(gonodontisCH, type = 'JSSAB',
  model = list(BN~t, phi~t, p~t))
```

We choose to plot 80% confidence intervals because the estimates are quite rough.

```
par(mar=c(4,4,2,2))
plot(fitCJS, yaxs = 'i', ylim = 0:1, alpha = 0.2, xoffset = 0.1,
  pch = 21, bg='white', xpd = TRUE)
plot(fitJSSAf, add = TRUE, type='o', col = 'red', alpha = 0.2, pch = 16)
```



2.4 Orongorongo Valley brushtail possums

2.4.1 Data summary

```
summary(FebpossumCH, terse = TRUE)

##           1980 1981 1982 1983 1984 1985 1986 1987 1988
## Occasions    10   8   6   4   4   4   5   5   6
## Detections  461 462 423 248 278 214 294 318 275
## Animals     142 146 147 138 129 106 133 141 114
## Detectors     1   1   1   1   1   1   1   1   1
```

```
m.array(FebpossumCH)

##           R 1981 1982 1983 1984 1985 1986 1987 1988 NRecap
## 1980 142   85    0    0    1    0    0    0    0    56
## 1981 146     95    3    2    0    0    0    0    0    46
## 1982 147          100   9    3    1    0    0    0    34
## 1983 138            98   5    1    0    0    0    0    34
## 1984 129              83   5    3    1    0    0    37
## 1985 106                69   7    2    0    0    28
## 1986 133                  85   4    0    0    0    44
## 1987 141                    86   0    0    0    0    55
## 1988 114                      114
```

2.4.2 CJS analyses

Pledger et al. (2003) analysed data from February samples in 1980–1988, using all captures.

```
# collapse because PPN did not use robust design
FebCH <- reduce(FebpossumCH, by = 'all', verify = FALSE)
m.array(FebCH) # identical to above

##           R 1981 1982 1983 1984 1985 1986 1987 1988 NRecap
## 1980 142   85    0    0    1    0    0    0    0    56
## 1981 146     95    3    2    0    0    0    0    0    46
## 1982 147          100   9    3    1    0    0    0    34
## 1983 138            98   5    1    0    0    0    0    34
## 1984 129              83   5    3    1    0    0    37
## 1985 106                69   7    2    0    0    28
## 1986 133                  85   4    0    0    0    44
## 1987 141                    86   0    0    0    0    55
## 1988 114                      114

FebCHF <- subset(FebCH, function(x) covariates(x)$sex=='F')
FebCHM <- subset(FebCH, function(x) covariates(x)$sex=='M')

baseargs <- list(capthist = 'FebCHF', type = 'CJS')
args <- rep(list(baseargs), 24)
args[[1]]$model <- list(p~t, phi~t)
args[[2]]$model <- list(p~t+h2, phi~t)
args[[3]]$model <- list(p~t*h2, phi~t)
args[[4]]$model <- list(p~t, phi~t+h2)
args[[5]]$model <- list(p~t+h2, phi~t+h2)
args[[6]]$model <- list(p~t, phi~t*h2)
```

```

args[[7]]$model <- list(p~t+h2, phi~t*h2)
args[[8]]$model <- list(p~t*h2, phi~t*h2)
for (i in 9:16) {
  args[[i]] <- args[[i-8]]
  args[[i]]$scaphist <- 'FebCHM'
}
for (i in 17:24) {
  args[[i]] <- args[[i-8]]
  args[[i]]$scaphist <- 'FebCH'
}

fitsCJS <- par.openCR.fit(args, ncores = 7)

```

```
## Completed in 0.653 minutes at 11:54:19 29 Jun 2019
```

```
# Females
```

```
AIC(openCRlist(fitsCJS[1:8]), sort = FALSE, criterion = 'AIC')[,-(5:6)]
```

##	model	npar	rank	logLik	dAIC	AICwt
## 1	p~t phi~t	16	14	-366.9	3.979	0.0531
## 2	p~t + h2 phi~t pmix~h2	18	16	-362.9	0.000	0.3883
## 3	p~t * h2 phi~t pmix~h2	25	21	-359.4	7.049	0.0114
## 4	p~t phi~t + h2 pmix~h2	18	15	-363.3	0.814	0.2585
## 5	p~t + h2 phi~t + h2 pmix~h2	19	17	-362.3	0.827	0.2568
## 6	p~t phi~t * h2 pmix~h2	25	16	-362.4	13.135	0.0000
## 7	p~t + h2 phi~t * h2 pmix~h2	26	17	-357.4	4.996	0.0319
## 8	p~t * h2 phi~t * h2 pmix~h2	33	22	-355.0	14.187	0.0000

```
# Males
```

```
AIC(openCRlist(fitsCJS[9:16]), sort = FALSE, criterion = 'AIC')[,-(5:6)]
```

##	model	npar	rank	logLik	dAIC	AICwt
## 1	p~t phi~t	16	15	-483.3	31.092	0.0000
## 2	p~t + h2 phi~t pmix~h2	18	17	-468.5	5.488	0.0459
## 3	p~t * h2 phi~t pmix~h2	25	17	-468.5	19.487	0.0000
## 4	p~t phi~t + h2 pmix~h2	18	16	-470.3	9.147	0.0074
## 5	p~t + h2 phi~t + h2 pmix~h2	19	17	-464.7	0.000	0.7136
## 6	p~t phi~t * h2 pmix~h2	25	19	-466.3	15.164	0.0000
## 7	p~t + h2 phi~t * h2 pmix~h2	26	23	-458.8	2.237	0.2332
## 8	p~t * h2 phi~t * h2 pmix~h2	33	23	-458.9	16.302	0.0000

```
# Combined
```

```
AIC(openCRlist(fitsCJS[17:24]), sort = FALSE, criterion = 'AIC')[,-(5:6)]
```

##	model	npar	rank	logLik	dAIC	AICwt
## 1	p~t phi~t	16	15	-867.0	46.571	0.0000
## 2	p~t + h2 phi~t pmix~h2	18	18	-842.4	1.309	0.3392
## 3	p~t * h2 phi~t pmix~h2	25	23	-840.2	11.020	0.0000
## 4	p~t phi~t + h2 pmix~h2	18	16	-849.3	15.121	0.0000
## 5	p~t + h2 phi~t + h2 pmix~h2	19	19	-840.7	0.000	0.6527
## 6	p~t phi~t * h2 pmix~h2	25	17	-848.3	27.205	0.0000
## 7	p~t + h2 phi~t * h2 pmix~h2	26	26	-838.1	8.774	0.0081
## 8	p~t * h2 phi~t * h2 pmix~h2	33	31	-837.6	21.773	0.0000

```
pred18 <- predict(fitsCJS[[18]], all.levels = TRUE)
```

```
pred21 <- predict(fitsCJS[[21]], all.levels = TRUE)
```

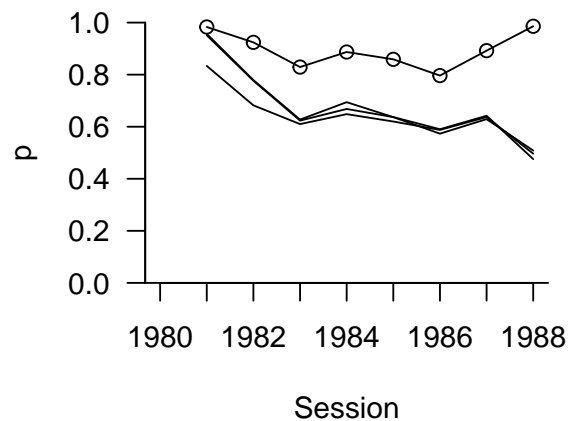
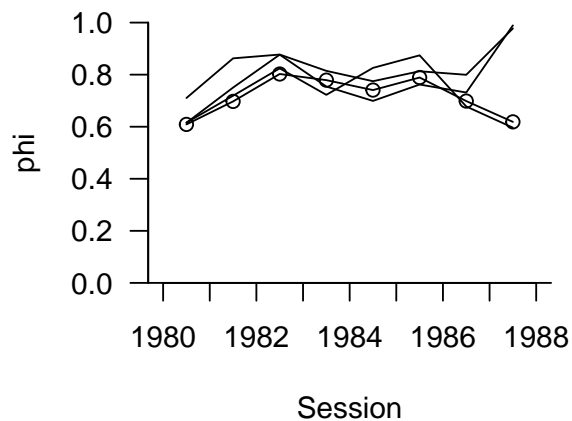
```

pred23 <- predict(fitsCJS[[23]], all.levels = TRUE)
avp18 <- pred18$pmix$estimate[1] * pred18$p$estimate[1:9] +
  pred18$pmix$estimate[2] * pred18$p$estimate[10:18]
avp21 <- pred21$pmix$estimate[1] * pred21$p$estimate[1:9] +
  pred21$pmix$estimate[2] * pred21$p$estimate[10:18]
avp23 <- pred23$pmix$estimate[1] * pred23$p$estimate[1:9] +
  pred23$pmix$estimate[2] * pred23$p$estimate[10:18]
avphi21 <- pred21$pmix$estimate[1] * pred21$phi$estimate[1:9] +
  pred21$pmix$estimate[2] * pred21$phi$estimate[10:18]
avphi23 <- pred23$pmix$estimate[1] * pred23$phi$estimate[1:9] +
  pred23$pmix$estimate[2] * pred23$phi$estimate[10:18]

xv <- (0:8)+0.5
par(mfrow = c(1,2), xpd = TRUE)
plot(fitsCJS[[17]], 'phi', ylim = c(0,1), type = 'o', lty = 2, CI = FALSE)
lines(xv, pred18$phi$estimate)
lines(xv, avphi21)
lines(xv, avphi23)

plot(fitsCJS[[17]], 'p', ylim = c(0,1), type = 'o', lty = 2, CI = FALSE)
lines(0:8, avp18)
lines(0:8, avp21)
lines(0:8, avp23)

```



As we saw in the initial summary, the number of trapping days per session varied from 4 to 10. Some variation in capture probability is due to varying effort. We compare the collapsed CJS analysis of Pledger et al. (2003) to a full robust-design CJS analysis.

```

baseargs <- list(capthist = 'FebpossumCH', type = 'CJS')
args <- rep(list(baseargs), 8)
args[[1]]$model <- list(p~t, phi~t)
args[[2]]$model <- list(p~t+h2, phi~t)
args[[3]]$model <- list(p~t*h2, phi~t)
args[[4]]$model <- list(p~t, phi~t+h2)
args[[5]]$model <- list(p~t+h2, phi~t+h2)

```

```

args[[6]]$model <- list(p~t, phi~t*h2)
args[[7]]$model <- list(p~t+h2, phi~t*h2)
args[[8]]$model <- list(p~t*h2, phi~t*h2)
fitsCJSRD <- par.openCR.fit(args, ncores = 8)

## Completed in 0.62 minutes at 11:54:57 29 Jun 2019
AIC(fitsCJSRD, criterion = 'AIC', sort = FALSE)[,-(5:6)]

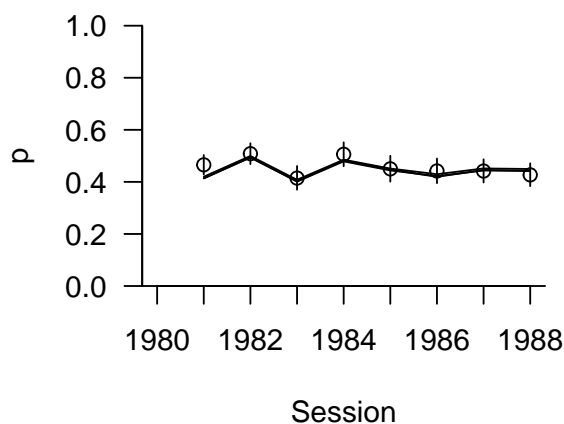
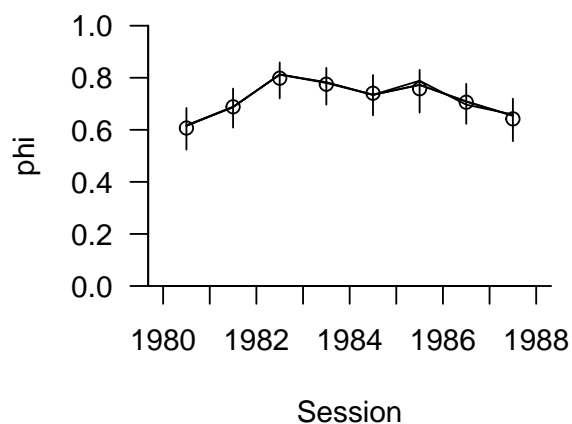
##           model npar rank logLik   dAIC  AICwt
## 1           p~t phi~t   16  16  -3541 422.904 0.0000
## 2    p~t + h2 phi~t pmix~h2  18  18  -3328   1.201 0.2596
## 3    p~t * h2 phi~t pmix~h2  25  25  -3323   3.931 0.0663
## 4    p~t phi~t + h2 pmix~h2  18  17  -3521 386.198 0.0000
## 5 p~t + h2 phi~t + h2 pmix~h2  19  19  -3328   2.885 0.1118
## 6    p~t phi~t * h2 pmix~h2  25  18  -3521 400.185 0.0000
## 7 p~t + h2 phi~t * h2 pmix~h2  26  26  -3320   0.000 0.4732
## 8 p~t * h2 phi~t * h2 pmix~h2  33  33  -3314   3.339 0.0891

average <- function (fit, parm = 'phi') {
  pred <- predict(fit, all = TRUE)
  nr <- nrow(pred[[parm]])
  pred$pmix$estimate[1] * pred[[parm]]$estimate[1:(nr/2)] +
    pred$pmix$estimate[2] * pred[[parm]]$estimate[(nr/2+1):nr]
}

avp2 <- average(fitsCJSRD[[2]], 'p')
avp3 <- average(fitsCJSRD[[3]], 'p')
avp5 <- average(fitsCJSRD[[5]], 'p')
avphi5 <- average(fitsCJSRD[[5]], 'phi')

par(mfrow=c(1,2))
xv <- (0:8)+0.5
plot(fitsCJSRD[[1]], ylim = c(0,1))
plot(fitsCJSRD[[2]], add = TRUE, CI = FALSE, type = 'l')
plot(fitsCJSRD[[3]], add = TRUE, CI = FALSE, type = 'l')
lines(xv, avphi5)
xv <- 0:8
plot(fitsCJSRD[[1]], 'p', ylim = c(0,1))
lines(xv, avp2)
lines(xv, avp3)
lines(xv, avp5)

```



2.4.3 JSSA analyses

Pledger et al. (2010) analysed data from February samples in 1980–1988, using captures from only the first day.

```
FebD1CH <- subset(FebpossumCH, occasion = 1)
JS.counts(FebD1CH)
```

```
##      n  R  m  r  z
## 1 65 65  0 36  0
## 2 78 78 27 53  9
## 3 82 82 44 62 18
## 4 85 85 57 57 23
## 5 76 76 58 46 22
## 6 70 70 54 41 14
## 7 46 46 34 30 21
## 8 78 78 42 22  9
## 9 37 37 31  0  0
```

```
m.array(FebD1CH)
```

```
##      R 1981 1982 1983 1984 1985 1986 1987 1988 NRecap
## 1980 65   27   5    2    1    1    0    0    0    29
## 1981 78     39   8    4    2    0    0    0    0    25
## 1982 82     47  10   4    0    1    0    0    20
## 1983 85     43   9    2    2    1    1    28
## 1984 76     38   5    2    1    2    1    30
## 1985 70     27  11   3    2    1    3    29
## 1986 46     26   4    1    2    1    4    16
## 1987 78     22   4    1    2    1    4    56
## 1988 37     22   4    1    2    1    4    37
```

We fit all the models fitted by Pledger et al. (2010)

```
baseargs <- list(caphist = 'FebD1CH', type = 'JSSAb')
args <- rep(list(baseargs), 24)
```



```

args[[1]]$model <- list(p~1, phi~1, b~t)
args[[2]]$model <- list(p~1, phi~t, b~t)
args[[3]]$model <- list(p~1, phi~h2, b~t)
args[[4]]$model <- list(p~1, phi~t+h2, b~t)
args[[5]]$model <- list(p~1, phi~t*h2, b~t)
args[[6]]$model <- list(p~t, phi~1, b~t)
args[[7]]$model <- list(p~t, phi~t, b~t)
args[[8]]$model <- list(p~t, phi~h2, b~t)
args[[9]]$model <- list(p~t, phi~t+h2, b~t)
args[[10]]$model <- list(p~t, phi~t*h2, b~t)
args[[11]]$model <- list(p~h2, phi~1, b~t)
args[[12]]$model <- list(p~h2, phi~t, b~t)
args[[13]]$model <- list(p~h2, phi~h2, b~t)
args[[14]]$model <- list(p~h2, phi~t+h2, b~t)
args[[15]]$model <- list(p~h2, phi~t*h2, b~t)
args[[16]]$model <- list(p~t+h2, phi~1, b~t)
args[[17]]$model <- list(p~t+h2, phi~t, b~t)
args[[18]]$model <- list(p~t+h2, phi~h2, b~t)
args[[19]]$model <- list(p~t+h2, phi~t+h2, b~t)
args[[20]]$model <- list(p~t+h2, phi~t*h2, b~t)
args[[21]]$model <- list(p~t*h2, phi~1, b~t)
args[[22]]$model <- list(p~t*h2, phi~t, b~t)
args[[23]]$model <- list(p~t*h2, phi~h2, b~t)
args[[24]]$model <- list(p~t*h2, phi~t+h2, b~t)
fits <- par.openCR.fit(args, ncores = 7)

```

Completed in 1.061 minutes at 11:56:02 29 Jun 2019

Reproducing Pledger et al. (2010) Table 1.

```

AICtable <- round(matrix(c(AIC(fits, sort = FALSE, criterion = 'AIC')$dAIC, NA), nrow = 5), 1)
dimnames(AICtable) <- list(c('phi(.)', 'phi(t)', 'phi(h2)', 'phi(t + h2)', 'phi(t x h2)'),
                           c('p(.)', 'p(t)', 'p(h2)', 'p(t + h2)', 'p(t x h2)'))

```

AICtable

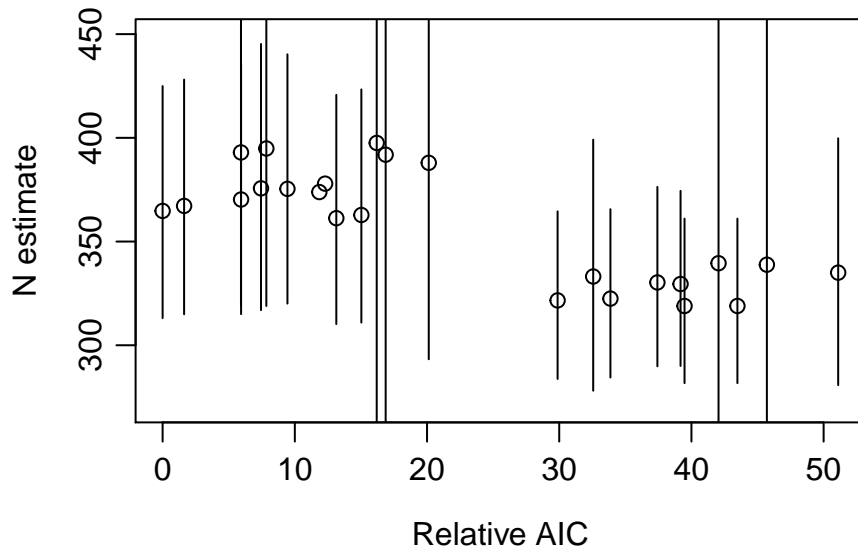
##	p(.)	p(t)	p(h2)	p(t + h2)	p(t x h2)
## phi(.)	39.5	37.4	13.1	5.9	12.3
## phi(t)	29.9	42.1	0.0	5.9	16.2
## phi(h2)	43.5	32.6	15.0	7.4	11.9
## phi(t + h2)	33.9	45.7	1.6	7.8	16.9
## phi(t x h2)	39.2	51.1	9.4	20.1	NA

Reproducing Pledger et al. (2010) Fig. 1.

```

par(mar=c(4,4,2,2), mgp=c(2.4,0.7,0))
Nhat <- sapply(lapply(predict(fits), '[', 'superN'), '[', 1, 'estimate')
Nhatlcl <- sapply(lapply(predict(fits), '[', 'superN'), '[', 1, 'lcl')
Nhatucl <- sapply(lapply(predict(fits), '[', 'superN'), '[', 1, 'ucl')
daic <- AIC(fits, sort = FALSE, criterion = 'AIC')$dAIC
plot(daic, Nhat, ylim = c(270,450), xlab = 'Relative AIC', ylab = 'N estimate')
segments(daic, Nhatlcl, daic, Nhatucl)

```



The superpopulation estimate for the model with lowest AIC was 364.8, compared to 393 for the $\{\phi \sim t, p \sim t+h^2\}$ model.

Reproducing Pledger et al. (2010) Fig. 3.

```
par(mar = c(4,4,2,2))
plot(fits[[17]], 'phi', pch = 16, ylim = c(0,1), CI = FALSE, type = 'o')
phi <- predict(fits[[17]])$phi$estimate
SEphi <- predict(fits[[17]])$phi$SE.estimate
xv <- (0:8)+0.5; segments(xv, phi-SEphi, xv, phi+SEphi)
plot(fits[[17]], 'b', add = TRUE, int = FALSE, CI = FALSE, col = 'red', pch = 16, type = 'o')
abline(h = seq(0,1,0.2), lty = 2)
```

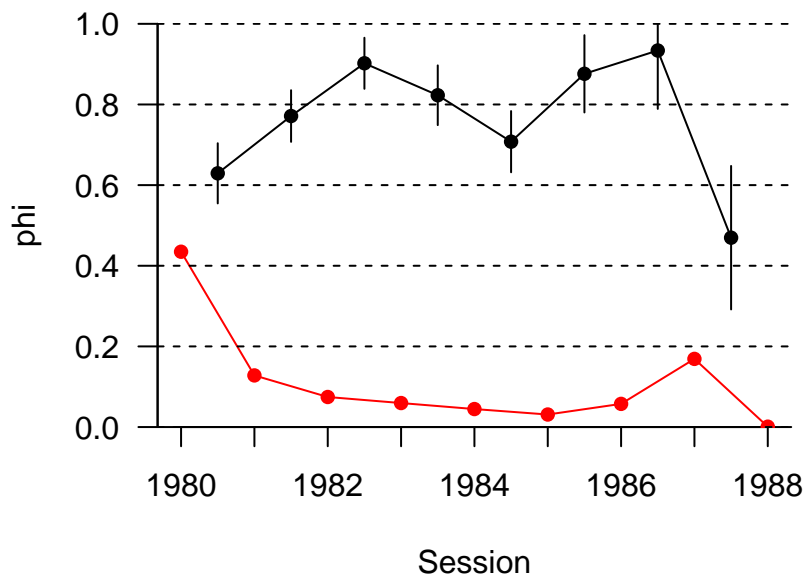


Fig. Estimates of apparent survival ϕ (black) and entry probability b (red) for Orongorongo possums 1980–1988. Bars are ± 1 SE.

3 Spatially explicit analyses

3.1 Kielder Forest field voles

Ergon and Gardner (2014) provided a robust design dataset from a trapping study on field voles *Microtus agrestis* in a clearcut within Kielder Forest, northern England – see also Ergon et al. (2011). The study aimed to describe sex differences in space-use, survival and dispersal among adult voles. Data were from one trapping grid in summer 2000.

Trapping was on a rectangular grid of 192 multi-catch (Ugglan Special) traps at 7-meter spacing. Traps were baited with whole barley grains and carrots; voles were marked with individually numbered ear tags. Traps were checked at about 12 hour intervals at around 6 am and 6 pm such that each primary trapping period had respectively 3, 5, 4 and 5 secondary trap checks. Four primary trapping sessions were begun at intervals of 21 to 23 days between 10 June and 15 August.

Ergon and Gardner (2014) focussed on models for dispersal (movement of home ranges between primary sessions). Modelling dispersal is expected to provide CJS estimates of survival ϕ free of the effect of emigration.

3.1.1 Data summary

```
JS.counts(fieldvoleCH)
```

```
##      n   R   m   r   z
## 1   94   91   0  69   0
## 2  106  105  66  88   3
## 3  109  109  90  89   1
## 4   95   94  90   0   0
```

```
m.array(fieldvoleCH)
```

```
##      R    2    3    4 NRecap
## 1   91   66    2    1     22
## 2  105     88    0    1     17
## 3  109     89    0    1     20
## 4   94     94    0    1     17
```

Form multi-session capthist for each sex:

```
chF <- subset(fieldvoleCH, function(x) covariates(x)$sex=='F')
chM <- subset(fieldvoleCH, function(x) covariates(x)$sex=='M')
```

First, a conventional CJS analysis on the collapsed data (not robust design). Both parameters p and ϕ are fitted as constant across sessions.

```
chF1 <- reduce(chF, by = 'all', verify = FALSE)
chM1 <- reduce(chM, by = 'all', verify = FALSE)
CJSfitF <- openCR.fit(chF1)
CJSfitM <- openCR.fit(chM1)
predict(CJSfitF)
```

```
## $p
## session estimate SE.estimate    lcl    ucl
```

```
## 1      1      NA          NA      NA      NA
## 2      2  0.9887    0.01113 0.9253 0.9984
## 3      3  0.9887    0.01113 0.9253 0.9984
## 4      4  0.9887    0.01113 0.9253 0.9984
##
## $phi
##  session estimate SE.estimate    lcl    ucl
## 1      1    0.7174    0.03488 0.6444 0.7806
## 2      2    0.7174    0.03488 0.6444 0.7806
## 3      3    0.7174    0.03488 0.6444 0.7806
## 4      4      NA          NA      NA      NA
```

```
predict(CJSfitM)
```

```
## $p
##  session estimate SE.estimate    lcl    ucl
## 1      1      NA          NA      NA      NA
## 2      2  0.9341    0.03545 0.8209 0.9777
## 3      3  0.9341    0.03545 0.8209 0.9777
## 4      4  0.9341    0.03545 0.8209 0.9777
##
## $phi
##  session estimate SE.estimate    lcl    ucl
## 1      1  0.8775    0.04542 0.7578 0.9425
## 2      2  0.8775    0.04542 0.7578 0.9425
## 3      3  0.8775    0.04542 0.7578 0.9425
## 4      4      NA          NA      NA      NA
```

These estimates match the nonspatial MCMC results reported by Ergon and Gardner (2014) in their Table 4 (section B).

Next, try a spatial analysis on the robust-design data. Ergon and Gardner (2014) appear to have used a 14-m buffer; this is rather small but we use it here to be consistent. In detection function ‘HVP’ the parameter z matches their exponent κ ($\kappa = 1$ corresponds to ‘HEX’ and $\kappa = 2$ to ‘HHN’).

```
mks <- make.mask(traps(chF), buffer = 14, spacing = 1, type='trapbuffer')
ampmdf <- attr(fieldvoleCH, 'ampm')
baseargs <- list(mask = msk, type = 'CJSsecr', detectfn = 'HVP',
                 model = list(lambda0~ampm, phi~1, sigma~1, z~1), timecov = ampmdf,
                 movementmodel = 'exponential', details = list(CJSsp1 = TRUE))
args <- rep(list(baseargs),2)
args[[1]]$capthist <- 'chF'
args[[2]]$capthist <- 'chM'
fits <- par.openCR.fit(args)
```

```
## Completed in 49.901 minutes at 12:46:07 29 Jun 2019
```

```
names(fits) <- c('exponF', 'exponM')
```

We could view estimates of all ‘real’ parameters for all models with

A more simple summary is

```
make.table(fits, 'phi')
```

```
##          session
## model      1      2      3 4
##  exponF 0.7496 0.7496 0.7496
```

```

##   exponM 0.8785 0.8785 0.8785
make.table(fits, 'lambda0')

##           session
## model      1      2      3      4
##   exponF 3.6777 3.6777 3.6777 3.6777
##   exponM 0.2939 0.2939 0.2939 0.2939
make.table(fits, 'sigma')

##           session
## model      1      2      3      4
##   exponF 1.174 1.174 1.174 1.174
##   exponM 10.861 10.861 10.861 10.861
make.table(fits, 'z')

##           session
## model      1      2      3      4
##   exponF 0.7145 0.7145 0.7145 0.7145
##   exponM 2.1217 2.1217 2.1217 2.1217
make.table(fits, 'move.a')

##           session
## model      1      2      3 4
##   exponF 1.511 1.511 1.511
##   exponM 2.354 2.354 2.354

```

These results differ somewhat from those of Ergon and Gardner (2014) Table 4.

3.2 Patuxent ovenbirds

Ovenbirds (*Seiurus aurocapilla*) were captured in 44 mist nets on 9–10 days during the breeding season in 5 consecutive years. Each received a uniquely numbered metal band. The `secr` capthist object `ovenCHp` uses the ‘proximity’ detector type: capture of an individual in a particular net on a particular day was a binary variable.

3.2.1 Data summary

```

summary(ovenCHp, terse = TRUE)

##           2005 2006 2007 2008 2009
## Occasions      9  10  10  10  10
## Detections     41  49  57  33  35
## Animals        20  22  26  19  16
## Detectors      44  44  44  44  44
m.array(ovenCHp)

##           R 2006 2007 2008 2009 NRecap
## 2005 20      9    2    1    0      8
## 2006 22           10    0    0     12
## 2007 26           3     3     20
## 2008 19           5     14
## 2009 15

```

3.2.2 Non-spatial analysis

Suppose we are interested in the overall population trend represented by the realised finite rate of increase (λ).

```
baseargs <- list(caphist = 'ovenCH')
args <- rep(list(baseargs), 10)
names(args) <- c('cjs', 'jssabCL', 'jssafCL', 'jssagCL', 'jssalCL',
                'jssab', 'jssaf', 'jssag', 'jssal', 'jssaN')
args[[1]] <- c(args[[1]], list(type = 'CJS', model = list(p~t, phi~t)))
args[[2]] <- c(args[[2]], list(type = 'JSSAbCL', model = list(p~t, phi~t, b~t)))
args[[3]] <- c(args[[3]], list(type = 'JSSAfCL', model = list(p~t, phi~t, f~t)))
args[[4]] <- c(args[[4]], list(type = 'JSSAgCL', model = list(p~t, phi~t, gamma~t)))
args[[5]] <- c(args[[5]], list(type = 'JSSAlCL', model = list(p~t, phi~t, lambda~t)))
args[[6]] <- c(args[[6]], list(type = 'JSSAb', model = list(p~t, phi~t, b~t)))
args[[7]] <- c(args[[7]], list(type = 'JSSAf', model = list(p~t, phi~t, f~t)))
args[[8]] <- c(args[[8]], list(type = 'JSSAg', model = list(p~t, phi~t, gamma~t)))
args[[9]] <- c(args[[9]], list(type = 'JSSAl', model = list(p~t, phi~t, lambda~t)))
args[[10]] <- c(args[[10]], list(type = 'JSSAN', model = list(p~t, phi~t, N~t)))
fits <- par.openCR.fit(args, ncores = 5)
```

```
## Completed in 0.302 minutes at 12:46:43 29 Jun 2019
```

```
make.table(fits, parm = "p")
```

```
##          session
## model      2005    2006    2007    2008    2009
##   cjs                0.16891 0.22441 0.04917 0.18504
##   jssabCL 0.14886 0.13841 0.16420 0.08566 0.17676
##   jssafCL 0.14886 0.13841 0.16420 0.08566 0.17676
##   jssagCL 0.14886 0.13841 0.16421 0.08566 0.17676
##   jssalCL 0.14886 0.13841 0.16420 0.08566 0.17676
##   jssab    0.14886 0.13841 0.16420 0.08566 0.17676
##   jssaf    0.14886 0.13841 0.16420 0.08566 0.17676
##   jssag    0.14886 0.13841 0.16420 0.08566 0.17676
##   jssal    0.14886 0.13841 0.16420 0.08566 0.17676
##   jssaN    0.14886 0.13841 0.16420 0.08566 0.17676
```

```
make.table(fits, parm = "phi")
```

```
##          session
## model      2005    2006    2007    2008    2009
##   cjs        0.6512 0.5308 0.4387 0.3377
##   jssabCL 0.6780 0.5600 0.3348 0.3784
##   jssafCL 0.6780 0.5600 0.3348 0.3784
##   jssagCL 0.6780 0.5600 0.3348 0.3784
##   jssalCL 0.6780 0.5600 0.3348 0.3784
##   jssab    0.6780 0.5600 0.3348 0.3784
##   jssaf    0.6780 0.5600 0.3348 0.3784
##   jssag    0.6780 0.5600 0.3348 0.3784
##   jssal    0.6780 0.5600 0.3348 0.3784
##   jssaN    0.6780 0.5600 0.3348 0.3784
```

All parameterizations of the JSSA model yield exactly the same estimates of p and ϕ .

For later reference, fit a nonspatial model with constant p and λ :

```
fitns <- openCR.fit(ovenCHp, type = 'JSSA1CL', model = phi ~ t)
predict(fitns)
```

```
## $p
##   session estimate SE.estimate   lcl   ucl
## 2005     1  0.1411     0.0124 0.1185 0.1672
## 2006     2  0.1411     0.0124 0.1185 0.1672
## 2007     3  0.1411     0.0124 0.1185 0.1672
## 2008     4  0.1411     0.0124 0.1185 0.1672
## 2009     5  0.1411     0.0124 0.1185 0.1672
##
## $phi
##   session estimate SE.estimate   lcl   ucl
## 2005     1  0.6327     0.10943 0.4063 0.8126
## 2006     2  0.5178     0.09646 0.3349 0.6960
## 2007     3  0.2815     0.08789 0.1432 0.4787
## 2008     4  0.5149     0.12646 0.2824 0.7412
## 2009     5      NA          NA     NA     NA
##
## $lambda
##   session estimate SE.estimate   lcl   ucl
## 2005     1  0.9551     0.06968 0.8279 1.102
## 2006     2  0.9551     0.06968 0.8279 1.102
## 2007     3  0.9551     0.06968 0.8279 1.102
## 2008     4  0.9551     0.06968 0.8279 1.102
## 2009     5      NA          NA     NA     NA
```

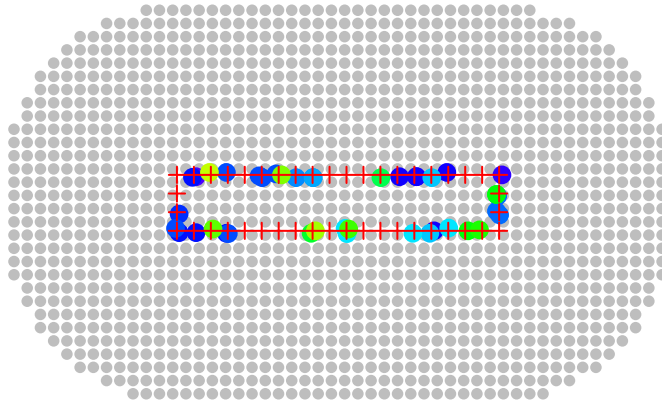
3.2.3 Spatial analysis

For spatial analyses we need to define a habitat mask; this represents the extent of relevant habitat.

```
par(mar = c(2,2,2,2))
ovenCHR <- rotate(ovenCHp, 90) # rotate for horizontal plot
nets <- traps(ovenCHR)[[1]]
msk <- make.mask(nets, buffer = 300, nx = 50, type = "trapbuffer")
plot(msk)
plot(ovenCHR[[1]], add = TRUE)
plot(nets, tracks = TRUE, add = TRUE)
```

2005

9 occasions, 41 detections, 20 animals



Now we can perform a spatial analysis equivalent to fits. This takes much longer to fit.

```
msh <- make.mask(traps(ovenCHp[[1]]), buffer = 300, nx = 25, type = "trapbuffer")
fitsp <- openCR.fit(ovenCHp, type = 'JSSAseclL', model = lambda0-t, mask = msh)
```

```
predict(fitsp)
```

```
## $lambda0
##      session estimate SE.estimate    lcl    ucl
## 2005         1  0.01970   0.004373 0.01275 0.03044
## 2006         2  0.02077   0.004012 0.01422 0.03033
## 2007         3  0.02983   0.005970 0.02015 0.04416
## 2008         4  0.01655   0.004229 0.01003 0.02731
## 2009         5  0.02211   0.006451 0.01248 0.03917
##
## $phi
##      session estimate SE.estimate    lcl    ucl
## 2005         1   0.5324   0.06202 0.4114 0.6498
## 2006         2   0.5324   0.06202 0.4114 0.6498
## 2007         3   0.5324   0.06202 0.4114 0.6498
## 2008         4   0.5324   0.06202 0.4114 0.6498
## 2009         5      NA      NA      NA      NA
##
## $lambda
##      session estimate SE.estimate    lcl    ucl
## 2005         1   0.9683   0.07757 0.8276 1.133
## 2006         2   0.9683   0.07757 0.8276 1.133
## 2007         3   0.9683   0.07757 0.8276 1.133
## 2008         4   0.9683   0.07757 0.8276 1.133
## 2009         5      NA      NA      NA      NA
##
## $sigma
##      session estimate SE.estimate    lcl    ucl
## 2005         1   99.55     7.423 86.01 115.2
## 2006         2   99.55     7.423 86.01 115.2
```



```
## 2007      3    99.55      7.423 86.01 115.2
## 2008      4    99.55      7.423 86.01 115.2
## 2009      5    99.55      7.423 86.01 115.2
```

Notice that the estimate of sigma is larger than for models fitted to the succession of closed populations using `secl.fit`. For example

```
collate(ovenbird.model.1)[,,'sigma']
```

```
##           estimate SE.estimate  lcl  ucl
## session=2005    78.58      6.386 67.02 92.12
## session=2006    78.58      6.386 67.02 92.12
## session=2007    78.58      6.386 67.02 92.12
## session=2008    78.58      6.386 67.02 92.12
## session=2009    78.58      6.386 67.02 92.12
```

We attribute this to year-to-year shifts in activity centre that inflate sigma for the open population model. Next we fit a model that allows birds to shift their home ranges from year to year using either a bivariate normal or exponential kernel. We can save a little time by starting at the estimates from the previous model.

```
fitsp2 <- openCR.fit(ovenCHp, type = 'JSSAseclCL', model = lambda0~t, mask = msk,
                    movementmodel = 'normal')
```

```
fitsp3 <- openCR.fit(ovenCHp, type = 'JSSAseclCL', model = lambda0~t, mask = msk,
                    movementmodel = 'exponential')
```

```
ocr <- openCRlist(static = fitsp, normal = fitsp2, exponential = fitsp3)
AIC(ocr)
```

```
##           model npar rank logLik  AIC AICc  dAIC
## static          lambda0~t phi~1 lambda~1 sigma~1      8   8 -1446 2908 2910 0.000
## normal          lambda0~t phi~1 lambda~1 sigma~1 move.a~1  9   8 -1447 2911 2914 3.236
## exponential      lambda0~t phi~1 lambda~1 sigma~1 move.a~1  9   9 -1447 2913 2916 4.853
##           AICwt
## static          0.7772
## normal          0.1541
## exponential      0.0687
```

Modelling between-year movement does not improve fit, and the scale of movement in the bivariate normal model could not be estimated (rank less than number of parameters). We therefore emphasise the static model, but for illustration also consider the exponential model.

```
make.table(ocr[-2], 'lambda0')
```

```
##           session
## model          2005  2006  2007  2008  2009
## fits.static    0.01970 0.02077 0.02983 0.01655 0.02211
## fits.exponential 0.02775 0.02633 0.03430 0.01609 0.02652
```

```
make.table(ocr[-2], 'lambda0', 'SE.estimate')
```

```
##           session
## model          2005  2006  2007  2008  2009
## fits.static    0.004373 0.004012 0.005970 0.004229 0.006451
## fits.exponential 0.007096 0.005844 0.007251 0.004595 0.007474
```

```
make.table(ocr[-2], 'sigma')
```

```
##           session
## model          2005  2006  2007  2008  2009
```

```
## fits.static      99.55 99.55 99.55 99.55 99.55
## fits.exponential 87.09 87.09 87.09 87.09 87.09
```

```
make.table(ocr[-2], 'sigma', 'SE.estimate')
```

```
##                session
## model          2005 2006 2007 2008 2009
## fits.static    7.423 7.423 7.423 7.423 7.423
## fits.exponential 8.386 8.386 8.386 8.386 8.386
```

The estimate of sigma is now more in line with that from the closed-population models. Interestingly, the constant survival rate has increased considerably. It would be rash to claim this fully accounts for the emigration component of apparent survival, but it may be getting close.

```
make.table(ocr[-2], 'phi')
```

```
##                session
## model          2005 2006 2007 2008 2009
## fits.static    0.5324 0.5324 0.5324 0.5324
## fits.exponential 0.5646 0.5646 0.5646 0.5646
```

```
make.table(ocr[-2], 'phi', 'SE.estimate')
```

```
##                session
## model          2005 2006 2007 2008 2009
## fits.static    0.06202 0.06202 0.06202 0.06202
## fits.exponential 0.06021 0.06021 0.06021 0.06021
```

3.3 Orongorongo Valley possums robust design

Brush-tail possums *Trichosurus vulpecula* were trapped from 1980–2006 according to a robust-design scheme with three primary sessions per year (nominally February, June and September). There is a single annual birth pulse in May; young are carried in the mother’s pouch through about October–November and ride on the mother’s back for some weeks after leaving the pouch. The three samples therefore correspond to post-independence (February), early pouch phase (June) and late pouch phase (September).

The dataset OVpossumCH in `secr` includes data for the six sessions in 1996 and 1997 (sessions 49–54). The population was at high density at this time.

3.3.1 Data summary

```
summary(OVpossumCH, terse = TRUE)
```

```
##           49  50  51  52  53  54
## Occasions    5   5   5   5   5   5
## Detections 450 494 328 383 372 375
## Animals     223 206 148 162 154 135
## Detectors   167 167 167 167 167 167
```

```
m.array(OVpossumCH)
```

```
##      R  50  51  52  53  54 NRecap
## 49 220 167   9   4   3   0     37
## 50 203   130  11   3   0     59
## 51 147     124   3   0     20
## 52 162     135   4     23
```

```
## 53 154          126    28
## 54 134          134
```

3.3.2 Analysis

Construct a habitat mask, using a forest map to exclude riverbed.

```
ovtrap <- traps(OVpossumCH[[1]])
if (!requireNamespace('rgdal')) stop ("this example requires package rgdal")
```

```
## Loading required namespace: rgdal
```

```
datadir <- system.file("extdata", package = "secr")
OVforest <- rgdal::readOGR(dsn = datadir, layer = "OVforest")
```

```
## OGR data source with driver: ESRI Shapefile
## Source: "C:\R\R-3.5.1\library\secr\extdata", layer: "OVforest"
## with 3 features
## It has 2 fields
```

```
ovmask <- make.mask(ovtrap, buffer = 120, type = 'trapbuffer',
  poly = OVforest[1:2,], spacing = 15, keep.poly = FALSE)
ovmask2 <- make.mask(ovtrap, buffer = 200, type = 'trapbuffer',
  poly = OVforest[1:2,], spacing = 15, keep.poly = FALSE)
intervals(OVpossumCH) <- c(123, 91, 154, 118, 85)/365 # annual
```

Fit three models, two with season as a covariate. Intervals were not included in the `secr` dataset, so we sneak them in here. Sexes and ages are pooled.

```
baseargs <- list(capthist = 'OVpossumCH', mask = ovmask, type = 'JSSAsecrfCL',
  sessioncov = c(1,2,3,1,2,3))
args <- rep(list(baseargs), 3)
names(args) <- c('null', 'seasonal.phi.f', 'seasonal.lambda0.phi.f')
args[[1]]$model <- list(lambda0~1, phi~1, f~1)
args[[2]]$model <- list(lambda0~1, phi~scov, f~scov)
args[[3]]$model <- list(lambda0~scov, phi~scov, f~scov)
fits <- par.openCR.fit(args, ncores = 3)
```

```
## Completed in 16.96 minutes at 13:17:15 29 Jun 2019
```

```
AIC(fits)
```

```
##
##                                model npar rank logLik  AIC  AICc
## seasonal.lambda0.phi.f lambda0~scov phi~scov f~scov sigma~1    7    7 -12460 24934 24935
## null                                lambda0~1 phi~1 f~1 sigma~1    4    4 -12464 24936 24936
## seasonal.phi.f                    lambda0~1 phi~scov f~scov sigma~1    6    6 -12464 24940 24940
##                                dAIC  AICwt
## seasonal.lambda0.phi.f 0.000 0.6430
## null                    1.434 0.3139
## seasonal.phi.f          5.408 0.0430
```

```
predict(fits)
```

```
## $null
## $null$lambda0
##   session estimate SE.estimate    lcl    ucl
## 49     1  0.0812    0.002531 0.07639 0.08632
## 50     2  0.0812    0.002531 0.07639 0.08632
```

```

## 51      3  0.0812    0.002531 0.07639 0.08632
## 52      4  0.0812    0.002531 0.07639 0.08632
## 53      5  0.0812    0.002531 0.07639 0.08632
## 54      6  0.0812    0.002531 0.07639 0.08632
##
## $null$phi
##   session estimate SE.estimate   lcl   ucl
## 49      1  0.6235     0.02744 0.5684 0.6756
## 50      2  0.6235     0.02744 0.5684 0.6756
## 51      3  0.6235     0.02744 0.5684 0.6756
## 52      4  0.6235     0.02744 0.5684 0.6756
## 53      5  0.6235     0.02744 0.5684 0.6756
## 54      6      NA         NA     NA     NA
##
## $null$f
##   session estimate SE.estimate   lcl   ucl
## 49      1  0.1043     0.02002 0.0716 0.1519
## 50      2  0.1043     0.02002 0.0716 0.1519
## 51      3  0.1043     0.02002 0.0716 0.1519
## 52      4  0.1043     0.02002 0.0716 0.1519
## 53      5  0.1043     0.02002 0.0716 0.1519
## 54      6      NA         NA     NA     NA
##
## $null$sigma
##   session estimate SE.estimate   lcl   ucl
## 49      1   36.13     0.4428 35.27 37.01
## 50      2   36.13     0.4428 35.27 37.01
## 51      3   36.13     0.4428 35.27 37.01
## 52      4   36.13     0.4428 35.27 37.01
## 53      5   36.13     0.4428 35.27 37.01
## 54      6   36.13     0.4428 35.27 37.01
##
##
## $seasonal.phi.f
## $seasonal.phi.f$lambda0
##   session scov estimate SE.estimate   lcl   ucl
## 49      1    1  0.08123    0.002539 0.0764 0.08636
## 50      2    2  0.08123    0.002539 0.0764 0.08636
## 51      3    3  0.08123    0.002539 0.0764 0.08636
## 52      4    1  0.08123    0.002539 0.0764 0.08636
## 53      5    2  0.08123    0.002539 0.0764 0.08636
## 54      6    3  0.08123    0.002539 0.0764 0.08636
##
## $seasonal.phi.f$phi
##   session scov estimate SE.estimate   lcl   ucl
## 49      1    1  0.6205     0.04092 0.5377 0.6968
## 50      2    2  0.6241     0.02819 0.5675 0.6776
## 51      3    3  0.6277     0.05105 0.5236 0.7212
## 52      4    1  0.6205     0.04092 0.5377 0.6968
## 53      5    2  0.6241     0.02819 0.5675 0.6776
## 54      6    3      NA         NA     NA     NA
##
## $seasonal.phi.f$f
##   session scov estimate SE.estimate   lcl   ucl

```

```

## 49      1      1      0.1076      0.03453 0.05737 0.2018
## 50      2      2      0.1043      0.02002 0.07158 0.1519
## 51      3      3      0.1011      0.03496 0.05132 0.1991
## 52      4      1      0.1076      0.03453 0.05737 0.2018
## 53      5      2      0.1043      0.02002 0.07158 0.1519
## 54      6      3          NA          NA      NA      NA
##
## $seasonal.phi.f$sigma
##      session scov estimate SE.estimate      lcl      ucl
## 49      1      1      36.13      0.4428 35.27 37.01
## 50      2      2      36.13      0.4428 35.27 37.01
## 51      3      3      36.13      0.4428 35.27 37.01
## 52      4      1      36.13      0.4428 35.27 37.01
## 53      5      2      36.13      0.4428 35.27 37.01
## 54      6      3      36.13      0.4428 35.27 37.01
##
##
## $seasonal.lambda0.phi.f
## $seasonal.lambda0.phi.f$lambda0
##      session scov estimate SE.estimate      lcl      ucl
## 49      1      1      0.07552      0.003149 0.06959 0.08195
## 50      2      2      0.08152      0.002552 0.07666 0.08668
## 51      3      3      0.08799      0.003735 0.08096 0.09562
## 52      4      1      0.07552      0.003149 0.06959 0.08195
## 53      5      2      0.08152      0.002552 0.07666 0.08668
## 54      6      3      0.08799      0.003735 0.08096 0.09562
##
## $seasonal.lambda0.phi.f$phi
##      session scov estimate SE.estimate      lcl      ucl
## 49      1      1      0.6136      0.04091 0.5310 0.6901
## 50      2      2      0.6227      0.02821 0.5660 0.6762
## 51      3      3      0.6317      0.05090 0.5276 0.7248
## 52      4      1      0.6136      0.04091 0.5310 0.6901
## 53      5      2      0.6227      0.02821 0.5660 0.6762
## 54      6      3          NA          NA      NA      NA
##
## $seasonal.lambda0.phi.f$f
##      session scov estimate SE.estimate      lcl      ucl
## 49      1      1      0.08583      0.03376 0.03971 0.1855
## 50      2      2      0.09753      0.02014 0.06507 0.1462
## 51      3      3      0.11083      0.03825 0.05635 0.2180
## 52      4      1      0.08583      0.03376 0.03971 0.1855
## 53      5      2      0.09753      0.02014 0.06507 0.1462
## 54      6      3          NA          NA      NA      NA
##
## $seasonal.lambda0.phi.f$sigma
##      session scov estimate SE.estimate      lcl      ucl
## 49      1      1      36.12      0.4426 35.26 37
## 50      2      2      36.12      0.4426 35.26 37
## 51      3      3      36.12      0.4426 35.26 37
## 52      4      1      36.12      0.4426 35.26 37
## 53      5      2      36.12      0.4426 35.26 37
## 54      6      3      36.12      0.4426 35.26 37

```

```

nonspOV <- openCR.fit(OVpossumCH, type = 'JSSAfCL', model = list(p~t, phi~t, f~t))
spOV <- openCR.fit(OVpossumCH, type = 'JSSAsecrfCL', model = list(lambda0~t, phi~t, f~t),
  mask = ovmask)
spmOV2 <- openCR.fit(OVpossumCH, type = 'JSSAsecrfCL',
  model = list(lambda0~t, phi~t, f~t, move.a~t),
  movementmodel = 'normal', mask = ovmask2, method = 'Nelder-Mead')
spmOV <- openCR.fit(OVpossumCH, type = 'JSSAsecrfCL',
  model = list(lambda0~t, phi~t, f~t, move.a~t),
  movementmodel = 'normal', mask = ovmask2)
save(spOV, spmOV, spmOV2, nonspOV, file = paste0(testdir, 'spOV.RData'))

```

```

load(paste0(testdir, 'spOV.RData'))
# format tables of results
formatOV <- function(ocrlist = list(nonspOV, spOV, spmOV), parm = 'phi', fmt = '%5.3f') {
  formatest <- function () {
    est <- sprintf(fmt, t(make.table(ocrlist, parm = parm, fields = 'estimate'))
    SE <- sprintf(fmt, t(make.table(ocrlist, parm = parm, fields = 'SE.estimate'))
    SE <- paste0 ('(', SE, ')')
    paste(est, SE)
  }
  m1 <- matrix(t(apply(matrix(formatest(), ncol = 3),1,paste, collapse = ' & ')), ncol = 1)
  m2 <- cbind(c('1996',' ',' ','1997',' ',' '), rep(c('Feb','Jun','Sep'),2),
    1:6, m1)
  m3 <- apply(m2, 1, paste, collapse = ' & ')
  out <- sapply(m3, cat, '\\\\ \\n')
}
formatOV(parm = 'phi')

```

```

## 1996 & Feb & 1 & 0.606 (0.055) & 0.613 (0.056) & 0.595 (0.058) \\
##      & Jun & 2 & 0.310 (0.051) & 0.333 (0.053) & 0.295 (0.052) \\
##      & Sep & 3 & 0.734 (0.054) & 0.754 (0.053) & 0.749 (0.055) \\
## 1997 & Feb & 4 & 0.655 (0.063) & 0.821 (0.060) & 0.799 (0.062) \\
##      & Jun & 5 & 0.456 (0.075) & 0.644 (0.093) & 0.616 (0.092) \\
##      & Sep & 6 &    NA (  NA) &    NA (  NA) &    NA (  NA) \\

```

```
formatOV(parm = 'f')
```

```

## 1996 & Feb & 1 & 0.175 (0.081) & 0.124 (0.071) & 0.149 (0.070) \\
##      & Jun & 2 & 0.063 (0.029) & 0.035 (0.022) & 0.028 (0.019) \\
##      & Sep & 3 & 0.287 (0.073) & 0.177 (0.061) & 0.176 (0.063) \\
## 1997 & Feb & 4 & 0.127 (0.050) & 0.030 (0.034) & 0.036 (0.039) \\
##      & Jun & 5 & 0.070 (0.037) & 0.019 (0.021) & 0.024 (0.025) \\
##      & Sep & 6 &    NA (  NA) &    NA (  NA) &    NA (  NA) \\

```

```
formatOV(parm = 'lambda0', fmt = '%5.3f')
```

```

## 1996 & Feb & 1 &    NA (  NA) & 0.062 (0.004) & 0.071 (0.004) \\
##      & Jun & 2 &    NA (  NA) & 0.080 (0.004) & 0.092 (0.005) \\
##      & Sep & 3 &    NA (  NA) & 0.069 (0.004) & 0.079 (0.005) \\
## 1997 & Feb & 4 &    NA (  NA) & 0.091 (0.005) & 0.102 (0.006) \\
##      & Jun & 5 &    NA (  NA) & 0.093 (0.005) & 0.105 (0.006) \\
##      & Sep & 6 &    NA (  NA) & 0.112 (0.007) & 0.127 (0.008) \\

```

```
formatOV(parm = 'move.a', fmt = '%4.1f')
```

```
## 1996 & Feb & 1 &    NA (  NA) &    NA (  NA) & 5.8 ( 1.0) \\
```

```
##      & Jun & 2 &   NA ( NA) &   NA ( NA) & 6.3 ( 1.2) \\
##      & Sep & 3 &   NA ( NA) &   NA ( NA) & 22.0 ( 2.2) \\
## 1997 & Feb & 4 &   NA ( NA) &   NA ( NA) & 13.2 ( 2.6) \\
##      & Jun & 5 &   NA ( NA) &   NA ( NA) & 6.6 ( 1.2) \\
##      & Sep & 6 &   NA ( NA) &   NA ( NA) &   NA ( NA) \\
```

```
make.table(list(nonspOV, spOV, spmOV), 'p')
```

```
##      session
## model      49      50      51      52      53      54
## fits1 0.3604 0.4349 0.3819 0.4417 0.4660 0.5447
## fits2
## fits3
```

```
make.table(list(nonspOV, spOV, spmOV), 'sigma')
```

```
##      session
## model      49      50      51      52      53      54
## fits1
## fits2 36.13 36.13 36.13 36.13 36.13 36.13
## fits3 33.67 33.67 33.67 33.67 33.67 33.67
```

```
make.table(list(nonspOV, spOV, spmOV), 'sigma', 'SE.estimate')
```

```
##      session
## model      49      50      51      52      53      54
## fits1
## fits2 0.4428 0.4428 0.4428 0.4428 0.4428 0.4428
## fits3 0.4631 0.4631 0.4631 0.4631 0.4631 0.4631
```

```
AIC(spOV, spmOV)
```

```
##      model npar rank logLik  AIC  AICc  dAIC  AICwt
## spmOV lambda0~t phi~t f~t sigma~1 move.a~t  22  22 -12357 24759 24762 0.00  1
## spOV      lambda0~t phi~t f~t sigma~1  17  17 -12400 24834 24836 75.47  0
```

4 References

- Bishop, J. A., Cook, L. M., and Muggleton, J. (1978). The response of two species of moth to industrialization in northwest England. II. Relative fitness of morphs and population size. *Philosophical Transactions of the Royal Society of London* **B281**, 517–540.
- Crosbie, S. F. (1979) *The mathematical modelling of capture–mark–recapture experiments on animal populations*. Ph.D. Thesis, University of Otago, Dunedin, New Zealand.
- Crosbie, S. F. and Manly, B. F. J. (1985) Parsimonious modelling of capture–mark–recapture studies. *Biometrics* **41**, 385–398.
- Ergon, T., Ergon, R., Begon, M., Telfer, S. and Lambin, X. (2011) Delayed density- dependent onset of spring reproduction in a fluctuating population of field voles. *Oikos* **120**, 934–940.
- Ergon, T. and Lambin, X. (2013) Data from: Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. Dryad Digital Repository. doi: 10.5061/dryad.r17n5
- Ergon, T. and Gardner, B. (2014) Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution* **5**, 1327–1336.

- Laake, J.L., Johnson, D. S. and Conn, P.B. (2013) marked: An R package for maximum-likelihood and MCMC analysis of capture-recapture data. *Methods in Ecology and Evolution* **4**, 885–890.
- Lebreton, J.-D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118.
- Link, W. A. and Barker, R. J. (2005) Modeling association among demographic parameters in analysis of open-population capture–recapture data. *Biometrics* **61**, 46–54.
- Link, W. A. and Barker, R. J. (2010) *Bayesian Inference with Ecological Applications*. Academic Press, Amsterdam.
- Marzolin, G. (1988) Polygynie du Cincle plongeur (*Cinclus cinclus*) dans les côtes de Lorraine. L’Oiseau et la Revue Francaise d’Ornithologie 58:277-286.
- Nichols, J. D., Pollock, K. H. and Hines, J. E (1984) The use of a robust capture–recapture design in small mammal population studies: a field example with *Microtus pennsylvanicus*. *Acta Theriologica* **29**, 357–365.
- Pledger, S., Pollock, K. H. and Norris, J. L. (2010) Open capture–recapture models with heterogeneity: II. Jolly-Seber model. *Biometrics* **66**, 883–890.
- Pollock, K. H., Nichols, J. D., Brownie, C. and Hines, J. E. (1990) Statistical inference for capture–recapture experiments. *Wildlife Monographs* **107**. 97pp.
- Pradel, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* **52**, 703–709.
- Schwarz, C. J. and Arnason, A. N. (1996) A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* **52**, 860–873.
- Schofield, M. and Barker, R. (2016) 50-year-old curiosities: ancillarity and inference in capture–recapture models. *Statistical Science* **31**, 161–174.
- Seber, G. A. F. (1982) *The estimation of animal abundance and related parameters*. 2nd edition. Griffin.
- Williams, B. K., Nichols, J. D. and Conroy, M. J. (2002) *Analysis and management of animal populations*. Academic Press, San Diego.