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NOTES AND COMMENTS

Dealing with many correlated covariates in capture–recapture models

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Abstract Capture–recapture models for estimating demographic parameters allow covariates to be incorporated to better understand population dynamics. However, high-dimensionality and multicollinearity can hamper estimation and inference. Principal component analysis is incorporated within capture–recapture models and used to reduce the number of predictors into uncorrelated synthetic new variables. Principal components are selected by sequentially assessing their statistical significance. We provide an example on seabird survival to illustrate our approach. Our method requires standard statistical tools, which permits an efficient and easy implementation using standard software.

Keywords Animal demography · Population dynamics · Principal-component capture–recapture model · Snow petrel · Survival estimation

Introduction

Capture–recapture (CR) methods (e.g., Lebreton et al. 1992) are widely used for assessing the effect of explanatory variables on demographic parameters such as survival (Pollock 2002). Generally however, complex situations arise where multiple covariates are required to capture patterns in survival. In such situations, one usually favors a multiple regression-like CR modeling framework that is however hampered by two issues: first, because it increases the number of parameters to be estimated, incorporating many covariates results in a loss of statistical power and a decrease in the precision of parameter estimates; second, correlation among the set of predictors—aka multicollinearity—may alter interpretation (see below).

To overcome these two issues, Grosbois et al. (2008) recommended to perform a principal component analysis (PCA) on the set of explanatory variables before fitting CR models. PCA is a multivariate technique that explains the variability of a set of variables in terms of a *reduced* set of *uncorrelated* linear combinations of such variables—aka principal components (PCs)—while maximizing the variance (Jolliffe 2002). Grosbois et al. (2008) then expressed survival as a function of the PCs that explained most of the variance in the set of original covariates, typically the first one or the first two ones.

However, the main drawback of this approach is that the PCs are selected based on covariates variation pattern alone, regardless of the response variable, and without guarantee that survival is most related to these PCs (Graham 2003). To deal with this issue in the context of logistic regression, Aguilera et al. (2006) proposed to test the significance of *all* PCs to decide which ones should be retained, instead of a priori relying on the PCs that explain most of the variation in the covariates.

In this paper, we implement the algorithm proposed by Aguilera et al. (2006) to deal with many possibly correlated covariates in CR models, a method we refer to as principal component capture–recapture (P2CR). We apply this new approach to a case study on survival of Snow petrels

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(*Pagodroma nivea*) that is possibly affected by climatic conditions. In this example, the issue of multicollinearity occurs, and summarizing the set of covariates in a subset of lower dimension is also crucial to get precise survival estimates. Overall, P2CR models can be fitted with statistical programs that perform PCA and CR data analysis. The data and R code are available from GitHub at https://github.com/oliviergimenez/p2cr.

Methods

We used capture–recapture (CR) models to study open populations over K capture occasions to estimate the probability ϕ_i ($i=1, \ldots, K-1$) that an individual survives to occasion $i+1$ given that it is alive at time i, along with the probability p_j ($j=2, \ldots, K$) that an individual is recaptured at time j—aka as the Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992). Covariates were incorporated in survival probabilities using a linear-logistic function:

$$\operatorname{logit}(\phi_i) = \log\left(\frac{\phi_i}{1-\phi_i}\right) = \alpha + \sum_{j=1}^{p} \beta_j X_{ij} \tag{1}$$

where α is the intercept parameter, X_{ij} is the value of covariate j ($j=1,\ldots, p$) in year i ($i=1,\ldots, K-1$), and β_j is its associated slope parameter. Covariates were standardized to avoid numerical instabilities. To assess the significance of a covariate in CR models, we used the analysis of deviance (ANODEV; Skalski et al. 1993) that compares the amount of deviance explained by this covariate with the amount of deviance not explained by this covariate, the CR model with fully time-dependent survival serving as a reference. The ANODEV test statistic is given by:

$$\text{ANODEV} = \frac{\text{Dev}(X) - \text{Dev(constant)}}{1} \bigg/ \frac{\text{Dev(time)} - \text{Dev}(X)}{K-1} \tag{2}$$

where Dev(constant), Dev(X) and Dev(time) stand for the deviance of models with constant, covariate-dependent and time-dependent survival probabilities. To obtain the associated P value, the value of the ANODEV is compared with the quantile of Fisher–Snedecor distribution with 1 and $K-1$ degrees of freedom.

To reduce the dimension of the set of covariates (X_1, …, X_p), we used PCA which aims at finding a small number of linear combinations of the original variables—the principal components (PCs)—while maximizing the variance in (X_1, …, X_p). Because the variables measurement units often differ, we performed the PCA on the correlation matrix (Jolliffe 2002). To select PCs, we used a forward model selection algorithm as proposed by Aguilera et al. (2006) for the logistic regression. The forward algorithm begins with no covariates in the model. Each PC is incorporated in simple linear regression-like CR models and the ANODEV P value calculated. The PC that has the lowest P value is added to the null model, say PC$_k$. Then the PCs that were not retained are incorporated along with PC$_k$ in multiple regression-like CR models, and ANODEV P values are calculated. In other words, we need to assess the effect of PC$_j$ for $j \neq k$ in the presence of PC$_k$ to decide whether PC$_j$ should be retained. To do so, Dev(constant) and Dev(X) are replaced by Dev(PC$_k$) and Dev(PC$_k$ + PC$_j$) in Eq. 2, where Dev(PC$_k$ + PC$_j$) is the deviance of the model with survival as a function of both principal components PC$_k$ and PC$_j$. We repeat the process until no remaining PC is selected.

All models were fitted using the maximum-likelihood method using MARK (White and Burnham 1999) called with R using package RMark (Laake 2013).

Case study

The Snow petrel is a medium sized Procellariiform species endemic to Antarctica that breeds in summer. Birds start to occupy breeding sites in early November, laying occurs in early December and chicks fledge in early March. This highly specialized species only forages within the pack-ice on crustaceans and fishes. Data on survival were obtained from a long-term CR study on Ile des Pétrels, Pointe Géologie Archipelago, Terre Adélie, Antarctica. We refer to Barbraud et al. (2000) for more details about data collection. We removed the first capture to limit heterogeneity among individuals, and worked with a total of 604 female capture histories from 1973 to 2002.

The following covariates were included to assess the effect of climatic conditions upon survival variation: sea ice extent (SIE; http://nsidc.org/data/seaice_index/); air temperature, which was obtained from the Météo France weather station at Dumont d'Urville, as a proxy for sea surface temperature; southern Oscillation Index (SOI) as a proxy for the overall climate condition (https://crudata.uea.ac.uk/cru/data/soi/). These environmental variables were averaged over seasonal time periods corresponding to the chick rearing period (January–March: summer period), the non-breeding period (April–June: autumn and July–September: winter), and the laying and incubation period of the same year (October–December: spring). In total, nine covariates were included in the analysis: sea ice extent in summer (SIEsummer), in autumn (SIEautumn), in winter (SIEwinter), in spring (SIEspring), annual SOI, air temperature in summer (Tsummer), in autumn (Tautumn), in winter (Twinter) and in spring (Tspring).

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Results

The CJS model poorly fitted the data ($\chi^2 = 221.2$, $df = 127$, $P < 0.01$), and a closer inspection of the results revealed that the lack of fit was explained by a trap-dependence effect (Test2CT, $\chi^2 = 103.1$, $df = 27$, $P < 0.01$). Consequently, we estimated two recapture probabilities that differed according to whether or not a recapture occurred the occasion before. By first attempting to simplify the structure of recapture probabilities, we were led to consider an additive effect of time and a trap effect (Electronic Supplementary material, ESM). Estimates of recapture probabilities ranged from 0.14 [standard error (SE) 0.07] to 0.79 (SE 0.09) when no recapture occurred the occasion before and from 0.25 (SE 0.18) to 0.89 (SE 0.09) when a recapture occurred the occasion before (ESM).

Because of multicollinearity, we were led to counter-intuitive estimates of regression parameters in the CR model including all covariates (ESM): the coefficient of SIE in autumn was estimated at 0.5 (SE 0.24) and that of SIE in winter was estimated at −0.5 (SE 0.21) while these two covariates were significantly positively correlated ($r_P = 0.67$, $P < 0.01$).

When we applied the P2CR approach, the algorithm selected two PCs, namely PC3 ($F_{1,27} = 7.34$, $P = 0.01$) at step 1 and PC4 ($F_{1,26} = 4.63$, $P = 0.04$) at step 2 (ESM), but never did we pick PC1 as we would have done using a classical approach (Grosbois et al. 2008). PC3 was positively correlated to SIE in summer and negatively correlated to temperature in winter, while PC4 was positively correlated to temperature in spring and negatively correlated to SIE in summer (ESM). Survival increased with increasing values of PC3 (Fig. 1), with high values of SIE in summer and low values of temperature in winter (resp. low values of SIE in summer and high values of temperature in winter) corresponding to high (resp. low) survival.

Survival decreased with increasing values of PC4 (Fig. 2), with high values of temperature in spring and low values of SIE in summer (resp. low values of temperature in spring and high values of SIE in summer) corresponding to low (resp. high) survival.

The P2CR approach also led to more precise survival estimates when compared to the model incorporating all original covariates (Fig. 3).

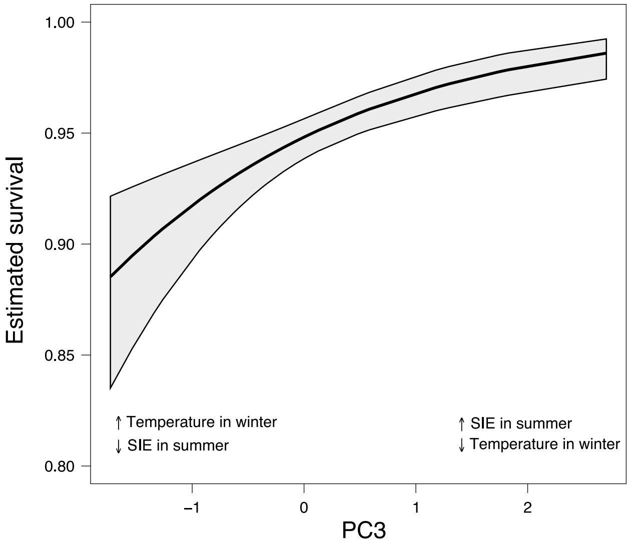

Fig. 1 Estimated survival of Snow petrel as a function of PC3 (*solid line*) with 95% confidence interval (*shaded area*). Low survival is associated with low values of PC3 that correspond to high values of air temperature in winter and low values of sea ice extent (SIE) in summer; high survival is associated with high values of PC3 that correspond to low values of air temperature in winter and high values of SIE in summer

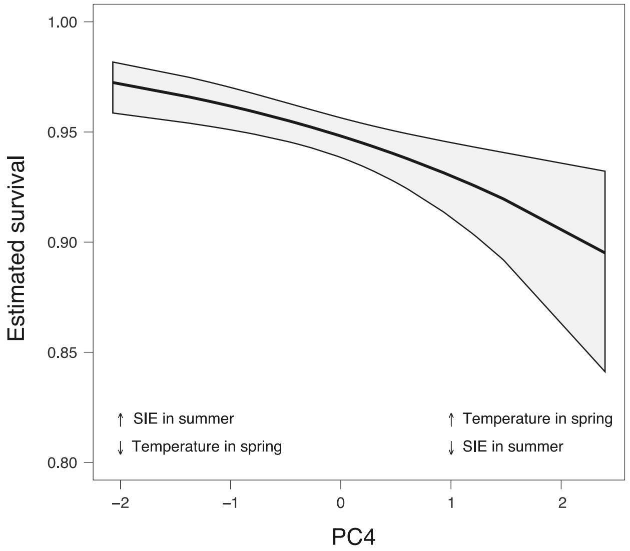

Fig. 2 Estimated survival of Snow petrel as a function of PC4 (*solid line*) with 95% confidence interval (*shaded area*). High survival is associated with low values of PC4 that correspond to low values of air temperature in spring and high values of sea ice extent (SIE) in summer; low survival is associated with high values of PC4 that correspond to high values of air temperature in spring and low values of SIE in summer

Discussion

We introduce a new approach combining principal component analysis and capture–recapture models to deal with many possibly correlated explanatory covariates. Our approach requires standard statistical tools, which allows an efficient and easy implementation using standard software.

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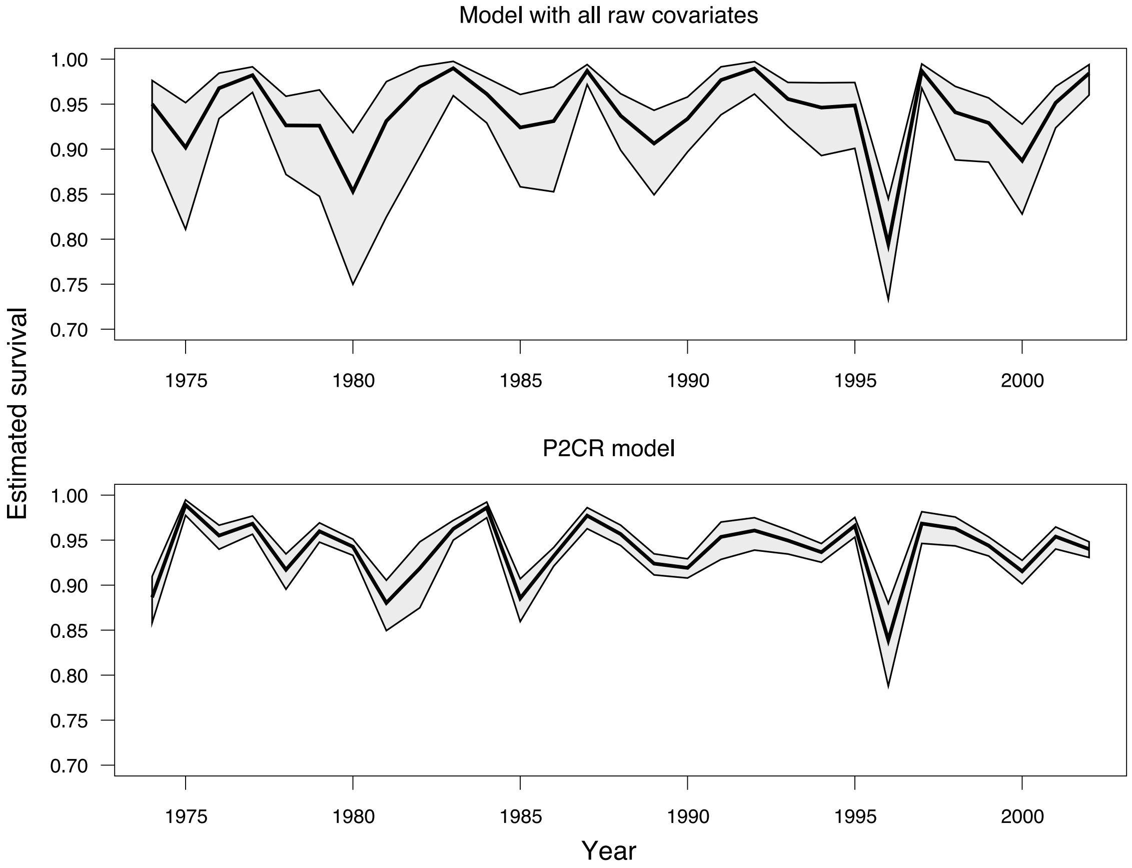

Fig. 3 Survival of Snow petrel over time as estimated from the model with all original covariates (*solid line, top panel*) vs. the PC2R model (*solid line, bottom panel*). 95% confidence intervals are also displayed (*shaded area*)

Snow petrels and climatic conditions

In summer, snow petrels exclusively forage within the pack-ice tens to hundreds of kilometers from the colony where they catch sea ice-associated species, such as Antarctic silverfish (*Pleuragramma antarcticum*) and Euphausiids, to feed their chick (Ridoux and Offredo 1989). This is an energetically demanding period for breeding adults and, during years with reduced sea-ice extent, food resources may be less abundant and snow petrels may be forced to cover larger distances to find suitable foraging habitats, with potential survival costs. Assuming air temperature was a proxy of sea surface temperature variations, the negative effect of warmer temperatures on survival is coherent with general patterns found between sea surface temperature and demographic parameters in seabirds (Barbraud et al. 2012). In many marine ecosystems warmer temperatures are associated with decreased primary production and food resources for top predators. Although the low survival in 1996 corresponded to a year with reduced sea-ice extent in summer, the drop in survival was high and remains unexplained at the moment.

Principal component CR models

When multiple covariates have to be considered to estimate survival, both issues of dimensionality and multicollinearity can lead to biased estimates, inflated precision as well as lack of statistical power. In such a context, the P2CR modeling framework has proved particularly useful in our example, mainly because few PCs were selected which were easily interpretable. We acknowledge that PCs with little interpretability might have been picked up by our method. To make the interpretation easier, PCA results can be post-processed by rotating axes to improve correlations between raw variables and PCs like in the varimax method (Kaiser 1958). Recent developments in the field of multivariate analyses could also be useful, like methods to handle with missing values in PCA (Dray and Josse 2015).

In statistical ecology, one of our objectives is to try and explain variation in state variables such as abundance, survival and the distribution of species. Dimension-reduction methods are promising to deal with many correlated covariates for the analysis of CR or occupancy data.

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Supplementary material for 'Dealing with many correlated covariates in capture-recapture models' by Gimenez and Barbraud.

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Introduction

We illustrate the principal component capture-recapture (P2CR) method for covariates selection in capture-recapture models using data on survival of Snow petrels in Pointe Géologie Archipelago, Terre Adélie, Antarctica. In total, the dataset consists of 604 female histories from 1973 to 2002. The objective is to investigate the effect of climatic conditions on adult survival.

Explore climatic covariates

First we explore the covariates sea ice extent in summer (SIE.Su), in autumn and winter (SIE.Au and SIE.Wi), in spring (SIE.Sp), annual southern oscillation index (SOI), air temperature in summer (T.Su), in autumn and winter (T.Au and T.Wi) and in spring (T.Sp).

Let us have a look to the correlations between these covariates:

```
cov <- read.table('cov-petrel.txt',header=T)
head(cov)
```

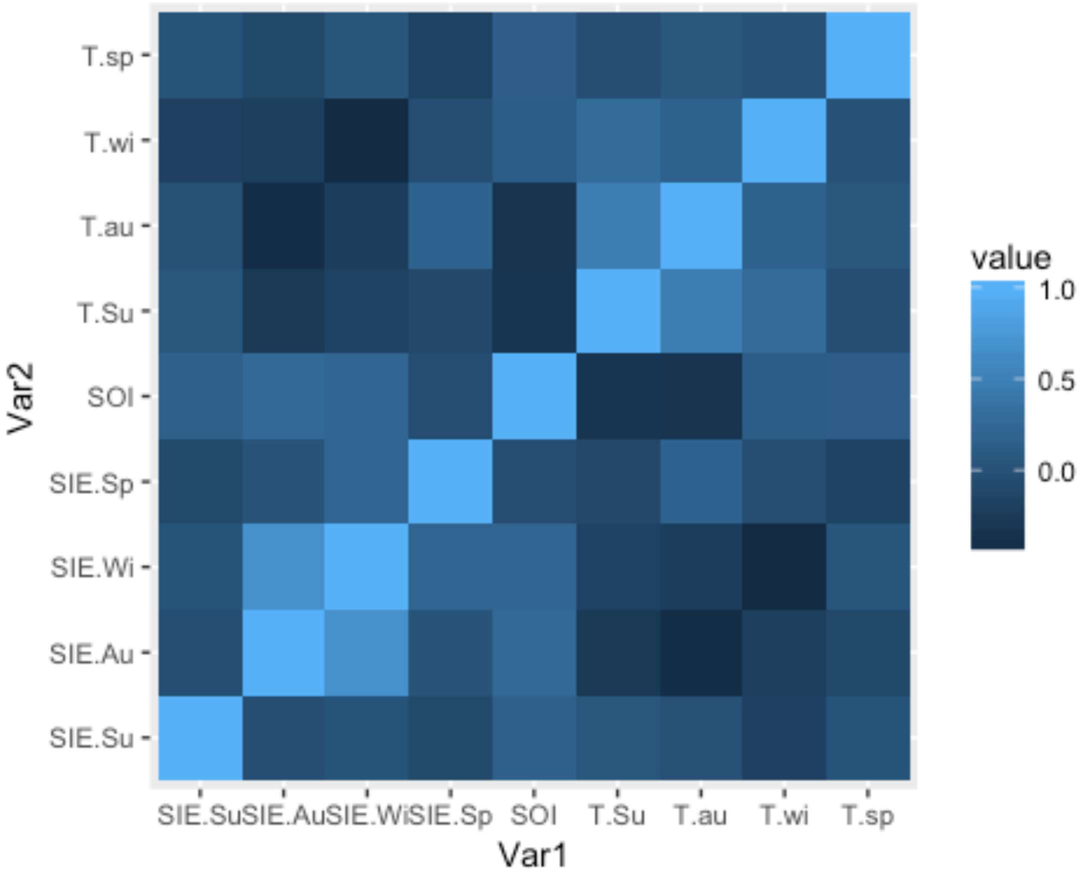
```
##   SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI      T.Su      T.au      T.wi
## 1      0    341    478    348  0.96 -5.233333 -14.98333 -17.01667
## 2    189    300    600    341  1.33 -4.150000 -15.08333 -17.85000
## 3     26    270    337    230  0.06 -5.033333 -16.51667 -16.51667
## 4     81    256    348    337 -1.14 -4.300000 -13.76667 -15.86667
## 5     22    207    389    437 -0.29 -4.716667 -14.30000 -15.63333
## 6    111    215    307    437 -0.26 -5.116667 -15.06667 -16.15000
##        T.sp
## 1 -6.700000
## 2 -7.250000
## 3 -7.683333
## 4 -7.650000
## 5 -7.916667
## 6 -6.766667
```

```
round(cor(cov),2)
```

```
##        SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI  T.Su  T.au  T.wi  T.sp
## SIE.Su   1.00  -0.05   0.01  -0.10  0.15  0.04 -0.02 -0.21  0.01
## SIE.Au  -0.05   1.00   0.67   0.02  0.26 -0.30 -0.43 -0.23 -0.12
## SIE.Wi    0.01   0.67   1.00   0.21  0.22 -0.18 -0.24 -0.47  0.04
## SIE.Sp   -0.10   0.02   0.21   1.00 -0.06 -0.11  0.19 -0.06 -0.18
## SOI       0.15   0.26   0.22  -0.06  1.00 -0.34 -0.37  0.13  0.14
## T.Su      0.04  -0.30  -0.18  -0.11 -0.34  1.00  0.47  0.27 -0.05
## T.au     -0.02  -0.43  -0.24   0.19 -0.37  0.47  1.00  0.17  0.06
## T.wi     -0.21  -0.23  -0.47  -0.06  0.13  0.27  0.17  1.00  0.00
## T.sp      0.01  -0.12   0.04  -0.18  0.14 -0.05  0.06  0.00  1.00
```

Visually, with a heatmap:

```
library(ggplot2)
library(reshape2)
qplot(x=Var1, y=Var2, data=melt(cor(cov)), fill=value, geom="tile")
```



What are the significant correlations?

```
library(psych)

corr.test(cov)

## Call:corr.test(x = cov)
## Correlation matrix
##         SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI  T.Su  T.au  T.wi  T.sp
## SIE.Su    1.00  -0.05   0.01  -0.10  0.15  0.04 -0.02 -0.21  0.01
## SIE.Au   -0.05   1.00   0.67   0.02  0.26 -0.30 -0.43 -0.23 -0.12
## SIE.Wi   0.01   0.67   1.00   0.21  0.22 -0.18 -0.24 -0.47  0.04
## SIE.Sp  -0.10   0.02   0.21   1.00 -0.06 -0.11  0.19 -0.06 -0.18
## SOI      0.15   0.26   0.22  -0.06  1.00 -0.34 -0.37  0.13  0.14
## T.Su     0.04  -0.30  -0.18  -0.11 -0.34  1.00  0.47  0.27 -0.05
## T.au    -0.02  -0.43  -0.24   0.19 -0.37  0.47  1.00  0.17  0.06
## T.wi    -0.21  -0.23  -0.47  -0.06  0.13  0.27  0.17  1.00  0.00
## T.sp     0.01  -0.12   0.04  -0.18  0.14 -0.05  0.06  0.00  1.00
## Sample Size 
## [1] 29
## Probability values (Entries above the diagonal are adjusted for multiple t
ests.) 
##        SIE.Su SIE.Au SIE.Wi SIE.Sp  SOI T.Su T.au T.wi T.sp
## SIE.Su   0.00   1.00   1.00   1.00 1.00 1.00 1.00 1.00    1
## SIE.Au   0.79   0.00   0.00   1.00 1.00 1.00 0.64 1.00    1
## SIE.Wi   0.96   0.00   0.00   1.00 1.00 1.00 1.00 0.37    1
## SIE.Sp   0.59   0.90   0.28   0.00 1.00 1.00 1.00 1.00    1
## SOI      0.43   0.17   0.25   0.77 0.00 1.00 1.00 1.00    1
## T.Su     0.83   0.12   0.35   0.56 0.07 0.00 0.33 1.00    1
## T.au     0.92   0.02   0.20   0.32 0.05 0.01 0.00 1.00    1
## T.wi     0.28   0.23   0.01   0.76 0.52 0.15 0.37 0.00    1
## T.sp     0.97   0.53   0.84   0.34 0.47 0.80 0.77 0.99    0
## 
##  To see confidence intervals of the correlations, print with the short=FAL
SE option
```

```
print(corr.test(cov),short=FALSE)
```

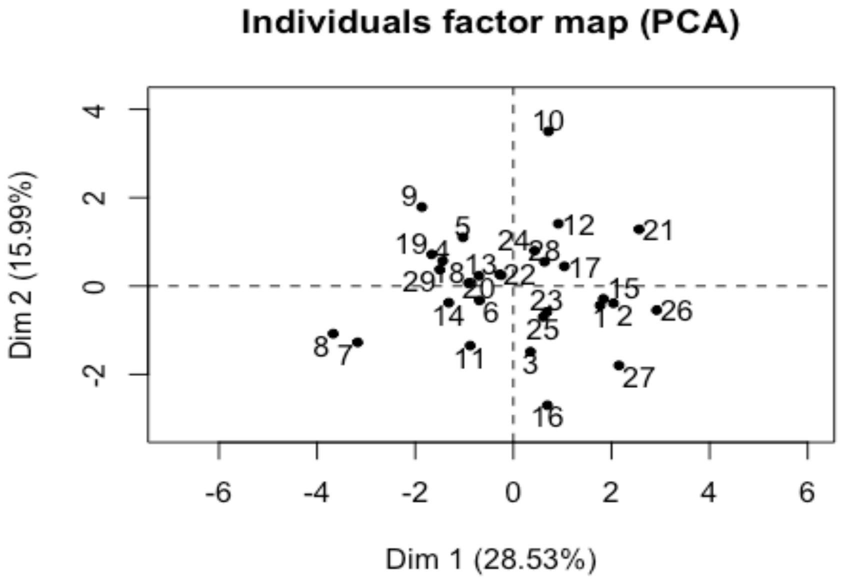
```
## Call:corr.test(x = cov)
## Correlation matrix 
##        SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI  T.Su  T.au  T.wi  T.sp
## SIE.Su   1.00  -0.05   0.01  -0.10  0.15  0.04 -0.02 -0.21  0.01
## SIE.Au  -0.05   1.00   0.67   0.02  0.26 -0.30 -0.43 -0.23 -0.12
## SIE.Wi   0.01   0.67   1.00   0.21  0.22 -0.18 -0.24 -0.47  0.04
## SIE.Sp  -0.10   0.02   0.21   1.00 -0.06 -0.11  0.19 -0.06 -0.18
## SOI      0.15   0.26   0.22  -0.06  1.00 -0.34 -0.37  0.13  0.14
## T.Su     0.04  -0.30  -0.18  -0.11 -0.34  1.00  0.47  0.27 -0.05
## T.au    -0.02  -0.43  -0.24   0.19 -0.37  0.47  1.00  0.17  0.06
## T.wi    -0.21  -0.23  -0.47  -0.06  0.13  0.27  0.17  1.00  0.00
## T.sp     0.01  -0.12   0.04  -0.18  0.14 -0.05  0.06  0.00  1.00
## Sample Size 
## [1] 29
## Probability values (Entries above the diagonal are adjusted for multiple t
ests.) 
##        SIE.Su SIE.Au SIE.Wi SIE.Sp  SOI T.Su T.au T.wi T.sp
## SIE.Su   0.00   1.00   1.00   1.00 1.00 1.00 1.00 1.00    1
## SIE.Au   0.79   0.00   0.00   1.00 1.00 1.00 0.64 1.00    1
## SIE.Wi   0.96   0.00   0.00   1.00 1.00 1.00 1.00 0.37    1
## SIE.Sp   0.59   0.90   0.28   0.00 1.00 1.00 1.00 1.00    1
## SOI      0.43   0.17   0.25   0.77 0.00 1.00 1.00 1.00    1
## T.Su     0.83   0.12   0.35   0.56 0.07 0.00 0.33 1.00    1
## T.au     0.92   0.02   0.20   0.32 0.05 0.01 0.00 1.00    1
## T.wi     0.28   0.23   0.01   0.76 0.52 0.15 0.37 0.00    1
## T.sp     0.97   0.53   0.84   0.34 0.47 0.80 0.77 0.99    0
##
##  To see confidence intervals of the correlations, print with the short=FAL
SE option
##
##  Confidence intervals based upon normal theory.  To get bootstrapped value
s, try cor.ci
##                lower     r upper    p
## SIE.Su-SIE.A  -0.41 -0.05  0.32 0.79
## SIE.Su-SIE.W  -0.36  0.01  0.38 0.96
## SIE.Su-SIE.Sp -0.45 -0.10  0.27 0.59
## SIE.Su-SOI    -0.23  0.15  0.49 0.43
## SIE.Su-T.Su   -0.33  0.04  0.40 0.83
## SIE.Su-T.au   -0.38 -0.02  0.35 0.92
## SIE.Su-T.wi   -0.53 -0.21  0.17 0.28
## SIE.Su-T.sp   -0.36  0.01  0.37 0.97
## SIE.A-SIE.W    0.40  0.67  0.83 0.00
## SIE.A-SIE.Sp  -0.35  0.02  0.39 0.90
## SIE.A-SOI     -0.12  0.26  0.57 0.17
## SIE.A-T.Su    -0.60 -0.30  0.08 0.12
## SIE.A-T.au    -0.69 -0.43 -0.08 0.02
## SIE.A-T.wi    -0.55 -0.23  0.15 0.23
## SIE.A-T.sp    -0.47 -0.12  0.26 0.53
## SIE.W-SIE.Sp  -0.17  0.21  0.53 0.28
## SIE.W-SOI     -0.16  0.22  0.54 0.25
## SIE.W-T.Su    -0.51 -0.18  0.20 0.35
## SIE.W-T.au    -0.56 -0.24  0.13 0.20
## SIE.W-T.wi    -0.71 -0.47 -0.12 0.01
## SIE.W-T.sp    -0.33  0.04  0.40 0.84
## SIE.Sp-SOI    -0.41 -0.06  0.32 0.77
## SIE.Sp-T.Su   -0.46 -0.11  0.26 0.56
## SIE.Sp-T.au   -0.19  0.19  0.52 0.32
## SIE.Sp-T.wi   -0.42 -0.06  0.31 0.76
## SIE.Sp-T.sp   -0.52 -0.18  0.20 0.34
## SOI-T.Su      -0.63 -0.34  0.03 0.07
## SOI-T.au      -0.65 -0.37  0.00 0.05
## SOI-T.wi      -0.25  0.13  0.47 0.52
## SOI-T.sp      -0.24  0.14  0.48 0.47
## T.Su-T.au      0.13  0.47  0.72 0.01
## T.Su-T.wi     -0.10  0.27  0.58 0.15
## T.Su-T.sp     -0.41 -0.05  0.32 0.80
## T.au-T.wi     -0.21  0.17  0.51 0.37
## T.au-T.sp     -0.32  0.06  0.41 0.77
## T.wi-T.sp     -0.37  0.00  0.37 0.99
```

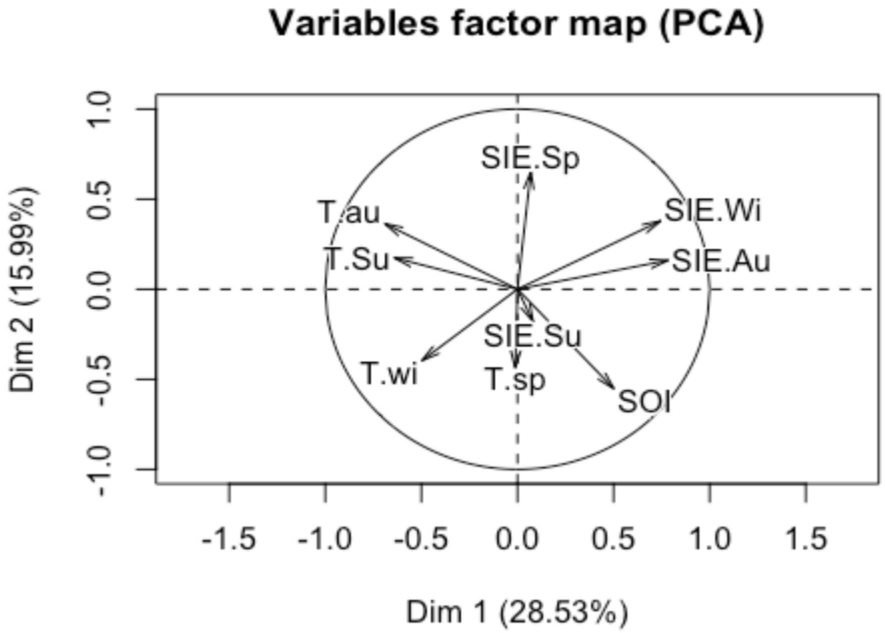
Seems like sea ice extent in autumn and winter are positively correlated, while sea ice extent in autumn and temperature in autumn are negatively correlated.

PCA on covariates

Let's perform a PCA on this set of covariates:

```
library(FactoMineR)
res.pca = PCA(cov,scale.unit=T,graph=T,ncp=9)
```





Find the covariates associated to each principal component:

```
dimdesc(res.pca,axes = 1:9)
```

```
## $Dim.1
## $Dim.1$quanti
##         correlation      p.value
## SIE.Au   0.7846343 4.703772e-07
## SIE.Wi   0.7444495 3.650675e-06
## SOI      0.5012694 5.604172e-03
## T.wi    -0.4966878 6.129402e-03
## T.Su    -0.6409107 1.798385e-04
## T.au    -0.6912833 3.291814e-05
##
##
## $Dim.2
## $Dim.2$quanti
##         correlation     p.value
## SIE.Sp   0.6505897 0.000132906
## SIE.Wi   0.3787178 0.042773054
## T.wi    -0.3960426 0.033438570
## T.sp    -0.4367718 0.017836263
## SOI     -0.5519112 0.001910053
##
##
## $Dim.3
## $Dim.3$quanti
##         correlation      p.value
## SIE.Su   0.7413696 4.205825e-06
## T.wi    -0.5808892 9.527347e-04
##
##
## $Dim.4
## $Dim.4$quanti
##         correlation      p.value
## T.sp     0.8228262 4.300265e-08
## SIE.Su  -0.3946619 3.411627e-02
##
##
## $Dim.5
## $Dim.5$quanti
##         correlation      p.value
## SIE.Sp   0.6329789 0.0002286769
## SOI      0.4046400 0.0294590693
## SIE.Su   0.4020185 0.0306294870
##
##
## $Dim.6
## $Dim.6$quanti
##       correlation     p.value
## T.Su   0.5642562 0.001431237
## T.wi   0.3861381 0.038548955
##
##
## $Dim.8
## NULL

#plot(res.pca)
```

Percentage of variance explained:

```
res.pca$eig[,3]

## [1]  28.53227  44.52647  57.72122  68.86126  79.32825  89.27306  93.70949
## [8]  97.95676 100.00000
```

The loadings:

```
res.pca$var$cor

##              Dim.1      Dim.2      Dim.3       Dim.4       Dim.5
## SIE.Su  0.08057735 -0.1786150  0.7413696 -0.39466187  0.40201850
## SIE.Au  0.78463426  0.1601660 -0.1358873 -0.02360527 -0.28475060
## SIE.Wi  0.74444946  0.3787178  0.1390330  0.26085759 -0.10566944
## SIE.Sp  0.06940453  0.6505897 -0.2874635  0.14838490  0.63297890
## SOI     0.50126942 -0.5519112 -0.1726551  0.02166076  0.40463998
## T.Su   -0.64091072  0.1741091  0.1976988 -0.02932482 -0.29134793
## T.au   -0.69128327  0.3642634  0.1570772  0.27691731  0.17674456
## T.wi   -0.49668781 -0.3960426 -0.5808892 -0.03417841  0.08316850
## T.sp   -0.01138968 -0.4367718  0.2940550  0.82282616  0.02694411
##              Dim.6       Dim.7       Dim.8       Dim.9
## SIE.Su  0.20439145  0.16833601  0.15205046 -0.03696014
## SIE.Au  0.32726859  0.07959270  0.31757770  0.21046404
## SIE.Wi  0.33851943 -0.03721296 -0.08556715 -0.28376578
## SIE.Sp  0.00660304  0.22829056 -0.08806289  0.08176243
## SOI     0.34355549 -0.29450675 -0.19246270  0.09112650
## T.Su    0.56425618  0.10752351 -0.30114518  0.11600140
## T.au    0.20978102 -0.36666032  0.27977904  0.01097100
## T.wi    0.38613805  0.19899778  0.18999768 -0.16165470
## T.sp   -0.04458262  0.19690112  0.03311646  0.05485501
```

Re-project each covariate on each principal component:

```
pcs = res.pca$ind$coord
round(pcs,2)

##    Dim.1 Dim.2 Dim.3 Dim.4 Dim.5 Dim.6 Dim.7 Dim.8 Dim.9
## 1   1.77 -0.44 -0.78  1.45 -0.08  0.12 -0.97 -0.13  0.85
## 2   2.04 -0.39  2.70 -0.78  1.49  1.99 -0.44 -0.63 -0.21
## 3   0.35 -1.49 -0.46 -1.19 -1.33 -1.04 -0.78 -0.45  0.16
## 4  -1.44  0.57  0.48 -0.86 -0.07 -0.20 -0.01  0.59 -0.01
## 5  -1.03  1.10 -1.26 -0.40  1.18 -0.56 -0.37 -0.76 -0.33
## 6  -0.69 -0.33  0.59  0.08  2.17 -0.99  1.00 -0.10  0.37
## 7  -3.17 -1.28 -0.08  0.21  0.39  0.83  0.91 -0.79 -0.37
## 8  -3.67 -1.08 -1.54  0.46  1.39  0.75 -0.45  0.80  0.20
## 9  -1.87  1.79  0.56  2.40  0.67 -1.92 -0.76 -0.42 -0.51
## 10  0.72  3.50  0.01 -1.05  0.25  0.99 -0.45  0.57  0.30
## 11 -0.88 -1.35  1.83 -1.38  0.28  0.08  0.51 -0.52  0.43
## 12  0.92  1.41 -1.34  0.60  0.12  0.57  0.57 -1.13  0.63
## 13 -0.24  0.25 -0.19  0.61 -2.19  1.61 -0.49 -1.09 -0.63
## 14 -1.32 -0.38  1.73  0.04 -1.37 -0.51  0.10  0.65 -0.05
## 15  1.84 -0.29  0.57  0.29  1.08  0.43 -0.21  0.27  0.32
## 16  0.69 -2.70 -0.83 -0.01 -0.08 -1.06  0.02  0.14  0.20
## 17  1.04  0.45 -0.63  0.50  0.31  0.52  0.94  0.61  0.12
## 18 -0.91  0.06  1.18  1.48 -1.31  1.58  0.28  1.16  0.03
## 19 -1.66  0.72 -0.74 -2.07 -1.05 -0.19 -0.27  0.38  0.33
## 20 -0.70  0.23 -0.57 -0.99 -1.25 -0.31  0.93 -0.87 -0.01
## 21  2.56  1.28 -0.60 -0.26 -0.47 -1.17  1.54  0.61 -0.63
## 22 -0.28  0.27  0.13 -1.18  0.92 -0.31 -0.72  0.59 -1.06
## 23  0.68 -0.59 -1.73  1.23  0.13  1.37  0.41 -0.03 -0.33
## 24  0.43  0.80  1.79  1.19 -0.77 -1.32  0.27 -0.05  0.56
## 25  0.61 -0.70  1.29  0.93 -0.25 -0.66 -0.18 -0.29 -0.39
## 26  2.92 -0.55 -0.47 -0.47  0.15 -0.83 -0.75 -0.23 -0.15
## 27  2.15 -1.80 -0.93  0.19 -0.11  0.10 -0.05  0.95 -0.38
## 28  0.64  0.55 -0.39 -0.99  0.36  0.24  0.05 -0.17  0.05
## 29 -1.50  0.37 -0.33 -0.03 -0.52 -0.12 -0.61  0.33  0.52
```

Model fitting

We're gonna fit various capture-recapture models to the petrel data. We use RMark because everything can be done in R, and it's cool for reproducible research. But other pieces of software could be used too, like e.g. E-SURGE.

Before fitting capture-recapture models to the data, we check whether the standard Cormack-Jolly-Seber model is fitting the data well. We use the R package R2ucare.

```
library(R2ucare)
geese = read_inp("females_petrel.inp")
petrel.ch = geese$encounter_histories
freq = geese$sample_size
test3sr(petrel.ch, freq)

## $test3sr
##      stat        df     p_val sign_test
##    29.095    27.000     0.356     0.903
##
## $details
##    component  stat p_val signed_test  test_perf
## 1          2 0.001 0.975      -0.032 Chi-square
## 2          3 0.249 0.618      -0.499     Fisher
## 3          4 0.213 0.644       0.462 Chi-square
## 4          5     0     1           0     Fisher
## 5           6 4.174 0.041       -2.043 Chi-square
## 6           7     0     1            0     Fisher
## 7           8     0     1            0     Fisher
## 8           9     0     0            0       None
## 9          10  1.13 0.288       -1.063 Chi-square
## 10         11     0     1            0     Fisher
## 11         12 1.766 0.184       -1.329     Fisher
## 12         13  1.19 0.275        1.091     Fisher
## 13         14     0     1            0     Fisher
## 14         15 1.224 0.269        1.106     Fisher
## 15         16 2.696 0.101       -1.642 Chi-square
## 16         17     0     1            0     Fisher
## 17         18     0     1            0     Fisher
## 18         19 3.695 0.055        1.922     Fisher
## 19         20     0     1            0     Fisher
## 20         21 1.885  0.17        1.373     Fisher
## 21         22 0.296 0.586        0.544     Fisher
## 22         23     0 0.984            0 Chi-square
## 23         24     0     1            0     Fisher
## 24         25 6.514 0.011        2.552     Fisher
## 25         26 0.749 0.387        0.865 Chi-square
## 26         27 0.102 0.749       -0.319 Chi-square
## 27         28     0     1            0     Fisher
## 28         29 3.211 0.073        1.792     Fisher
```

```
test3sm(petrel.ch, freq)
```

```
## $test3sm
##   stat     df  p_val
## 39.260 31.000  0.147
##
## $details
##    component   stat df p_val  test_perf
## 1           2  0.756  1 0.384 Chi-square
## 2           3  4.883  1 0.027 Chi-square
## 3           4  0.172  2 0.918 Chi-square
## 4           5      0  1     1     Fisher
## 5           6  1.022  1 0.312 Chi-square
## 6           7  0.748  1 0.387 Chi-square
## 7           8      0  1     1     Fisher
## 8           9  0.294  1 0.588     Fisher
## 9          10  0.939  1 0.333 Chi-square
## 10         11   2.88  3 0.411 Chi-square
## 11         12  1.709  1 0.191 Chi-square
## 12         13   0.19  1 0.663 Chi-square
## 13         14      0  1     1     Fisher
## 14         15  5.705  1 0.017     Fisher
## 15         16 14.009  2 0.001 Chi-square
## 16         17  0.309  1 0.578 Chi-square
## 17         18  0.305  1 0.581 Chi-square
## 18        19       0  1      1     Fisher
## 19        20   1.337  1  0.248 Chi-square
## 20        21   0.547  1   0.46 Chi-square
## 21        22       0  1      1     Fisher
## 22        23       0  1      1     Fisher
## 23        24   1.867  1  0.172 Chi-square
## 24        25   0.657  1  0.417     Fisher
## 25        26   0.456  1    0.5 Chi-square
## 26        27   0.212  1  0.645 Chi-square
## 27        28   0.263  1  0.608     Fisher
## 28        29       0  0      0       None
```

```
test2ct(petrel.ch, freq)
```

```
## $test2ct
##      stat        df     p_val sign_test
##   103.115    27.000     0.000    -8.441
##
## $details
##    component dof   stat p_val signed_test  test_perf
## 1           2   1  0.013 0.908       0.114 Chi-square
## 2           3   1    8.1 0.004      -2.846     Fisher
## 3           4   1  2.599 0.107      -1.612 Chi-square
## 4           5   1  1.207 0.272      -1.099 Chi-square
## 5           6   1  1.162 0.281      -1.078 Chi-square
## 6           7   1  0.499  0.48      -0.706 Chi-square
## 7           8   1  0.958 0.328      -0.979 Chi-square
## 8           9   1  0.977 0.323      -0.988 Chi-square
## 9          10   1  6.397 0.011      -2.529 Chi-square
## 10         11   1  2.674 0.102      -1.635 Chi-square
## 11         12   1   8.56 0.003      -2.926 Chi-square
## 12         13   1  0.056 0.814      -0.237 Chi-square
## 13         14   1  0.015 0.903       0.122 Chi-square
## 14         15   1  5.736 0.017      -2.395 Chi-square
## 15         16   1  5.291 0.021        -2.3 Chi-square
## 16         17   1  2.057 0.152      -1.434 Chi-square
## 17         18   1 10.988 0.001      -3.315 Chi-square
## 18         19   1  7.809 0.005      -2.794 Chi-square
## 19         20   1  0.149 0.699      -0.386 Chi-square
## 20         21   1  5.228 0.022      -2.286 Chi-square
## 21         22   1  9.259 0.002      -3.043 Chi-square
## 22         23   1  3.826  0.05      -1.956 Chi-square
## 23         24   1  9.147 0.002      -3.024 Chi-square
## 24         25   1      0     1           0 Chi-square
## 25         26   1  6.442 0.011      -2.538 Chi-square
## 26         27   1      0 0.984           0 Chi-square
## 27         28   1  3.966 0.046      -1.991 Chi-square
```

```
test2cl(petrel.ch, freq)
```

```
## $test2cl
##   stat     df  p_val
## 49.741 42.000  0.192
##
## $details
##    component dof  stat p_val  test_perf
## 1          2   1     0     1     Fisher
## 2          3   1 1.077 0.299     Fisher
## 3          4   1  1.42 0.233 Chi-square
## 4          5   1 0.033 0.855 Chi-square
## 5          6   3 0.246  0.97 Chi-square
## 6          7   3 0.955 0.812 Chi-square
## 7          8   2 0.906 0.636 Chi-square
## 8          9   1 0.101  0.75 Chi-square
## 9         10   1 0.808 0.369 Chi-square
## 10        11   3 8.064 0.045 Chi-square
## 11        12   2 0.545 0.761 Chi-square
## 12        13   2 0.973 0.615 Chi-square
## 13        14   1 1.709 0.191 Chi-square
## 14        15   2 1.416 0.493 Chi-square
## 15        16   3 7.218 0.065 Chi-square
## 16        17   3  9.25 0.026 Chi-square
## 17        18   2 3.995 0.136 Chi-square
## 18        19   2 4.387 0.112 Chi-square
## 19        20   1 0.402 0.526 Chi-square
## 20        21   1 0.545  0.46 Chi-square
## 21        22   1 0.683 0.408 Chi-square
## 22        23   1 1.155 0.283 Chi-square
## 23        24   1 2.093 0.148     Fisher
## 24        25   1 0.229 0.633 Chi-square
## 25        26   1 1.319 0.251 Chi-square
## 26        27   1 0.212 0.645 Chi-square
```

```
overall_CJS(petrel.ch, freq)
```

```
##                              chi2 degree_of_freedom p_value
## Gof test for CJS model: 221.211               127       0
```

It sounds like there is a strong trap-dependence effect. Let's deal with it and create an individual time-varying covariate for trap-dependence (see appendix C of the Gentle introduction to Mark):

```
# let's read in the data:
library(RMark)
```

```
## This is RMark 2.2.0
```

```
petrel=convert.inp("females_petrel")
petrel.ch <- unlist(strsplit(petrel$ch, ""))
nocc <- nchar(petrel$ch[1])
petrel.td <- matrix(as.numeric(petrel.ch), ncol = nocc, byrow = TRUE)
petrel.td <- petrel.td[, 1:(nocc - 1)]
petrel.td <- as.data.frame(petrel.td)
begin.time <- 1974
names(petrel.td) <- paste('td', (begin.time + 1):(begin.time + nocc - 1), sep
= "")
#head(petrel.td) # dim 430 x 29
dim(petrel.td)

## [1] 430  29

petrel <- cbind(petrel, petrel.td)
#head(petrel)
```

Now process the data:

```
petrel.processed=process.data(petrel, model="CJS", begin.time=1974)
```

Create the default design matrix:

```
design.p=list(time.varying=c('td')) #td
design.parameters <- list(p=design.p)
petrel.ddl <- make.design.data(petrel.processed,parameters=design.parameters)
```

Standardize the covariates:

```
# standardize
moy = apply(cov,2,mean)
prec = apply(cov,2,sd)
moymat = matrix(rep(moy,nrow(cov)),ncol=ncol(cov),byrow=T)
precmat = matrix(rep(prec,nrow(cov)),ncol=ncol(cov),byrow=T)
covstar = (cov - moymat)/precmat
#apply(covstar,2,mean)
#apply(covstar,2,sd)
cov = covstar
```

Add raw covariates to the design matrix:

```
petrel.ddl$Phi$x1=0
petrel.ddl$Phi$x2=0
petrel.ddl$Phi$x3=0
petrel.ddl$Phi$x4=0
petrel.ddl$Phi$x5=0
petrel.ddl$Phi$x6=0
petrel.ddl$Phi$x7=0
petrel.ddl$Phi$x8=0
petrel.ddl$Phi$x9=0
ind=1
for (i in 1974:2002){
  petrel.ddl$Phi$x1[petrel.ddl$Phi$time==i]=cov[ind,1]
  petrel.ddl$Phi$x2[petrel.ddl$Phi$time==i]=cov[ind,2]
  petrel.ddl$Phi$x3[petrel.ddl$Phi$time==i]=cov[ind,3]
  petrel.ddl$Phi$x4[petrel.ddl$Phi$time==i]=cov[ind,4]
  petrel.ddl$Phi$x5[petrel.ddl$Phi$time==i]=cov[ind,5]
  petrel.ddl$Phi$x6[petrel.ddl$Phi$time==i]=cov[ind,6]
  petrel.ddl$Phi$x7[petrel.ddl$Phi$time==i]=cov[ind,7]
  petrel.ddl$Phi$x8[petrel.ddl$Phi$time==i]=cov[ind,8]
  petrel.ddl$Phi$x9[petrel.ddl$Phi$time==i]=cov[ind,9]
  ind=ind+1
}
```

Specify the effects on survival and detection probabilities:

```
#  for survival probabilities
Phidot=list(formula=~1) # constant
Phitime=list(formula=~time) # time
PhiCov=list(formula=~x1+x2+x3+x4+x5+x6+x7+x8+x9) # all covariates
#  Define range of models for detection probabilities
pdot=list(formula=~td) # constant, with trap-dependence
ptime=list(formula=~time+td) # additive effect of time and trap-dependence (n
o interaction because of severe identifiability issues Gimenez et al. 2003)
```

Fit models:

```
# phi,p
phip = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phidot,p=pd
ot),output = FALSE,delete=T)
# phit,p
phitp = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phitime,p=
pdot),output = FALSE,delete=T)
# phi,pt
phipt = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phidot,p=p
time),output = FALSE,delete=T)
# phit,pt
phitpt = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phitime,p
=ptime),output = FALSE,delete=T)
```

Compare models

```
collect.models()

##                       model npar     AICc DeltaAICc       weight Deviance
## 4 Phi(~time)p(~time + td)   59 6535.213   0.00000 1.000000e+00 6414.843
## 2    Phi(~1)p(~time + td)   31 6580.016  44.80257 1.867433e-10 6517.358
## 3        Phi(~time)p(~td)   31 7035.204 499.99017 0.000000e+00 6972.546
## 1           Phi(~1)p(~td)    3 7141.081 605.86732 0.000000e+00 7135.073
```

Clearly, there is time variation in the detection process. Also, it's worth investigating further time variation in survival.

Now, let's fit a model with all covariates:

```
phixpt = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=PhiCov,p=
ptime),output = FALSE,delete=T)
```

And have a look to the parameter estimates:

```
phixpt$results$beta

##                    estimate        se        lcl        ucl
## Phi:(Intercept)  3.0215027 0.1266500  2.7732686  3.2697368
## Phi:x1          -0.0214576 0.1238148 -0.2641346  0.2212193
## Phi:x2           0.5045058 0.2438022  0.0266534  0.9823581
## Phi:x3          -0.5050225 0.2135759 -0.9236313 -0.0864136
## Phi:x4          -0.1875442 0.1633865 -0.5077816  0.1326933
## Phi:x5          -0.3384226 0.1285907 -0.5904604 -0.0863848
## Phi:x6           0.0366735 0.1194053 -0.1973609  0.2707079
## Phi:x7           0.4200931 0.2218857 -0.0148029  0.8549890
## Phi:x8          -0.5388508 0.1450647 -0.8231777 -0.2545240
## Phi:x9          -0.1858322 0.1744092 -0.5276742  0.1560098
## p:(Intercept)   -0.2762133 0.3518067 -0.9657543  0.4133278
## p:time1976       1.4053121 0.5015022  0.4223678  2.3882563
## p:time1977       1.1939267 0.4353984  0.3405459  2.0473075
## p:time1978      -1.3620787 0.3974020 -2.1409866 -0.5831708
## p:time1979       0.8851171 0.4070317  0.0873350  1.6828992
## p:time1980      -1.3972306 0.4109121 -2.2026184 -0.5918429
## p:time1981      -0.8393120 0.4093691 -1.6416754 -0.0369486
## p:time1982      -1.4862563 0.4314896 -2.3319760 -0.6405367
## p:time1983       1.0600671 0.4128135  0.2509526  1.8691817
## p:time1984       0.4538590 0.3939755 -0.3183330  1.2260510
## p:time1985      -1.0118973 0.3845834 -1.7656808 -0.2581137
## p:time1986       0.0048467 0.3855301 -0.7507922  0.7604857
## p:time1987      -1.0459573 0.3890010 -1.8083993 -0.2835153
## p:time1988       0.5125888 0.3873746 -0.2466655  1.2718431
## p:time1989       1.1524762 0.4016411  0.3652597  1.9396928
## p:time1990      -0.3716563 0.3782383 -1.1130033  0.3696907
## p:time1991       0.6520759 0.3844498 -0.1014458  1.4055976
## p:time1992       0.6619091 0.3826238 -0.0880335  1.4118518
## p:time1993       0.6817374 0.3839835 -0.0708703  1.4343450
## p:time1994       0.0532153 0.3753604 -0.6824912  0.7889217
## p:time1995       0.7756711 0.3815839  0.0277667  1.5235755
## p:time1996       1.6026013 0.4091297  0.8007071  2.4044955
## p:time1997       1.4893316 0.4098044  0.6861150  2.2925482
## p:time1998       0.4982784 0.3783386 -0.2432652  1.2398220
## p:time1999       1.4753445 0.4081701  0.6753310  2.2753580
## p:time2000       0.5118000 0.3840496 -0.2409372  1.2645371
## p:time2001      -0.1193068 0.3820731 -0.8681701  0.6295565
## p:time2002      -0.0079716 0.3829367 -0.7585277  0.7425844
## p:time2003       0.2303389 0.3863065 -0.5268217  0.9874996
## p:td             0.7281680 0.0827993  0.5658814  0.8904547
```

The covariates are in that order: SIE.Su (x1), SIE.Au (x2), SIE.Wi (x3), SIE.Sp (x4), SOI (x5), T.Su (x6), T.au (x7), T.wi (x8) and T.sp (x9). Remember, from our preliminary exploration step above, we know that covariates 2 and 3 are highly positively correlated. However by inspecting the estimates here, these covariates seem to have an opposite effect on survival!

Standard forward stepwise covariate selection approach

Following a referee's suggestion, we perform here a forward covariate selection. Bearing in mind that we found strong correlation among covariates (see above), we do not recommend performing this analysis without first dealing with the multicollinearity issue.

In the first step of the analysis, we consider each covariate separately:

```
Phix1=list(formula=~x1)
Phix2=list(formula=~x2)
Phix3=list(formula=~x3)
Phix4=list(formula=~x4)
Phix5=list(formula=~x5)
Phix6=list(formula=~x6)
Phix7=list(formula=~x7)
Phix8=list(formula=~x8)
Phix9=list(formula=~x9)
phix1 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix1,p=pt
ime),output = FALSE,delete=T)
phix2 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix2,p=pt
ime),output = FALSE,delete=T)
phix3 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix3,p=pt
ime),output = FALSE,delete=T)
phix4 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix4,p=pt
ime),output = FALSE,delete=T)
phix5 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix5,p=pt
ime),output = FALSE,delete=T)
phix6 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix6,p=pt
ime),output = FALSE,delete=T)
phix7 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix7,p=pt
ime),output = FALSE,delete=T)
phix8 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix8,p=pt
ime),output = FALSE,delete=T)
phix9 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix9,p=pt
ime),output = FALSE,delete=T)
```

We now use ANODEV to test the significance of these covariates:

```
# get info on model with time-dependent survival
devtime = phitpt$results$lnl
npartime = phitpt$results$npar

# get info on model with constant survival
devct = phipt$results$lnl
nparct = phipt$results$npar

# test each covariate:
stat = rep(NA,9)
df1 = rep(NA,9)
df2 = rep(NA,9)
```

```
for (i in 1:9){
    name = paste('phix',i,sep="")
    devco = get(name)$results$lnl
    nparco = get(name)$results$npar
    num = (devct - devco)/(nparco-nparct)
    den = (devco - devtime)/(npartime-nparco)
    stat[i] <- num/den
    df1[i] <- nparco-nparct
    df2[i] <- npartime-nparco
}
# calculate p-value
pval = 1-pf(stat,df1,df2)
stat

## [1] 1.43111265 0.01122451 0.75434906 1.85305569 7.96593098 0.56817195
## [7] 0.11635867 7.75091055 1.77150769

df1

## [1] 1 1 1 1 1 1 1 1 1

df2

## [1] 27 27 27 27 27 27 27 27 27

pval

## [1] 0.241982884 0.916408601 0.392757731 0.184681802 0.008838179 0.45750976
8
## [7] 0.735658189 0.009686743 0.194326441
```

It seems like SOI (x_5) and temperature in winter (x_8) have a significant effect. In step 2 of the analysis, we keep these two covariates and test the significance of the other covariates:

```
Phix0=list(formula=~x5+x8) # constant model in the current ANODEV
Phix1=list(formula=~x5+x8+x1)
Phix2=list(formula=~x5+x8+x2)
Phix3=list(formula=~x5+x8+x3)
Phix4=list(formula=~x5+x8+x4)
Phix5=list(formula=~x5+x8+x6)
Phix6=list(formula=~x5+x8+x7)
Phix7=list(formula=~x5+x8+x9)
phix58 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix1,p=p
time),output = FALSE,delete=T)
phix581 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix1,p=
ptime),output = FALSE,delete=T)
phix582 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix2,p=
ptime),output = FALSE,delete=T)
phix583 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix3,p=
ptime),output = FALSE,delete=T)
phix584 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix4,p=
ptime),output = FALSE,delete=T)
```

```
phix585 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix5,p=
ptime),output = FALSE,delete=T)
phix586 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix6,p=
ptime),output = FALSE,delete=T)
phix587 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phix7,p=
ptime),output = FALSE,delete=T)
```

Then, we perform ANODEV tests to assess the significance of the remaining covariates in presence of both x_5 and x_8.

```
stat = rep(NA,7)
df1 = rep(NA,7)
df2 = rep(NA,7)
for (i in 1:7){
    name = 'phix58'
    devct = get(name)$results$lnl
    nparct = get(name)$results$npar
    namex = paste('phix58',i,sep="")
    devco = get(namex)$results$lnl
    nparco = get(namex)$results$npar
    df1[i] <- 1 # we add a single covariate
    df2[i] <- npartime-nparco
    num = (devct - devco)/df1[i]
    den = (devco - devtime)/df2[i]
    if (devct == devco) stat[i] <- 0 # it happens for covariate x1
  if (devct != devco) stat[i] <- num/den
}

pval = 1-pf(stat,df1,df2)
stat

## [1]  0.0000000  0.1697841  2.2834398  0.8267684 -0.3533329  0.3438980
## [7] -0.3574468

df1

## [1] 1 1 1 1 1 1 1

df2

## [1] 25 25 25 25 25 25 25

pval

## [1] 1.0000000 0.6838155 0.1432996 0.3718918 1.0000000 0.5628460 1.0000000
```

There is no more significant covariates.

P2CR analysis

In this section, we show how to perform a P2CR analysis. First, we amend the design matrix we built before, and add the coordinates of the raw covariates on the principal components:

```r
petrel.ddl$Phi$pc1=0
petrel.ddl$Phi$pc2=0
petrel.ddl$Phi$pc3=0
petrel.ddl$Phi$pc4=0
petrel.ddl$Phi$pc5=0
petrel.ddl$Phi$pc6=0
petrel.ddl$Phi$pc7=0
petrel.ddl$Phi$pc8=0
petrel.ddl$Phi$pc9=0
ind=1
for (i in 1974:2002){
  petrel.ddl$Phi$pc1[petrel.ddl$Phi$time==i]=pcs[ind,1]
  petrel.ddl$Phi$pc2[petrel.ddl$Phi$time==i]=pcs[ind,2]
  petrel.ddl$Phi$pc3[petrel.ddl$Phi$time==i]=pcs[ind,3]
  petrel.ddl$Phi$pc4[petrel.ddl$Phi$time==i]=pcs[ind,4]
  petrel.ddl$Phi$pc5[petrel.ddl$Phi$time==i]=pcs[ind,5]
  petrel.ddl$Phi$pc6[petrel.ddl$Phi$time==i]=pcs[ind,6]
  petrel.ddl$Phi$pc7[petrel.ddl$Phi$time==i]=pcs[ind,7]
  petrel.ddl$Phi$pc8[petrel.ddl$Phi$time==i]=pcs[ind,8]
  petrel.ddl$Phi$pc9[petrel.ddl$Phi$time==i]=pcs[ind,9]
  ind=ind+1
}
```

In the first step of the P2CR analysis, we consider each PC separately:

```r
Phipc1=list(formula=~pc1)
Phipc2=list(formula=~pc2)
Phipc3=list(formula=~pc3)
Phipc4=list(formula=~pc4)
Phipc5=list(formula=~pc5)
Phipc6=list(formula=~pc6)
Phipc7=list(formula=~pc7)
Phipc8=list(formula=~pc8)
Phipc9=list(formula=~pc9)
phipc1 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc1,p=
ptime),output = FALSE,delete=T)
phipc2 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc2,p=
ptime),output = FALSE,delete=T)
phipc3 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc3,p=
ptime),output = FALSE,delete=T)
phipc4 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc4,p=
ptime),output = FALSE,delete=T)
phipc5 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc5,p=
ptime),output = FALSE,delete=T)
phipc6 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc6,p=
ptime),output = FALSE,delete=T)
phipc7 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc7,p=
ptime),output = FALSE,delete=T)
phipc8 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc8,p=
ptime),output = FALSE,delete=T)
```

```
phipc9 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc9,p=
ptime),output = FALSE,delete=T)
```

We now use ANODEV to to test the significance of these PCs:

```
# get info on model with time-dependent survival
devtime = phitpt$results$lnl
npartime = phitpt$results$npar

# get info on model with constant survival
devct = phipt$results$lnl
nparct = phipt$results$npar

# test each PC:
stat = rep(NA,9)
df1 = rep(NA,9)
df2 = rep(NA,9)
for (i in 1:9){
    name = paste('phipc',i,sep="")
    devco = get(name)$results$lnl
    nparco = get(name)$results$npar
    num = (devct - devco)/(nparco-nparct)
    den = (devco - devtime)/(npartime-nparco)
    stat[i] <- num/den
    df1[i] <- nparco-nparct
    df2[i] <- npartime-nparco
}
# calculate p-value
pval = 1-pf(stat,df1,df2)
stat

## [1] 0.4561618 2.0348053 7.3439558 3.0089184 3.0594652 2.4351876 0.1359247
## [8] 0.3111153 0.7808127

df1

## [1] 1 1 1 1 1 1 1 1 1

df2

## [1] 27 27 27 27 27 27 27 27 27

pval

## [1] 0.50516694 0.16519557 0.01154684 0.09421181 0.09162924 0.13028569
## [7] 0.71524166 0.58159232 0.38469346
```

We can reject the null hypothesis that PC3 has no effect on survival.

In step 2 of the P2CR, we keep PC3 and test the significance of the other PCs:

```
Phipc1=list(formula=~pc1+pc3)
Phipc2=list(formula=~pc2+pc3)
Phipc3=list(formula=~pc4+pc3)
Phipc4=list(formula=~pc5+pc3)
Phipc5=list(formula=~pc6+pc3)
Phipc6=list(formula=~pc7+pc3)
Phipc7=list(formula=~pc8+pc3)
Phipc8=list(formula=~pc9+pc3)
phipc11 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc1,p
=ptime),output = FALSE,delete=T)
phipc21 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc2,p
=ptime),output = FALSE,delete=T)
phipc31 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc3,p
=ptime),output = FALSE,delete=T)
phipc41 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc4,p
=ptime),output = FALSE,delete=T)
phipc51 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc5,p
=ptime),output = FALSE,delete=T)
phipc61 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc6,p
=ptime),output = FALSE,delete=T)
phipc71 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc7,p
=ptime),output = FALSE,delete=T)
phipc81 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc8,p
=ptime),output = FALSE,delete=T)

stat = rep(NA,8)
df1 = rep(NA,8)
df2 = rep(NA,8)
for (i in 1:8){
    name = paste('phipc',3,sep="")
    devct = get(name)$results$lnl
    nparct = get(name)$results$npar
    namex = paste('phipc',paste(i,'1',sep=""),sep="")
    devco = get(namex)$results$lnl
    nparco = get(namex)$results$npar
    num = (devct - devco)/(nparco-nparct)
    den = (devco - devtime)/(npartime-nparco)
    stat[i] <- num/den
    df1[i] <- nparco-nparct
    df2[i] <- npartime-nparco

}

pval = 1-pf(stat,df1,df2)
stat

## [1] 0.115032061 2.935263243 4.629627302 2.517956493 3.502807470 0.27595235
4
## [7] 0.006486012 0.723243675
```

```
df1

## [1] 1 1 1 1 1 1 1 1

df2

## [1] 26 26 26 26 26 26 26 26

pval

## [1] 0.73721058 0.09856598 0.04088835 0.12464492 0.07255722 0.60381802
## [7] 0.93642787 0.40284611
```

Now PC4 is significant according the ANODEV (remember that PC3 was removed from the list).

In step 3 of the P2CR analysis, we reiterate the process, that is we test the significance of the other PCs in presence of PC3 and PC4:

```
Phipc1=list(formula=~pc1+pc3+pc4)
Phipc2=list(formula=~pc2+pc3+pc4)
Phipc3=list(formula=~pc5+pc3+pc4)
Phipc4=list(formula=~pc6+pc3+pc4)
Phipc5=list(formula=~pc7+pc3+pc4)
Phipc6=list(formula=~pc8+pc3+pc4)
Phipc7=list(formula=~pc9+pc3+pc4)
phipc12 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc1,p
=ptime),output = FALSE,delete=T)
phipc22 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc2,p
=ptime),output = FALSE,delete=T)
phipc32 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc3,p
=ptime),output = FALSE,delete=T)
phipc42 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc4,p
=ptime),output = FALSE,delete=T)
phipc52 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc5,p
=ptime),output = FALSE,delete=T)
phipc62 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc6,p
=ptime),output = FALSE,delete=T)
phipc72 = mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc7,p
=ptime),output = FALSE,delete=T)
```

What does the ANODEV tell us?

```
stat = rep(NA,7)
df1 = rep(NA,7)
df2 = rep(NA,7)
for (i in 1:7){
    name = paste('phipc',31,sep="")
    devct = get(name)$results$lnl
    nparct = get(name)$results$npar
    namex = paste('phipc',paste(i,'2',sep=""),sep="")
    devco = get(namex)$results$lnl
    nparco = get(namex)$results$npar
    num = (devct - devco)/(nparco-nparct)
    den = (devco - devtime)/(npartime-nparco)
    stat[i] <- num/den
    df1[i] <- nparco-nparct
    df2[i] <- npartime-nparco

}

pval = 1-pf(stat,df1,df2)
stat

## [1] 0.074403780 1.878326793 1.383423294 0.547418815 0.235266864 0.00226589
3
## [7] 1.282105461

df1

## [1] 1 1 1 1 1 1 1

df2

## [1] 25 25 25 25 25 25 25

pval

## [1] 0.7872701 0.1827058 0.2505979 0.4662660 0.6318690 0.9624122 0.2682518
```

No more significant PC, the algorithm stops here.

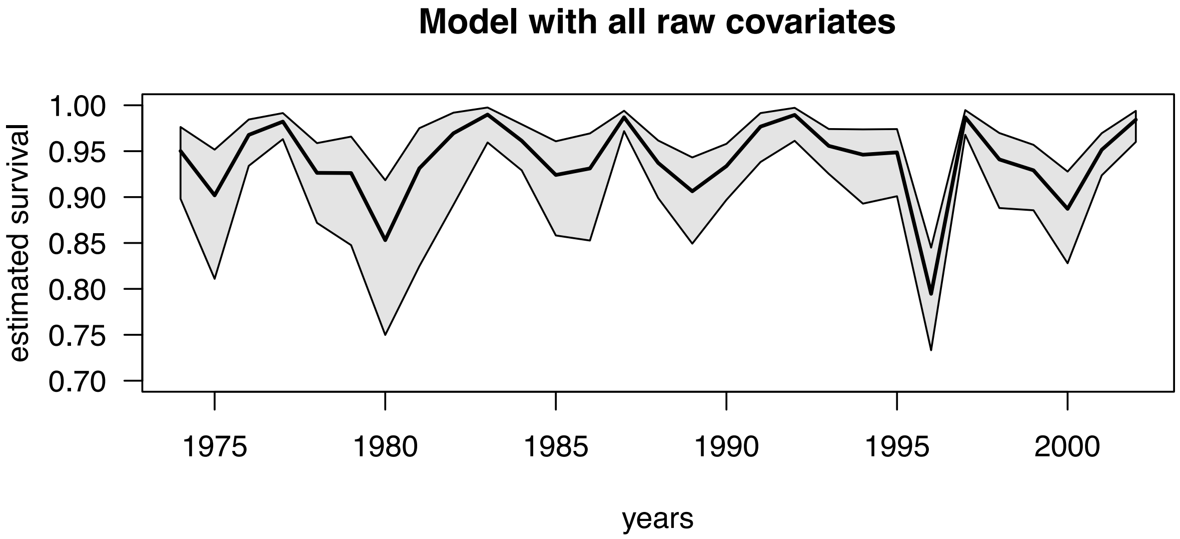
Post-process results

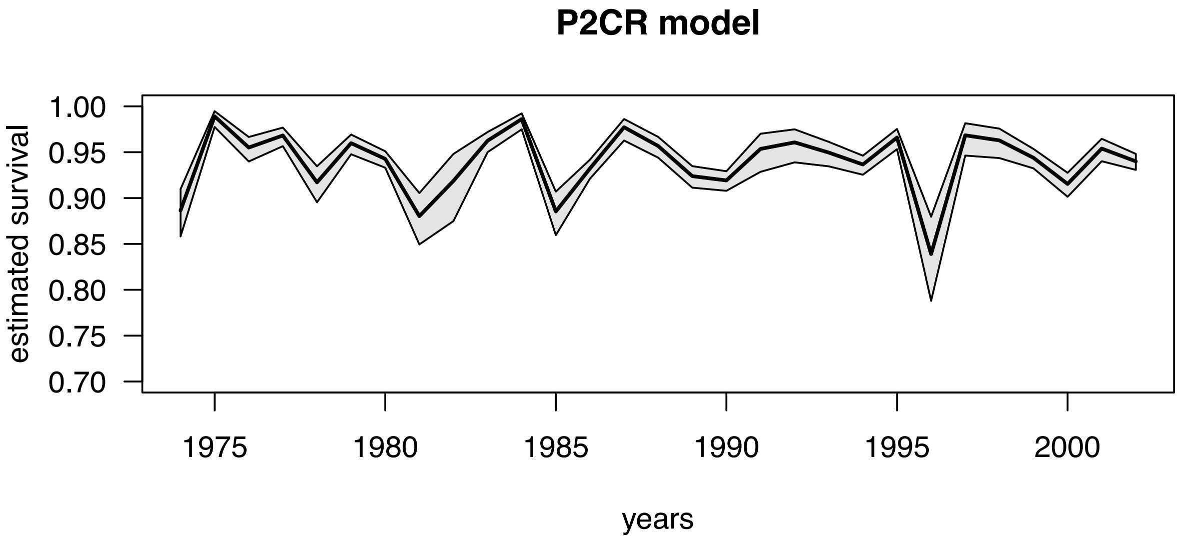
We will make two plots, one with time-varying survival estimates, and another oneto illustrate the relationship between survival and the selected PCs.

First, a figure displaying the time variation in survival according to a model with all raw covariates and the PC2R model:

```
#phit_mle <- phitpt$results$real[1:29,]
phicov_mle <- phixpt$results$real[1:29,]
phipca_mle <- phipc31$results$real[1:29,]
# Make a 6x6 inch image at 300dpi
#ppi <- 300
#png("time_survival_allcov.png", width=6*ppi, height=6*ppi, res=ppi)
par(mfrow=c(2,1))
plot(1974:2002,phicov_mle[,1],lwd=2,col='black',type='n',ylim=c(0.7,1),xlab='
years',ylab='estimated survival',main='Model with all raw covariates')
polygon(x=c(1974:2002, rev(1974:2002)),y=c(phicov_mle[,3], rev(phicov_mle[,4]
)),col='grey90')
lines(1974:2002,phicov_mle[,1],lwd=2,col='black')
#dev.off()
#png("time_survival_p2cr.png", width=6*ppi, height=6*ppi, res=ppi)
```

```
plot(1974:2002,phipca_mle[,1],lwd=2,col='black',type='n',ylim=c(0.7,1),xlab='
years',ylab='estimated survival',main='P2CR model')
polygon(x=c(1974:2002, rev(1974:2002)),y=c(phipca_mle[,3], rev(phipca_mle[,4]
)),col='grey90')
lines(1974:2002,phipca_mle[,1],lwd=2,col='black')
```





```
#dev.off()
```

Second, a figure displaying the relationship between survival and the PCs selected by the P2CR analysis.

Get the coefficient estimates for each PC and the intercept:

```
phipc31$results$beta[1:3,]
```

```
##                    estimate         se        lcl        ucl
## Phi:(Intercept)  2.9065529 0.0930352  2.7242038  3.0889019
## Phi:pc4         -0.3179566 0.0937601 -0.5017265 -0.1341868
## Phi:pc3          0.4987768 0.1117004  0.2798440  0.7177096
```

Get estimates of recapture probabilities:

```
# recapture given no recapture before
lp1=phipc31$results$beta$estimate[4] + phipc31$results$beta$estimate[5:32]
p1 = 1/(1+exp(-lp1))
p1

##  [1] 0.6849745 0.6950768 0.1598928 0.6532744 0.1491627 0.2186211 0.1380853
##  [8] 0.6799227 0.5559287 0.2101187 0.4365715 0.2081895 0.5650883 0.7013976
## [15] 0.3322994 0.5843023 0.5899872 0.6135580 0.4454382 0.6270110 0.7892106
## [22] 0.7614156 0.5662430 0.7626804 0.5415123 0.3768221 0.4066764 0.4896956

# recapture given recapture before
lp2=phipc31$results$beta$estimate[4]+phipc31$results$beta$estimate[5:32]+phip
c31$results$beta$estimate[33]
p2 = 1/(1+exp(-lp2))
p2

##  [1] 0.8225428 0.8293326 0.2886225 0.8006571 0.2720511 0.3736061 0.2545782
##  [8] 0.8191144 0.7274251 0.3618676 0.6228950 0.3591787 0.7347352 0.8335369
## [15] 0.5147804 0.7497731 0.7541473 0.7719290 0.6313058 0.7818291 0.8886590
## [22] 0.8718481 0.7356502 0.8726254 0.7157292 0.5631322 0.5936851 0.6716636

# get min/max for p1 with SEs
ind.min = which.min(p1) # index min p1
ind.max = which.max(p1) # index max p1
varlp1 = phipc31$results$beta$se[4]^2 + phipc31$results$beta$se[5:32]^2 # var
of p1 on logit scale
lp1mi = lp1[ind.min]
varlp1mi = varlp1[ind.min]
library(msm)
sep1mi = deltamethod(~ 1/(1+exp(-x1)), lp1mi, varlp1mi)
min(p1)

## [1] 0.1380853

sep1mi

## [1] 0.06614093

lp1ma = lp1[ind.max]
varlp1ma = varlp1[ind.max]
sep1ma = deltamethod(~ 1/(1+exp(-x1)), lp1ma, varlp1ma)
max(p1)

## [1] 0.7892106

sep1ma
```

```
## [1] 0.08957705

# get min/max for p2 with SEs
ind.min = which.min(p2) # index min p2
ind.max = which.max(p2) # index max p2
varlp2 = phipc31$results$beta$se[4]^2 + phipc31$results$beta$se[5:32]^2 + phi
pc31$results$beta$estimate[33]^2# var of p2 on logit scale
lp2mi = lp2[ind.min]
varlp2mi = varlp2[ind.min]
sep2mi = deltamethod(~ 1/(1+exp(-x1)), lp2mi, varlp2mi)
min(p2)

## [1] 0.2545782

sep2mi

## [1] 0.1781993

lp2ma = lp2[ind.max]
varlp2ma = varlp2[ind.max]
sep2ma = deltamethod(~ 1/(1+exp(-x1)), lp2ma, varlp2ma)
max(p2)

## [1] 0.888659

sep2ma

## [1] 0.09191182
```

Get confidence intervals using the delta-method:

```
library(msm)
PC3 = pcs[,3]
PC4 = pcs[,4]
phi_SE3 = matrix(0, nrow = 29, ncol = 1)
estmean3 <- c(2.9065503,0.4987728)
estvar3 <- diag(c(0.0930351,0.1117004)^2)
phi_SE4 = matrix(0, nrow = 29, ncol = 1)
estmean4 <- c(2.9065503,-0.3179579)
estvar4 <- diag(c(0.0930351,0.0937603)^2)
for (i in 1:29){
    temp3 <- PC3[i]
    temp4 <- PC4[i]
    phi_SE3[i,] <- deltamethod(~ x1+x2*temp3, estmean3, estvar3)
    phi_SE4[i,] <- deltamethod(~ x1+x2*temp4, estmean4, estvar4)
}

ilogitphi3 <- estmean3[1] + estmean3[2] * PC3
ilogitphi3lb <- ilogitphi3 - 1.96 * as.vector(phi_SE3)
ilogitphi3ub <- ilogitphi3 + 1.96 * as.vector(phi_SE3)
phi3lb <- 1/(1+exp(-(ilogitphi3lb)))
phi3ub <- 1/(1+exp(-(ilogitphi3ub)))
```

```
phi3 <- 1/(1+exp(-(ilogitphi3)))

ilogitphi4 <- estmean4[1] + estmean4[2] * PC4
ilogitphi4lb <- ilogitphi4 - 1.96 * as.vector(phi_SE4)
ilogitphi4ub <- ilogitphi4 + 1.96 * as.vector(phi_SE4)
phi4lb <- 1/(1+exp(-(ilogitphi4lb)))
phi4ub <- 1/(1+exp(-(ilogitphi4ub)))
phi4 <- 1/(1+exp(-(ilogitphi4)))
```

Before plotting the survival as a function of the PC values, we need to find out about the raw covariates that were used to build these PCs:

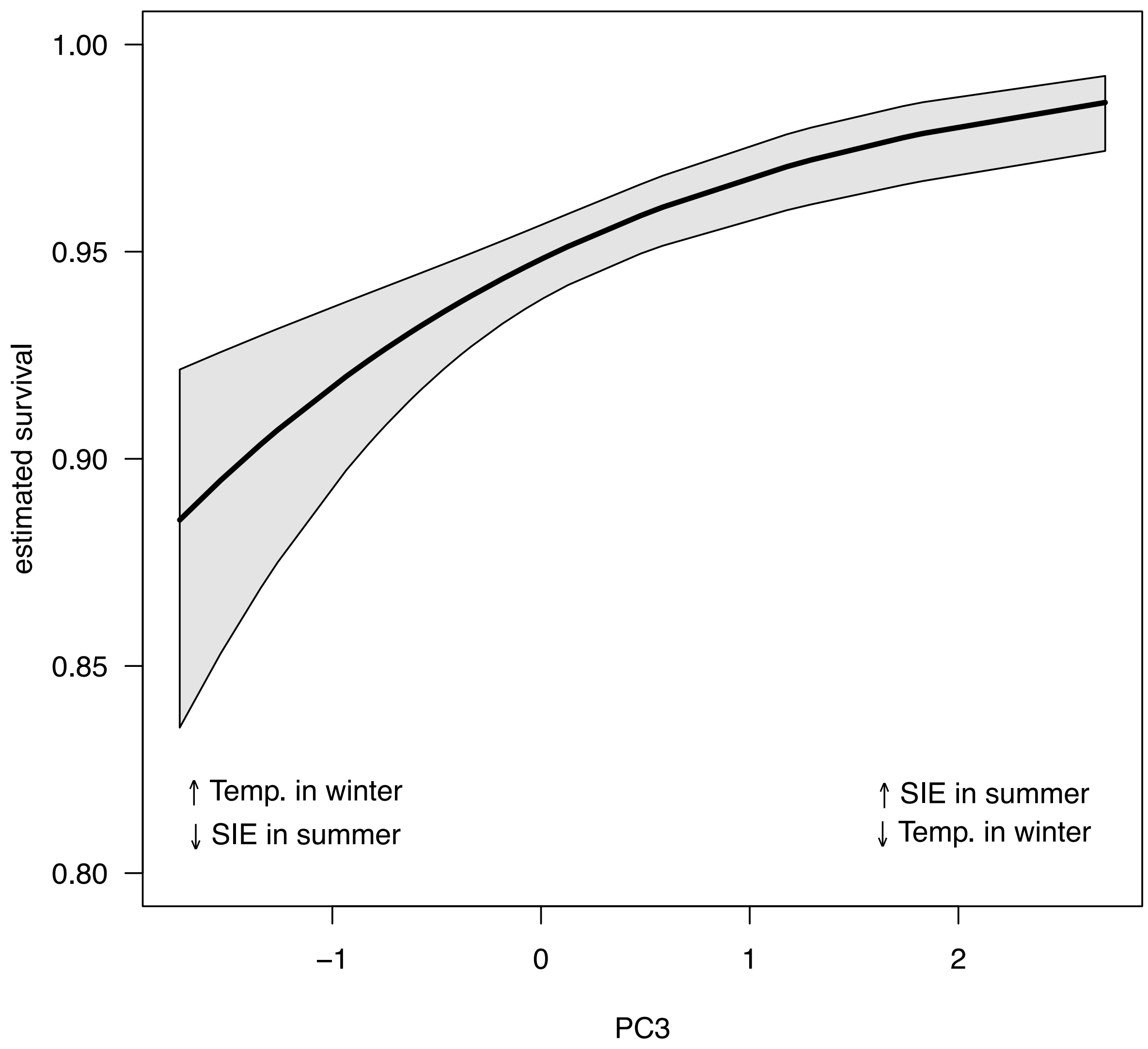
```
dimdesc(res.pca,axes = c(3:4))

## $Dim.3
## $Dim.3$quanti
##        correlation      p.value
## SIE.Su   0.7413696 4.205825e-06
## T.wi    -0.5808892 9.527347e-04
##
##
## $Dim.4
## $Dim.4$quanti
##        correlation      p.value
## T.sp     0.8228262 4.300265e-08
## SIE.Su  -0.3946619 3.411627e-02
```

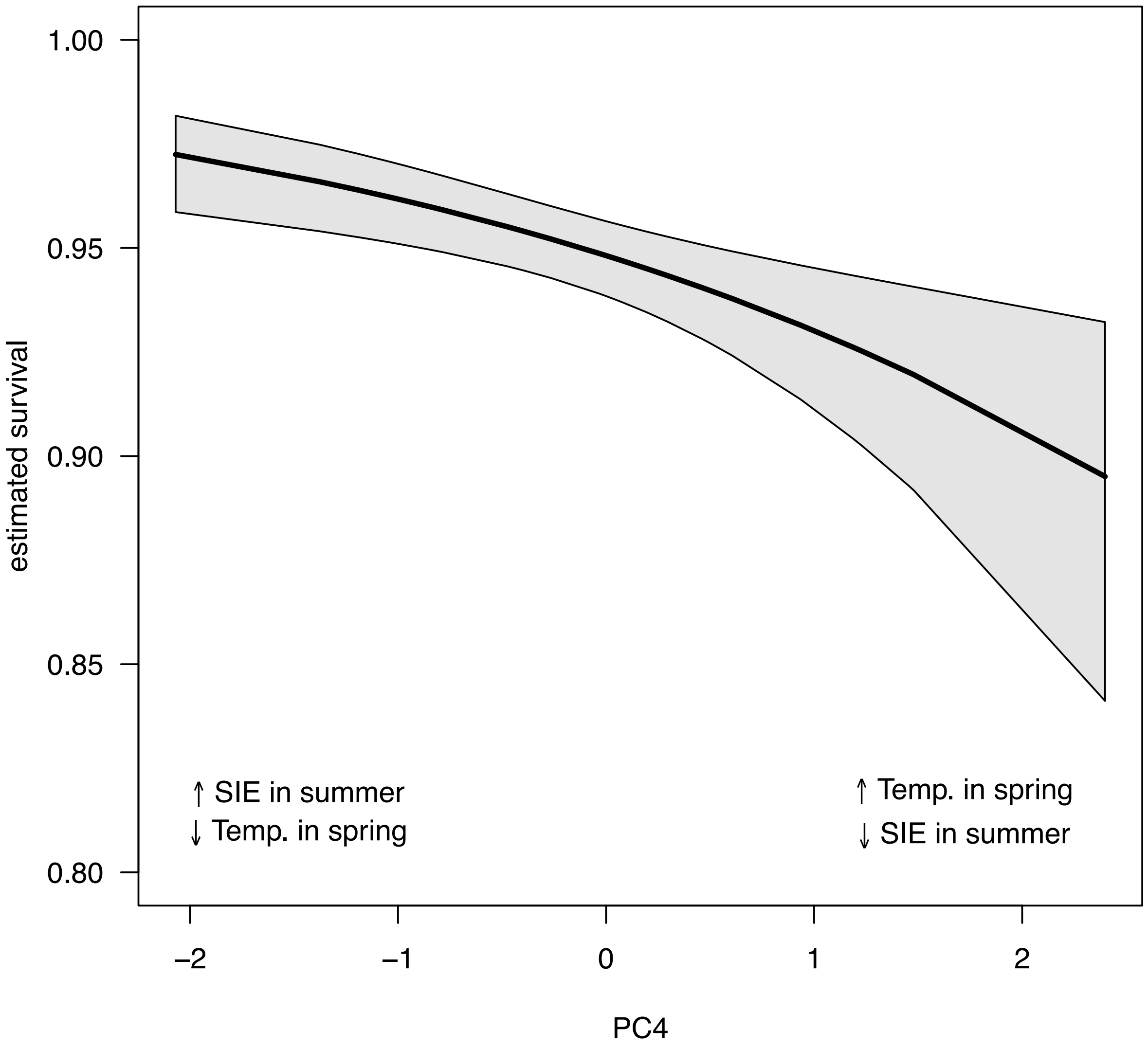
High (resp. low) values of PC3 mean high (resp. low) values of SIE in summer and low (resp. high) values of temperature in winter. High (resp. low) values of PC4 mean high (resp. low) values of temperature in spring and low (resp. high) values of SIE in summer.

Now we can plot the survival - PC relationships, and add the interpretation of the PCs:

```
# Make a 6x6 inch image at 300dpi
#ppi <- 300
#png("pc3_survival.png", width=6*ppi, height=6*ppi, res=ppi)
ord<-order(PC3)
plot(PC3[ord],phi3[ord],lwd=3,col='black',type='n',xlab='PC3',ylab='estimated survival',main='',ylim=c(0.8,1))
polygon(x=c(PC3[ord], rev(PC3[ord])),y=c(phi3lb[ord], rev(phi3ub[ord])),col='grey90')
lines(PC3[ord],phi3[ord],lwd=3,col='black')
text(-1.2,0.82,expression('' %up% 'Temp. in winter'),cex=1)
text(-1.2,0.81,expression('' %down% 'SIE in summer'),cex=1)
text(2.1,0.82,expression('' %up% 'SIE in summer'),cex=1)
text(2.1,0.81,expression('' %down% 'Temp. in winter'),cex=1)
```



```
ord<-order(PC4)
#dev.off()
#png("pc4_survival.png", width=6*ppi, height=6*ppi, res=ppi)
plot(PC4[ord],phi4[ord],lwd=3,col='black',type='n',xlab='PC4',ylab='estimated
survival',main='',ylim=c(0.8,1))
polygon(x=c(PC4[ord], rev(PC4[ord])),y=c(phi4lb[ord], rev(phi4ub[ord])),col='
grey90')
lines(PC4[ord],phi4[ord],lwd=3,col='black')
text(-1.5,0.82,expression('' %up% 'SIE in summer'),cex=1)
text(-1.5,0.81,expression('' %down% 'Temp. in spring'),cex=1)
text(1.7,0.82,expression('' %up% 'Temp. in spring'),cex=1)
text(1.7,0.81,expression('' %down% 'SIE in summer'),cex=1)
```


1.00
0.95
0.90
0.85
0.80
estimated survival
–2
–1
0
1
2
PC4
↑ SIE in summer
↓ Temp. in spring
↑ Temp. in spring
↓ SIE in summer

```
#dev.off()
```

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NOTES AND COMMENTS

Dealing with many correlated covariates in capture–recapture models

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Abstract Capture–recapture models for estimating demographic parameters allow covariates to be incorporated to better understand population dynamics. However, high-dimensionality and multicollinearity can hamper estimation and inference. Principal component analysis is incorporated within capture–recapture models and used to reduce the number of predictors into uncorrelated synthetic new variables. Principal components are selected by sequentially assessing their statistical significance. We provide an example on seabird survival to illustrate our approach. Our method requires standard statistical tools, which permits an efficient and easy implementation using standard software.

Keywords Animal demography · Population dynamics · Principal-component capture–recapture model · Snow petrel · Survival estimation

Introduction

Capture–recapture (CR) methods (e.g., Lebreton et al. 1992) are widely used for assessing the effect of explanatory variables on demographic parameters such as survival (Pollock 2002). Generally however, complex situations arise where multiple covariates are required to capture patterns in survival. In such situations, one usually favors a multiple regression-like CR modeling framework that is however hampered by two issues: first, because it increases the number of parameters to be estimated, incorporating many covariates results in a loss of statistical power and a decrease in the precision of parameter estimates; second, correlation among the set of predictors—aka multicollinearity—may alter interpretation (see below).

To overcome these two issues, Grosbois et al. (2008) recommended to perform a principal component analysis (PCA) on the set of explanatory variables before fitting CR models. PCA is a multivariate technique that explains the variability of a set of variables in terms of a *reduced* set of *uncorrelated* linear combinations of such variables—aka principal components (PCs)—while maximizing the variance (Jolliffe 2002). Grosbois et al. (2008) then expressed survival as a function of the PCs that explained most of the variance in the set of original covariates, typically the first one or the first two ones.

However, the main drawback of this approach is that the PCs are selected based on covariates variation pattern alone, regardless of the response variable, and without guarantee that survival is most related to these PCs (Graham 2003). To deal with this issue in the context of logistic regression, Aguilera et al. (2006) proposed to test the significance of *all* PCs to decide which ones should be retained, instead of a priori relying on the PCs that explain most of the variation in the covariates.

In this paper, we implement the algorithm proposed by Aguilera et al. (2006) to deal with many possibly correlated covariates in CR models, a method we refer to as principal component capture–recapture (P2CR). We apply this new approach to a case study on survival of Snow petrels

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(*Pagodroma nivea*) that is possibly affected by climatic conditions. In this example, the issue of multicollinearity occurs, and summarizing the set of covariates in a subset of lower dimension is also crucial to get precise survival estimates. Overall, P2CR models can be fitted with statistical programs that perform PCA and CR data analysis. The data and R code are available from GitHub at https://github.com/oliviergimenez/p2cr.

Methods

We used capture–recapture (CR) models to study open populations over K capture occasions to estimate the probability ϕ_i ($i=1, \ldots, K-1$) that an individual survives to occasion $i+1$ given that it is alive at time i, along with the probability p_j ($j=2, \ldots, K$) that an individual is recaptured at time j—aka as the Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992). Covariates were incorporated in survival probabilities using a linear-logistic function:

$$\text{logit}\left(\phi_i\right) = \log\left(\frac{\phi_i}{1-\phi_i}\right) = \alpha + \sum_{j=1}^{p} \beta_j X_{ij} \tag{1}$$

where α is the intercept parameter, X_{ij} is the value of covariate j ($j=1,\ldots, p$) in year i ($i=1,\ldots, K-1$), and β_j is its associated slope parameter. Covariates were standardized to avoid numerical instabilities. To assess the significance of a covariate in CR models, we used the analysis of deviance (ANODEV; Skalski et al. 1993) that compares the amount of deviance explained by this covariate with the amount of deviance not explained by this covariate, the CR model with fully time-dependent survival serving as a reference. The ANODEV test statistic is given by:

$$\text{ANODEV} = \frac{\text{Dev}(X) - \text{Dev}(\text{constant})}{1} \Big/ \frac{\text{Dev}(\text{time}) - \text{Dev}(X)}{K-1} \tag{2}$$

where Dev(constant), Dev(X) and Dev(time) stand for the deviance of models with constant, covariate-dependent and time-dependent survival probabilities. To obtain the associated P value, the value of the ANODEV is compared with the quantile of Fisher–Snedecor distribution with 1 and $K-1$ degrees of freedom.

To reduce the dimension of the set of covariates (X_1, …, X_p), we used PCA which aims at finding a small number of linear combinations of the original variables—the principal components (PCs)—while maximizing the variance in (X_1, …, X_p). Because the variables measurement units often differ, we performed the PCA on the correlation matrix (Jolliffe 2002). To select PCs, we used a forward model selection algorithm as proposed by Aguilera et al. (2006) for the logistic regression. The forward algorithm begins with no covariates in the model. Each PC is incorporated in simple linear regression-like CR models and the ANODEV P value calculated. The PC that has the lowest P value is added to the null model, say PC$_k$. Then the PCs that were not retained are incorporated along with PC$_k$ in multiple regression-like CR models, and ANODEV P values are calculated. In other words, we need to assess the effect of PC$_j$ for $j \neq k$ in the presence of PC$_k$ to decide whether PC$_j$ should be retained. To do so, Dev(constant) and Dev(X) are replaced by Dev(PC$_k$) and Dev(PC$_k$ + PC$_j$) in Eq. 2, where Dev(PC$_k$ + PC$_j$) is the deviance of the model with survival as a function of both principal components PC$_k$ and PC$_j$. We repeat the process until no remaining PC is selected.

All models were fitted using the maximum-likelihood method using MARK (White and Burnham 1999) called with R using package RMark (Laake 2013).

Case study

The Snow petrel is a medium sized Procellariiform species endemic to Antarctica that breeds in summer. Birds start to occupy breeding sites in early November, laying occurs in early December and chicks fledge in early March. This highly specialized species only forages within the pack-ice on crustaceans and fishes. Data on survival were obtained from a long-term CR study on Ile des Pétrels, Pointe Géologie Archipelago, Terre Adélie, Antarctica. We refer to Barbraud et al. (2000) for more details about data collection. We removed the first capture to limit heterogeneity among individuals, and worked with a total of 604 female capture histories from 1973 to 2002.

The following covariates were included to assess the effect of climatic conditions upon survival variation: sea ice extent (SIE; http://nsidc.org/data/seaice_index/); air temperature, which was obtained from the Météo France weather station at Dumont d'Urville, as a proxy for sea surface temperature; southern Oscillation Index (SOI) as a proxy for the overall climate condition (https://crudata.uea.ac.uk/cru/data/soi/). These environmental variables were averaged over seasonal time periods corresponding to the chick rearing period (January–March: summer period), the non-breeding period (April–June: autumn and July–September: winter), and the laying and incubation period of the same year (October–December: spring). In total, nine covariates were included in the analysis: sea ice extent in summer (SIEsummer), in autumn (SIEautumn), in winter (SIEwinter), in spring (SIEspring), annual SOI, air temperature in summer (Tsummer), in autumn (Tautumn), in winter (Twinter) and in spring (Tspring).

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Results

The CJS model poorly fitted the data ($\chi^2 = 221.2$, $df = 127$, $P < 0.01$), and a closer inspection of the results revealed that the lack of fit was explained by a trap-dependence effect (Test2CT, $\chi^2 = 103.1$, $df = 27$, $P < 0.01$). Consequently, we estimated two recapture probabilities that differed according to whether or not a recapture occurred the occasion before. By first attempting to simplify the structure of recapture probabilities, we were led to consider an additive effect of time and a trap effect (Electronic Supplementary material, ESM). Estimates of recapture probabilities ranged from 0.14 [standard error (SE) 0.07] to 0.79 (SE 0.09) when no recapture occurred the occasion before and from 0.25 (SE 0.18) to 0.89 (SE 0.09) when a recapture occurred the occasion before (ESM).

Because of multicollinearity, we were led to counter-intuitive estimates of regression parameters in the CR model including all covariates (ESM): the coefficient of SIE in autumn was estimated at 0.5 (SE 0.24) and that of SIE in winter was estimated at −0.5 (SE 0.21) while these two covariates were significantly positively correlated ($r_P = 0.67$, $P < 0.01$).

When we applied the P2CR approach, the algorithm selected two PCs, namely PC3 ($F_{1,27} = 7.34$, $P = 0.01$) at step 1 and PC4 ($F_{1,26} = 4.63$, $P = 0.04$) at step 2 (ESM), but never did we pick PC1 as we would have done using a classical approach (Grosbois et al. 2008). PC3 was positively correlated to SIE in summer and negatively correlated to temperature in winter, while PC4 was positively correlated to temperature in spring and negatively correlated to SIE in summer (ESM). Survival increased with increasing values of PC3 (Fig. 1), with high values of SIE in summer and low values of temperature in winter (resp. low values of SIE in summer and high values of temperature in winter) corresponding to high (resp. low) survival.

Survival decreased with increasing values of PC4 (Fig. 2), with high values of temperature in spring and low values of SIE in summer (resp. low values of temperature in spring and high values of SIE in summer) corresponding to low (resp. high) survival.

The P2CR approach also led to more precise survival estimates when compared to the model incorporating all original covariates (Fig. 3).

Discussion

We introduce a new approach combining principal component analysis and capture–recapture models to deal with many possibly correlated explanatory covariates. Our approach requires standard statistical tools, which allows an efficient and easy implementation using standard software.

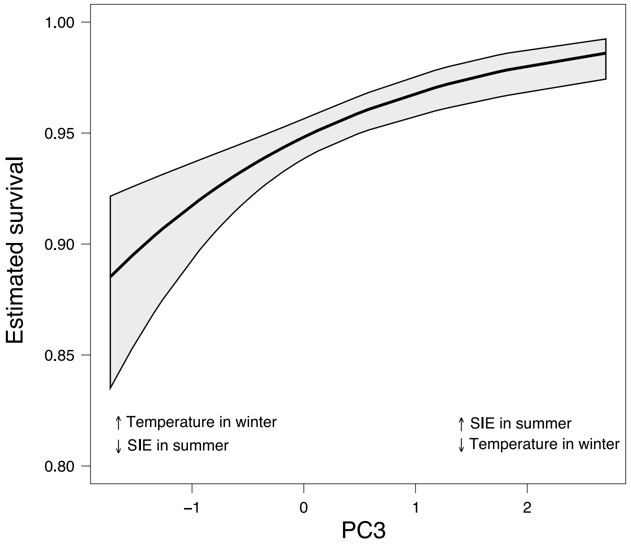

Fig. 1 Estimated survival of Snow petrel as a function of PC3 (*solid line*) with 95% confidence interval (*shaded area*). Low survival is associated with low values of PC3 that correspond to high values of air temperature in winter and low values of sea ice extent (SIE) in summer; high survival is associated with high values of PC3 that correspond to low values of air temperature in winter and high values of SIE in summer

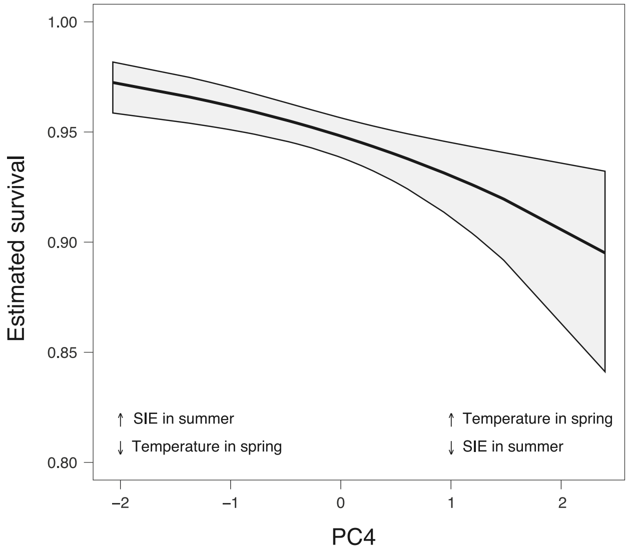

Fig. 2 Estimated survival of Snow petrel as a function of PC4 (*solid line*) with 95% confidence interval (*shaded area*). High survival is associated with low values of PC4 that correspond to low values of air temperature in spring and high values of sea ice extent (SIE) in summer; low survival is associated with high values of PC4 that correspond to high values of air temperature in spring and low values of SIE in summer

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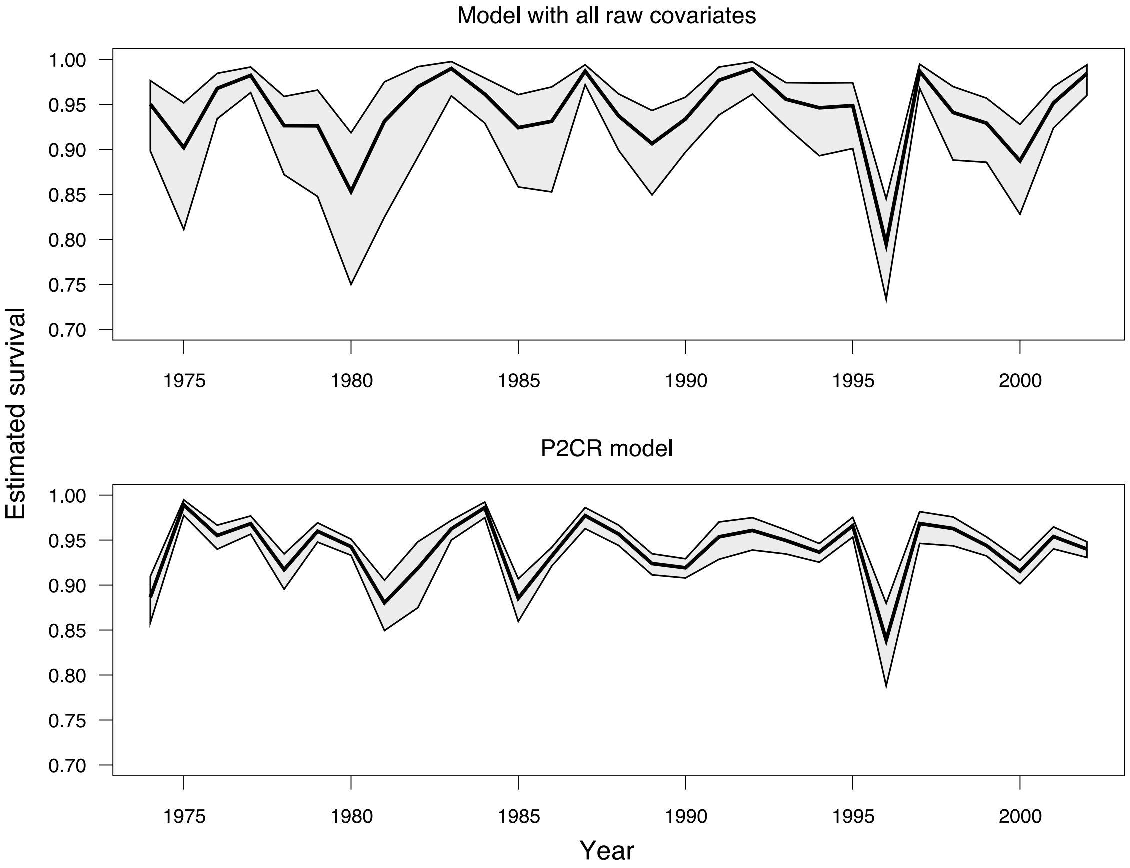

Fig. 3 Survival of Snow petrel over time as estimated from the model with all original covariates (*solid line, top panel*) vs. the PC2R model (*solid line, bottom panel*). 95% confidence intervals are also displayed (*shaded area*)

Snow petrels and climatic conditions

In summer, snow petrels exclusively forage within the pack-ice tens to hundreds of kilometers from the colony where they catch sea ice-associated species, such as Antarctic silverfish (*Pleuragramma antarcticum*) and Euphausiids, to feed their chick (Ridoux and Offredo 1989). This is an energetically demanding period for breeding adults and, during years with reduced sea-ice extent, food resources may be less abundant and snow petrels may be forced to cover larger distances to find suitable foraging habitats, with potential survival costs. Assuming air temperature was a proxy of sea surface temperature variations, the negative effect of warmer temperatures on survival is coherent with general patterns found between sea surface temperature and demographic parameters in seabirds (Barbraud et al. 2012). In many marine ecosystems warmer temperatures are associated with decreased primary production and food resources for top predators. Although the low survival in 1996 corresponded to a year with reduced sea-ice extent in summer, the drop in survival was high and remains unexplained at the moment.

Principal component CR models

When multiple covariates have to be considered to estimate survival, both issues of dimensionality and multicollinearity can lead to biased estimates, inflated precision as well as lack of statistical power. In such a context, the P2CR modeling framework has proved particularly useful in our example, mainly because few PCs were selected which were easily interpretable. We acknowledge that PCs with little interpretability might have been picked up by our method. To make the interpretation easier, PCA results can be post-processed by rotating axes to improve correlations between raw variables and PCs like in the varimax method (Kaiser 1958). Recent developments in the field of multivariate analyses could also be useful, like methods to handle with missing values in PCA (Dray and Josse 2015).

In statistical ecology, one of our objectives is to try and explain variation in state variables such as abundance, survival and the distribution of species. Dimension-reduction methods are promising to deal with many correlated covariates for the analysis of CR or occupancy data.

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