Ecography

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Fernández-Chacón, A., Genovart, M., Pradel, R., Tavecchia, G., Bertolero, A., Piccardo, J., Forero, M. G., Afán, I., Muntaner, J. and Oro, D. 2013. When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population. – Ecography 36: xxx–xxx.

Supplementary material

Appendix 1

Specification of the multi-event modeling approach in program E-SURGE

Multi-event models were built in several stages using program E-SURGE (Choquet and Nogue 2010). Each step represents one of the different parameters to estimate (Φ, d, ψ, p', p, see below). This is done by means of row-stochastic matrices, i.e. each row corresponds to a multinomial. Consequently, the total of cell probabilities is 1. Because of this constraint, one and only one cell probability in each row will be calculated as the complement to 1 of the others. This particular cell is denoted with a '*' symbol. Inactive cells, i.e. cells whose associated probability is structurally 0 are denoted with a '-' symbol. An active cell receives an arbitrary letter. Note that the same Greek letter in two cells does not mean that the two values should be equal.

The individual states considered are:

E, Individual breeding at the Ebro Delta that was not resighted the previous year (unaware state).

C, Individual breeding at the Columbretes archipelago (regardless of having been resighted or not the previous year at the same site).

X, Individual breeding at the Chafarinas islands that was not resighted the previous year (unaware state).

M, Individual breeding at Southern Mallorca (regardless of having been resighted or not the previous year at the same site).

G, Individual alive but out of the study area (*Ghost* site)

E', Individual breeding at the Ebro Delta that was resighted the previous year (aware state).

X', Individual breeding at the Chafarinas islands that was resighted the previous year (aware state).

†, Dead.

The possible events are:

1, seen at the Ebro Delta.

2, seen at the Columbretes archipelago.

3, seen at the Chafarinas islands.

4, seen at Southern Mallorca.

0, not seen.

The symbols for parameters are:

Y, Initial state probability

Φ, survival probability

d, departure probability (1-fidelity probability)

ψ, settlement probability

p', Unaware-aware transition probability (=recapture probability for the Ebro Delta and Chafarinas sites)

p, event probability (=recapture probability for Columbretes and Southern Mallorca sites)

Initial State probabilities ("Dead" cannot be an initial state)

1x7

E	C	X	M	G	E'	X'
-	Y	-	Y	-	Y	*

Transition probabilities, step 1: Survival

8x8

From/to	**E**	**C**	**X**	**M**	**G**	**E’**	**X’**	**†**
E	**Φ**	-	-	-	-	-	-	*
C	-	**Φ**	-	-	-	-	-	*
X	-	-	**Φ**	-	-	-	-	*
M	-	-	-	**Φ**	-	-	-	*
G	-	-	-	-	**Φ**	-	-	*
E’	-	-	-	-	-	**Φ**	-	*
X’	-	-	-	-	-	-	**Φ**	*
†	-	-	-	-	-	-	-	*

Transition probabilities, step 2: Departure (Note: Departure = ”out” and Fidelity = ”in”; here we estimate only departure and leave fidelity as the complement “*”).

8x15

From/to	**E**in	**E**out	**C**in	**C**out	**X**in	**X**out	**M**in	**M**out	**G**in	**G**out	**E’**in	**E’**out	**X’**in	**X’**out	**†**
D	*	**d**	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	*	**d**	-	-	-	-	-	-	-	-	-	-	-
X	-	-	-	-	*	**d**	-	-	-	-	-	-	-	-	-
M	-	-	-	-	-	-	*	**d**	-	-	-	-	-	-	-
G	-	-	-	-	-	-	-	-	*	**d**	-	-	-	-	-
D’	-	-	-	-	-	-	-	-	-	-	*	**d**	-	-	-
X’	-	-	-	-	-	-	-	-	-	-	-	-	*	**d**	-
†	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*

Transition probabilities, step 3: Settlement

15x8

From/to	**E**	**C**	**X**	**M**	**G**	**E'**	**X'**	**†**
Ein	*	-	-	-	-	-	-	-
Eout	-	**Ψ**	**Ψ**	**Ψ**	*	-	-	-
Cin	-	*	-	-	-	-	-	-
Cout	**Ψ**	-	**Ψ**	**Ψ**	*	-	-	-
Xin	-	-	*	-	-	-	-	-
Xout	**Ψ**	**Ψ**	-	**Ψ**	*	-	-	-
Min	-	-	-	*		-	-	-
Mout	**Ψ**	**Ψ**	**Ψ**	-	*	-	-	-
Gin	-	-	-	-	*	-	-	-
Gout	**Ψ**	**Ψ**	**Ψ**	*	-	-	-	-
E'in	*	-	-	-	-	-	-	-
E'out	-	**Ψ**	**Ψ**	**Ψ**	*	-	-	-
X'in	-	-	*	-	-	-	-	-
X'out	**Ψ**	**Ψ**	-	**Ψ**	*	-	-	-
†	-	-	-	-	-	-	-	*

Transition probabilities, step 4: recapture (Unaware-Aware transitions)

8x8

From/to	**E**	**C**	**X**	**M**	**G**	**E'**	**X'**	**†**
E	*	-	-	-	-	***p'***	-	-
C	-	*	-	-	-	-	-	-
X	-	-	*	-	-	-	***p'***	-
M	-	-	-	*	-	-	-	-
G	-	-	-	-	*	-	-	-
E'	*	-	-	-	-	***p'***	-	-
X'	-	-	*	-	-	-	***p'***	-
†	-	-	-	-	-	-	-	*

Event probabilities, step 1: recapture

8x5

From/to	Not seen (**0**)	Seen at the Ebro Delta (**1**)	Seen at Columbretes (**2**)	Seen at Chafarinas (**3**)	Seen at Southern Mallorca (**4**)
E	*	-	-	-	-
C	*	-	***p***	-	-
X	*	-	-	-	-
M	*	-	-	-	***p***
G	*	-	-	-	-
E'	-	*	-	-	-
X'	-	-	-	*	-
†	*	-	-	-	-

Choquet, R. and Nogue, E. 2010. E-SURGE 1.7 user's manual. - CEFE, Montpellier.

Appendix 2

Post hoc linear models for settlement estimates

Problem: the effect of covariates on settlement probabilities cannot be built in the CR model because the desirable link function (logit) is not available. An alternative is to retrieve the estimates of a model without constraint and run a post hoc analysis. However, because the estimates come with a variance matrix, a GLM is not appropriate. A generalized least square is the solution. There are two main difficulties:

1. Obtaining the variance matrix of the right quantities
2. Finding a statistical program that does the GLS model

1. Deriving the Variance matrix:

We used E-SURGE to estimate the settlement probabilities. E-SURGE provides the variance matrix of the mathematical parameters (but only the individual standard errors of the reconstituted biological parameters). We can use the delta method to obtain the variance matrix of the reconstituted settlement probabilities. However, because we want to fit a logit linear model, we will have to apply the delta method a second time after that.

Settlement probabilities are estimated for migrants. Thus, there is a settlement probability μ_{ij} for each pair of site (departure=*i*, arrival=*j*) with $i \neq j$. In our study, there are 4 sites (1=D=Ebro Delta, 2=C=Columbretes Islands, 3=X=Chafarinas Islands, 4=M= Mallorca) plus a catchall fifth site that we call the ghost location (G) and which serves for all individuals that go to unmonitored sites or skip breeding altogether. Settlement probabilities from a given site of departure *i* sum to 1. One of them is thus computed as the complement of the others. For our study, it is convenient to choose the 'settlement on the Ghost Location' as the complement.

The settlement probabilities from a given site of departure *i* are estimated in E-SURGE through a generalized logit link function. This is a multivariate function, the exact form of which depends on which settlement probability is computed as the complement of the others. With the 'settlement on the Ghost Location' taken as the complement, the generalized logit for settlement probabilities of individuals departing from the Ebro Delta takes the form:

$$(\mu_{DC} \quad \mu_{DX} \quad \mu_{DM}) \rightarrow (\beta_{D1} \quad \beta_{D2} \quad \beta_{D3})$$

where

$$\beta_{D1} = \ln\left(\frac{\mu_{DC}}{1 - \mu_{DC} - \mu_{DX} - \mu_{DM}}\right),$$

$$\beta_{D2} = \ln\left(\frac{\mu_{DX}}{1 - \mu_{DC} - \mu_{DX} - \mu_{DM}}\right),$$

$$\beta_{D3} = \ln\left(\frac{\mu_{DM}}{1 - \mu_{DC} - \mu_{DX} - \mu_{DM}}\right).$$

There is no simple correspondence between the individual μs and βs. In particular, the first β, β_{D1}, does not reflect the sole probability of settlement at the Columbretes, reason why its second index is a 1 and not a C.

The generalized logit can be inverted:

$$\mu_{DC} = \frac{e^{\beta_{D1}}}{1 + e^{\beta_{D1}} + e^{\beta_{D2}} + e^{\beta_{D3}}}$$

$$\mu_{DX} = \frac{e^{\beta_{D2}}}{1 + e^{\beta_{D1}} + e^{\beta_{D2}} + e^{\beta_{D3}}}$$

$$\mu_{DM} = \frac{e^{\beta_{D3}}}{1 + e^{\beta_{D1}} + e^{\beta_{D2}} + e^{\beta_{D3}}}$$

Although the β on the numerator does not correspond strictly to the μ on the other side of the equality, it may be simpler to use the same indexes and this is what E-SURGE does. This abuse of notation simplifies the writing of formulas. If we take the 'settlement on the Ghost Location' as the complement whatever the site of departure, and replace D, C, X and M respectively with 1, 2, 3 and 4, then we have

$$\mu_{ij} = \frac{e^{\beta_{ij}}}{1 + \sum_{k \neq i} e^{\beta_{ik}}}$$ for i=1 to 4; j=1 to 4; k=1 to 4 and i≠j

To apply the delta method, we need the partial derivatives of the μs with respect to the βs. After some algebra, we get

$$\frac{\partial \mu_{ij}}{\partial \beta_{ik}} = -\mu_{ij}\mu_{ik}, k \neq j$$

$$\frac{\partial \mu_{ij}}{\partial \beta_{ik}} = \mu_{ij}(1 - \mu_{ij}), k = j$$

$$\frac{\partial \mu_{ij}}{\partial \beta_{lk}} = 0, i \neq l$$

The matrix D_μ of the first derivatives of the μs (in rows) with respect to the βs (in columns) is thus

	β_{12}	β_{13}	β_{14}	β_{21}	β_{23}	β_{24}	β_{31}	β_{32}	β_{34}	β_{41}	β_{42}	β_{43}
μ_{12}	$\mu_{12}(1-\mu_{12})$	$-\mu_{12}\mu_{13}$	$-\mu_{12}\mu_{14}$	0	0	0	0	0	0	0	0	0
μ_{13}	$-\mu_{13}\mu_{12}$	$\mu_{13}(1-\mu_{13})$	$-\mu_{13}\mu_{14}$	0	0	0	0	0	0	0	0	0
μ_{14}	$-\mu_{14}\mu_{12}$	$-\mu_{14}\mu_{13}$	$\mu_{14}(1-\mu_{14})$	0	0	0	0	0	0	0	0	0
μ_{21}	0	0	0	$\mu_{21}(1-\mu_{21})$	$-\mu_{21}\mu_{23}$	$-\mu_{21}\mu_{24}$	0	0	0	0	0	0
μ_{23}	0	0	0	$-\mu_{23}\mu_{21}$	$\mu_{23}(1-\mu_{23})$	$-\mu_{23}\mu_{24}$	0	0	0	0	0	0
μ_{24}	0	0	0	$-\mu_{24}\mu_{21}$	$-\mu_{24}\mu_{23}$	$\mu_{24}(1-\mu_{24})$		0	0	0	0	0
μ_{31}	0	0	0	0	0	0	$\mu_{31}(1-\mu_{31})$	$-\mu_{31}\mu_{32}$	$-\mu_{31}\mu_{34}$	0	0	0
μ_{32}	0	0	0	0	0	0	$-\mu_{32}\mu_{31}$	$\mu_{32}(1-\mu_{32})$	$-\mu_{32}\mu_{34}$	0	0	0
μ_{34}	0	0	0	0	0	0	$-\mu_{34}\mu_{31}$	$-\mu_{34}\mu_{32}$	$\mu_{34}(1-\mu_{34})$	0	0	0
μ_{41}	0	0	0	0	0	0	0	0	0	$\mu_{41}(1-\mu_{41})$	$-\mu_{41}\mu_{42}$	$-\mu_{41}\mu_{43}$
μ_{42}	0	0	0	0	0	0	0	0	0	$-\mu_{42}\mu_{41}$	$\mu_{42}(1-\mu_{42})$	$-\mu_{42}\mu_{43}$
μ_{43}	0	0	0	0	0	0	0	0	0	$-\mu_{43}\mu_{41}$	$-\mu_{43}\mu_{42}$	$\mu_{43}(1-\mu_{43})$

As per the Delta method, the variance matrix V(μ) of the μs is approximated by

$$D_\mu V(\beta) D_\mu^{\,T}$$

Where V(β) is the variance matrix of the βs and $D_\mu^{\,T}$ is the transpose of D_μ.

2. Retrieving the Variance matrix of the βs in the E-SURGE output:

The difficult point is to identify the βs corresponding to the settlement probabilities among all the mathematical parameters. I proceeded in the following way. In E-SURGE, select the option 'from last model', retrieve the model of interest, and open IVFV. Find the settlement probabilities in IVFV (actually their β transforms) and look at the numerical values. In the sheet 'Beta' of the Excel output of the same model, find the same values. I did this with model46. The settlement probabilities were the parameters 62 to 76 and with IVFV, I can see that the first one is β_{21}, the next one β_{31} etc... Then going to sheet 'Var-Cov', I can extract the submatrix corresponding to these βs.

I could then calculate D_μ and V(μ). This last calculation involving matrix products was done in R.

```
#R-script Delta method for settlement

D<-matrix(0,12,12)

D[1,]<-c(0.117146837,-0.106032943,-0.011113894,0,0,0,0,0,0,0,0,0)

D[2,]<-c(-0.106032943,0.10760978,-0.001576837,0,0,0,0,0,0,0,0,0)

D[3,]<-c(-0.011113894,-0.001576837,0.012690731,0,0,0,0,0,0,0,0,0)

D[4,]<-c(0,0,0,0.046502306,-2.85332E-09,-0.033254435,0,0,0,0,0,0)

D[5,]<-c(0,0,0,-2.85332E-09,3E-09,-1.04892E-10,0,0,0,0,0,0)
```

```
D[6,]<-c(0,0,0,-0.033254435,-1.04892E-10,0.033741443,0,0,0,0,0,0)

D[7,]<-c(0,0,0,0,0,0,0.129466761,-0.004614051,-4.91625E-07,0,0,0)

D[8,]<-c(0,0,0,0,0,0,-0.004614051,0.029280926,-9.71293E-08,0,0,0)

D[9,]<-c(0,0,0,0,0,0,-4.91625E-07,-9.71293E-08,3.21699E-06,0,0,0)

D[10,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)

D[11,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)

D[12,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)

M<-c(0.864490279,0.122653714,0.012856008,0.951107187,0.000000003,0.034963919,0.152821028,0.030192514,0.000003217,1,0,0)

VCV<-matrix(0,12,12)

VCV[1,]<-c(0.20614054,0.15905685,0.03321758,1.04026856,-0.05664936,1.14629378,-0.01732456,-0.01418431,-0.03188666,0,0,0)

VCV[2,]<-c(0.15905685,0.17940281,0.05448564,1.01921411,-0.05570602,1.15025645,-0.01077763,-0.02180492,-0.03172129,0,0,0)

VCV[3,]<-c(0.03321758,0.05448564,0.15419649,0.67031994,-0.03361497,0.69258843,-0.00492457,-0.01481698,-0.01980359,0,0,0)

VCV[4,]<-c(1.04026856,1.01921411,0.67031994,7.30974251,-0.38204743,7.87568008,-0.08578104,-0.12440104,-0.22089041,0,0,0)

VCV[5,]<-c(-0.05664936,-0.05570602,-0.03361497,-0.38204743,0.02101213,-0.41914279,0.00456552,0.00640252,0.01176308,0,0,0)
```

```
VCV[6,]<-c(1.14629378,1.15025645,0.69258843,7.87568008,-0.41914279,8.72916172,-
0.09225856,-0.14225517,-0.24183528,0,0,0)

VCV[7,]<-c(-0.01732456,-0.01077763,-0.00492457,-0.08578104,0.00456552,-
0.09225856,0.03589406,0.02909819,0.0022974,0,0,0)

VCV[8,]<-c(-0.01418431,-0.02180492,-0.01481698,-0.12440104,0.00640252,-
0.14225517,0.02909819,0.42137069,0.00252894,0,0,0)

VCV[9,]<-c(-0.03188666,-0.03172129,-0.01980359,-0.22089041,0.01176308,-
0.24183528,0.0022974,0.00252894,0.00677493,0,0,0)

VCV[10,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)

VCV[11,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)

VCV[12,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)

#delta method

D%*%VCV%*%t(D)
```

---

3. Calculating the Variance matrix for the logit of the μs:

Using again the delta method, we get

$$cov\big(logit(u), logit(v)\big) = \frac{cov(u, v)}{u(1-u)v(1-v)}$$

$$var\big(logit(u), logit(v)\big) = \frac{var(u, v)}{u^2(1-u)^2}$$

The variance matrix of the logits can thus be derived from that of the μs.

4. Post-hoc analysis of the effect of the distance (Standardized distance or distN) :

Because we work with *estimates* of the logit(μ)=LTMU, not the logit(μ) themselves, we must account for their variances and covariances with a generalized least square approach. This procedure is implemented in MATLAB with the function lscov and in R with the function lm.gls of the library MASS.

MATLAB code:

```
A=[ones(12,1) distN]

A =

 1.0000 -1.3491
 1.0000  1.0343
 1.0000 -0.6367
 1.0000 -1.3491
 1.0000  0.7592
 1.0000 -0.8010
 1.0000  1.0343
 1.0000  0.7592
 1.0000  0.9933
 1.0000 -0.6367
 1.0000 -0.8010
 1.0000  0.9933
```

LTMU

LTMU =

1.902573483

-2.015301302

-4.393265995

3.136467656

-19.11382792

-3.325105816

-1.747501714

-3.897856223

-14.92720776

18

-18

-18

VLTMU

VLTMU =

0.070	-0.067	-0.080	0.019	-0.015	-0.019	-0.007	0.012	0.001	0.000	0.000	0.000
-0.067	0.066	0.057	-0.024	0.013	0.026	0.007	-0.013	-0.001	0.000	0.000	0.000
-0.080	0.057	0.264	0.036	0.027	-0.049	0.007	-0.007	-0.001	0.000	0.000	0.000
0.019	-0.024	0.036	0.245	-0.449	-0.198	-0.003	0.002	-0.002	0.000	0.000	0.000
-0.015	0.013	0.027	-0.449	2.053	0.103	-0.001	0.079	0.012	0.000	0.000	0.000
-0.019	0.026	-0.049	-0.198	0.103	0.215	0.003	-0.019	0.000	0.000	0.000	0.000

-0.007 0.007 0.007 -0.003 -0.001 0.003 0.030 0.006 -0.004 0.000 0.000 0.000

0.012 -0.013 -0.007 0.002 0.079 -0.019 0.006 1.018 -0.021 0.000 0.000 0.000

0.001 -0.001 -0.001 -0.002 0.012 0.000 -0.004 -0.021 0.001 0.000 0.000 0.000

0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000

0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000

0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000

V=VLTMU+eye(12)*0.00001

V =

0.070 -0.067 -0.080 0.019 -0.015 -0.019 -0.007 0.012 0.001 0.000 0.000 0.000

-0.067 0.066 0.057 -0.024 0.013 0.026 0.007 -0.013 -0.001 0.000 0.000 0.000

-0.080 0.057 0.264 0.036 0.027 -0.049 0.007 -0.007 -0.001 0.000 0.000 0.000

0.019 -0.024 0.036 0.245 -0.449 -0.198 -0.003 0.002 -0.002 0.000 0.000 0.000

-0.015 0.013 0.027 -0.449 2.053 0.103 -0.001 0.079 0.012 0.000 0.000 0.000

-0.019 0.026 -0.049 -0.198 0.103 0.215 0.003 -0.019 0.000 0.000 0.000 0.000

-0.007 0.007 0.007 -0.003 -0.001 0.003 0.030 0.006 -0.004 0.000 0.000 0.000

0.012 -0.013 -0.007 0.002 0.079 -0.019 0.006 1.018 -0.021 0.000 0.000 0.000

0.001 -0.001 -0.001 -0.002 0.012 0.000 -0.004 -0.021 0.001 0.000 0.000 0.000

0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.00001 0.000

0.000

0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.00001 0.000

0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.00001

```
[x,stdx,mse,S]=lscov(A,LTMU,V)

% x(1) is the intercept; x(2) the slope of the distance

x =

   -5.5960

   -7.7173

% stdx gives the standard errors

stdx =

    3.6554

    4.9807

mse =

  7.5699e+006

% S is the variance covariance matrix of the intercept and slope

S =

   13.3621    6.6140

    6.6140   24.8077
```

5. problems with boundary parameters:

Two settlement probabilities were estimated at 0 and one was estimated at 1. Their asymptotic variances could not be computed by E-SURGE. This led to a non-invertible variance matrix. To solve this problem a solution is to add a small quantity on the diagonal. We added 0.00001 on the diagonal of V(logit μ). [V=VLTMU+eye(12)*0.00001]

Appendix 3

Backward approach for the selection of the best predictor of settlement

In this backward approach, we are proceeding from the full regression model (with all covariates) and removing the least significant until all remaining covariates are significant (see table A). Significance is determined by performing t-tests using the slope estimates and their standard errors (see Table B).

Table A. p-values for each element in the regression function and the effects removed (in bold) at each step of the backward approach, departing from the full regression model.

	Step 1	**Step 2**	**Step 3**	**Step 4**
	t-test df = 7	t-test df=8	t-test df=9	t-test df=10
Intercept	0.1863	0.1340	0.1145	0.1690
Distance	0.5644	0.3667	**0.3468**	-
Num. breeding pairs	0.0974	0.0573	0.0098	0.0035
Foraging area	**0.9236**	**-**	**-**	**-**
Breeding success	0.6753	**0.6613**	**-**	**-**

The removed least significant effects are (in chronological order): Foraging area, Breeding success and Distance.

Table B: Slope estimates and Standard errors (in parenthesis) for each step of the backward approach.

	Step 1	**Step 2**	**Step 3**	**Step 4**
Intercept	-5.4796 (3.7400)	-5.3278 (3.1953)	-4.5868 (2.6250)	-3.5981 (2.4269)
Distance	-4.3425 (7.1805)	-3.7640 (3.9341)	-3.7283 (3.7560)	11.6134 (3.0581)
Num. breeding pairs	12.9490 (6.7718)	12.6553 (5.7031)	10.5686 (3.2363)	-
Foraging area	-0.7569 (7.6182)	-	-	-
Breeding success	-2.6419 (6.0456)	-2.4849 (5.4624)	**-**	-