Bayesian integrated population modeling using JAGS

Some further examples of integrated population models

Example 1:
Identifying demographic reasons of the UK lapwing decline

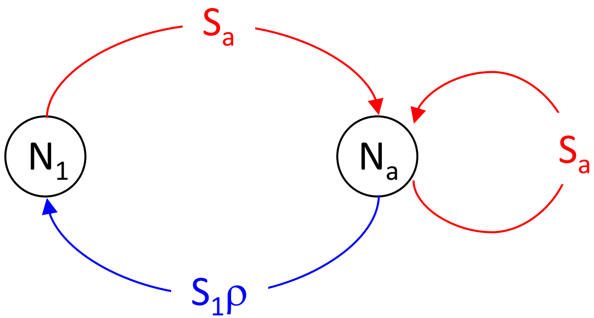
Background:

- Numbers declining in UK
- Demographic reasons unknown
- Brooks et al. (2004)

Available data:

- Population counts from Common Bird Census (CBC)
- Recoveries of dead individuals ringed as chicks

1. Set up a population model



Stochastic population model:

$$N_{1,t+1} \sim \text{Po}\left(N_{a,t}\rho_t S_{1,t}\right)$$

$$N_{a,t+1} \sim \text{Bin}\left(N_{1,t} + N_{a,t}, S_{a,t}\right)$$

<u>Parameters</u>
S: survival probability
ρ: productivity
N_1: population size of 1y
N_a: population size of adults

2. Likelihood for the different data sets

A. Counts: state-space model

State process equations:

$$N_{1,t+1} \sim \text{Po}\left(N_{a,t}\rho_t S_{1,t}\right)$$

$$N_{a,t+1} \sim \text{Bin}\left(N_{1,t} + N_{a,t}, S_{a,t}\right)$$

Observation process equation:

Only breeding bird are counted, thus

$$y_t \sim \text{N}\left(N_{a,t}, \sigma_y^2\right)$$

<u>Parameters</u>

S: survival probability

ρ: productivity

N_1: population size of 1y

N_a: population size of adults

y: count data

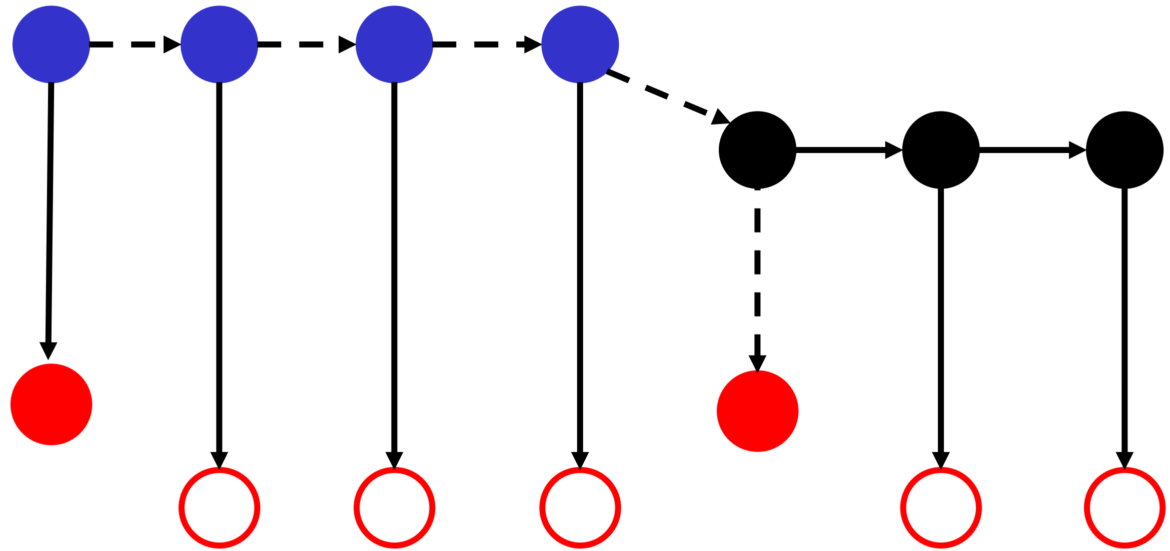
σ^2_y: census/residual error

B. Dead-recovery data

State process

Alive

Dead



Recovered

Not recovered

Observation process

Stochastic process

Deterministic process

B. Dead-recovery data

1. Survival process

$$z_{i,first} = 1$$

$$z_{i,t} \sim Bernoulli\left(z_{i,t-1} s_{i,t-1}\right)$$

where,

$z_{i,t}$: matrix, indicating whether individual *i* is alive at time *t* (z = 1), or dead (z = 0)

$s_{i,t}$: survival probability for individual *i* from time *t* to *t*+1

2. Observation process

$$y_{i,t} \sim Bernoulli\left(\left[z_{i,t-1} - z_{i,t}\right] r_{i,t}\right)$$

where,

$y_{i,t}$: is the observed capture history for individual *i* at time *t*

$r_{i,t}$: recovery probability for individual *i* at time *t*

<u>Parameters</u>

S: survival probability

r: ring recovery probability

3. Joint likelihood

- State-space model likelihood

  $L_s(N_1, N_a, \rho, S_1, S_a, \sigma_y^2)$

- Dead recovery model likelihood

  $L_r(S_1, S_a, r)$

- Joint likelihood

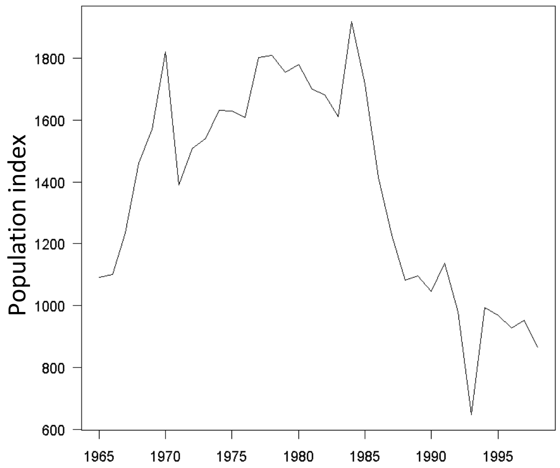
  $L_j(N_1, N_a, \rho, \sigma_y^2, S_1, S_a, r) =$

  $L_s(N_1, N_a, \rho, S_1, S_a, \sigma_y^2) L_r(S_1, S_a, r)$

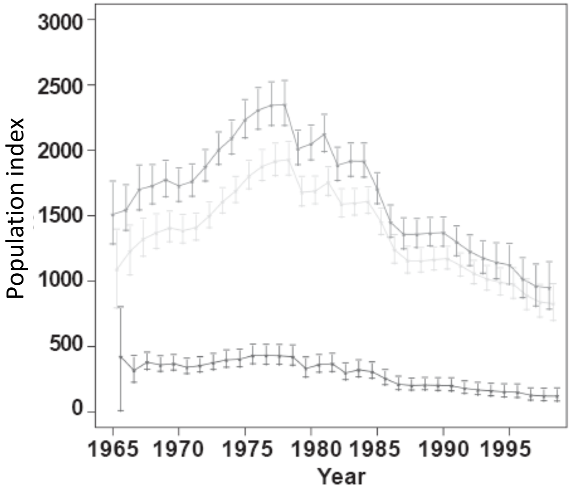
Results

1. Population development

observed

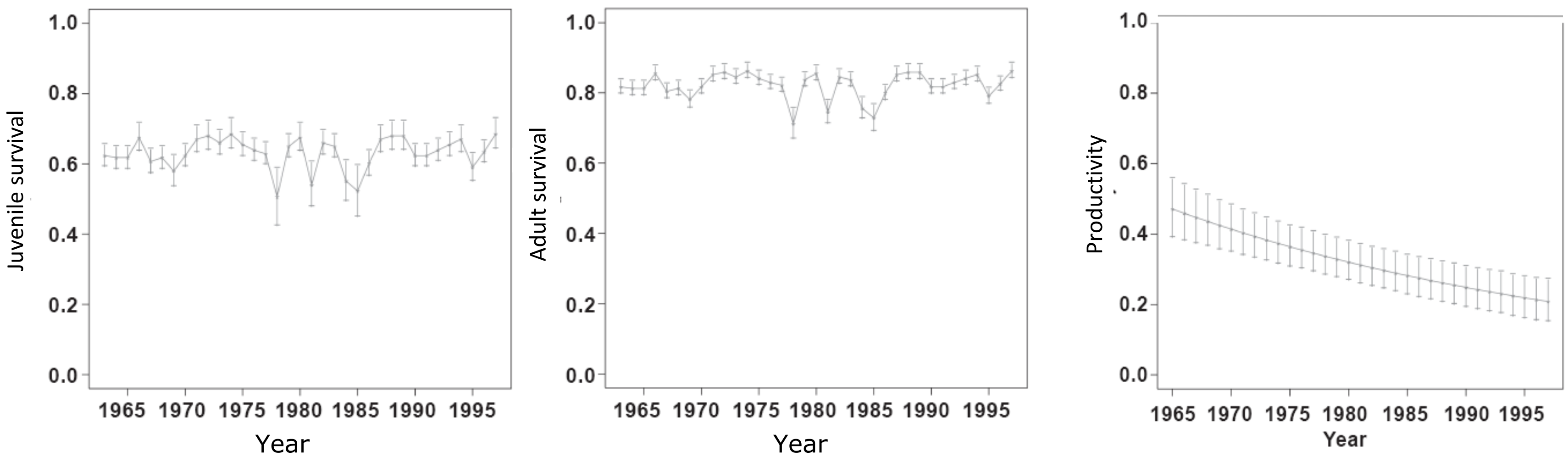


estimated



Results

2. Demographic rates



Conclusions

- Population decline confirmed by model
- Decline of productivity as a major demographic reason for the decline of the lapwing population in the UK

Benefits of integrated modelling for the lapwing example

- Estimate of productivity
- Smooth population index with confidence limits (both age classes)

Example 2:
Immigration in a little owl population

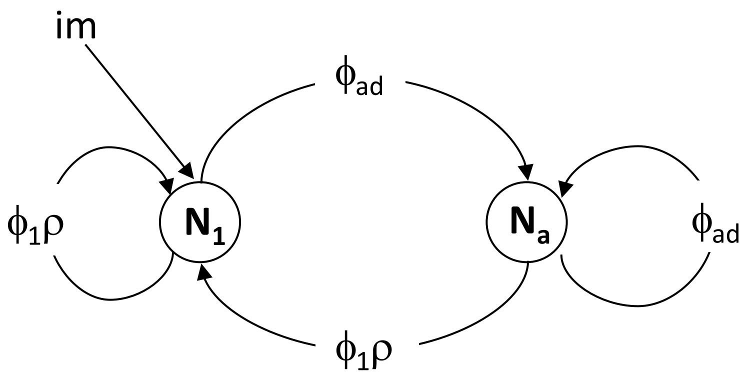
Background:

- Nest box population (SW Germany)
- Impact of vole density on immigration?
- Abadi et al. (2010), J. Appl. Ecol.

Available data (1978-2003):

- Capture-recapture data
- Reproductive success
- Number of breeding pairs

1. Set up a population model



Stochastic population equations:

$$N_{1,t+1} \sim \text{Po}\left[\left(N_{1,t} + N_{a,t}\right)\left(\phi_{1,t}\rho_t + im_t\right)\right]$$

$$N_{a,t+1} \sim \text{Bin}\left(N_{1,t} + N_{a,t}, \phi_{a,t}\right)$$

<u>Parameters</u>

ϕ: local survival probability
ρ: productivity
im: immigration rate
N_1: population size of 1y
N_a: population size of adults

2. Likelihood for the different data sets

A. Counts: state-space model

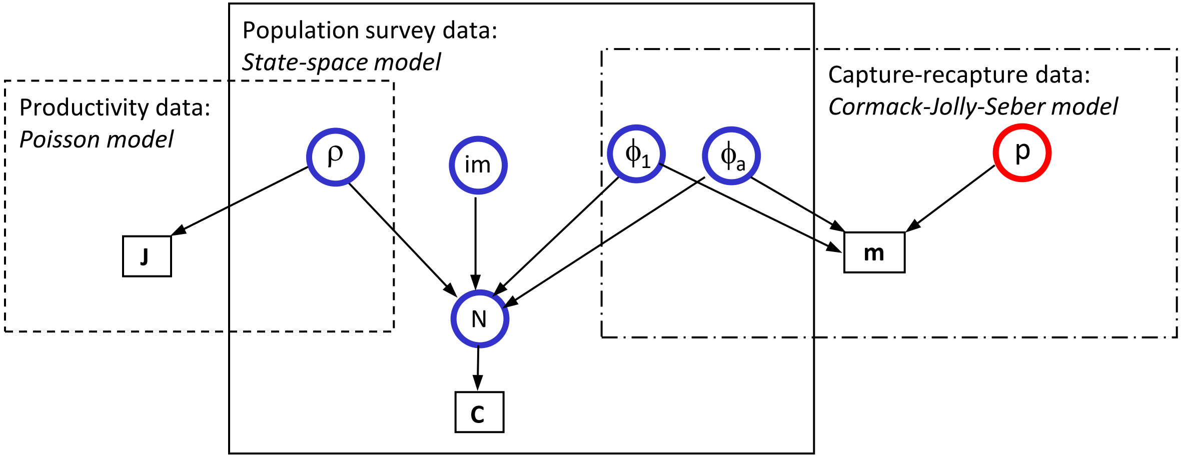
B. Capture-recapture data: Cormack-Jolly-Seber model

C. Number of fledglings: Poisson regression model

3. Joint likelihood

$$L_j(N_1, N_a, \rho, im, \phi_1, \phi_a, p) = L_s(N_1, N_a, \rho, im, \phi_1, \phi_a) L_r(\phi_1, \phi_a, p) L_n(\rho)$$

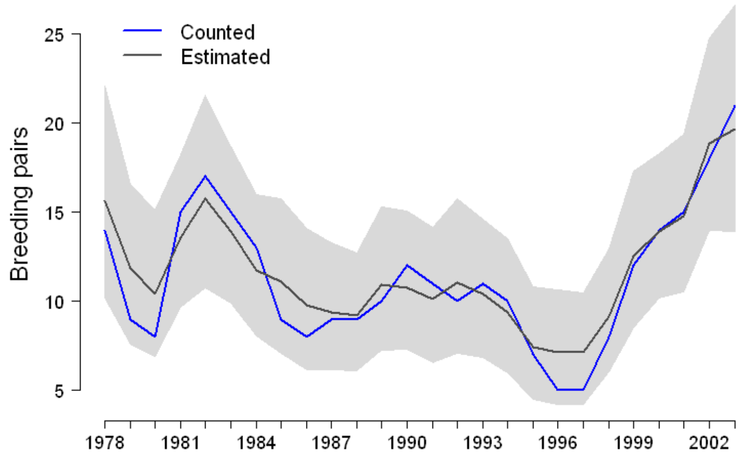
Graphical relationship between data and parameter:

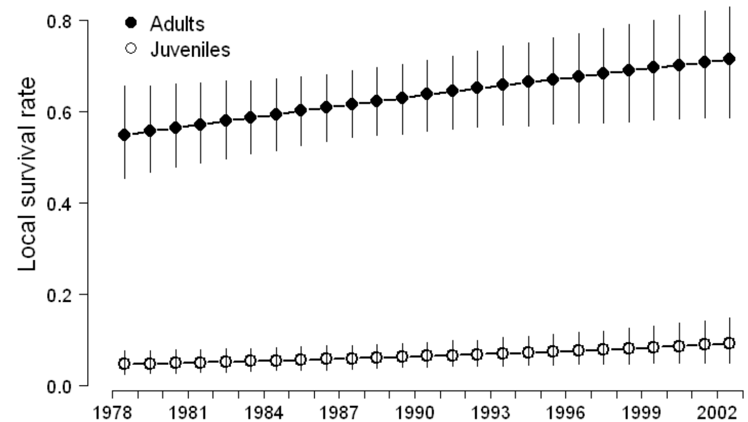


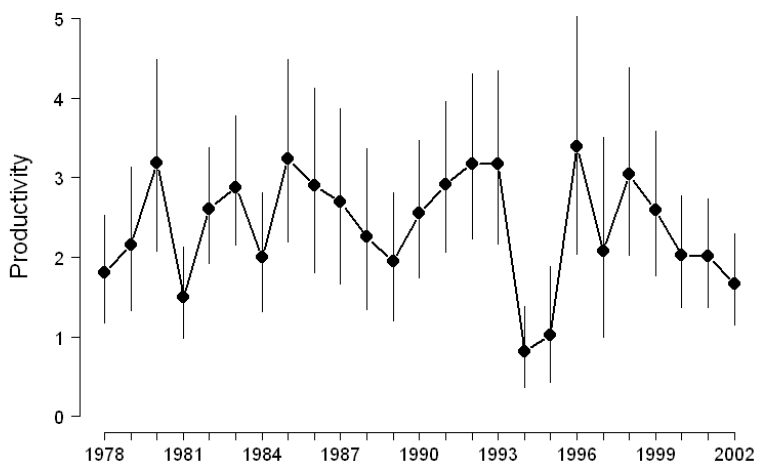
Modelling immigration rate:

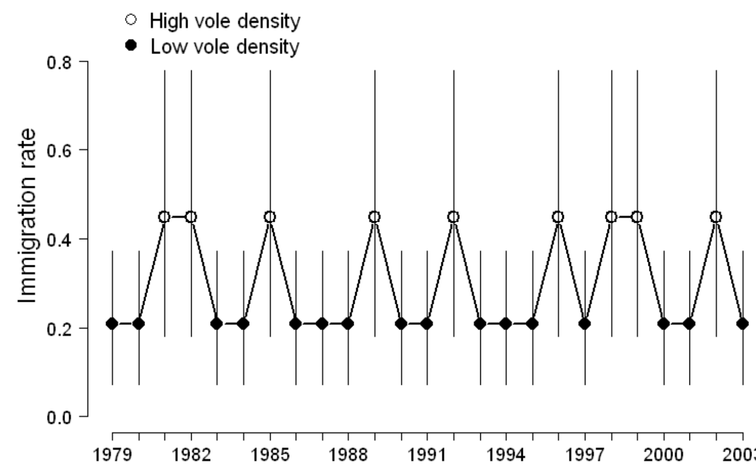
$$\log(im_t) = \beta_0 + \beta_1 vole_t$$

Results


Counted
Estimated
Breeding pairs
25
20
15
10
5
1978
1981
1984
1987
1990
1993
1996
1999
2002


Adults
Juveniles
Local survival rate
0.8
0.6
0.4
0.2
0.0
1978
1981
1984
1987
1990
1993
1996
1999
2002


Productivity
5
4
3
2
1
0
1978
1981
1984
1987
1990
1993
1996
1999
2002


High vole density
Low vole density
Immigration rate
0.8
0.6
0.4
0.2
0.0
1979
1982
1985
1988
1991
1994
1997
2000
2003

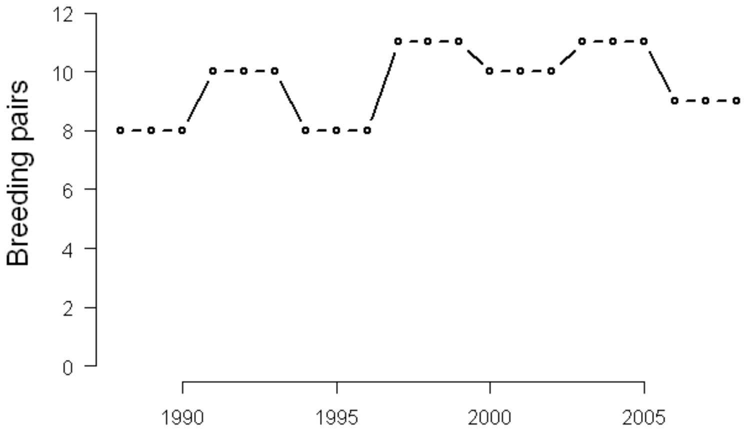
Conclusions

- Immigration was substantial
- Immigration to the population was higher in years with abundant prey

Benefits of integrated modelling for the little owl example

- Estimate of immigration rate
- Modelling covariate effects on immigration

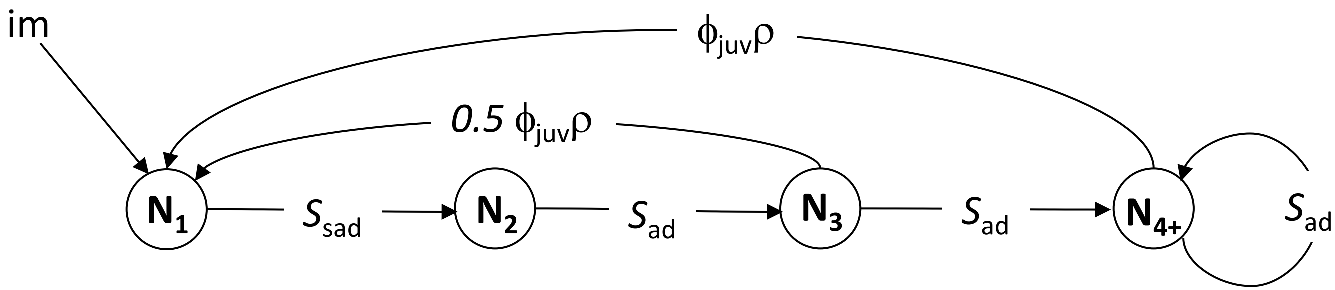
Example 3:
Demographic assessment of a small eagle owl population



Background:
- Population study from the Valais
- Why does the population not increase?
- Schaub et al. (2010), Biol. Cons.

Available data (1988-2008):
- Number of breeding pairs
- Number of fledglings per year
- Telemetry data of fledglings
- Age-ratios from museum skins

1. Set up a population model



Stochastic population sizes:

$$N_{1,t+1} \sim \text{Po}\left[\left(\frac{1}{2}N_{3,t} + N_{4,t}\right)\left(\phi_{juv,t}\rho_t + im_t\right)\right]$$

$$N_{2,t+1} \sim \text{Bin}\left(N_{1,t}, S_{sad,t}\right)$$

$$N_{3,t+1} \sim \text{Bin}\left(N_{2,t}, S_{ad,t}\right)$$

$$N_{4+,t+1} \sim \text{Bin}\left(\left(N_{3,t} + N_{4,t}\right), S_{ad,t}\right)$$

<u>Parameters</u>

ϕ_{juv}: local juvenile survival probability
S_{sad}: subadult survival probability
S_{ad}: adult survival probability
ρ: productivity
im: immigration rate
N_1: population size of 1y
N_2: population size of 2y
N_3: population size of 3y
N_{4+}: population size of 4y or older

2. Likelihood for the different data sets

A. Counts: state-space model

B. Telemetry data of fledglings

- 28 owls tracked in the period 2002 – 2008
- Capture-recapture type of analysis with trap-dependence
- Survey area: Valais and some adjacent valleys

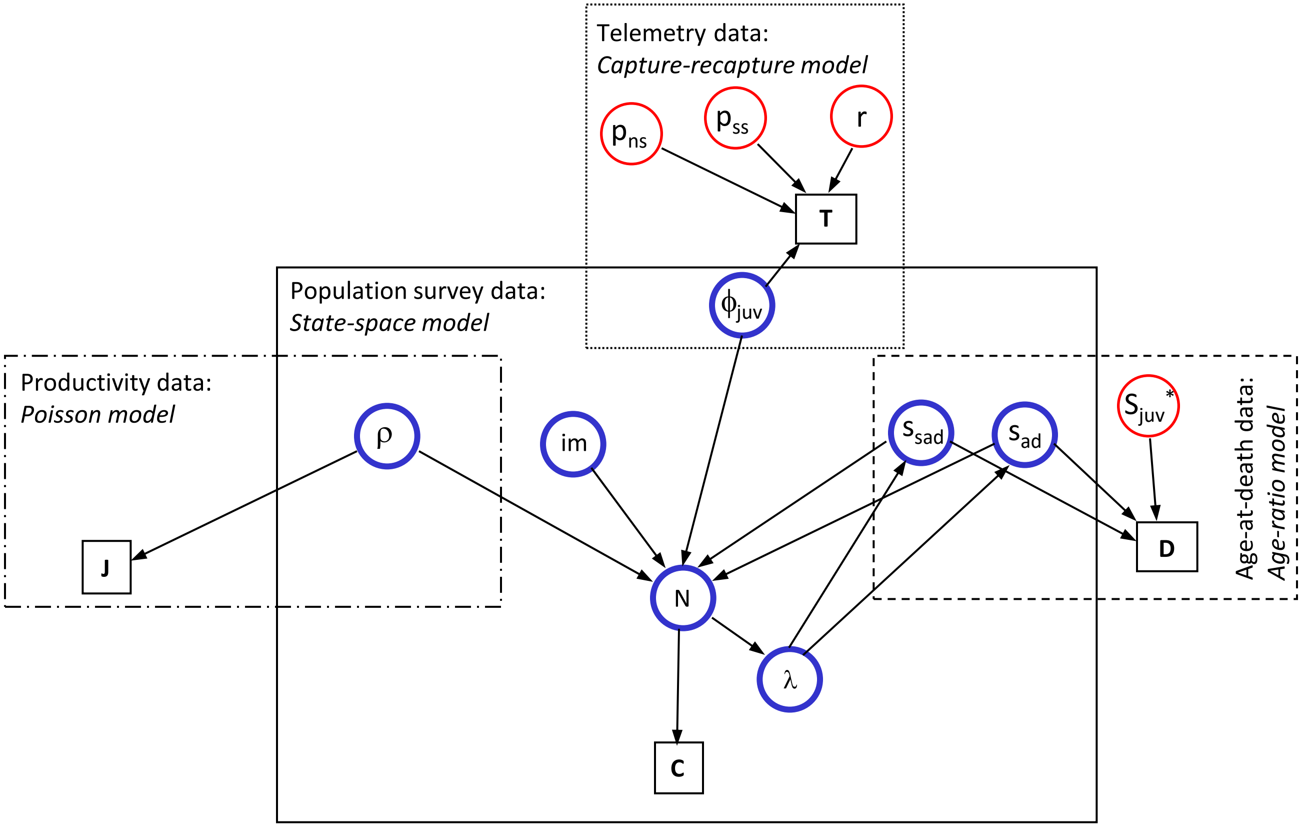
C. Age-ratio from museum skins

- 102 owls from the period 1988 – 2008 from whole Switzerland
- Age-ratio methods (Udevitz & Ballachey 1998)
    - Population growth rate must be known
    - Stable age distribution
    - Finding probability independent of age

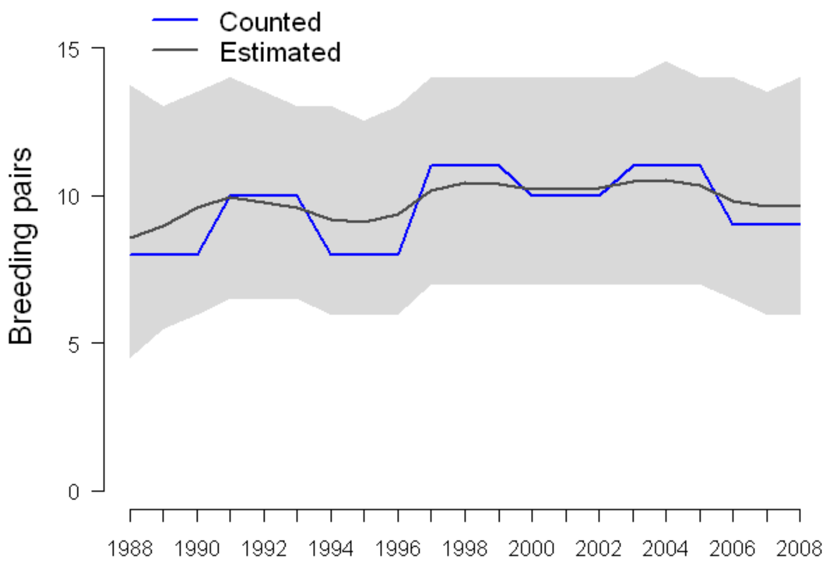
D. Number of fledglings: Poisson regression model

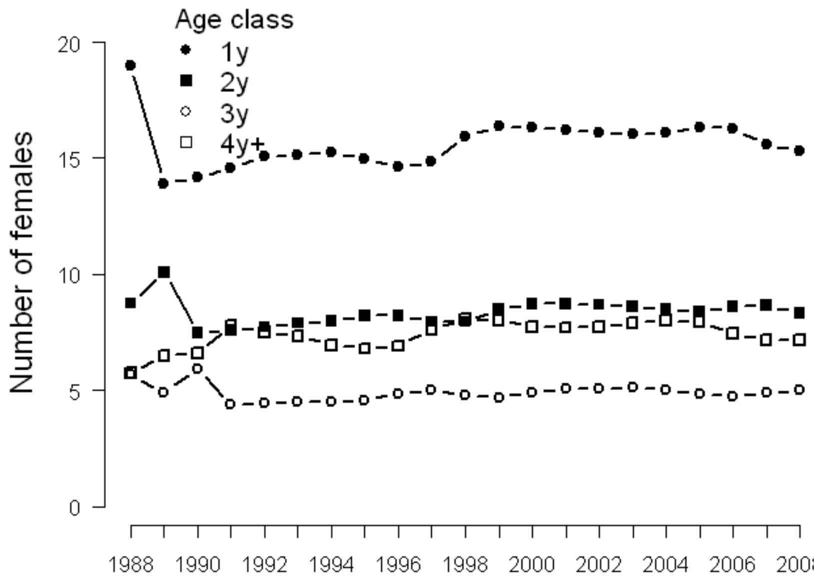
3. Joint likelihood

Graphical relationship between data and parameter:



Results: population sizes



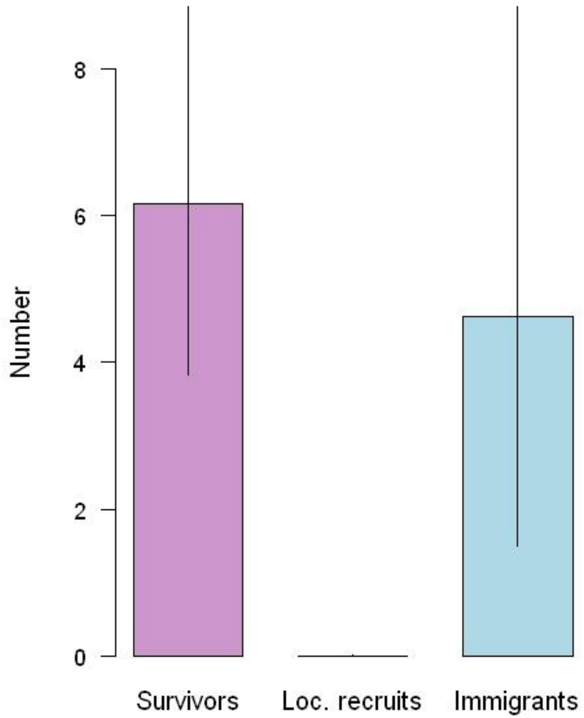


Results

Estimates of demographic rates

	Mean	SD
Local juvenile survival	0.09	0.05
Subadult survival	0.54	0.06
Adult survival	0.61	0.07
Productivity	0.93	0.10
Immigration rate	1.59	0.66
Population growth rate	1.01	0.01

Population composition



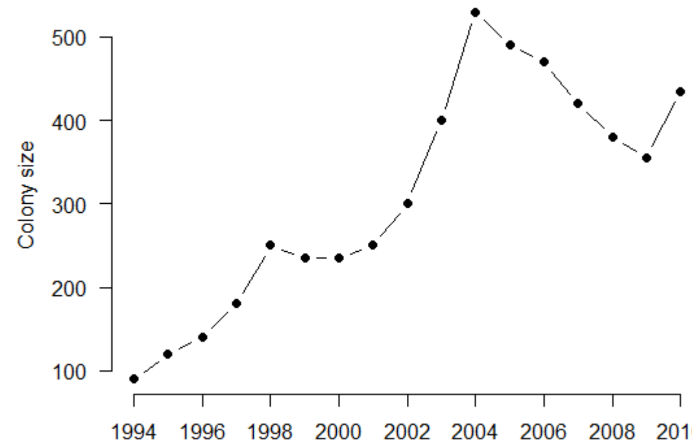
Conclusions

- Stable population only due to massive immigration
- Population not self-sustainable
- Mortality very high, most of it human-induced

Benefits of integrated modelling for the eagle owl example

- Estimates of immigration and adult survival
- Estimates of population sizes

Example 4: **Correlates of immigration in a common tern colony**



Background:

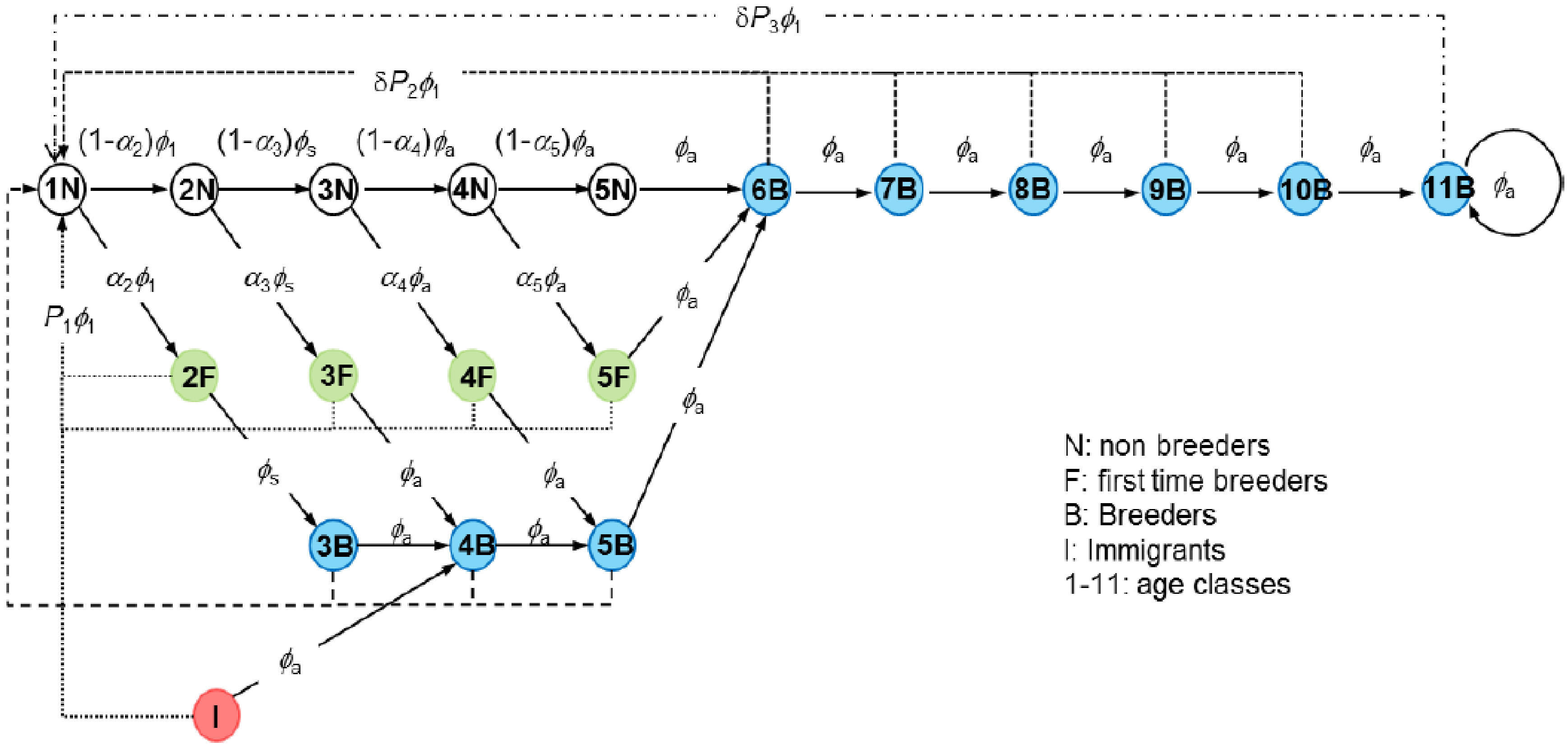
- Population study in the Wadden Sea
- Immmigration important at all?
- By which factors are immigrants attracted?
  - Conspecific attraction?
  - Public information?

Available data (1994-2010):

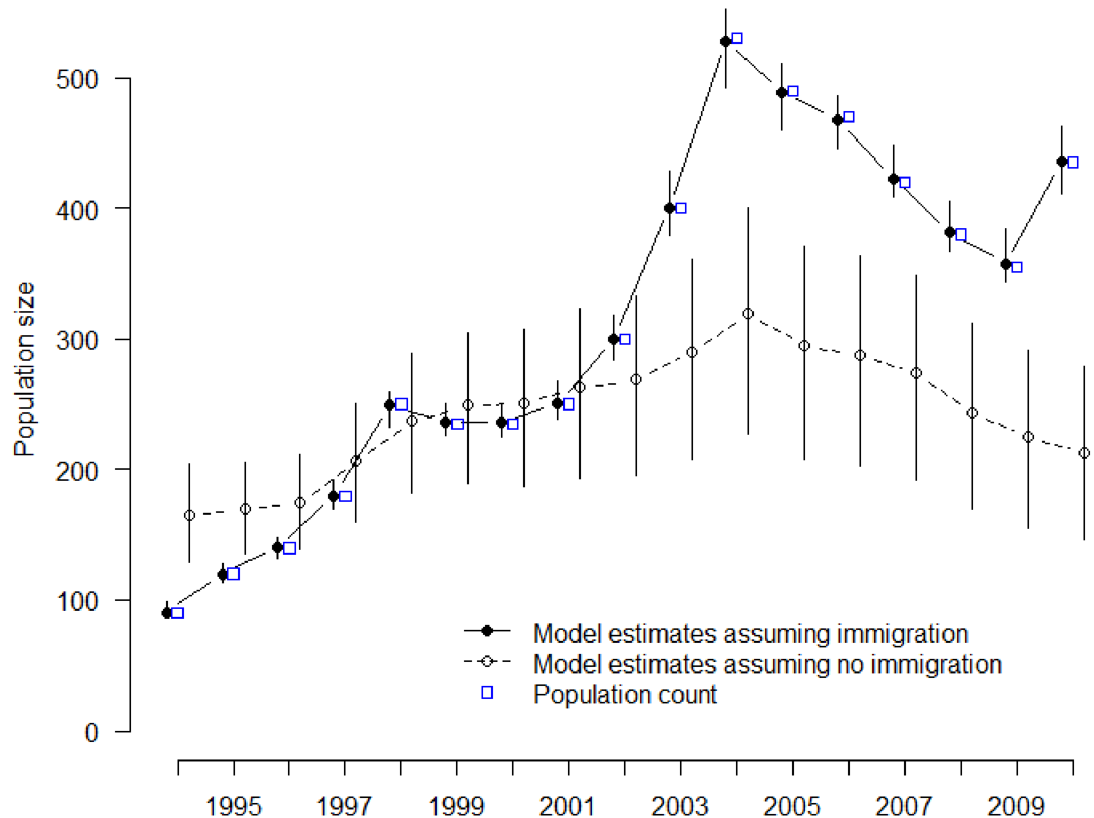
- Number of breeding pairs
- Number of fledglings per year
- Capture-recapture data

Szostek *et al.* (2014) J. Anim Ecol.

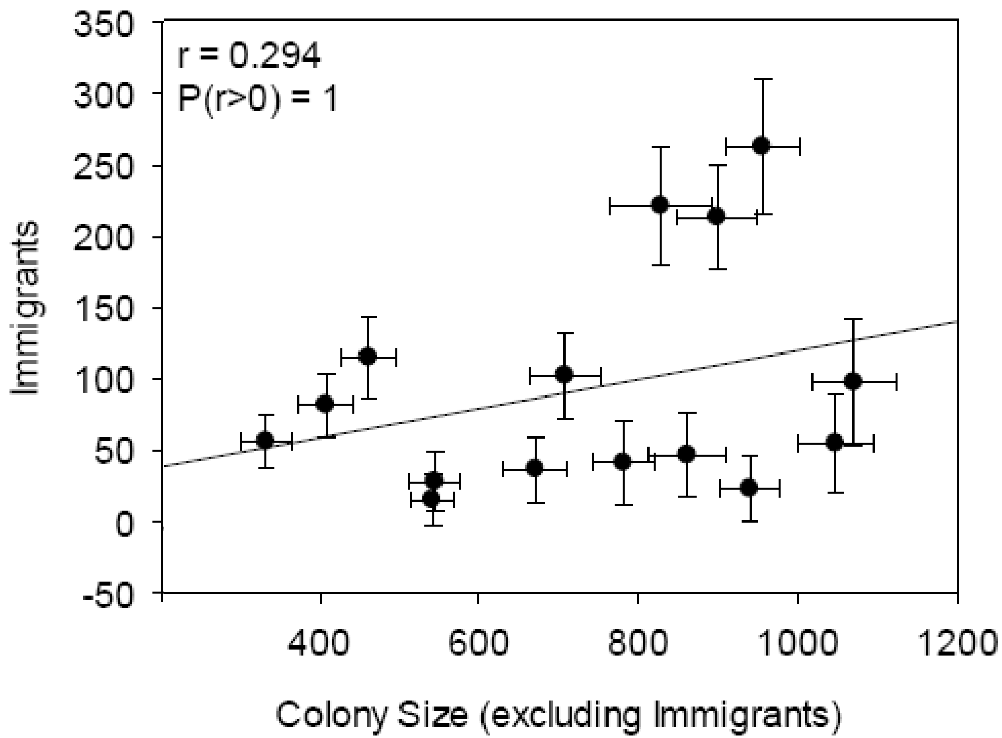
Life cycle graph



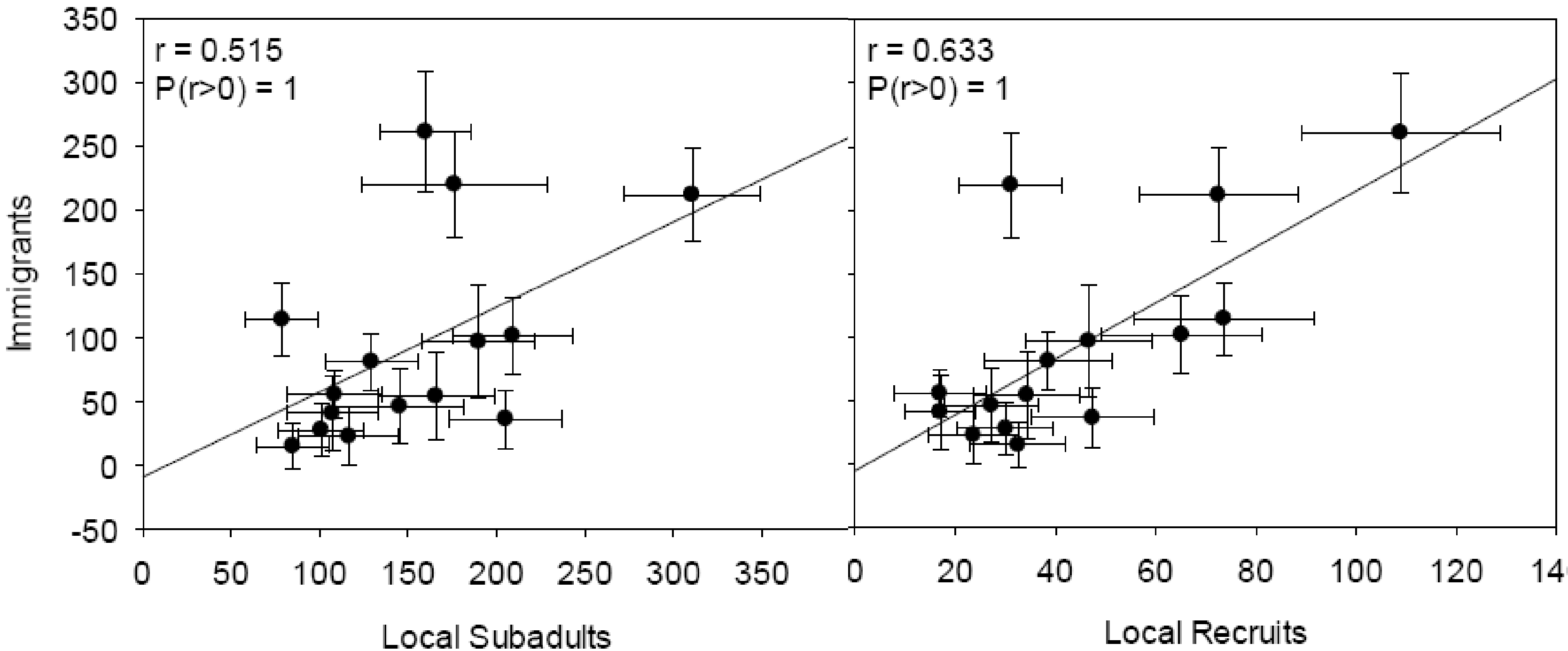
Immigration was important for the tern colony growth



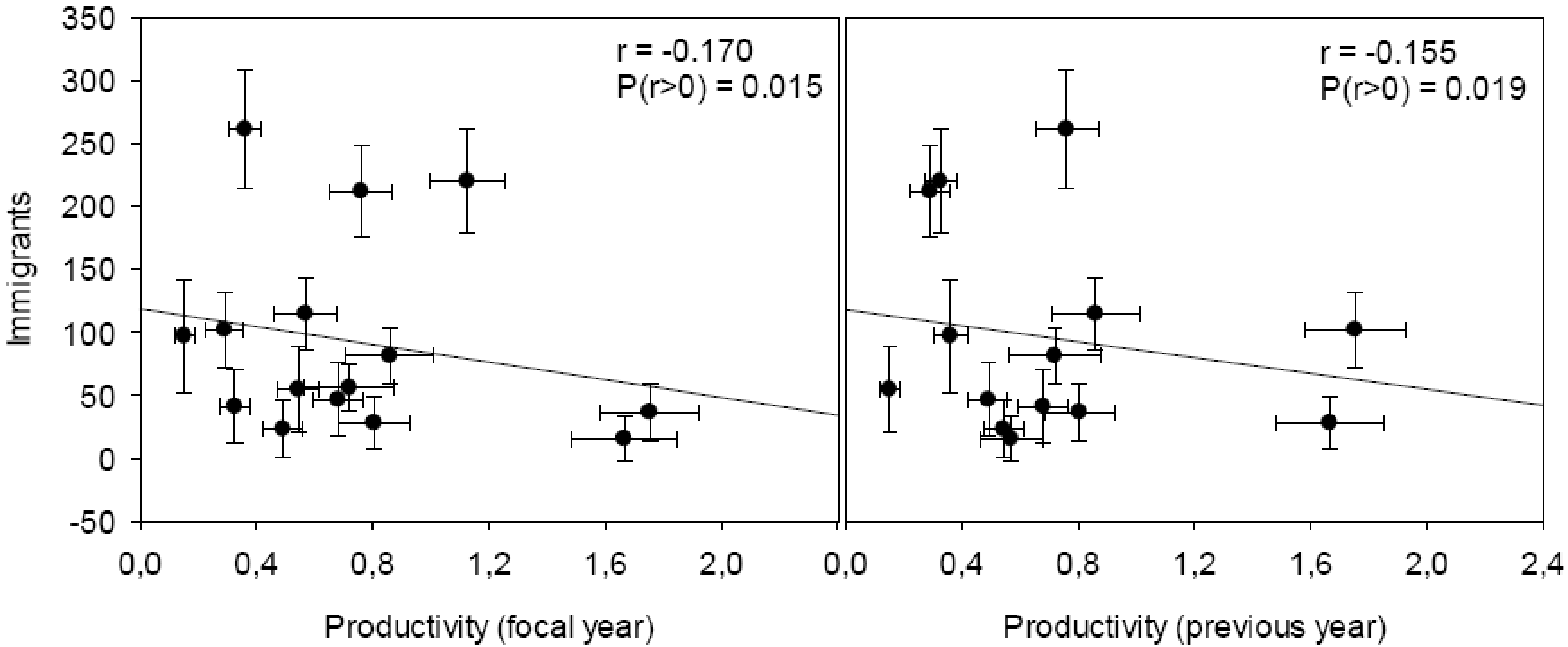
Conspecific attraction?



Conspecific attraction?

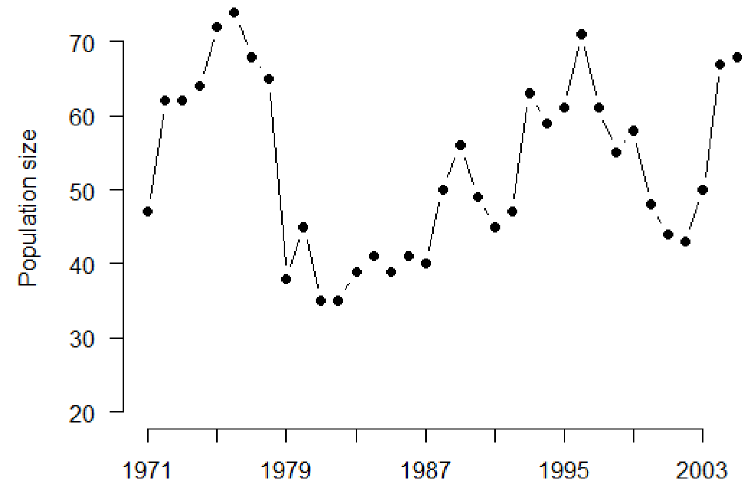


Public information?



- Immigration was an important demographic driver of the tern colony dynamics
- Conspecific attraction is most likely a driver for immigrants and for the settlement decision
- Public information about productivity was not important for the settlement decision

Example 5: **Significance of immigration for the dynamics of a red-backed shrike population**



Background:

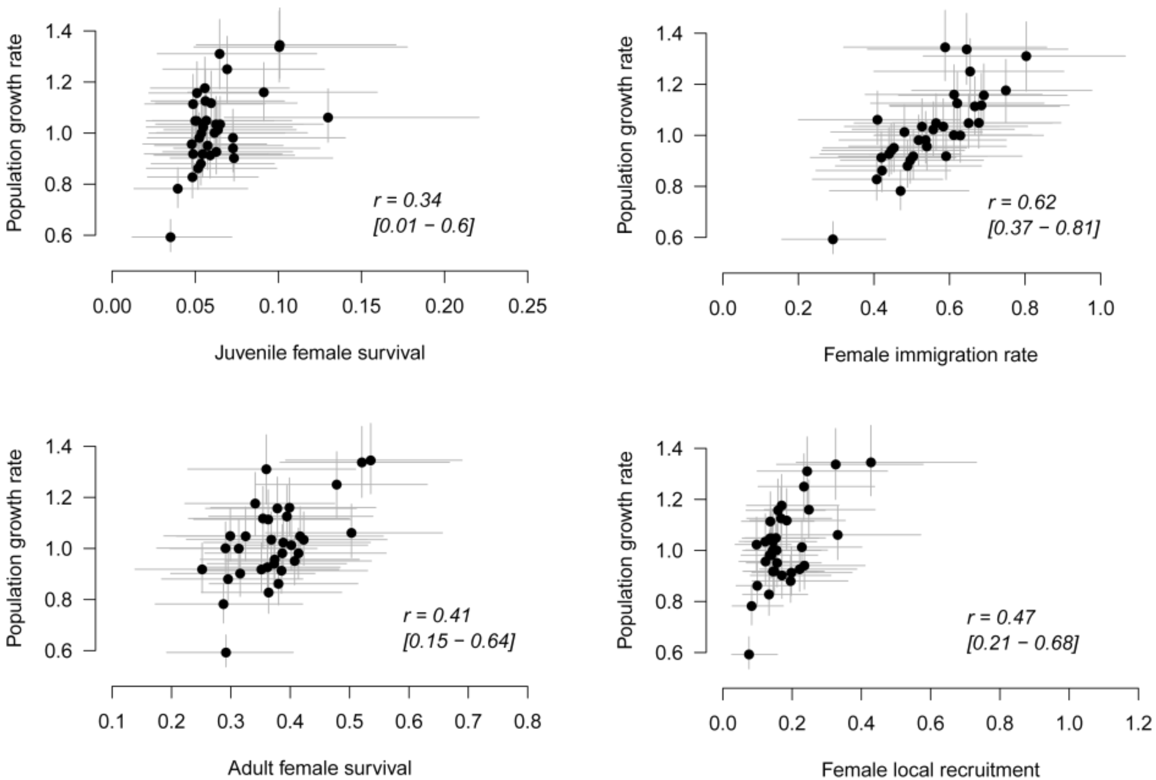
- Population study in southern Germany
- Has immigration contributed to the dynamics?
- Can immigration contribute to population regulation?
- Composition of the population

Available data (1971-2006):

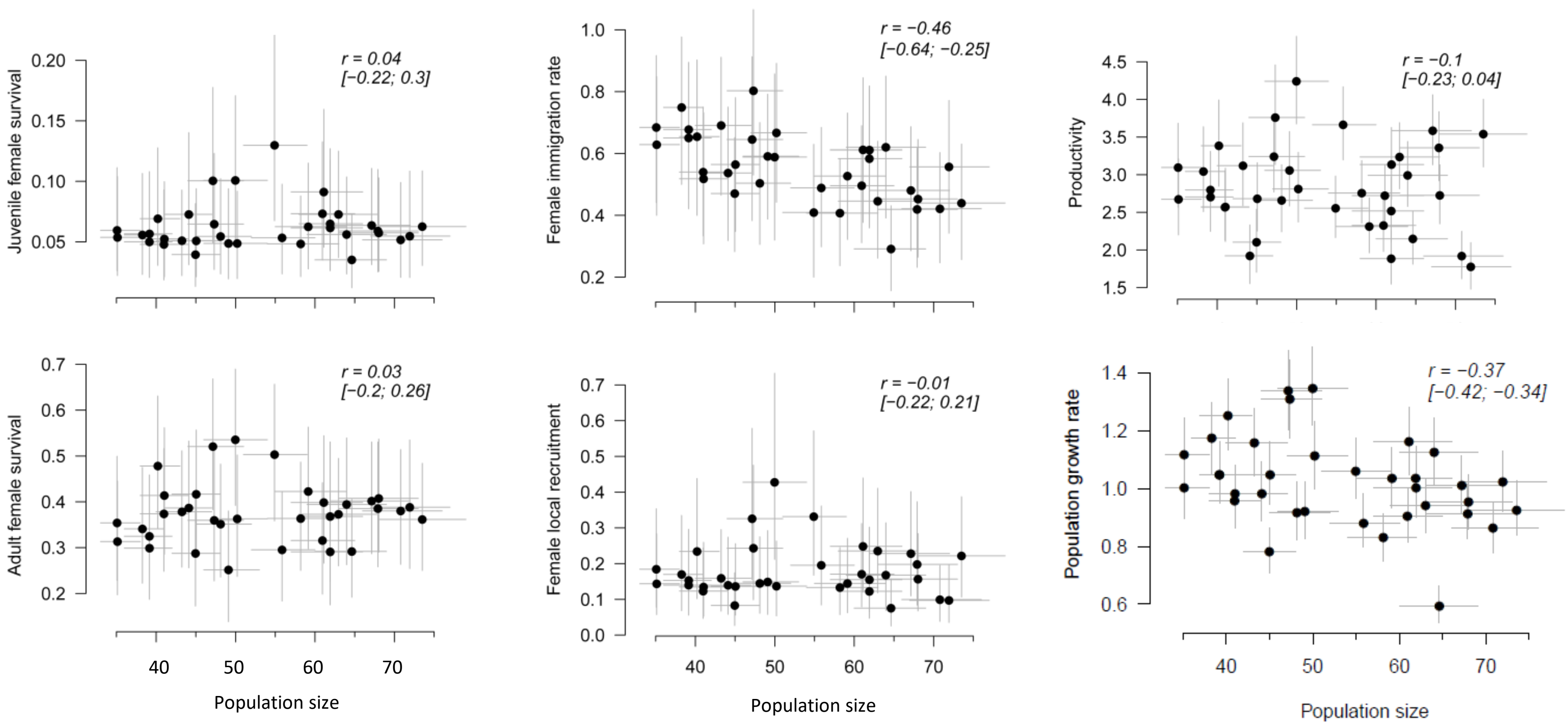
- Number of breeding pairs
- Number of fledglings per year
- Capture-recapture data

Schaub et al. 2013, Ecology

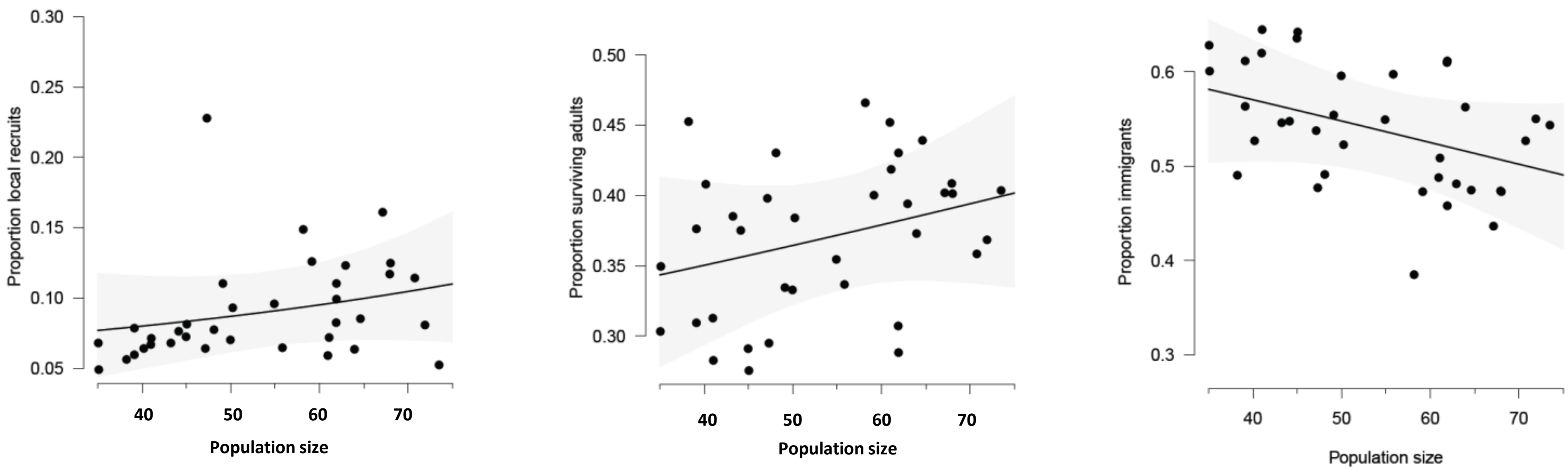
Impact of the variation of demographic rates on the variation of population growth



Density-dependence

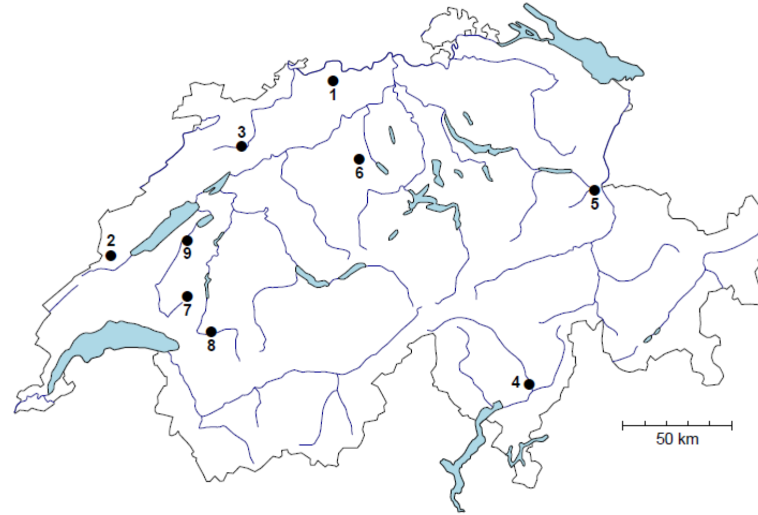


Change of population composition with population size



- Immigration was the most important factor for the dynamics of the red-backed shrike population
- Population regulation (density-dependence) operated mainly via immigration
- The composition of the population changed with population size

Example 6: **Population synchrony in barn swallows**



Background:

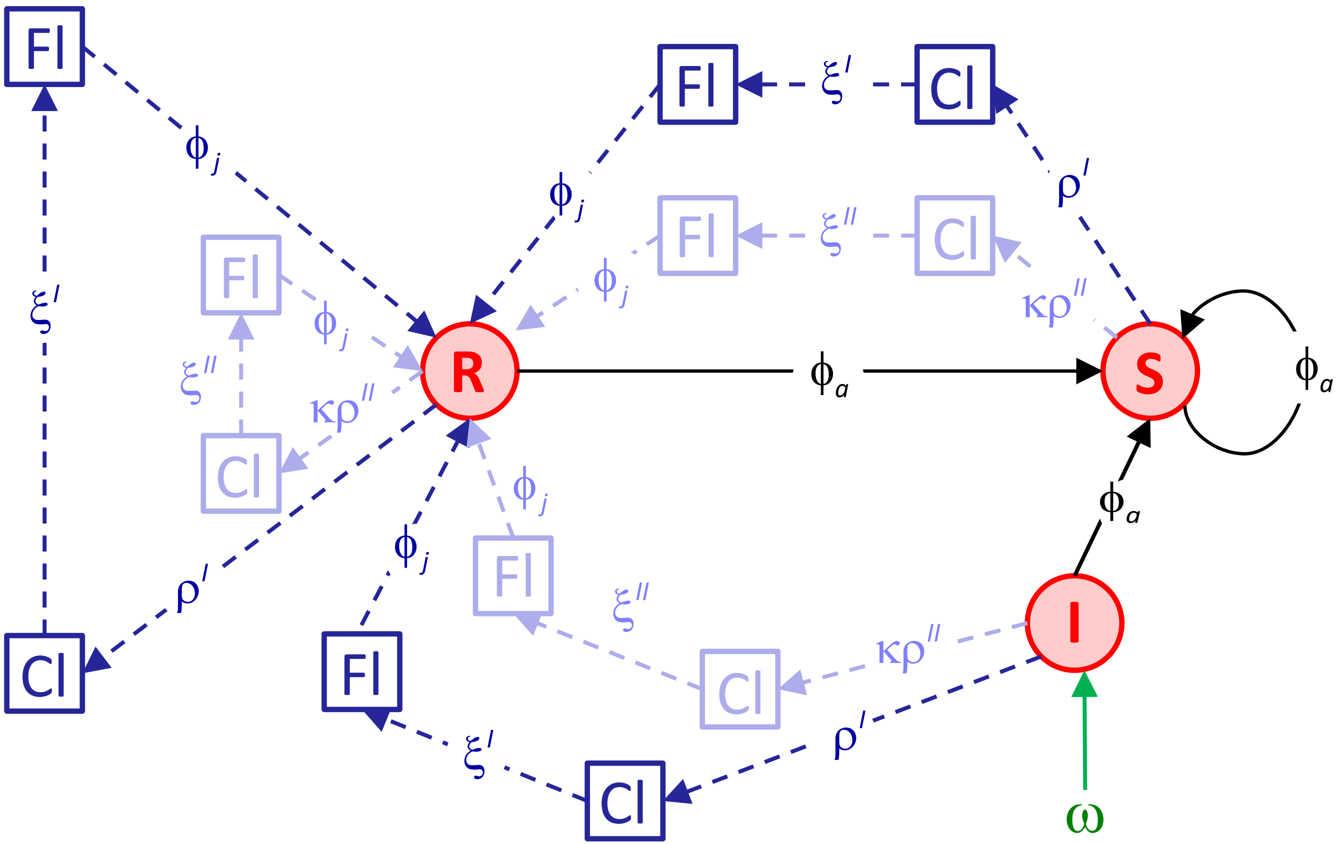
- Assess synchrony of population growth and of underlying demographic rates
- Insights into demographic mechanisms of population synchrony

Available data:

- 9 sites
- Number of breeding pairs
- Clutch size (1 & 2 brood)
- Num. of fledglings (1^{st} & 2^{nd} brood)
- Whether an indv. is double brooding
- Capture-recapture data

Schaub et al. 2015, J. Anim. Ecol.

Life cycle graph



Population composition

S: Survivors

R: Local recruits

I: Immigrants

Demographic processes

Survival

- ϕ_a : adult apparent survival

Local recruitment

First brood

- ρ' : clutch size
- ξ' : fledging success
- ϕ_j : juv. apparent survival

Second brood

- ρ'' : clutch size
- ξ'' : fledging success
- κ : prob. second brood

Immigration

- ω : immigration rate

Integrated population model

- State-space model for the count data

State process equations

$$S_{i,t+1} \sim \text{Binomial}\left(N_{i,t}, \phi_{i,a,t}\right)$$
$$R_{i,t+1} \sim \text{Binomial}\left(Fl_{i,t}, \phi_{i,j,t}\right)$$
$$Fl_{i,t} \sim \text{Poisson}\left(N_{i,t}\left(\rho^{I}_{i,t}\xi^{I}_{i,t} + \kappa_{i,t}\rho^{II}_{i,t}\xi^{II}_{i,t}\right)\right)$$
$$I_{i,t+1} \sim \text{Poisson}\left(N_{i,t}\omega_{i,t}\right)$$
$$N_{i,t} = R_{i,t} + I_{i,t} + S_{i,t}$$

Observation equations

$$y_{i,t} \sim \log\text{Normal}\left(N_{i,t}, \sigma_i^2\right)$$

$y_{i,t}$: Counts (site *i*, year *t*)

σ_i^2 : Residual error at site *i*

Likelihood:

$$L_{SS}\left(\mathbf{y} \middle| \mathbf{N}, \boldsymbol{\phi}_j, \boldsymbol{\phi}_a, \boldsymbol{\rho}^{I}, \boldsymbol{\xi}^{I}, \boldsymbol{\kappa}, \boldsymbol{\rho}^{II}, \boldsymbol{\xi}^{II}, \boldsymbol{\omega}, \boldsymbol{\sigma}^2\right)$$

Integrated population model

- Cormack-Jolly-Seber models for capture-recapture data:
  - Estimation of juvenile and adults apparent survival probabilities
  - Example of a capture history: m_i = { 1 0 1 0 0 0 }
  - Imperfect detection has to be taken into account
  - Define latent state variable **z**:

    if individual i is alive at t → $z_{i,t} = 1$, otherwise $z_{i,t} = 0$
  - Then, $z_{i,t} \mid z_{i,t-1} = 1 \sim Bernoulli\left(\phi_{i,t-1}\right)$

    $y_{i,t} \mid z_{i,t} = 1 \sim Bernoulli\left(p_{i,t}\right)$ p: recapture probability
  - Likelihood: $L_{CJS}\left(\mathbf{m} \mid \phi_j, \phi_a, \mathbf{p}\right)$

Integrated population model

- Poisson regression model for clutch sizes

$$c^{I}_{i,t,k} \sim \text{Poisson}\left(\rho^{I}_{i,t}\right),\ \ c^{II}_{i,t,k} \sim \text{Poisson}\left(\rho^{II}_{i,t}\right)$$

- Logistic regression for fledging success

$$u^{I}_{i,t,k} \sim \text{Binomial}\left(c^{I}_{i,t,k}, \xi^{I}_{i,t}\right),\ \ u^{II}_{i,t,k} \sim \text{Binomial}\left(c^{II}_{i,t,k}, \xi^{II}_{i,t}\right)$$

- Logistic regression for probability of double brooding

$$d_{i,t,k} \sim \text{Bernoulli}\left(\kappa_{i,t}\right)$$

- Likelihoods:

$$L^{I}_{R1} = \left(\mathbf{c}^{\mathbf{I}} \middle| \rho^{I}\right),\ L^{II}_{R1} = \left(\mathbf{c}^{\mathbf{II}} \middle| \rho^{II}\right),\ L^{I}_{R2} = \left(\mathbf{u}^{\mathbf{I}}, \mathbf{c}^{\mathbf{I}} \middle| \xi^{I}\right),\ L^{II}_{R2} = \left(\mathbf{u}^{\mathbf{II}}, \mathbf{c}^{\mathbf{II}} \middle| \xi^{II}\right),\ L_{R3} = \left(\mathbf{d} \middle| \kappa\right)$$

- **Joint likelihood**:

$$L_{IMP} = L_{SS} \times L_{CJS} \times L^{I}_{R1} \times L^{II}_{R1} \times L^{I}_{R2} \times L^{II}_{R2} \times L_{R3}$$

Models for demographic rates

- Data from all 9 populations analysed jointly
- Hierarchical model for each demographic parameter θ:

$$g\left(\boldsymbol{\theta}_{i,t}\right) = \boldsymbol{\mu}_i + \boldsymbol{\varepsilon}_t + \boldsymbol{\omega}_{i,t}$$

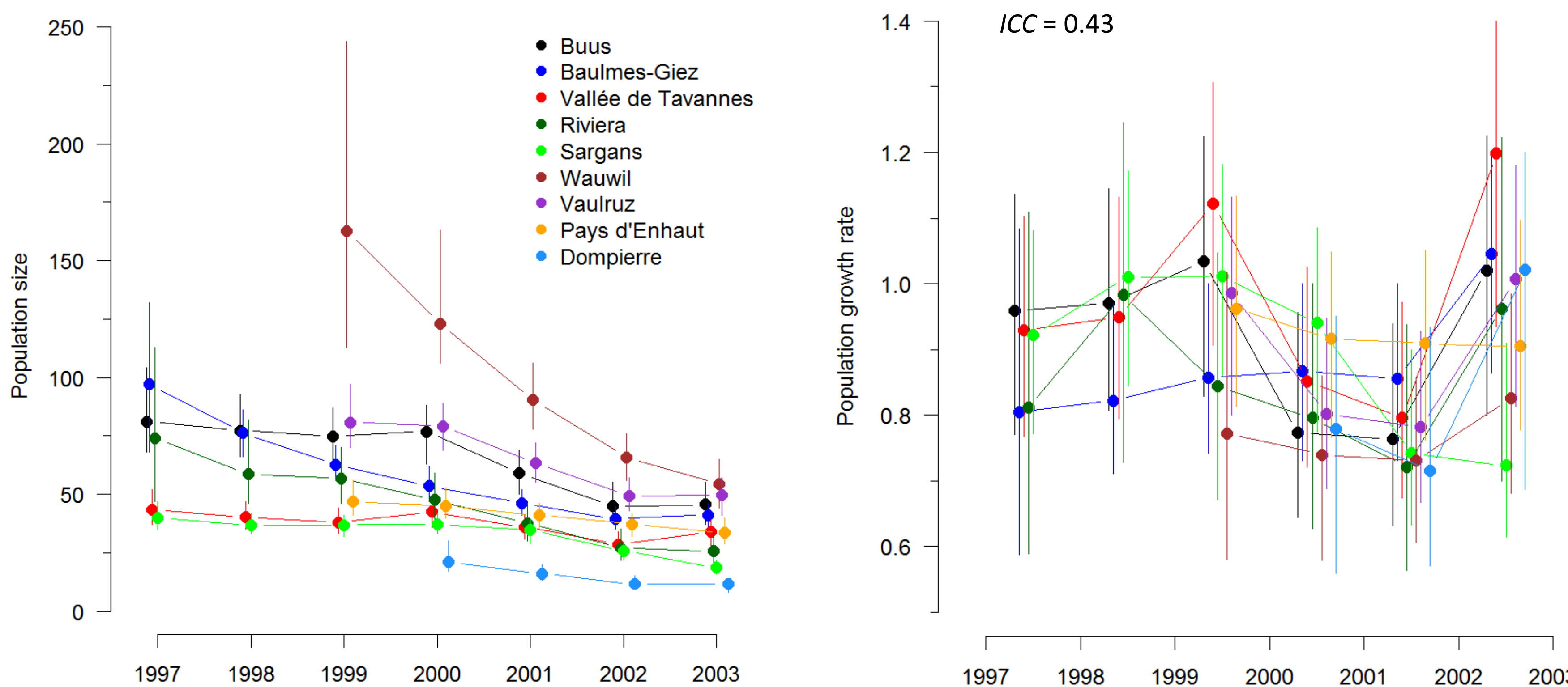
$$\boldsymbol{\varepsilon}_t \sim Normal\left(0, \boldsymbol{\sigma}_t^2\right)$$

$$\boldsymbol{\omega}_{i,t} \sim Normal\left(0, \boldsymbol{\sigma}^2\right)$$

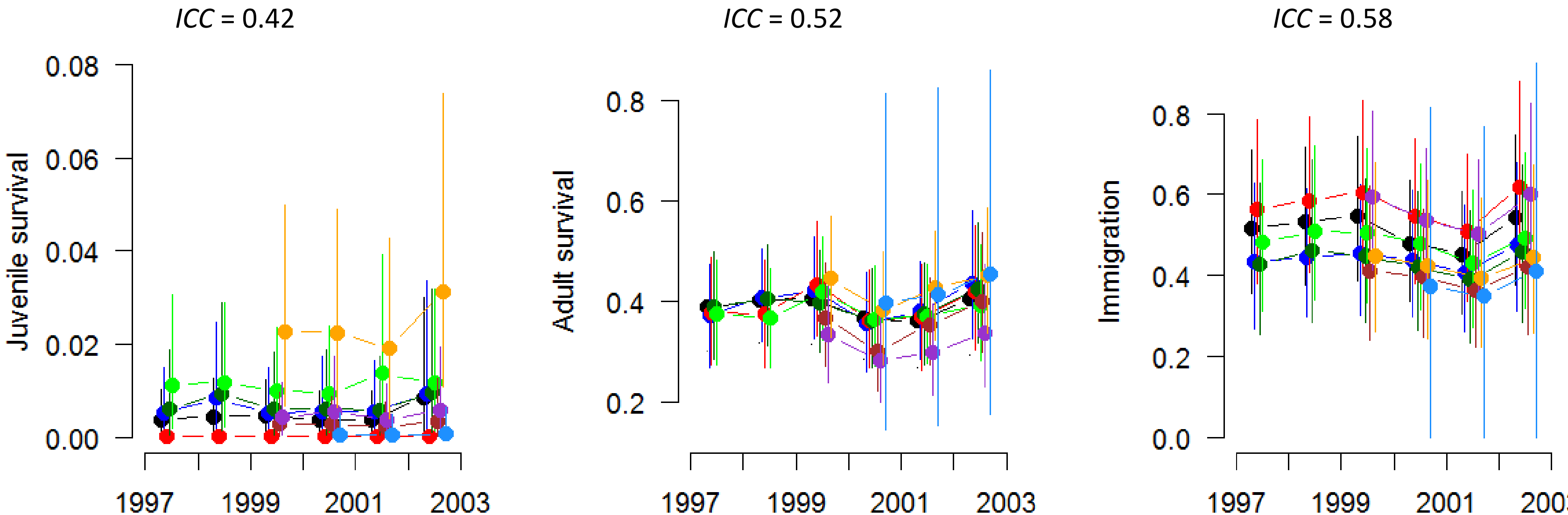
- Intraclass correlation:

$$ICC = \frac{\boldsymbol{\sigma}_t^2}{\boldsymbol{\sigma}_t^2 + \boldsymbol{\sigma}^2}$$

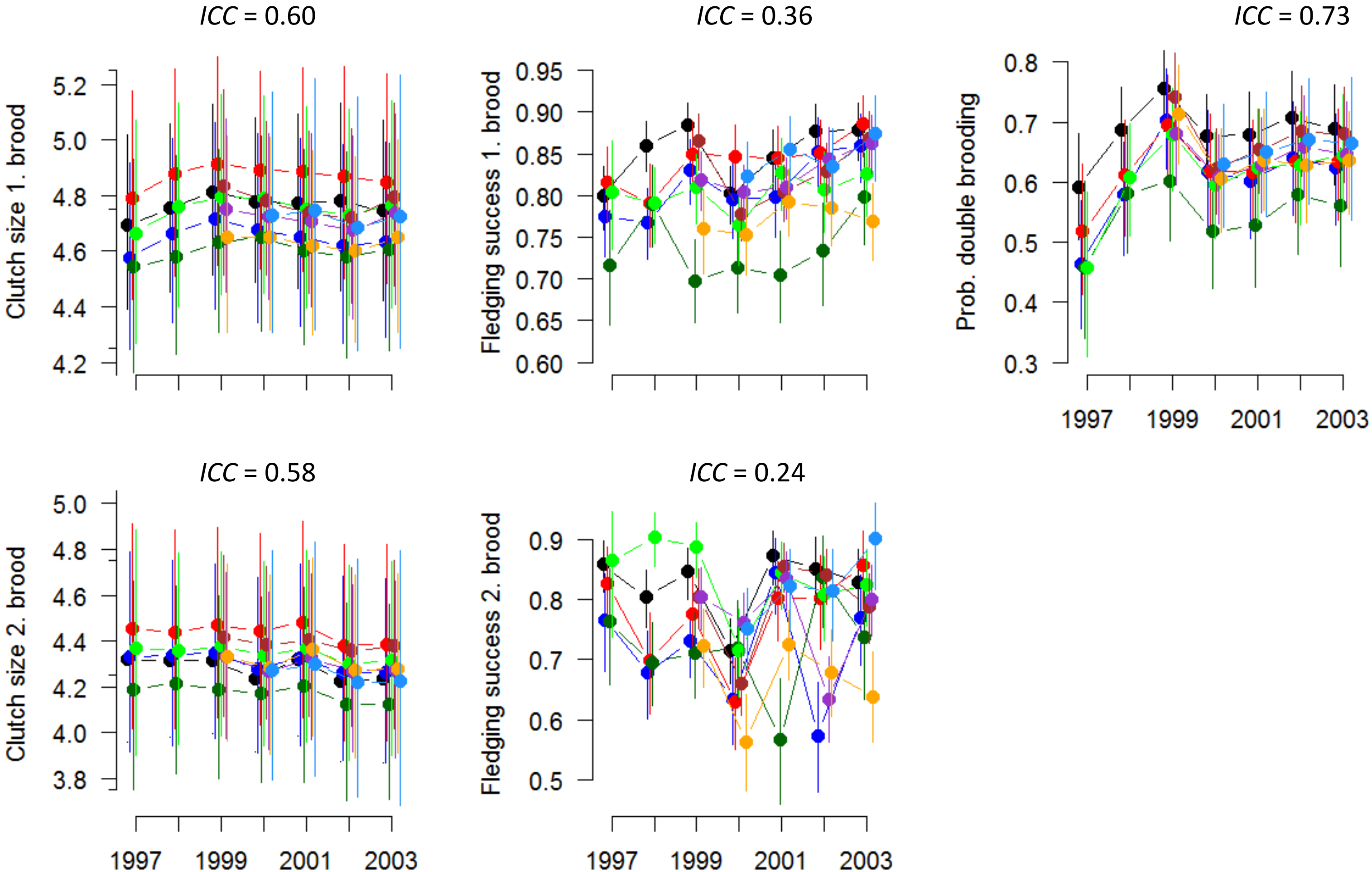
Results: population synchrony



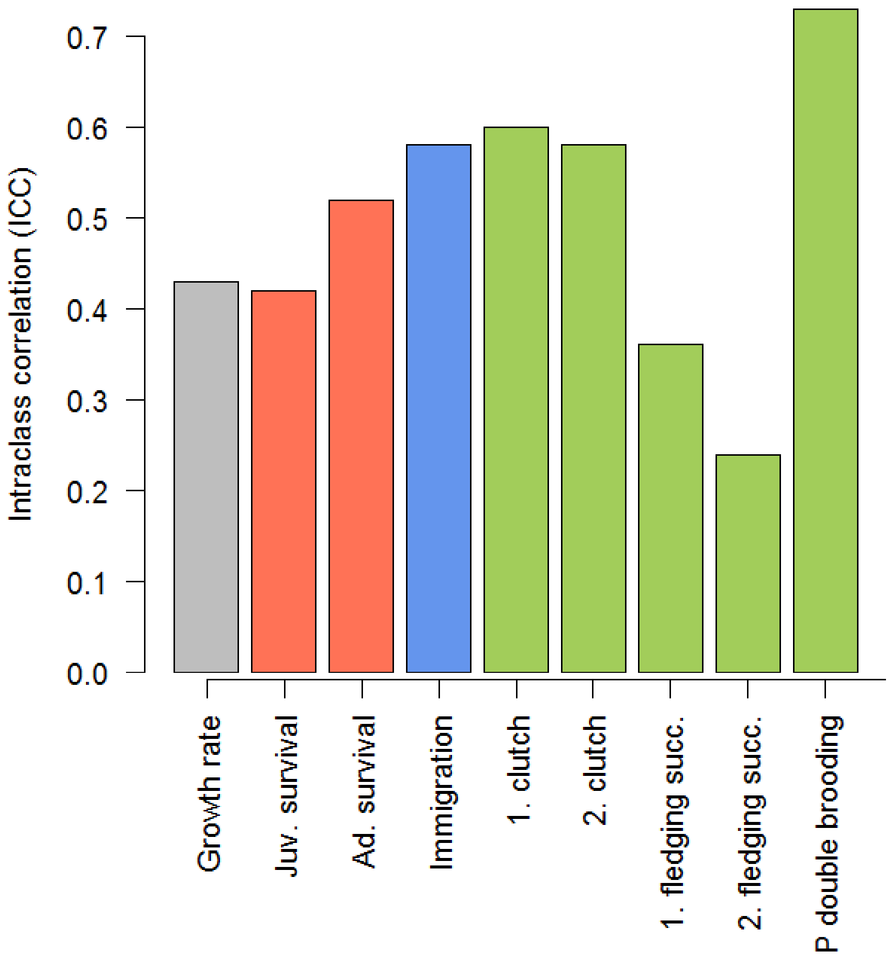
Results: synchrony of demographic rates



Results: synchrony of demographic rates



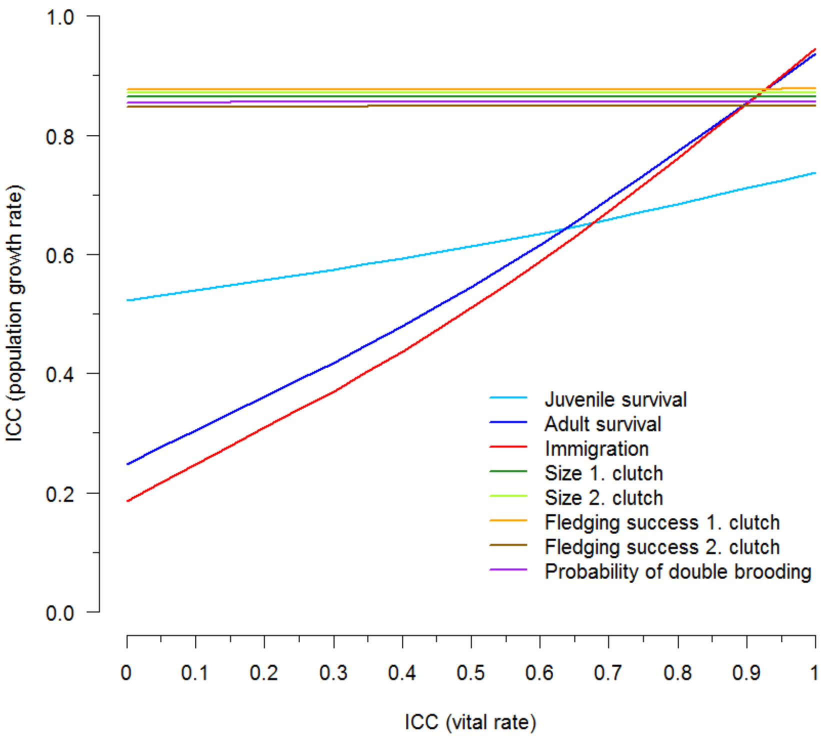
Results: Intraclass correlations



Discussion

- Dynamics driven by variation of survivors (*adult survival*) and gains (*local recruitment + immigration*)
- Survivors:
  - Synchrony of adult survival directly induces synchrony of survivors → contributes to population synchrony
- Gains:
  - *Local recruitment*: small due to strong natal dispersal → hardly contributes to population synchrony
  - *Immigration*:
    - Immigrants are mostly first time breeders
    - Related to the number of fledglings produced in neighbouring populations
    - Synchrony of immigration is a consequence of synchrony of productivity
    - Operates via natal dispersal, appears as immigration in the models for local dynamics

How much can synchrony of demographic rates contribute to population synchrony?



- Simulation study

$$\sigma^2_{total} = \sigma^2_t + \sigma^2$$

$$\varepsilon_t \sim \text{Normal}\left(0, \sigma^2_{total} \times ICC\right)$$

$$\omega_{i,t} \sim \text{Normal}\left(0, \sigma^2_{total} \times (1 - ICC)\right)$$

$$g(\theta) = \mu_i + \varepsilon_t + \omega_{i,t}$$

- Change ICC of demographic rates in turn
- $\lambda_{i,t} = \phi_{i,a,t} + \phi_{i,j,t}\left(\rho^{I}_{i,t}\xi^{I}_{i,t} + \kappa_{i,t}\rho^{II}_{i,t}\xi^{II}_{i,t}\right)\frac{1}{2} + \omega_{i,t}$
- Calculate ICC at the population level

Example 8: **Redhead population dynamics**

Background:

- Mid continent states & provinces
- Assess population dynamics in relation to
  - Breeding habitat availability
  - Density-dependence
  - Hunting regulation

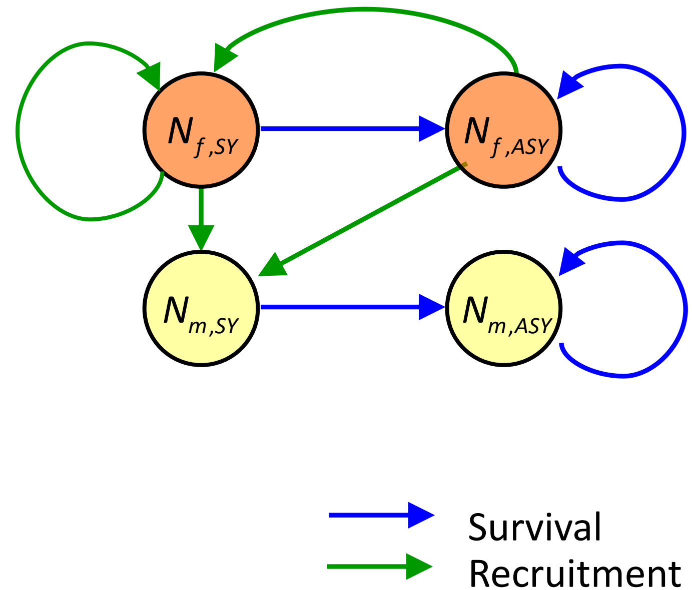
Available data (1960-2009)

- Breeding population survey (from Waterfowl Breeding Population and Habitat Survey data base)
- Banding and recovery data
- Harvested duck wings (age and sex ratios)

Péron et al. 2012, J. Anim. Ecol.

Structured life cycle

- 2 age classes
- 2 sexes
- pre-breeding census
- By the next spring a recruited bird enters its second year (SY) and it can breed



$N_{f,SY}$: Second-year females

$N_{f,ASY}$: After-second year females

$N_{m,SY}$: Second-year males

$N_{m,ASY}$: After-second year males

State-space model for population survey data

State process equations:

$$N_{f,SY,t+1} \sim Poisson\left(N_{f,SY,t}\tau F_t S_{f,j,t} 0.5 + N_{f,ASY,t} F_t S_{f,j,t} 0.5\right)$$

$$N_{f,ASY,t+1} \sim Binomial\left(S_{f,a,t}, N_{f,SY,t} + N_{f,ASY,t}\right)$$

$$N_{m,SY,t+1} \sim Poisson\left(N_{f,SY,t}\tau F_t S_{m,j,t} 0.5 + N_{f,ASY,t} F_t S_{m,j,t} 0.5\right)$$

$$N_{m,ASY,t+1} \sim Binomial\left(S_{m,a,t}, N_{m,SY,t} + N_{m,ASY,t}\right)$$

Observation equations:

$$y_t \sim Normal\left(\tau N_{f,SY,t} + N_{f,ASY,t} + N_{m,SY,t} + N_{m,ASY,t}, \sigma_t^2\right)$$

$$\sigma_t^2 = \theta_0 y_t$$

Likelihood: $L_{SS}\left(y \middle| \mathbf{N}, \mathbf{S}, F, \tau, \theta_0\right)$

$S_{f,j}$: Juvenile survival of females

$S_{f,a}$: Adult survival of females

$S_{m,j}$: Juvenile survival of males

$S_{m,a}$: Adult survival of males

F : Fecundity

τ : Proportion of SY females that reproduce

Band-recovery model for band-recovery data

Likelihood: $L_{CR}\left(m \middle| \mathbf{S},\mathbf{r}\right)$

$\mathbf{r}$: Age- and sex-specific recovery rates

Binomial models for age- and sex ratio data

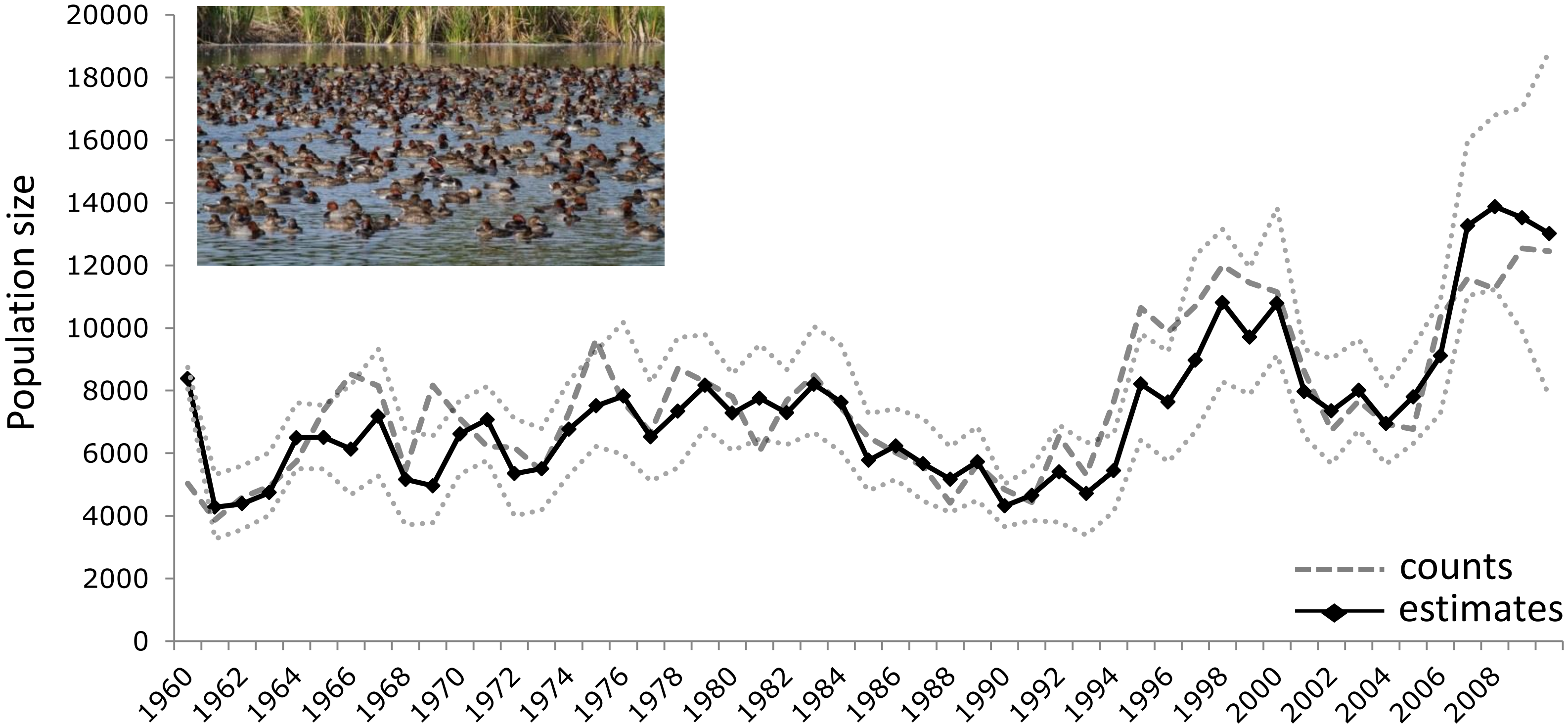
$$w_{f,SY,t} \sim Binomial\left(\eta_{f,SY,t}, w_{f,t}\right)$$

$\mathbf{w}_t$: Age- and sex-specific number of retrieved wings in year t

$$\eta_{f,SY,t} = \frac{0.5F_t\left(\tau N_{f,SY,t} + N_{f,ASY,t}\right)\left(1 - S_{f,j,t}\right)r_{f,j,t}}{0.5F_t\left(\tau N_{f,SY,t} + N_{f,ASY,t}\right)\left(1 - S_{f,j,t}\right)r_{f,j,t} + \left(N_{f,SY,t} + N_{f,ASY,t}\right)\left(1 - S_{f,a,t}\right)r_{f,a,t}}$$

Likelihood: $L_W\left(w \middle| \tau, \mathbf{N}, F, \mathbf{S}, \mathbf{r}\right)$

Population development



Demographic rates and discussion

	Mean (SD)
Fecundity	
Offspring per female (F)	1.50 (0.14)
Presence of HY females (τ)	0.52 (0.10)
Survival probability (S)	
Juvenile females	0.47 (0.02)
Adult females	0.65 (0.01)
Juvenile males	0.45 (0.02)
Adult males	0.71 (0.01)
Recovery probability (r)	
Juvenile females	0.04 (0.005)
Adult females	0.02 (0.002)
Juvenile males	0.05 (0.005)
Adult males	0.04 (0.002)

- Interactive effects of pond numbers and density-dependence on fecundity
- No effect of hunting regulation on survival
- Density-dependence of female juvenile survival
- Population booms occurred after wet years