

# Integrated Population Models (IPM)

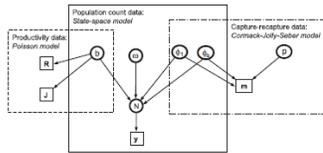


Diagram of Integrated Population Model from Schaub and Abadi (2011; J Ornithol.)

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## Overview

- Introduction
- Basic steps
  - Links between abundance and vital rates
  - Likelihoods of data sets
  - Loading data
  - Coding and running model in JAGS
  - Interpreting posteriors
- Some variants
  - Demographic stochasticity
  - Environmental stochasticity
  - "Missing" vital rates
    - Immigration
  - Density dependence
  - Predictive models
- Using JAGS



Photo credit Megumi Aita

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## Motivations

- Have both individual-based and count data
- Want to estimate vital rates and yearly abundance
- Want to make more efficient use of precious data
- Especially with rare and declining species, often
  - Have several streams of data
  - But each stream of data doesn't get us far on its own
- May want to estimate something we have no direct data on
- Also want to project population into future, incorporating uncertainty

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### State-space Modeling

- Time-series models
- True state of system (e.g. annual population size) measured imperfectly
- Connected models for population dynamics and observation
- Observation error can be modeled as normal (classical state-space), Poisson, or binomial/detection probability (Dail and Madsen)

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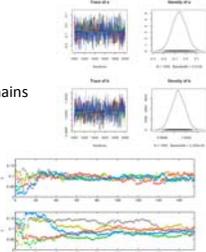
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### Bayesian Inference

- Specify priors, make inference from posteriors
- Markov chain Monte Carlo (MCMC) sampling
- Convergence diagnostics
  - Gelman-Rubin diagnostic (R-hat) based on multiple chains
  - Visual examination of chains
  - Others



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### Integrated Population Models (IPM)

- Tool used for both estimating parameters and projecting populations
- Single, unified analysis of population count data and demographic data
- Use state-space models
  - Process models
  - Detection models
  - Bayesian or classical
- Useful for including multiple sources of data

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# Basic Steps

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## Links Between Vital Rates and Abundance

- How? Matrix model!
- Example: bird population with pre-breeding census

$$\begin{bmatrix} N_1 \\ N_{ad} \end{bmatrix}_{t+1} = \begin{bmatrix} \frac{f_1}{2} \phi_{juv} & \frac{f_{ad}}{2} \phi_{juv} \\ \phi_{ad} & \phi_{ad} \end{bmatrix} \begin{bmatrix} N_1 \\ N_{ad} \end{bmatrix}_t$$

$$N_{1,t+1} = N_{1,t} \phi_{juv} \frac{f_{1,t}}{2} + N_{ad,t} \phi_{juv} \frac{f_{ad,t}}{2}$$

$$N_{ad,t+1} = N_{1,t} \phi_{ad,t} + N_{ad,t} \phi_{ad,t}$$


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## Likelihoods of Individual Datasets

- State-space model – population dynamics part already shown
- Count data options
  - Normal error:  $y_t \sim \text{Normal}(N_{1,t} + N_{ad,t}, \sigma_y^2)$
  - Poisson error:  $y_t \sim \text{Poisson}(N_{1,t} + N_{ad,t})$
  - Binomial error:  $y_t \sim \text{Binomial}(N_{1,t} + N_{ad,t}, p_{y,t})$
- Likelihood
 
$$L_{ss}(y | N, \Phi, f, \sigma_y^2) = L_u(y | N, \sigma_y^2) \times L_s(N | \Phi, f)$$

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### Likelihoods of Individual Datasets

- Capture-mark-recapture data
  - Capture history as matrix of 0s and 1s ( $\mathbf{C}$ )
- CMR analysis using state-space formulation
  - Each alive individual can be alive or dead next time step (latent state,  $z_{i,t}$ )
  - If alive, can be observed or not ( $C_{i,t}$ )
- In example, two age classes ( $\mathbf{x}$ )
  - Survival probability depends on age ( $\phi_{juv}$  and  $\phi_{ad}$ )
  - Capture probability does not ( $p$ )
- Likelihood  
 $L_{CMS}(\mathbf{C}, \mathbf{x} | \Phi, \mathbf{p})$

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### Likelihoods of Individual Datasets

- Reproductive success data
  - Number of females monitored by age class and year
  - Number of offspring by mother age class and year
- Model  
 $J_{1,t} \sim \text{Poisson}(R_{1,t} f_{1,t})$   
 $J_{ad,t} \sim \text{Poisson}(R_{ad,t} f_{ad,t})$
- Likelihood  
 $L_p(\mathbf{J}, \mathbf{R} | \mathbf{f})$

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### Joint Likelihood

- Assume datasets are independent
- What if they're not?
  - Falsely high precision of estimates
  - Abadi et al. (2010) found little effect in many cases
  - Can be dependent on specific model and data
- Joint likelihood is product of individual likelihoods  
 $L_{JPM}(y, \mathbf{C}, \mathbf{x}, \mathbf{J}, \mathbf{R} | \mathbf{N}, \Phi, \mathbf{f}, \mathbf{p}, \sigma_y^2) = L_y(y | \mathbf{N}, \sigma_y^2) \times L_N(\mathbf{N} | \Phi, \mathbf{f}) \times L_{CMS}(\mathbf{C}, \mathbf{x} | \Phi, \mathbf{p}) \times L_p(\mathbf{J}, \mathbf{R} | \mathbf{f})$

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### Initial Priors

- Uninformative priors on  $p, \phi_{juv}, \phi_{adv}, f_{1v}, f_{adv}, \sigma_v^2$ , etc.
- Example:
  - $p \sim \text{Uniform}(0,1)$
  - or
  - $\beta_0^e \sim \text{Normal}(0,1000)$
  - $\text{logit}(p) = \beta_0^e$

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### Loading or Simulating Data

- Can be useful to simulate data (e.g. in R)
  - See how well IPM works when it matches the simulation model exactly
  - See how well it works when it doesn't
  - Because you know the "truth" can assess accuracy
  - Can diagnose problems you have with real data
- May be good to wait until you know amount and type of data before simulating
- Both formatting real data and simulating data can take time

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### Coding and Running Model

- Options for MCMC engine
  - WinBUGS, OpenBUGS, **JAGS**
  - STAN
  - PyMC in Python
  - Code your own
- If having trouble with one engine, can try another
- Will give examples in JAGS at end of lecture and in lab
- Other examples out there

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### Interpreting Results

- Check for convergence
- Check means for
  - Compatibility with simulated values or
  - Plausibility
- Check SD and credible intervals
  - Coverage
  - Precision of estimates
- Graphing results several ways can be very helpful

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### Some Variants




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### Demographic Stochasticity

- More the default for IPMs
- From our example
  - Instead of:
 
$$N_{i,t+1} = N_{i,t} \phi_{juv,i} \frac{f_{i,t}}{2} + N_{ad,i} \phi_{juv,i} \frac{f_{ad,i}}{2}$$

$$N_{ad,t+1} = N_{i,t} \phi_{ad,i} + N_{ad,t} \phi_{ad,i}$$
  - We have:
 
$$N_{i,t+1} \sim \text{Poisson} \left( N_{i,t} \phi_{juv,i} \frac{f_{i,t}}{2} + N_{ad,t} \phi_{juv,i} \frac{f_{ad,i}}{2} \right)$$

$$N_{ad,t+1} \sim \text{Binomial} (N_{i,t} + N_{ad,t}, \phi_{ad,i})$$

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### Non-constant Environmental

- Vital rates change between years – environmental stochasticity
  - Random
  - External covariates
- Logit link for survival, log link for fecundity, e.g.:
 
$$\log(f_{i,t}) = \beta_{i,t}^f + \beta_{i,t}^f HDD_t + \varepsilon_{i,t}$$

$$\varepsilon_{i,t} \sim \text{Normal}(0, \sigma_i^2)$$
- If multiple vital rates affected by stochasticity, either:
  - Specify correlation (0, 1, etc.)
  - Try to estimate correlation

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### Missing Vital Rate Data

- Because have information on dynamics from multiple sources
  - Individual-based data on vital rates
  - Count data on abundance
- Can estimate a vital rate with no direct data on it (e.g. fecundity)
- “Filled-in” from other data

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### Immigration

- For open populations,  $N_{t+1} = N_t + B + I - D - E$
- Apparent survival incorporates death and emigration
- Seldom have direct data on immigration
- Can use IPMs to “fill-in” immigration
- Can be specified as rate or number
 
$$N_{i,t+1} \sim \text{Poisson}((N_{i,t} + N_{ad,t} + N_{im,t})\phi_t)$$
 Or
 
$$N_{i,t+1} \sim \text{Poisson}(I_t)$$

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### Density Dependence

- Have abundance as one of the parameters estimating in model
- Can have it affect vital rate(s)
- Example:  

$$\text{logit}(\phi_{juv,t}) = \beta_{juv,0}^{\phi} + \beta_{juv,N}^{\phi} (N_{1,t} + N_{ad,t})$$

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### Predictive Models

- Can project populations into future with these models
- Account for parametric uncertainty, stochasticity, etc.
- Just designate number of years from past and number from future
  - Data all come from past years
  - Vital rates assigned for all years
  - Population projected in all years
- Population viability analysis (PVA)
  - Can estimate probabilities of extinction and quasi-extinction
  - Not straightforward to estimate uncertainty in those, however

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### Even More Variants

- Multiple populations
- Additional data types
  - Recoveries
  - Telemetry
- Spatial capture-recapture
- Full annual-cycle population modeling (in progress)

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Running JAGS




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Coding in BUGS/JAGS

- Somewhere in between coding in R and writing statistical equations
- Program doesn't have to run in order (can define variable after using it)
- Some distributions specified in "strange" ways
  - For example: Normal (dnorm)
    - Most commonly specified with mean and variance
    - In R, parameterized with mean and standard deviation
    - In BUGS, parameterized with mean and precision (1/variance)
  - For binomial (dbin) probability before total
- JAGS is a powerful engine but can be finicky

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Running JAGS

- Can be run stand-alone, but more frequently run through R
- Several R packages can be used as interfaces (using jagsUI here)
- Can write JAGS code to disk from R using sink function:

```
sink("filename.jags")
cat("
model {
[code]
}
", fill = TRUE)
sink()

```

- Careful using Tinn-R

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### Sample JAGS Code (1 of 7)

```

model {
#-----
# 1. Define the priors for the parameters
#-----
# Observation error
tauy <- pow(sigma.y, -2)
sigma.y ~ duni f(0, 50)
sigma2.y <- pow(sigma.y, 2)

# Initial population sizes
n1 ~ dnorm(50, tauy)T(0,) # 1-year
nad ~ dnorm(50, tauy)T(0,) # Adults
N1[1] <- n1
Nad[1] <- nad
    
```

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### Sample JAGS Code (2 of 7)

```

# Survival and recapture probabilities, as well as productivity
for (t in 1:(nYears - 1)){
  phi.juv[t] <- mean.phi[1]
  phi.ad[t] <- mean.phi[2]
  f.juv[t] <- mean.fec[1]
  f.ad[t] <- mean.fec[2]
} # t

for (i in 1:nMarked){
  for (t in first[i]:(nYears - 1)){
    phi[i,t] <- mean.phi[x[i,t]]
    p[i,t] <- mean.p
  } #t
} #i
    
```

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### Sample JAGS Code (3 of 7)

```

for (u in 1:2){
  mean.phi[u] ~ duni f(0, 1) # Priors for age-specific survival
  mean.fec[u] ~ duni f(0, 20) # Priors for age-specific fecundity
}
mean.p ~ duni f(0, 1)

#-----
# 2. Derived parameters
#-----
# Population growth rate
for (t in 1:(nYears - 1)){
  lambda[t] <- Ntot[t + 1] / Ntot[t]
}
    
```

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## Sample JAGS Code (4 of 7)

```
#-----
# 3. The likelihoods of the single data sets
#-----
# 3.1. Likelihood for population population count data (state-space model)
# 3.1.1 System process
for (t in 2:nYears) {
  N1[t] <- f.juv[t - 1] / 2 * phi.juv[t - 1] * N1[t - 1] +
    f.ad[t - 1] / 2 * phi.juv[t - 1] * Nad[t - 1]
  Nad[t] <- phi.ad[t - 1] * Ntot[t - 1]
}
for (t in 1:nYears) {
  Ntot[t] <- Nad[t] + N1[t]
}
```

Introduction Basic Steps Variants JAGS

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## Sample JAGS Code (5 of 7)

```
#-----
# 3. The likelihoods of the single data sets
#-----
# 3.1. Likelihood for population population count data (state-space model)
# 3.1.1 System process
for (t in 2:nYears) {
  N1[t] <- f.juv[t - 1] / 2 * phi.juv[t - 1] * N1[t - 1] +
    f.ad[t - 1] / 2 * phi.juv[t - 1] * Nad[t - 1]
  Nad[t] <- phi.ad[t - 1] * Ntot[t - 1]
}
for (t in 1:nYears) {
  Ntot[t] <- Nad[t] + N1[t]
}
# 3.1.2 Observation process
for (t in 1:nYears) {
  y[t] ~ dnorm(Ntot[t], tau0)
}
```

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## Sample JAGS Code (6 of 7)

```
# 3.2 Likelihood for capture-recapture data: CJS model (2 age classes)
for (i in 1:nMarked){
  # Define latent state at first capture
  z[i, first[i]] <- 1
  for (t in (first[i] + 1):nYears) {
    # State process
    z[i, t] ~ dbern(mu1[i, t])
    mu1[i, t] <- phi[i, t - 1] * z[i, t - 1]
    # Observation process
    CH[i, t] ~ dbern(mu2[i, t])
    mu2[i, t] <- p[i, t - 1] * z[i, t]
  } #t
} #i
```

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### Sample JAGS Code (7 of 7)

```
# 3.3. Likelihood for productivity data: Poisson regression (2 age classes)
for (t in 1:(nYears - 1)) {
  J[1, t] ~ dpois(rho1[t])
  rho1[t] <- R[1, t] * f.juv[t]
  J[2, t] ~ dpois(rho2[t])
  rho2[t] <- R[2, t] * f.ad[t]
} #t
} #model
```

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### Sample R Code

```
library(jagsUI)
# Load data
load('IPM_inputs1.RData')
# Bundle data
jags.data <- list(CH = CH, y = y, J = J, R = R, nYears = nYears, first = first,
                 x = x, nMarked = nMarked, z = known.state.cjs(CH))
# Initial values
inits <- function(){list(mean.phi = runif(2, 0, 1), mean.p = runif(1, 0, 1),
                        mean.fec = runif(2, 0, 10), z = cjs.init.z(CH, first),
                        sigma.y = runif(1, 0, 1), n1 = rpois(1, 50), nad = rpois(1, 50))}
# Parameters monitored
parameters <- c("mean.phi", "mean.fec", "mean.p", "N1", "Nad", "Ntot", "sigma.y",
               "lambda")
```

Introduction Basic Steps Variants JAGS

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### Sample R Code cont.

```
# MCMC settings
ni <- 2000
nt <- 1
nb <- 500
nc <- 3

# Call JAGS from R (BRT 2 min)
ipm <- jags(jags.data, inits, parameters, "ipm.simple.jags", n.chains = nc,
           n.thin = nt, n.iter = ni, n.burnin = nb, DIC = F)

print(ipm)
plot(ipm)
```

Introduction Basic Steps Variants JAGS

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### Sample Output

JAGS output for model 'ipm.simple.jags', generated by jagsUI.  
 Estimates based on 3 chains of 2000 iterations,  
 burn-in = 500 iterations and thin rate = 1,  
 yielding 4500 total samples from the joint posterior.  
 MCMC ran for 1.048 minutes at time 2016-03-01 12:21:27.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
mean.phi [1]	0.252	0.016	0.223	0.254	0.280	FALSE	1	1.163	20
mean.phi [2]	0.559	0.025	0.519	0.554	0.611	FALSE	1	1.189	18
mean.fec[1]	3.095	0.143	2.819	3.089	3.390	FALSE	1	1.003	1470
mean.fec[2]	4.191	0.172	3.878	4.179	4.554	FALSE	1	1.012	193
mean.p	0.393	0.034	0.329	0.392	0.462	FALSE	1	1.002	1720
N1[1]	46.691	7.807	30.904	46.797	61.832	FALSE	1	1.009	243

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### Sample Output, cont.

```
...
lambda[11] 1.024 0.005 1.013 1.024 1.033 FALSE 1 1.002 2010
lambda[12] 1.024 0.005 1.013 1.024 1.033 FALSE 1 1.002 2010
lambda[13] 1.024 0.005 1.013 1.024 1.033 FALSE 1 1.002 2010
lambda[14] 1.024 0.005 1.013 1.024 1.033 FALSE 1 1.002 2010
```

**\*\*WARNING\*\*** Rhat values indicate convergence failure.  
 Rhat is the potential scale reduction factor (at convergence, Rhat=1).  
 For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.  
 f is the proportion of the posterior with the same sign as the mean;  
 i.e., our confidence that the parameter is positive or negative.

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