Lecture 18

CORMACK- JOLLY- SEBER MODEL

Survival and Capture Probability Estimation (Ch 17)

Exam 2 Next Week

Open Population Models

(More than two samples necessary)

Additions: Births or Immigrants (not separable)

Deletions: Deaths or Emigrants (not separable)

These models allow estimation of "apparent survival rates" and "recruitment" as well as population sizes.

FULL JOLLY-SEBER MODEL PARAMETERS AND UNOBSERVED RANDOM VARIABLES

*Population Sizes	$N_1, N_2, \ldots, N_{k-1}, N_k$
Survival Rates	$\phi_1, \phi_2, \ldots, \phi_{k-2}, \phi_{k-1}$
Capture Probabilities	$p_1, p_2, \ldots, p_{k-1}, p_k$
Recruitment Numbers	$B_1, B_2, \ldots, B_{k-2}, B_{k-1}$
*Marked Population Sizes	$M_1, M_2, \ldots, M_{k-1}, M_k$

JOLLY-SEBER MODEL

This model makes the following assumptions:

1. Every animal present in the population at the time of i th sample (i = 1, 2, …, k) has the same probability of capture (p_i).

2. Every marked animal present in the population immediately after the i th sample has the same probability of survival (ϕ_i) until the (i + 1)th sampling time (i = 1, 2, …, k-1).

3. Marks are not lost or overlooked.

4. All samples are instantaneous and each release is made immediately after the sample.

5. All emigration is permanent.

6. Fates of animals are independent

FULL JOLLY-SEBER MODEL

Population Sizes $N_1, \hat{N}_2, \ldots, \hat{N}_{k-1}, N_k$

Survival Rates $\hat{\phi}_1, \hat{\phi}_2, \ldots, \hat{\phi}_{k-2}, \phi_{k-1}$

Capture Probabilities $p_1, \hat{p}_2, \ldots, \hat{p}_{k-1}, p_k$

Marked Population Size $M_1, \hat{M}_2, \ldots, \hat{M}_{k-1}, M_k$

Recruitment Numbers $B_1, \hat{B}_2, \ldots, \hat{B}_{k-2}, B_{k-1}$

OPEN CAPTURE- RECAPTURE MODELS FOR ESTIMATING DEMOGRAPHIC PARAMETERS

Components of Data

Recaptures - this component is where we estimate survival and capture probabilities. You can see that from the intuitive estimators.

First Captures and Recaptures- allows estimation of population sizes and recruitment parameters (and also survival and capture probabilities). You also can see that from the intuitive estimators.

OPEN CAPTURE- RECAPTURE MODELS FOR ESTIMATING DEMOGRAPHIC PARAMETERS

We do not discuss the likelihoods much in this class but---

There are three components of the Full Likelihood for the Jolly-Seber Model.

$L = L_1$(First Captures)*L_2(Losses on Capture)*L_3(Recaptures)

L_1(First Captures) - allows estimation of population sizes and recruitment parameters (and also includes survival and capture probabilities).

L_2(Losses on Capture) - important that we allow for this but these parameters are not of biological interest.

L_3(Recaptures) - this is the reduced Cormack-Jolly-Seber likelihood and this component is where we estimate survival and capture probabilities

CORMACK-JOLLY-SEBER MODEL(Ch 17)

Survival Rates $\hat{\phi}_1, \hat{\phi}_2, \ldots, \hat{\phi}_{k-2}, \phi_{k-1}$

Capture Probabilities $p_1, \hat{p}_2, \ldots, \hat{p}_{k-1}, p_k$

Marked Population Sizes $M_1, \hat{M}_2, \ldots, \hat{M}_{k-1}, M_k$

WE JUST FOLLOW THE MARKED ANIMALS AND DON'T USE MARKED TO TOTAL RATIOS TO GET POPN SIZE OR BIRTH NUMBERS.

CORMACK-JOLLY SEBER MODEL

* Comprehensive Survival Modeling

* Extension to Stage Structured Models for survival within a stage and movement between stages.

SURVIVAL MODELING EUROPEAN DIPPER EXAMPLE

- Illustrated by European Dipper data taken from Lebreton at al. (1992) using SURGE. (MARK better now and I reanalysed in that program).There are seven years with one recapture event per year. There were data for the two sexes separately but they were found to be similar so I combined them for ease of presentation

- Five models were compared using AIC (Akaike Information Criteria) and we show details of our analysis for those models.

Dipper Combined Sex Analysis

Model	AICc	Delta AICc	AICc Weight	#Par
{Phi(f) p(.) PIM}	666.160	0.00*	0.89445	3
{Phi(.) p(.) PIM}	670.866	4.71	0.08505	2
{Phi(t) p(.) PIM}	673.998	7.84	0.01776	7
{Phi(.) p(t) PIM}	678.748	12.59	0.00165	7
{Phi(t) p(t) PIM}	679.588	13.43	0.00109	11

*Best Model

Model Details

- First we will look at the full CJS Model
- Next Look at the “Best Model” where survival differs between flood and nonflood years and where p is constant over years.

Dipper Full CJS Model {Phi(t) p(t) PIM}Output

Parameter	Estimate	Standard Error	Lower	Upper
1:Phi	0.7181818	0.1555470	0.3610409	0.9199575
2:Phi	0.4346708	0.0688290	0.3075047	0.5710588
3:Phi	0.4781705	0.0597091	0.3643839	0.5942685
4:Phi	0.6261177	0.0592656	0.5048461	0.7333741
5:Phi	0.5985335	0.0560517	0.4855434	0.7019412
6:Phi	*0.7284299	0.0000000	0.7284299	0.7284299
7:p	0.6962027	0.1657637	0.3302969	0.9141508
8:p	0.9230769	0.0728778	0.6161497	0.9889758
9:p	0.9130435	0.0581758	0.7140650	0.9778505
10:p	0.9007892	0.0538330	0.7360176	0.9672856
11:p	0.9324138	0.0458025	0.7684926	0.9828579
12:p	*0.7284328	0.0000000	0.7284328	0.7284328

** Last phi and p and not separately estimable

EUROPEAN DIPPER EXAMPLE

THREE PARAMETER “BEST” MODEL {Phi(f) p(.) PIM}

FLOOD SURVIVAL

$$\hat{\phi}_f = 0.469 \ \ (0.043)$$

NONFLOOD SURVIVAL

$$\hat{\phi}_n = 0.607 \ \ (0.031)$$

CAPTURE PROBABILITY

$$\hat{p} = 0.90 \ \ (0.029)$$

A simple, but useful example of MARK’S utility in Model selection and estimation.

EUROPEAN DIPPER EXAMPLE SUMMARY

- Very nice example which shows the value of the AIC procedure

- Very simple model is adequate –only 2 survival parameters estimated and 1 capture probability.

- Estimates are much more precise than for the full CJS model.

Meadow Vole Example from Text

P436-439 in Text

There are 6 sampling occasions and 2 sexes. The approach will be to look at the full CJS for both sexes first.

Then we will show you can do better using AIC on a set of submodels. An additive model on survival across sexes combined with a constant capture probability turns out to be best.

TABLE 17.8 Model Selection Statistics for Different Models of Time- and Sex-Specific Variation in Capture and Survival Probabilities of Meadow Voles[a]

Model	Parameters[b]	Deviance	ΔAIC_c
(φ_{s+t}, p)	7	74.9	0.00
(φ_t, p)	6	78.2	1.23
(φ_{s+t}, p_s)	8	74.2	1.33
(φ_{s+t}, p_{s*t})	14	61.7	1.40
(φ_t, p_s)	7	76.9	1.98
(φ_{s+t}, p_t)	10	72.5	3.82
(φ_{s*t}, p)	11	70.5	3.94
(φ_{s*t}, p_s)	12	68.6	4.14
(φ_t, p_{s*t})	14	64.9	4.60
(φ_{s+t}, p_{s+t})	11	71.4	4.77
(φ_t, p_{s+t})	10	73.8	5.12
(φ_{s*t}, p_{s*t})	17	59.1	5.25
(φ_t, p_t)	9	76.2	5.40
(φ_{s*t}, p_t)	14	68.4	8.17
(φ_{s*t}, p_{s+t})	15	66.7	8.50
(φ_s, p_{s*t})	9	85.0	14.22
(φ, p_{s*t})	8	87.9	15.05
(φ_s, p_{s+t})	7	94.6	19.67
(φ_s, p_t)	6	97.1	20.13
(φ, p_{s+t})	6	97.6	20.67
(φ, p_t)	5	100.4	21.44
(φ_s, p)	3	108.2	25.15
(φ_s, p_s)	4	106.6	25.62
(φ, p_s)	3	109.8	26.74
(φ, p)	2	112.0	26.90

[a] At Patuxent Wildlife Research Center, 1981; see data in Tables 17.5 and 17.6.

[b] Parameter numbers computed in program MARK (White and Burnham, 1999).

TABLE 17.7 Parameter Estimates under the General Two-Sex CJS model (φ_{s*t}, p_{s*t}) for Meadow Voles Studied at Patuxent Wildlife Research Center, Laurel, Maryland, 1981[a]

		Capture probability		Survival probability	
		Female	Male	Female	Male
Capture period	Sampling dates	$\hat{p}_i$ ($\widehat{SE}[\hat{p}_i]$)	$\hat{p}_i$ ($\widehat{SE}[\hat{p}_i]$)	$\hat{\varphi}_i$ ($\widehat{SE}[\hat{\varphi}_i]$)	$\hat{\varphi}_i$ ($\widehat{SE}[\hat{\varphi}_i]$)
1	6/27–7/1	—[b]	—[b]	0.89 (0.052)	0.86 (0.052)
2	8/1–8/5	0.88 (0.055)	0.96 (0.039)	0.78 (0.066)	0.58 (0.066)
3	8/29–9/2	0.90 (0.057)	0.82 (0.071)	0.68 (0.066)	0.71 (0.072)
4	10/3–10/7	0.96 (0.037)	0.91 (0.059)	0.69 (0.069)	0.59 (0.069)
5	10/31–11/4	1.00 —[c]	0.83 (0.069)	—[b]	—[b]
6	12/4–12/8	—[b]	—[b]	—[b]	—[b]

[a] See data in Tables 17.5 and 17.6.
[b] Parameter not estimable under CJS model.
[c] Standard error not estimated.

Full Model Summary

Capture probabilities high and fairly constant over time and sexes.

Survival probabilities vary over time and seem higher for females.

Lets see if we can get a simpler model to use.

Multiple Group Model Notation

s*t - each sex and time has a distinct parameter

s+t -there is a constant additive effect of sex at each time (see next panels)

s - there is a sex effect but no time variation

t - there is time variation but no effect of sex

. - there is no time variation and no effect of sex

Multiple Group Model Notation

s * t Model

$$Logit(\phi_{ij}) = \gamma + \alpha_i + \beta_j$$

i = sex, j = time period

s Model

$$Logit(\phi_{ij}) = \gamma + \alpha_i$$

t Model

$$Logit(\phi_{ij}) = \gamma + \beta_j$$

. Model

$$Logit(\phi_{ij}) = \gamma$$

Multiple Group Model Notation

Model s + t -there is a constant additive effect of sex at each time

$$Logit(\phi_{ij}) = \alpha s + \beta_j$$

with $s = 0$ Female or 1 Male.

Female

$$Logit(\phi_{ij}) = \beta_j$$

Male

$$Logit(\phi_{ij}) = \alpha + \beta_j$$

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[a] At Patuxent Wildlife Research Center, 1981; see data in Tables 17.5 and 17.6.

[b] Parameter numbers computed in program MARK (White and Burnham, 1999).

Additive Survival, Constant Capture Model

Much simpler summary than the full model.

Survival estimates plotted in next figure

Capture probability estimate is constant at

$$\hat{p} = 0.90$$

$$SE(\hat{p}) = 0.02$$

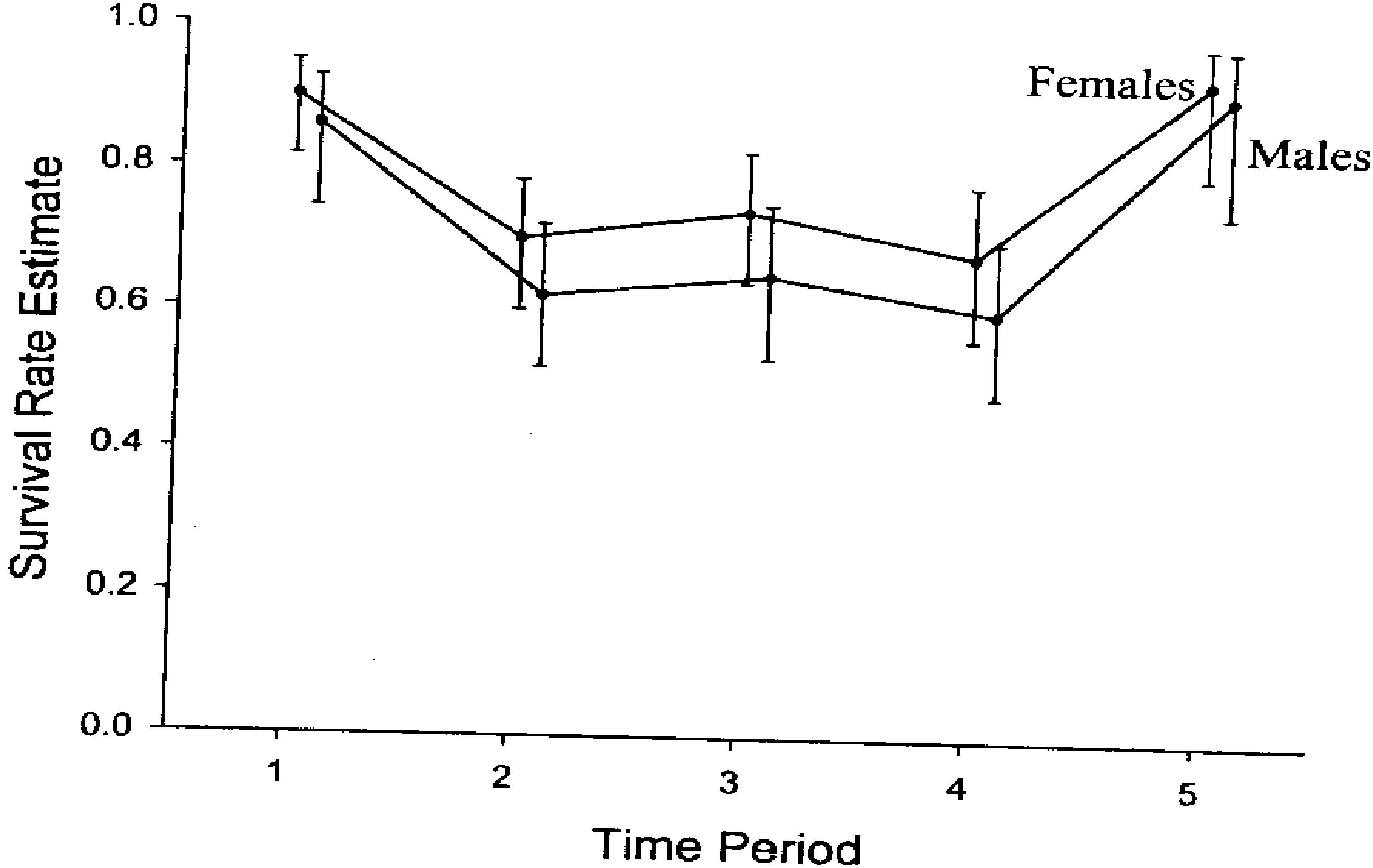


FIGURE 17.2 Estimated monthly survival probabilities and 95% confidence intervals from model (φ_{s+t}, p) for male and female meadow voles at Patuxent Wildlife Research Center, 1981.

Mark Demonstration: Dipper

- Two groups make it a bit more complex
- Open Existing File (to see Gary White analyses already there)
- Open New Analysis

  -Non estimable parameters in the full CJS model

  -Use of Predefined Models approach to save time it takes to use the PIMS.

  - Use of PIMS to account for the flood vs nonflood years models which don't fit into that.

Mark Demonstration: Dipper

- PIMS Structures
  - -There are 4 PIMS now Male and Female Survival, Male and Female Capture probabilities.

Mark Demonstration: Dipper

- PIMS Structures
  - -There are 4 PIMS now Male and Female Survival, Male and Female Capture probabilities.

Mark Demonstration: Dipper

PIMS Structures Survival Full Model

Males

```
1 2 3 4 5 6
  2 3 4 5 6
    3 4 5 6
      4 5 6
        5 6
          6
```

Females

```
7 8 9 10 11 12
  8 9 10 11 12
    9 10 11 12
      10 11 12
         11 12
            12
```

Mark Demonstration: Dipper

PIMS Structures Survival Best Model

Males

```
1 2 2 1 1 1
  2 2 1 1 1
    2 1 1 1
      1 1 1
        1 1
          1
```

Females

```
1 2 2 1 1 1
  2 2 1 1 1
    2 1 1 1
      1 1 1
        1 1
          1
```

Mark Demonstration: Dipper

PIMS Structures Capture Best Model

Males

3 3 3 3 3 3
3 3 3 3 3
3 3 3 3
3 3 3
3 3
3

Females

3 3 3 3 3 3
3 3 3 3 3
3 3 3 3
3 3 3
3 3
3

CORMACK-JOLLY SEBER MODEL

* Extension to Stage Structured Models for survival within a stage and movement between stages.

Open C-R Models for Multiple States

Survival and Movement Modeling for Multiple Sites or States
(Arnason, Schwarz, Nichols, Brownie, Pollock)

State transitions are now uncertain unlike age where an animal automatically moves to the next age.

Estimate: State-specific transition probabilities

State-specific survival probabilities

State-specific movement probabilities

Uses: Meta-population modeling

Breeding proportions and costs of reproduction

Testing condition-related survival (weight classes)

PARAMETER NOTATION

ϕ_i^{rs} = transition probability ie. The probability that an animal, alive and in state r at time i, is alive and in state s at time i + 1.

p_i^s = capture / resighting probability for an animal in state s at time i.

Table. Possible trajectories for animals released in location A at sampling period one of a two-period, two-location study (A or B) of an open population.

$$A \;\rightarrow\; A \;\rightarrow\; \text{Capture} \rightarrow \text{AA History}$$

$$\phi_1^{AA} \qquad p_2^{A} \qquad\qquad \phi_1^{AA} p_2^{A}$$

$$A \;\rightarrow\; B \;\rightarrow\; \text{Capture} \rightarrow \text{AB History}$$

$$\phi_1^{AB} \qquad p_2^{B} \qquad\qquad \phi_1^{AB} p_2^{B}$$

$$A \;\rightarrow\; A \;\rightarrow\; \text{No Capture} \rightarrow A0 \text{ History}$$

$$A \;\rightarrow\; B \;\rightarrow\; \text{No Capture} \rightarrow A0 \text{ History}$$

$$1 - \phi_1^{AA} p_2^{A} - \phi_1^{AB} p_2^{B}$$

Table. Possible capture histories and their probabilities for animals released in location A or B at sampling period one of a two-period, two-location study of an open population.

Location A	Probability
AA	$\phi_1^{AA} p_2^{A}$
AB	$\phi_1^{AB} p_2^{B}$
A0	$(1 - \phi_1^{AA} p_2^{A} - \phi_1^{AB} p_2^{B})$

Location B	Probability
BB	$\phi_1^{BB} p_2^{B}$
BA	$\phi_1^{BA} p_2^{A}$
B0	$(1 - \phi_1^{BB} p_2^{B} - \phi_1^{BA} p_2^{A})$

CAPTURE HISTORY FORMAT

Now our capture histories generalize to include state as well as caught or not.

Next is an example with 5 periods and two possible states.

EXAMPLE

Some of many Possible Capture Histories

Five Periods and Two States A and B

0 means not detected in either state

AA0AA

ABA0A

A0BA0

A0000

BBA00

BAA00

000BA

0A0B0

MULTI-STATE MODELS

- Can Use of SURVIV, MSSURVIV and MARK on two examples to illustrate this methodology.

- Microtus Mass Class Model

  A ⟶ B ⟶ C ⟶ D

  Nichols et al. (1992) Ecology

- Canada Geese going to three different wintering grounds, A,B,C

  Mid Atlantic, Chesapeake, Carolinas

  Hestbeck et al.(1991) Ecology

MICROTUS MASS CLASS EXAMPLE

- Small field mouse studied over 4 periods (months)

- Interested in weight transitions - survival and movement from stage to stage between periods.

A	< 22 g	Juveniles
B	22 -33 g	Subadults
C	34- 45 g	Small adults
D	> 45 g	Large adults

MICROTUS MASS CLASS EXAMPLE

TRANSITION (Survival + Movement)PROBABILITIES (ϕ^{rs})

Transition[#]	Estimate(St Error)
AB	0.87(0.05)
B B	0.51(0.06)
B C	0.24(0.06)
C C	0.66(0.05)
C D	0.08(0.08)
D C*	0.22(0.22)
D D	0.56(0.06)

[#] Not all transitions are shown as some do not occur.

*The animals lost weight.

WINTERING CANADA GEESE

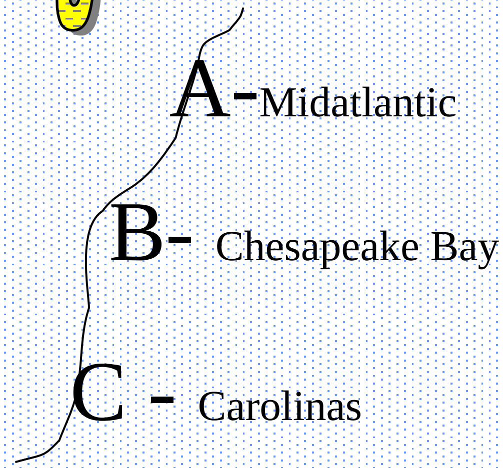
* Mark-resight of neck collared migratory geese in the winter, 1983-84 to 1985-86. 3 different winters where estimates possible
* A – Mid Atlantic Region

  (NY, NJ, DE, PA)
* B - Chesapeake Bay Region

  (MD, VA)
* C- Carolinas Region

  (NC, SC)
* All birds breed in Canada and come south for winter only
* transition probabilities between years estimated and then survival and movement probabilities estimated

Wintering Geese



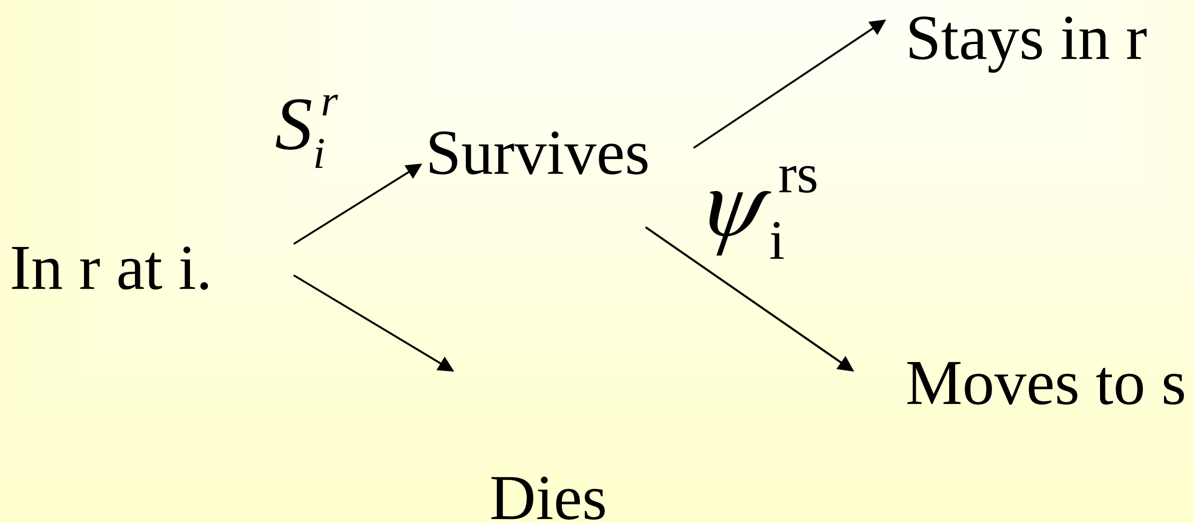
Estimation of survival and movement probs

$A \rightarrow A$	$A \rightarrow B$	$A \rightarrow C$
$B \rightarrow A$	$B \rightarrow B$	$B \rightarrow C$
$C \rightarrow A$	$C \rightarrow B$	$C \rightarrow C$

SEPARATION OF SURVIVAL AND MOVEMENT

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = S_i^r \psi_{\mathrm{i}}^{\mathrm{rs}}$$

If movement is at end of interval



WINTERING CANADA GEESE

SURVIVAL PROBS SHOWN HERE (S^r)

Location	Estimate(SE)
A	0.58 (0.015)
B	0.66 (0.016)
C	0.49 (0.019)

WINTERING CANADA GEESE

MOVEMENT PROBS ONLY SHOWN HERE* (ψ^{rs})

Transition	Estimate(SE)
A A	0.71(0.016)
A B	0.29(0.016)
A C	0.00(0.001)
B A	0.10(0.006)
B B	0.89(0.007)
B C	0.02(0.002)
C A	0.07(0.010)
C B	0.37(0.024)
C C	0.56(0.025)

*Probability of movement given survived and they assumed the animals moved at the end of interval.They add to 1 in each set.

WINTERING CANADA GEESE

MOVEMENT PROBABILITIES

Birds in the Carolinas are much less likely to return there the next winter (0.56) than for the other areas.

Whereas 0.71 returning to Midatlantic

And 0.89 of returning to Chesapeake. (Most faithful birds)

Conclusions and Complex Applications

Survival and Movement Applications

- Meta-popn modeling in different patches of fragmented habitat.
Distance between patches as a covariate.
- Stages can be life stages (microtus example)
- Combine tag returns & recaptures to evaluate value of marine reserves
- Use of radio telemetry to get more detailed info on movement.

RESEARCH ON SEPARATION OF SURVIVAL AND MOVEMENT PARAMETERS

- Recent work has focused on how to separate transition probabilities into survival and movement probabilities more generally.This is not easy to accomplish realistically.

- Work has been joint with my former Ph D student Mi-Jeom Joe.

- Reference is Joe and Pollock (2002) Journal of Applied Statistics.Proceedings of the EURING conference.

Mark:MSSURVIV Example

- I will open the example and show you the basic structures

SEPARATION OF SURVIVAL AND MOVEMENT

Additional Slides on Our research-Not covered in Class

SEPARATION OF SURVIVAL AND MOVEMENT

t fixed

We began by pretending that we knew the movement time t between the two sampling periods i and i+1. We then have:

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = (S_i^r)^t \psi_{\mathrm{i}}^{\mathrm{rs}} (S_i^s)^{1-t}$$

Where we have

S_i^r is the survival rate from i to i+1 given the animal is alive at i and the animal is in state r for the whole interval .

$\psi_{\mathrm{i}}^{\mathrm{rs}}$ is the probability of moving from state r to state s at i+t for an animal alive in state r at i+t

Note that $\psi_{\mathrm{i}}^{\mathrm{rr}} = 1 - \psi_{\mathrm{i}}^{\mathrm{rs}}$ in a two stage (or patch system).

SEPARATION OF SURVIVAL AND MOVEMENT

t fixed

In previous work the animals were assumed to move at the beginning or the end of the interval so that

t=0

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = S_i^s \psi_{\mathrm{i}}^{\mathrm{rs}}$$

or t=1.

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = S_i^r \psi_{\mathrm{i}}^{\mathrm{rs}}$$

SEPARATION OF SURVIVAL AND MOVEMENT

t random variable

- We continue by assuming the movement time t between the two sampling periods i and i+1 comes from a known distribution f(t). We then have:

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = \int_0^1 (S_i^r)^t \psi_{\mathrm{i}}^{\mathrm{rs}} (S_i^s)^{1-t} \, \mathrm{f(t)} \, \mathrm{dt}$$

An important special case is where f(t) is uniform which corresponds to the movement time being randomly distributed in the interval.For this case we can obtain an explicit form for the integral

SEPARATION OF SURVIVAL AND MOVEMENT

t uniform random variable

We continue by assuming f(t) is uniform. We then have:

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = \psi_{\mathrm{i}}^{\mathrm{rs}} \int_0^1 (S_i^r)^t (S_i^s)^{1-t} \, \mathrm{dt}$$

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = \psi_{\mathrm{i}}^{\mathrm{rs}} S_i^s [(S_i^r / S_i^s) - 1] / \ln(S_i^r / S_i^s)$$

and

$$\phi_{\mathrm{i}}^{\mathrm{rs}} = \psi_{\mathrm{i}}^{\mathrm{rs}} S_i^s \text{ if } S_i^r = S_i^s$$

SEPARATION OF SURVIVAL AND MOVEMENT

t uniform random variable

Simulations

When the movement rates were high:

- High correlations between estimates
- Some failure to converge
- High relative standard errors

When the movement rates were low:

- Estimates are much better behaved

Currently planning to apply to some butterfly data of Haddad

SEPARATION OF SURVIVAL AND MOVEMENT

t another random variable

- We continued by assuming f(t) is beta with known parameters.

- In practice we would have to estimate the distribution from telemetered animals.