

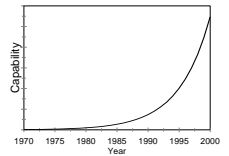
Program MARK Parameter Estimation from Marked Animals

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1

Advances since 1985

- More complex time/space models
- Covariates – more realistic biology
- New models – innovative data collection



2

- Standard tags, leg bands, or neck collars
- Radios (implants)
- PIT tags
- Camera “traps”
- DNA samples

Estimable Parameters

- **Survival**
- **Movement**
- **Emigration/immigration**
- **Reproduction/recruitment**
- **Population size**
- **Rate of population change**

5

Models in MARK

- Live encounters – Cormack, Jolly, Seber
- Dead encounters – Band or ring recovery
- Joint live and dead – Burnham, Barker, Lindberg
- Known fate – radio-tracking
- Closed capture-recapture – likelihood only, including individual heterogeneity
- Robust design – Pollock, Kendall
- Multistrata design – Brownie, Nichols, with dead recoveries – Barker
- Jolly-Seber – POPAN – Pradel – Link-Barker (7 parameterizations)
- Nest success
- Occupancy estimation, with robust design

6

- **Multiple attribute groups**
- **Time, group and individual covariates**
- **Unequal time intervals**
- **Model management**
- **AIC model selection**
- **Quasi-likelihood**
- **Variance Components**
- **Model Averaging**

- **Windows 95/98/NT/2000/ME/XP**
- **Structure of models**
- **Design matrix and link functions**
- **AIC, model selection**
- **Maximum likelihood estimation**
- **Sharp knives cut people**

Data are Required to Gain Reliable Knowledge

**A statistician's primary
function is to prevent, or
at least impede research.**

9

Computer Requirements

- Windows 95/98/NT 4.0/
2000/ME/XP
- CPU speed to compute
estimates in reasonable
amount of time
- ≥ 128 Mb RAM

10

- Interface written in Computer
Associates Visual Objects
- Numerical analysis in 32 bit
FORTRAN 95 code
- Communication by files

Basic Data

Encounter Histories

- LDLDL...
 - Dead recoveries
 - Joint live and dead
 - Known fate
- LLLLLL...
 - Live recaptures
 - Closed capture-recapture
- Dead recovery matrices
- Known fate

13

Likelihood Function

Maximum Likelihood Estimation

$$\text{Likelihood} = \text{Pr}(\text{Enc. Hist.})^{\text{Observed}}$$

$$\log_e(\text{Likelihood}) = \text{Num. Observed} \times \log_e[\text{Pr}(\text{Enc. Hist.})]$$

14

- How are encounter histories translated into probabilities that are a function of the parameters of interest?

		Encounter History (LD)	
	S	Live	10 S
Releases		r	Reported 11 (1 - S)r
	1 - S	Dead	
		1 - r	Not Reported 10 (1 - S)(1 - r)

Seber 1970

Brownie et al.: $f_i = (1 - S_i)r_i$

$$\begin{array}{cccc}
 (1-S_1)r_1 & S_1(1-S_2)r_2 & S_1S_2(1-S_3)r_3 & S_1S_2S_3(1-S_4)r_4 \\
 & (1-S_2)r_2 & S_2(1-S_3)r_3 & S_2S_3(1-S_4)r_4 \\
 & & (1-S_3)r_3 & S_3(1-S_4)r_4 \\
 & & & (1-S_4)r_4
 \end{array}$$

17

Brownie et al. 1985 Model

$$\begin{array}{cccc}
 f_1 & S_1f_2 & S_1S_2f_3 & S_1S_2S_3f_4 \\
 & f_2 & S_2f_3 & S_2S_3f_4 \\
 & & f_3 & S_3f_4 \\
 & & & f_4
 \end{array}$$

18



Dead Encounters

00100001

$$S_2 S_3 (1 - S_4) r_4$$



21

Dead Encounters

00000011

$$(1 - S_4) r_4$$



22



Dead Encounters

Model notation:

$$\{S(.) r(t)\}$$

$$S_1 = S_2 = \dots = S_t;$$

$$r_1, r_2, \dots, r_t$$

25

Dead Encounters

Model notation:

$$\{S(t) r(.)\}$$

$$S_1, S_2, \dots, S_t;$$

$$r_1 = r_2 = \dots = r_t$$

26

Model notation:

$$\{S(g^*t) r(g^*t)\}$$

$$S_{11}, S_{12}, \dots, S_{1t},$$

$$S_{21}, S_{22}, \dots, S_{2t};$$

$$r_{12}, r_{13}, \dots, r_{1t}, r_{22}, r_{23}, \dots, r_{2t}$$

Dead Encounters

Model notation:

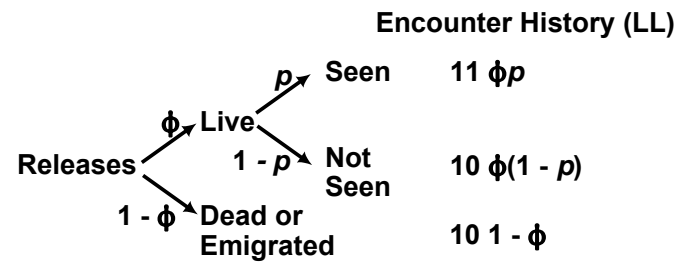
$\{S(g) r(g)\}$

$S_{1.}, S_{2.}, \dots, S_{g.}$

$r_{1.}, r_{2.}, \dots, r_{g.}$

29

Live Encounters (CJS)



30

Live Encounters (CJS)

0101

$$\phi_2(1 - p_3)\phi_3p_4$$

33

Live Encounters (CJS)

1110

$$\phi_1p_2\phi_2p_3$$
$$[\phi_3(1 - p_4) + (1 - \phi_3)]$$

34

Live Encounters (CJS)

Model notation:

$$\{\phi(.) p(.)\}$$

$$\phi_1 = \phi_2 = \dots = \phi_{t-1};$$

$$p_2 = p_3 = \dots = p_t$$

37

Live Encounters (CJS)

Model notation:

$$\{\phi(t) p(.)\}$$

$$\phi_1, \phi_2, \dots, \phi_{t-1};$$

$$p_2 = p_3 = \dots = p_t$$

38

Model notation:

$$\{\phi(g^*t) p(g^*t)\}$$

$$\phi_{11}, \phi_{12}, \dots, \phi_{1t-1};$$

$$\phi_{21}, \phi_{22}, \dots, \phi_{2t-1};$$

$$p_{12}, p_{13}, \dots, p_{1t};$$

Model notation:

$$\{\phi(g) p(g)\}$$

$$\phi_{1.}, \phi_{2.}, \dots, \phi_{g.};$$

$$p_{1.}, p_{2.}, \dots, p_{g.}$$

Extensions to CJS

Extensions allow additional parameters to be estimated.

- Multi-strata
- Jolly-Seber (Pradel, POPAN, Link-Barker)
- Robust design
- Incorporate dead encounters

41

Multi-Strata Model

- Allows transitions between categories, e.g.:
 - Life stages
 - Areas (e.g., wintering grounds)
 - Breeding status

42

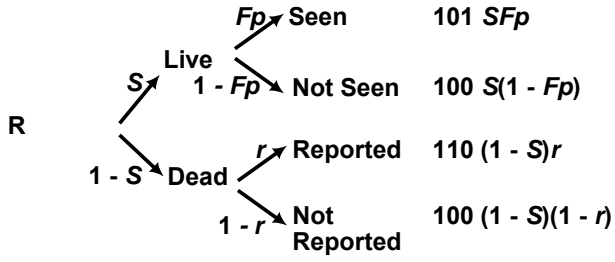
- Estimates of ϕ and p
- “Leading Zeros” used to estimate:
 - Lambda ($\lambda = N_{t+1}/N_t = \phi + f$)
 - Recruitment ($f = \lambda - \phi$)
 - Seniority (γ)
 - Population size (N_t)

- Multiple trapping occasions close together where no population change is assumed
- Estimates of:
 - Temporary emigration
 - Population size (N)

Joint Encounters

Both live and dead encounters

Encounter History (LDL)



45

Joint Encounters

4 encounter occasions

LDLDDL

S - survival prob.

r - reporting prob.

p - capture prob.

F - fidelity prob. ($\phi = SF$)

46

Joint Encounters

10101001

$$S_1 F_2 p_2 S_2 F_3 p_3 S_3 \\ [F_4(1 - p_4) + (1 - F_4)] \\ (1 - S_4)r_4$$

49

Barker Live-Dead Model

- Extension of joint live and dead recoveries model that allows resightings during intervals
- Estimation of survival and fidelity to study area

50

- Barker model extended to include robust design (also see Lindberg et al. 2001)
- Estimate temporary and permanent emigration, survival, and population size.

- For wildlife applications, this general model could incorporate data from DNA, radios, harvest, and casual resightings of marked animals
- Estimates of survival, temporary and permanent emigration, and population size

Multi-strata with Live and Dead Encounters

- Strata-specific live encounters, dead encounters ignore strata
- Estimation of transition probabilities, true survival, strata-specific live encounter probability, and dead encounter probability

53

Joint Encounters: Estimation of Radio Effects

- Group 1: regular live/dead encounters
 - 00100001
- Group 2: known fate data entered as joint live/dead encounter history
 - 00101011
 - $p = 1$
 - $r = 1$
- Compare S -hat and F -hat for 2 groups

54

				Encounter History (LL)	
				Seen	Not Seen
U	p	Seen	c	11	pc
		Not Seen	$1 - c$	10	$p(1 - c)$
	$1 - p$	Seen	p	01	$(1 - p)p$
		Not Seen	$1 - p$	00	$(1 - p)(1 - p)$

Closed Captures

$$\blacksquare N = M_{t+1} / [1 - (1-p_1)(1-p_2)\dots(1-p_4)]$$

57

Closed Captures

$$1111$$
$$p_1 c_2 c_3 c_4$$

58

Closed Captures

0100

$$(1 - p_1)p_2(1 - c_3)(1 - c_4)$$

61

Closed Captures

0000

$$(1 - p_1)(1 - p_2)(1 - p_3)(1 - p_4)$$

62

$$\blacksquare p_i = \pi p_a + (1 - \pi)p_b$$

where π is probability animal is from mixture distribution a which has p_a initial capture probability

▪ Similarly for remaining p_i and c_i

Closed Captures with Heterogeneity

Model notation with 2 mixtures (a, b):

$$\{\pi, p_a(t), p_b(t), c_a(t), c_b(t), N(\cdot)\}$$

$\pi;$

$$p_{a1}, p_{a2}, \dots, p_{at}; p_{b1}, p_{b2}, \dots, p_{bt};$$

$$c_{a2}, c_{a3}, \dots, c_{at}; c_{b2}, c_{b3}, \dots, c_{bt};$$

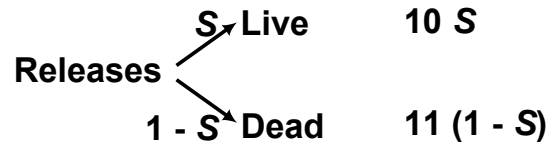
$N.$

65

Known Fate

Radio-tracking Data

Encounter History (LD)



66

Known Fate

00101011
 $S_2 S_3 (1 - S_4)$

69

Known Fate

10100011
 $S_1 S_2 (1 - S_4)$

70

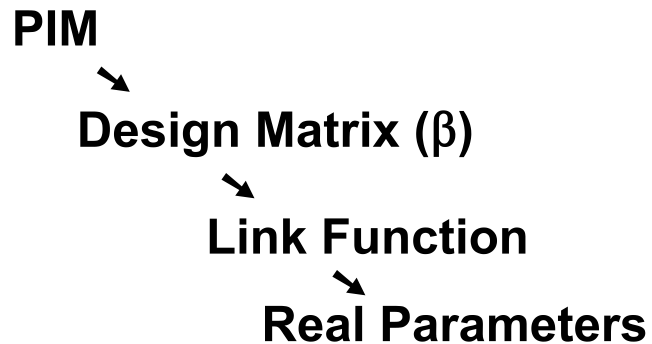
- KM estimate is product of survival estimates for fixed time intervals
- Staggered entry
 - 0000101010
 - 0000101011
- Right censoring or missing intervals
 - 10100000101000

Advantages of Using MARK Known Fate over Kaplan-Meier

- Alternative models
- Covariates
- Model selection
- Model averaging
- Variance components

73

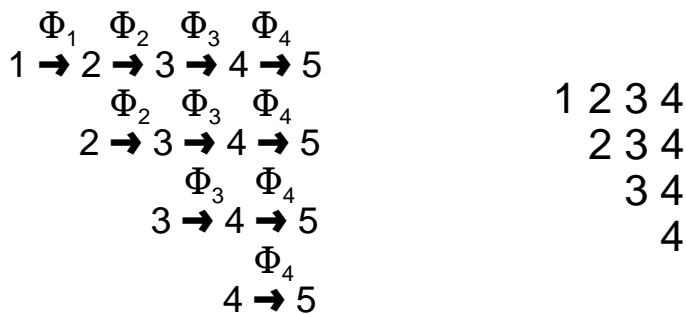
Model Building



74

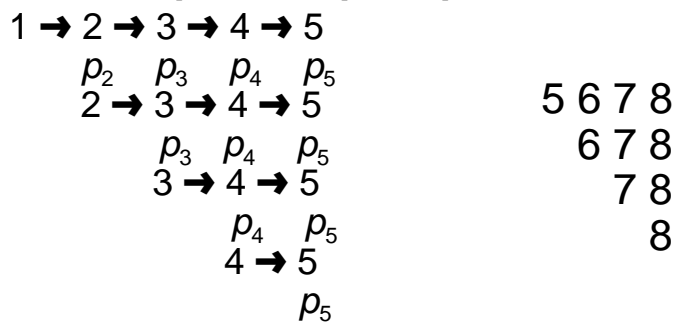
Parameter Index Matrix – PIM

Time-specific apparent survival



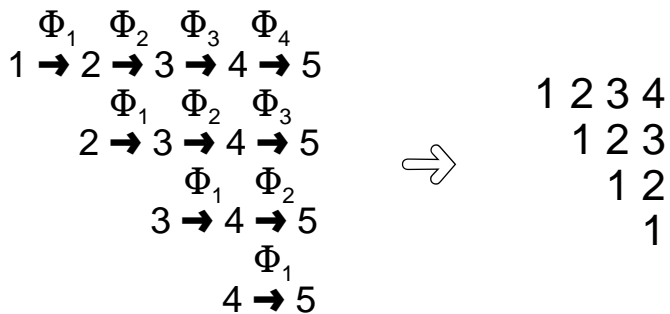
Parameter Index Matrix – PIM

Time-specific capture probabilities



Parameter Index Matrix – PIM

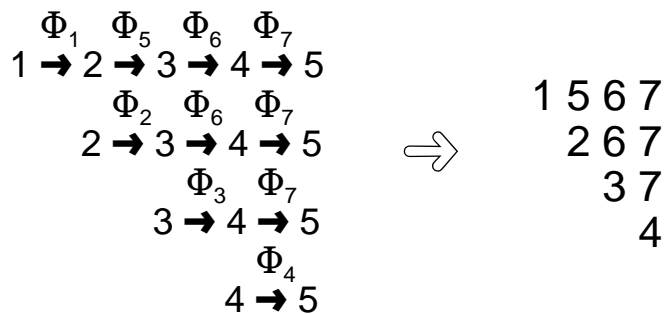
Age-specific apparent survival



77

Parameter Index Matrix – PIM

Age- and time-specific apparent survival, 2 age classes



78

Parameter Index Matrix – PIM

2 Groups, Survival Different, Time-specific Model $\{S(g^*t)\}$

<u>Group 1</u>	<u>Group 2</u>
1 2 3 4 5	6 7 8 9 10
2 3 4 5	7 8 9 10
3 4 5	8 9 10
4 5	9 10
5	10

Parameter Index Matrix – PIM

2 Groups, Survival Same, Time-specific Model $\{S(t)\}$

<u>Group 1</u>	<u>Group 2</u>
1 2 3 4 5	1 2 3 4 5
2 3 4 5	2 3 4 5
3 4 5	3 4 5
4 5	4 5
5	5

Parameter Index Matrix – PIM

2 Groups, Survival Different,
Model $\{S(g)\}$

<u>Group 1</u>	<u>Group 2</u>
1 1 1 1 1	2 2 2 2 2
1 1 1 1	2 2 2 2
1 1 1	2 2 2
1 1	2 2
1	2

81

Parameter Index Matrix – PIM

2 Groups, Survival Same,
Model $\{S(\cdot)\}$

<u>Group 1</u>	<u>Group 2</u>
1 1 1 1 1	1 1 1 1 1
1 1 1 1	1 1 1 1
1 1 1	1 1 1
1 1	1 1
1	1

82

- Time-specific (current PIM or all)
- Age-specific (current PIM or all)
- Constant (current PIM or all)
- Diagonal, Row, Column changes
- Change a single cell
- Exchange or copy whole PIMs
- Paste or copy to clipboard
- Renumber (with or without overlap)

- Visually assess PIMs
- Drag boxes to copy PIMs
- Right click to select menu choices

Design Matrix

- Allows additional constraints not possible using PIMs
 - ▶ Additive models with parallelism between groups, ages
- Covariates, including individual covariates

85

Individual Covariates

- Included in Encounter Histories File
- Attached to animal's encounter history

86

PIMs for Design Matrix Examples 5 intervals (6 occasions), 3 groups

Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

```

Group 1  Group 2  Group 3
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
2 3 4 5   7 8 9 10 12 13 14 15
3 4 5    8 9 10 13 14 15
4 5     9 10 14 15
5      10 15
  
```

Model $\{\theta(g^*t)\}$

```

1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0
  
```

Link Functions

- Sin
- Logit
- Log-Log
- Complementary Log-Log
- Log
- Identity
- Multinomial Logit
- Cumulative Logit

89

Design Matrix Identity Link

Unbounded

$$\text{Real Estimate} = X\beta$$

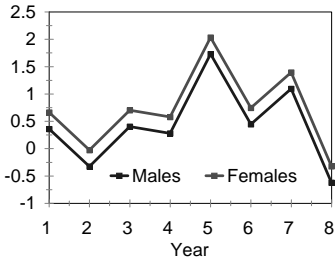
90

Bounded 0-1

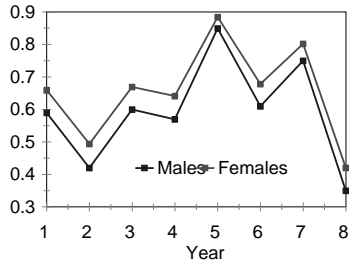
Bounded 0-1

Logit vs. Real Parameters

Logit Scale



Real Scale

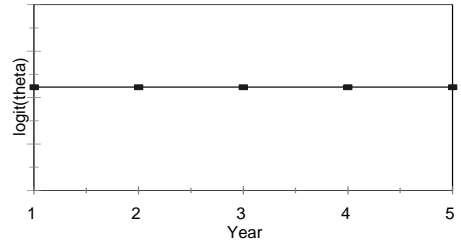


93

Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model {theta(.)}

1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1
1



94

Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model {theta(g)}

110
110
110
110
110
110
101
101
101
101
101
100
100
100
100
100
100
100

Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model {theta(t)}

11000
10100
10010
10001
10000
11000
10100
10010
10001
10000
11000
10100
10010
10001
10000
11000
10100
10010
10001
10000
10000

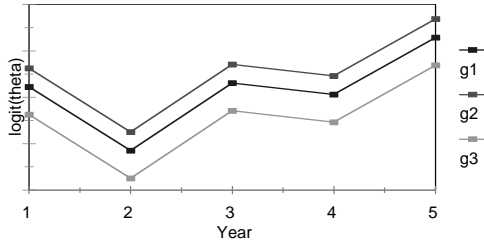
Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model {theta(g + t)}

```

1101000
1100100
1100010
1100001
1100000
1011000
1010100
1010010
1010001
1010000
1001000
1000100
1000010
1000001
1000000

```



Variation in theta by time and by group
Additive model with no interactions

97

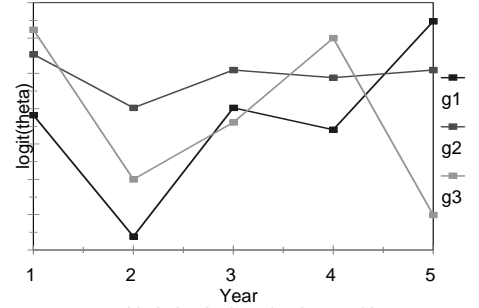
Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model {theta(g*t)}

```

110100010000000
110010001000000
110001000100000
110000100010000
110000010001000
110000001000000
101100000000100
101010000000100
101001000000010
101000100000001
101000010000000
100100000000000
100010000000000
100001000000000
100000100000000
100000010000000
100000001000000
100000000100000
100000000010000
100000000001000
100000000000100
100000000000010
100000000000001
100000000000000

```



Variation in theta by time and by group

98

Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model {theta(T)}

```

11
12
13
14
15
11
12
13
14
15
11
12
13
14
15

```

Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model {theta(g + T)}

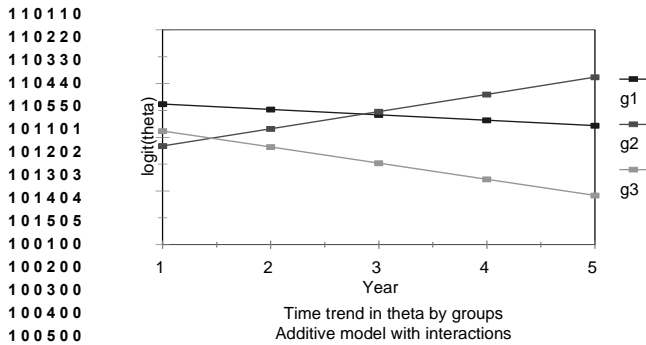
```

1101
1102
1103
1104
1105
1011
1012
1013
1014
1015
1001
1002
1003
1004
1005

```

Group 1	Group 2	Group 3
1 2 3 4 5	6 7 8 9 10	11 12 13 14 15
2 3 4 5	7 8 9 10	12 13 14 15
3 4 5	8 9 10	13 14 15
4 5	9 10	14 15
5	10	15

Model $\{\theta(g \cdot T)\}$



101

Design Matrix Manipulation

- Add and delete columns
- Products of columns or copy a column
- Intercept or trend covariates
- Identity matrix
- Time or group indicator variables
- Covariates or individual covariate names
- Functions of columns and/or individual covariates
- Copy values or rotate column up/down
- Paste values from clipboard
- Retrieve columns from previous models

102

- Separate FORTRAN code
- Runs as a separate process in a different thread
- Can be used separately from interface program

- Encounter histories parsed to compute probability as function of parameters
- Numerical optimization of likelihood with quasi-Newton algorithm
- Singular value decomposition of information matrix to obtain VC matrix and rank

Features of Results Browser

- Retrieve PIMs and Design Matrix of models to construct a new model
- Retrieve full output
- Retrieve parameter estimates
- Retrieve variance-covariance matrix
- Output to a NotePad window, to Excel, to the clipboard, or printed directly
- Graphics

105

Hypothesis Tests

- Likelihood ratio tests
- Analysis of Deviance (ANODEV)

106

- Program RELEASE
- Programs ESTIMATE/BROWNIE
- Parametric bootstrap with deviance or Pearson chi-square

- Model averaging
- Variance components estimation
- Quasi-likelihood to correct for overdispersion
- Bootstrap procedure

Model Selection Older Approaches

- Forward selection
- Backward selection
- Best R^2
- All possible models

109

Model Selection Information-Theoretic Approach

- AIC
- Akaike's Information Criterion
- $AIC = -2\log(\mathcal{L}(\beta)) + 2K$
- MARK ranks models based on their AIC values

110

Burnham and Anderson (1998)

- $AIC = -2\log(\mathcal{L}(\beta)) + 2K$
- $AIC_c = -2\log(\mathcal{L}(\beta)) + 2K + 2K(K+1)/(n-K-1)$
- $\Delta AIC_c = AIC_c - \min AIC_c$
- $w_i = \exp(-\Delta/2) / \sum \exp(-\Delta/2)$

Model Averaging

- Incorporate model selection uncertainty into parameter variances
- Obtain proper confidence interval coverage

113

Model Averaging

Program MARK Interface - San Luis Valley Mallard Data, from Brownie et al. 1985, page 92 (C:\Mark...)

File Delete Order Output Retrieve PIM Design Run Simulations Tests Adjustments Window Help

Results Browser - Brownie et al. Recoveries

Model	AICc	Delta AICc	AICc Weight	No. Par.	Deviance
{S(a*) f(a*)}	20718.55	0.00	0.53519	34	68.492
{S(a) f(a*)}	20718.84	0.28	0.46481	20	96.873
{S(a) f(a)}	20763.73	45.18	0.00000	4	173.819

10:54:03 AM

114

San Luis Valley Mallard Data, from Brownie et al. 1985, page 92

Survival Parameter (S) Adults Parameter 1

Model	Weight	Estimate	Standard Error
{S(a*) f(a*)}	0.53519	0.57906230	0.1140629
{S(a) f(a*)}	0.46481	0.6522073	0.0120278
Weighted Average		0.6130607	0.0666361
Unconditional SE			0.0827347
95% CI for Wgt. Ave. Est. (logit trans.) is 0.4443819 to 0.7583747			
Percent of Variation Attributable to Model Variation is 35.13%			

Variance Components

- **Sampling Variance, e.g., Standard Errors**
- **Process Variance, e.g., Variance across time**
- **Sum is Total Variance**

117

Process Variance σ^2

- **Needed for valid Population Viability Analysis**
- **Forecasting population trends**

118

Variance Components

- Mean
- Linear Trend
- User-defined linear function

121

Example

Beta-hat SE(Beta-hat)

0.362423 0.038221

S-hat SE(S-hat) S-tilde SE(S-tilde) RMSE(S-tilde)

0.377622 0.164105 0.382632 0.096390 0.096520

0.620369 0.193238 0.493115 0.100578 0.162203

...

0.097701 0.060745 0.124123 0.051765 0.058118

0.249997 0.169099 0.291019 0.098057 0.106292

Estimate of $\sigma^2 = 0.0135$ with 95% CI (0.0027 to 0.0666)

122

- Animal fates are independent
- Binomial variation
- Violations lead to overdispersion

Quasi-likelihood Estimation

- Correction for overdispersion
- Variance inflation factor \hat{c}
- $QAIC = -2\log(\hat{\mathcal{L}}(\beta)) / \hat{c} + 2K$
- $QAIC_c = -2\log(\hat{\mathcal{L}}(\beta)) / \hat{c} + 2K + 2\sqrt{K(K+1)/(n-K-1)}$
- $SE(\hat{\theta}) = \sqrt{\frac{Var(\hat{\theta})}{\hat{c}}}$

125

Goodness of Fit

- Estimate of over dispersion, c
- Rejection of global model as fitting the data

126

Decide if $c > 1$ for global model

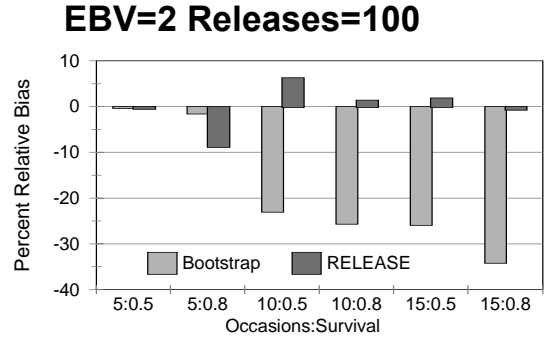
- Program RELEASE
- Programs ESTIMATE/BROWNIE
- Deviance
- $2\log(\hat{\mathcal{L}} \text{ model}) - 2\log(\hat{\mathcal{L}} \text{ saturated})$
- Bootstrap procedure

Bootstrap Procedure

- Compute estimates from data
- Compute parametric bootstraps from estimates
- Determine likelihood of observed deviance
- Estimate $\hat{\epsilon}$ as observed deviance divided by mean of bootstrap deviances (or Pearson chi-square)

129

Goodness of Fit – Bootstrap Approach



130

- Help file
- WWW
 - Gentle introduction
 - Evan Cooch
 - Theory description
 - David Anderson
 - Ken Burnham
- Various other publications

<http://www.cnr.colostate.edu/~gwhite>

- Single 13Mb zipped setup file
- Nine 1.4Mb zipped setup disks
- Update zip file of executable files

→ Includes help file and examples