

Basic overview/features of CMR for paleobiology

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Friedrich-Alexander-Universität
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THE ESSENCE OF CAPTURE RECAPTURE APPROACHES

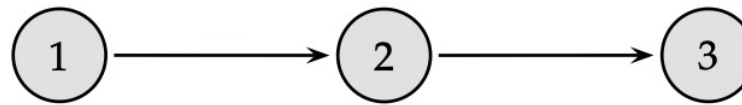


"Careful—it might be a trap!"

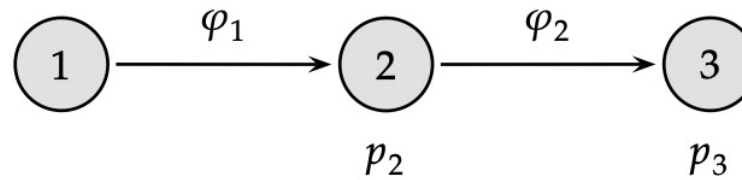
$$\frac{\text{marked Day 2}}{\text{total for Day 2}} = \frac{\text{marked Day 1}}{\text{Estimated Total}}$$

The **Lincoln–Petersen method** (Petersen–Lincoln index)

Encounter history



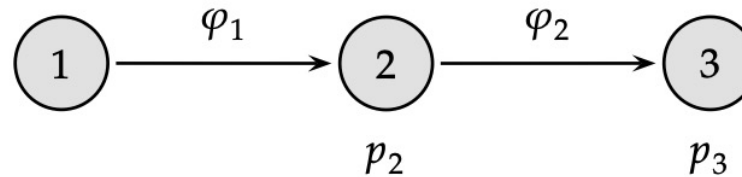
Encounter history



<i>encounter history</i>	<i>probability of encounter history</i>
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111	$\varphi_1 p_2 \varphi_2 p_3$
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Encounter history

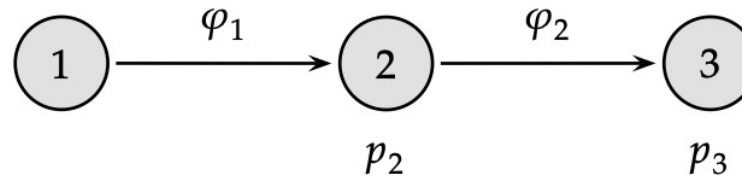


<i>encounter history</i>	<i>probability of encounter history</i>
--------------------------	---

111	$\varphi_1 p_2 \varphi_2 p_3$
-----	-------------------------------

110	$\varphi_1 p_2 [\varphi_2 (1 - p_3) + (1 - \varphi_2)]$ $= \varphi_1 p_2 (1 - \varphi_2 p_3)$
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Encounter history



<i>encounter history</i>	<i>probability of encounter history</i>
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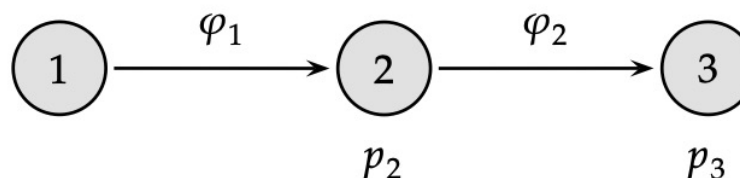
111	$\varphi_1 p_2 \varphi_2 p_3$
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110	$\varphi_1 p_2 [\varphi_2 (1 - p_3) + (1 - \varphi_2)]$ $= \varphi_1 p_2 (1 - \varphi_2 p_3)$
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101	$\varphi_1 (1 - p_2) \varphi_2 p_3$
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Encounter history

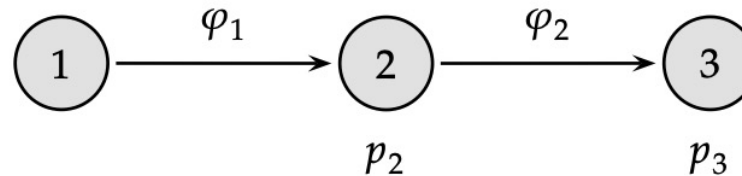


<i>encounter history</i>	<i>probability of encounter history</i>
111	$\varphi_1 p_2 \varphi_2 p_3$
110	$\varphi_1 p_2 [\varphi_2 (1 - p_3) + (1 - \varphi_2)]$ $= \varphi_1 p_2 (1 - \varphi_2 p_3)$
101	$\varphi_1 (1 - p_2) \varphi_2 p_3$
100	$(1 - \varphi_1) + \varphi_1 (1 - p_2) (1 - \varphi_2) + \varphi_1 (1 - p_2) \varphi_2 (1 - p_3)$ $= 1 - \varphi_1 p_2 - \varphi_1 (1 - p_2) \varphi_2 p_3$

Trilobite taxa



Encounter history

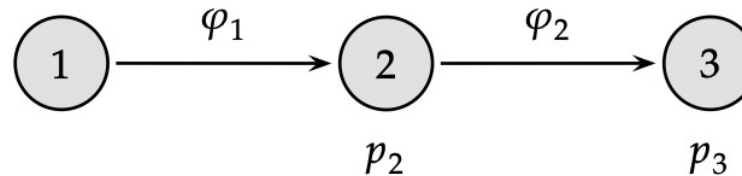


	<i>encounter history</i>	<i>probability of encounter history</i>
Trilobite taxon A	111	$\varphi_1 p_2 \varphi_2 p_3$
Trilobite taxon B	110	$\varphi_1 p_2 [\varphi_2 (1 - p_3) + (1 - \varphi_2)]$ $= \varphi_1 p_2 (1 - \varphi_2 p_3)$
Trilobite taxon C	101	$\varphi_1 (1 - p_2) \varphi_2 p_3$
Trilobite taxon D	100	$(1 - \varphi_1) + \varphi_1 (1 - p_2) (1 - \varphi_2) + \varphi_1 (1 - p_2) \varphi_2 (1 - p_3)$ $= 1 - \varphi_1 p_2 - \varphi_1 (1 - p_2) \varphi_2 p_3$

Trilobite taxa



Encounter history



	<i>encounter history</i>	<i>probability of encounter history</i>
A, X, P	111	$\varphi_1 p_2 \varphi_2 p_3$
B, E	110	$\varphi_1 p_2 [\varphi_2 (1 - p_3) + (1 - \varphi_2)]$ $= \varphi_1 p_2 (1 - \varphi_2 p_3)$
C, Q R, T, S, X, Z	101	$\varphi_1 (1 - p_2) \varphi_2 p_3$
D, G H, J, K, Y	100	$(1 - \varphi_1) + \varphi_1 (1 - p_2) (1 - \varphi_2) + \varphi_1 (1 - p_2) \varphi_2 (1 - p_3)$ $= 1 - \varphi_1 p_2 - \varphi_1 (1 - p_2) \varphi_2 p_3$

THE DATA

Taxon	Time intervals							
	1	2	3	4	5	6	7	8
A	0	0	1	1	0	0	1	0
B	0	1	0	0	0	0	0	0
C	0	0	0	0	0	1	1	1
D	1	0	1	1	0	1	0	0
E	0	0	0	1	0	0	1	1
F	0	1	0	0	1	1	0	1
G	0	0	0	1	0	1	1	0
H	0	0	0	0	0	1	1	0
I	0	0	1	0	1	1	0	1
J	1	0	0	0	0	0	0	0
K	0	0	0	0	1	0	1	1
L	0	0	1	1	0	0	0	0
M	0	1	0	1	1	0	0	0
N	1	1	0	0	1	0	1	0
O	0	0	0	1	0	1	1	1
P	0	0	1	0	0	0	0	0
Q	0	0	0	0	0	0	1	0
R	0	0	1	0	1	1	0	1
S	0	0	0	0	1	0	0	1
T	0	0	0	1	0	0	0	0

Liow L.H. & Nichols, J.D. 2010 Estimating rates and probabilities of origination and extinction using taxonomic occurrence data: Capture-recapture approaches. In Quantitative Paleobiology Short Course. Eds. Alroy J. & Hunt G. Paleontological Society pp. 81-94

DETECTION HISTORIES

Time interval	1	2	3	4	5	6	7	8
L	0	1	1	0	0	0	0	0
M	0	1	0	1	1	0	0	0

Encounter/detection histories

- Series of ones and zeros
- Ones are taken as true presences
- Two types of zeros
 - Not sampled
 - Not sampled or truly absent

		Time intervals							
Taxon		1	2	3	4	5	6	7	8
A		0	0	1	1	0	0	1	0
B		0	1	0	0	0	0	0	0
C		0	0	0	0	0	1	1	1
D		1	0	1	1	0	1	0	0
E		0	0	0	1	0	0	1	1
F		0	1	0	0	1	1	0	1
G		0	0	0	0	0	1	1	0
H		0	0	0	0	0	1	1	0
I		0	0	0	0	0	1	0	1
J		0	0	0	0	0	0	0	0
K		0	0	0	0	1	0	1	1
L		0	0	1	1	0	0	0	0
M		0	1	0	1	1	0	0	0
N		1	1	0	0	1	0	1	0
O		0	0	0	1	0	1	1	1
P		0	0	1	0	0	0	0	0
Q		0	0	0	0	0	0	1	0
R		0	0	1	0	1	1	0	1
S		0	0	0	0	1	0	0	1
T		0	0	0	1	0	0	0	0

Detection
probability

$$\hat{p}_6 = 5 / 10 = 0.5$$

		Time intervals							
Taxon		1	2	3	4	5	6	7	8
A		0	0	1	1	0	0	1	0
B		0	1	0	0	0	0	0	0
C		0	0	0	0	0	1	1	1
D		1	0	1	1	0	1	0	0
E		0	0	0	1	0	0	1	1
<div> $\hat{S}_6 = s_6 / \hat{p}_6 = 8 / 0.5 = 16$ </div>							1	0	1
							1	1	0
							1	1	0
							1	0	1
							1	0	0
I		0	0	1	0	1	0	0	1
J		1	0	0	0	0	0	0	0
K		0	0	0	0	1	0	1	1
L		0	0	1	1	0	0	0	0
M		0	1	0	1	1	0	0	0
N		1	1	0	0	1	0	1	0
O		0	0	0	1	0	1	1	1
P		0	0	1	0	0	0	0	0
Q		0	0	0	0	0	0	1	0
R		0	0	1	0	1	1	0	1
S		0	0	0	0	1	0	0	1
T		0	0	0	1	0	0	0	0

		Time intervals							
Taxon		1	2	3	4	5	6	7	8
Extinction probability	A	0	0	1	1	0	0	1	0
	B	0	1	0	0	0	0	0	0
	C	0	0	0	0	0	1	1	1
	D	1	0	1	1	0	1	0	0
				0	1	0	0	1	1
				0	0	1	1	0	1
				0	1	0	1	1	0
				0	0	0	1	1	0
				1	0	1	1	0	1
				0	0	0	0	0	0
				0	0	1	0	1	1
				1	1	0	0	0	0
				0	1	1	0	0	0
				0	0	1	0	1	0
				0	1	0	1	1	1
	P	0	0	1	0	0	0	0	0
	Q	0	0	0	0	0	0	1	0
	R	0	0	1	0	1	1	0	1
	S	0	0	0	0	1	0	0	1
	T	0	0	0	1	0	0	0	0

$$\hat{\mathcal{E}}_5 = 1 - (\hat{M}'_6 / s_5)$$

		Time intervals							
Taxon		1	2	3	4	5	6	7	8
Extinction probability	A	0	0	1	1	0	0	1	0
	B	0	1	0	0	0	0	0	0
	C	0	0	0	0	0	1	1	1
	D	1	0	1	1	0	1	0	0
				0	1	0	0	1	1
				0	0	1	1	0	1
				0	1	0	1	1	0
				0	0	0	1	1	0
				1	0	1	1	0	1
				0	0	0	0	0	0
				0	0	1	0	1	1
				1	1	0	0	0	0
				0	1	1	0	0	0
				0	0	1	0	1	0
				0	1	0	1	1	1
	P	0	0	1	0	0	0	0	0
	Q	0	0	0	0	0	0	1	0
	R	0	0	1	0	1	1	0	1
	S	0	0	0	0	1	0	0	1
	T	0	0	0	1	0	0	0	0

$$\hat{\epsilon}_5 = 1 - (\hat{M}'_6 / s_5)$$

$$= 1 - (\frac{m'_6}{\hat{p}_6})$$

$$= 1 - (\frac{3 / 0.5}{16})$$

		Time intervals							
Taxon		1	2	3	4	5	6	7	8
Extinction probability	A	0	0	1	1	0	0	1	0
	B	0	1	0	0	0	0	0	0
	C	0	0	0	0	0	1	1	1
	D	1	0	1	1	0	1	0	0
				0	1	0	0	1	1
				0	0	1	1	0	1
				0	1	0	1	1	0
				0	0	0	1	1	0
				1	0	1	1	0	1
				0	0	0	0	0	0
				0	0	1	0	1	1
				1	1	0	0	0	0
				0	1	1	0	0	0
				0	0	1	0	1	0
				0	1	0	1	1	1
	P	0	0	1	0	0	0	0	0
	Q	0	0	0	0	0	0	1	0
	R	0	0	1	0	1	1	0	1
	S	0	0	0	0	1	0	0	1
	T	0	0	0	1	0	0	0	0

Alive in T 5 and 6

Alive in T5

Survival
Probability
From T5 to T6

$$\hat{\epsilon}_5 = 1 - (\hat{M}'_6 / s_5)$$

$$= 1 - (m'_6 / \hat{p}_6)$$

$$= 1 - (3 / 0.5)$$

$$= 1 - (16)$$

Representing detection/encounter histories

1	2	3	4	5	6	7	8
0	0	1	0	1	1	0	0
			p_4	p_5	p_6	p_7	p_8

Detection probabilities

			ϵ_3	ϵ_4	ϵ_5	ϵ_6	ϵ_7	
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Extinction probabilities

eh = 0 0 1 0 1 1 0 0

Pr(eh = 0 0 1 0 1 1 0 0 | initial encounter in interval 3) =

CJS model

Representing detection/encounter histories

1	2	3	4	5	6	7	8
0	0	1	0	1	1	0	0
			p_4	p_5	p_6	p_7	p_8

Detection probabilities

			ϵ_3	ϵ_4	ϵ_5	ϵ_6	ϵ_7	
--	--	--	--------------	--------------	--------------	--------------	--------------	--

Extinction probabilities

eh = 0 0 1 0 1 1 0 0

$\Pr(\text{eh} = 0\ 0\ 1\ 0\ 1\ 1\ 0\ 0 \mid \text{initial encounter in interval } 3) =$

$$(1-\epsilon_3)(1-p_4) (1-\epsilon_4)p_5 (1-\epsilon_5)p_6 [\epsilon_6 + (1-\epsilon_6)(1-p_7)\{\epsilon_7+(1-\epsilon_7)(1-p_8)\}]$$

Representing detection/encounter histories

1	2	3	4	5	6	7	8
0	0	1	0	1	1	0	0
			p_4	p_5	p_6	p_7	p_8

Detection probabilities

			ϵ_3	ϵ_4	ϵ_5	ϵ_6	ϵ_7	
--	--	--	--------------	--------------	--------------	--------------	--------------	--

Extinction probabilities

eh = 0 0 1 0 1 1 0 0

$\Pr(\text{eh} = 0\ 0\ 1\ 0\ 1\ 1\ 0\ 0 \mid \text{initial encounter in interval } 3) =$

$$(1-\epsilon_3)(1-p_4) (1-\epsilon_4)p_5 (1-\epsilon_5)p_6 [\epsilon_6 + (1-\epsilon_6)(1-p_7)\{\epsilon_7+(1-\epsilon_7)(1-p_8)\}]$$

Representing detection/encounter histories

1	2	3	4	5	6	7	8
0	0	1	0	1	1	0	0
			p_4	p_5	p_6	p_7	p_8

Detection probabilities

			ϵ_3	ϵ_4	ϵ_5	ϵ_6	ϵ_7	
--	--	--	--------------	--------------	--------------	--------------	--------------	--

Extinction probabilities

eh = 0 0 1 0 1 1 0 0

$\Pr(\text{eh} = 0\ 0\ 1\ 0\ 1\ 1\ 0\ 0 \mid \text{initial encounter in interval } 3) =$

$$(1-\epsilon_3)(1-p_4) (1-\epsilon_4)p_5 (1-\epsilon_5)p_6 [\epsilon_6 + (1-\epsilon_6)(1-p_7)\{\epsilon_7+(1-\epsilon_7)(1-p_8)\}]$$

Representing detection/encounter histories

1	2	3	4	5	6	7	8	
0	0	1	0	1	1	0	0	
			p_4	p_5	p_6	p_7	p_8	Detection probabilities
			ϵ_3	ϵ_4	ϵ_5	ϵ_6	ϵ_7	Extinction probabilities

eh = 0 0 1 0 1 1 0 0

Pr(eh = 0 0 1 0 1 1 0 0 | initial encounter in interval 3) =

$$+ (1-\epsilon_6)(1-p_7)\{\epsilon_7+(1-\epsilon_7)(1-p_8)\}$$

Representing detection/encounter histories

1	2	3	4	5	6	7	8	
0	0	1	0	1	1	0	0	
			p_4	p_5	p_6	p_7	p_8	Detection probabilities
			ϵ_3	ϵ_4	ϵ_5	ϵ_6	ϵ_7	Extinction probabilities

eh = 0 0 1 0 1 1 0 0

$\Pr(\text{eh} = 0\ 0\ 1\ 0\ 1\ 1\ 0\ 0 \mid \text{initial encounter in interval } 3) =$

$(1-\epsilon_3)(1-p_4) (1-\epsilon_4)p_5 (1-\epsilon_5)p_6 [\epsilon_6 + (1-\epsilon_6)(1-p_7)\{\epsilon_7+(1-\epsilon_7)(1-p_8)\}]$

"sampling" and vital parameters are both explicit! (closer to generating process of the data)

We have detection histories – now what?

$\Pr(\text{eh} = 0\ 0\ 1\ 0\ 1\ 1\ 0\ 0) =$

$(1-\varepsilon_3)(1-p_4) (1-\varepsilon_4)p_5 (1-\varepsilon_5)p_6 [\varepsilon_6 + (1-\varepsilon_6)(1-p_7)\{\varepsilon_7+(1-\varepsilon_7)(1-p_8)\}]= H1$

Likelihood (parameters | data) = $H_1^{\text{No. cases}}$ $H_2^{\text{No. cases}}$ $H_x^{\text{No. cases}}$

0001010010	10
0010001101	3
0101010100	4
1001000000	18
0001010111	2
0011101000	1
	3
	No. cases

Maximum likelihood estimation

- statistical approach for estimating the parameters of a model
- parameters are chosen to maximize the likelihood for the assumed model given the data

So do to MLE, we have to

- assume a model (e.g. data generating process) for the data in questions
- derive the likelihood function for our data, given our assumed model

- The event of falling right
- The event of falling left
- The falling : call it y
- There are only two discrete values for y , 1 or 0 (right and left)
- What's the probability of fall left? Or right?



The Data

I	y	what
1	0	L
2	1	R
3	1	R
4	0	L
5	0	L
6	1	R
7	1	R
8	1	R
9	0	L
10	0	L



Probability mass function (PMF) for Bernoulli: $p^{y_i}(1 - p)^{1-y_i}$

$$y_i = 0$$

Negative outcome - falling left

$$y_i = 1$$

Positive outcome - falling right

PMF Example :

if $y_i = 1$, and $p = 0.5$

$$p^{y_i}(1 - p)^{1-y_i}$$

$$0.5^1(1 - 0.5)^{1-1} = 0.5$$

The likelihood function is the joint probability distribution (multiplication) of the PMFs for each observation. We are simply multiplying all the PMFs together

$$p^{y_1}(1 - p)^{1-y_1} \cdot p^{y_2}(1 - p)^{1-y_2} \dots \cdot p^{y_n}(1 - p)^{1-y_n}$$

joint probability distribution



$$L(\theta) = \prod_{i=1}^n p^{y_i} (1-p)^{1-y_i}$$

likelihood function

We want to maximize this function. Rather than doing calculus to figure this out, let's play around with different values of p to see how it affects the likelihood. You can try it out using [this workbook](#) (tab: fair_coin).

p=0.3				p=0.5				p=0.7			
i	y	p(y)	PMF(y)	i	y	p(y)	PMF(y)	i	y	p(y)	PMF(y)
1	0	0.3	0.7	1	0	0.5	0.5	1	0	0.7	0.3
2	0	0.3	0.7	2	0	0.5	0.5	2	0	0.7	0.3
3	0	0.3	0.7	3	0	0.5	0.5	3	0	0.7	0.3
4	1	0.3	0.3	4	1	0.5	0.5	4	1	0.7	0.7
5	1	0.3	0.3	5	1	0.5	0.5	5	1	0.7	0.7
6	0	0.3	0.7	6	0	0.5	0.5	6	0	0.7	0.3
7	1	0.3	0.3	7	1	0.5	0.5	7	1	0.7	0.7
8	1	0.3	0.3	8	1	0.5	0.5	8	1	0.7	0.7
9	1	0.3	0.3	9	1	0.5	0.5	9	1	0.7	0.7
10	0	0.3	0.7	10	0	0.5	0.5	10	0	0.7	0.3
L=			0.0004	L=			0.0010	L=			0.0004

Likelihood of Detection histories

1. Estimate parameters (by maximizing the likelihood)
2. Estimate uncertainty in parameters
3. Compare models
 - e.g. same or different p 's or ε 's
 - e.g. with or without covariates (important factors that you think might influence p and ε)
 - i. Akaike Information Criteria, AIC
 - ii. classical hypothesis testing
 - iii. extendable to Bayesian approaches
4. Good statistical properties

Assumptions of the CJS model

- 1. After initial encounters, detection/encounter probabilities are equal for all taxa in the data/group of interest**
- 2. After initial encounters, extinction probabilities for all taxa are equal**
- 3. Sampling intervals are short relative to the time over which extinction is to be estimated**
- 4. The fate of each taxon (with respect to extinction and encounter) is independent of the fate of every other taxon**

Assumptions of the CJS model

1. After initial encounters, detection/encounter probabilities are equal for all taxa in the data/group of interest
 - Taxon specific covariates
2. After initial encounters, extinction probabilities for all taxa are equal
3. Sampling intervals are short relative to the time over which extinction is to be estimated
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Assumptions of the CJS model

1. After initial encounters, detection/encounter probabilities are equal for all taxa in the data/group of interest
2. After initial encounters, extinction probabilities for all taxa are equal
3. **Sampling intervals are short relative to the time over which extinction is to be estimated**
 - **Simulations show that this is not a big problem; other models (e.g. robust design models, never applied in paleo) tackle this head-on**
4. The fate of each taxon (with respect to extinction and encounter) is independent of the fate of every other taxon

Assumptions of the CJS model

1. After initial encounters, detection/encounter probabilities are equal for all taxa in the data/group of interest
2. After initial encounters, extinction probabilities for all taxa are equal
3. Sampling intervals are short relative to the time over which extinction is to be estimated
4. The fate of each taxon (with respect to extinction and encounter) is independent of the fate of every other taxon
 - Corrections for over-dispersion
 - Co-occurrence analyses

Covariate modeling

- A way to include factors or variables that may be important in explaining variation in the parameters (e.g. extinction, sampling) you are interested in
- Allows us to compare models with different [or no] covariates (Model Comparison and Selection)
- models to compare
 - $\epsilon(\text{constant})p(\text{time-varying})$
 - $\epsilon(\text{time-varying})p(\text{sea-levels})$

Covariate modeling via link functions

$$\text{logit}(\varepsilon_{i,t}) = \log\left(\frac{\varepsilon_{i,t}}{1 - \varepsilon_{i,t}}\right) = \beta_0 + \beta_1 x_i + \beta_2 y_t$$

Taxon specific covariates

- size
- minerology
- taxonomic group

Covariate modeling via link functions

$$\text{logit}(\varepsilon_{i,t}) = \log\left(\frac{\varepsilon_{i,t}}{1 - \varepsilon_{i,t}}\right) = \beta_0 + \beta_1 x_i + \beta_2 y_t$$

Time specific covariates

- Duration of bin
- Sea-level
- Temperature

Covariate modeling via link functions

$$\text{logit}(\varepsilon_{i,t}) = \log\left(\frac{\varepsilon_{i,t}}{1 - \varepsilon_{i,t}}\right) = \boxed{\beta_0} + \boxed{\beta_1}x_i + \boxed{\beta_2}y_t$$

$$\varepsilon_{i,t} = \frac{e^{\boxed{\beta_0} + \boxed{\beta_1}x_i + \boxed{\beta_2}y_t}}{1 + e^{\boxed{\beta_0} + \boxed{\beta_1}x_i + \boxed{\beta_2}y_t}}$$

“Some simple rules of thumb are often useful in assessing the relative merits of models in the set: Models having $\Delta i \leq 2$ have substantial support (evidence), those in which $4 \leq \Delta i \leq 7$ have considerably less support, and models having $\Delta i > 10$ have essentially no support.” Burnham & Anderson 2004 – see dAIC

$$\Delta_i(AIC) = AIC_i - \min(AIC)$$

$$L \propto \exp\left(-\frac{1}{2}\Delta_i(AIC)\right)$$

$$AIC = -2 \ln(L) + 2k$$

$$w_i(AIC) = \frac{\exp\left(-\frac{1}{2}\Delta_i(AIC)\right)}{\sum_{k=1}^K \exp\left(-\frac{1}{2}\Delta_k(AIC)\right)}$$

	Model	Npar (k)	Rank	logLik (L)	AIC	AICc	dAIC	AICwt
Model A	p~1 phi~1	2	2	-333	670	671	0	0.79
Model B	p~1 phi~t	7	7	-330	673	676	2.9	0.19
Model C	p~t phi~1	7	7	-332	678	678	7.6	0.02
Model D	p~t phi~t	12	12	-328	681	688	10.1	0.00

Model selection is cool, but don't stop there

Look at your parameter estimates and check if they make sense!

Why Capture-Mark-Recapture (CMR) ?

- Detection probability
- Separating between
 - probability of detection (given presence)
 - probability of the parameters in question
(e.g. survivorship, origination, occupancy, immigration)
and derived parameters such as species richness/diversity

The probability of detection or sampling is sometimes only a nuisance but sometimes interesting in itself.

- Covariates can be EASILY included in models for both vital parameters and sampling/detection estimates.
- Covariates can be modeled at a variety of levels (e.g. group factors, individual traits, temporal characteristics)

Chapters in MARK book most relevant (if not using MARK)

- Chapter 1 (introduction)
- Chapter 4 (dipper example, but skip the MARK specific bits)
- Chapter 5 (goodness of fit –not covered in lectures but important)
- Chapter 6 (more on covariates and link functions)
- Chapter 11 (individual covariates)
- Chapter 12 (Pradel) and 13 (JS models in general)

<http://www.phidot.org/software/mark/docs/book/>

Some newer fossil papers using CMR (but oldies are goodies too)

- Schachat et al. **2021**. A Cretaceous peak in family-level insect diversity estimated with mark–recapture methodology. *Proceedings of the Royal Society, B* 286:20192054.
- Monarrez et al. **2021** Mass extinctions alter extinction and origination dynamics with respect to body size *Proceedings of the Royal Society, B* <https://doi.org/10.1098/rspb.2021.1681>
- Cohen et al. **2022** Plio-Pleistocene environmental variability in Africa and its implications for mammalian evolution, *PNAS* 119 (16) e2107393119
- Wilson et al. **2024**. Unveiling the underlying drivers of Phanerozoic marine diversification. *Proceedings of the Royal Society, B* 291: 20240165
- Leventhal S, Samuels-Fair M. **2025** Larval brooding correlated with high early origination rates in cheilostome Bryozoa. *Paleobiology*. 51(2):261-267