RMark Workshop

Spring 2024
February 27–29

What is RMark?

Program MARK is the most widely used software for analyzing data from marked individuals (capture-recapture data)

RMark is an R package that provides an interface between R and Program MARK

*These programs are much more than capture-recapture models; they allow us to conduct **population analysis** more generally*

What is Ecology?

A classical view: *the study of **distribution** & **abundance** and the mechanisms driving their change*

Two seminal textbooks in Ecology:

1. *The **Distribution** and **Abundance** of Animals* (Andrewartha and Birch, 1954)
2. *Ecology: The Experimental Analysis of **Distribution** & **Abundance*** (Krebs, 2001)

RMark Workshop – State Variables and Rate Parameters

RMark Workshop – State Variables and Rate Parameters

Abundance

dispersal

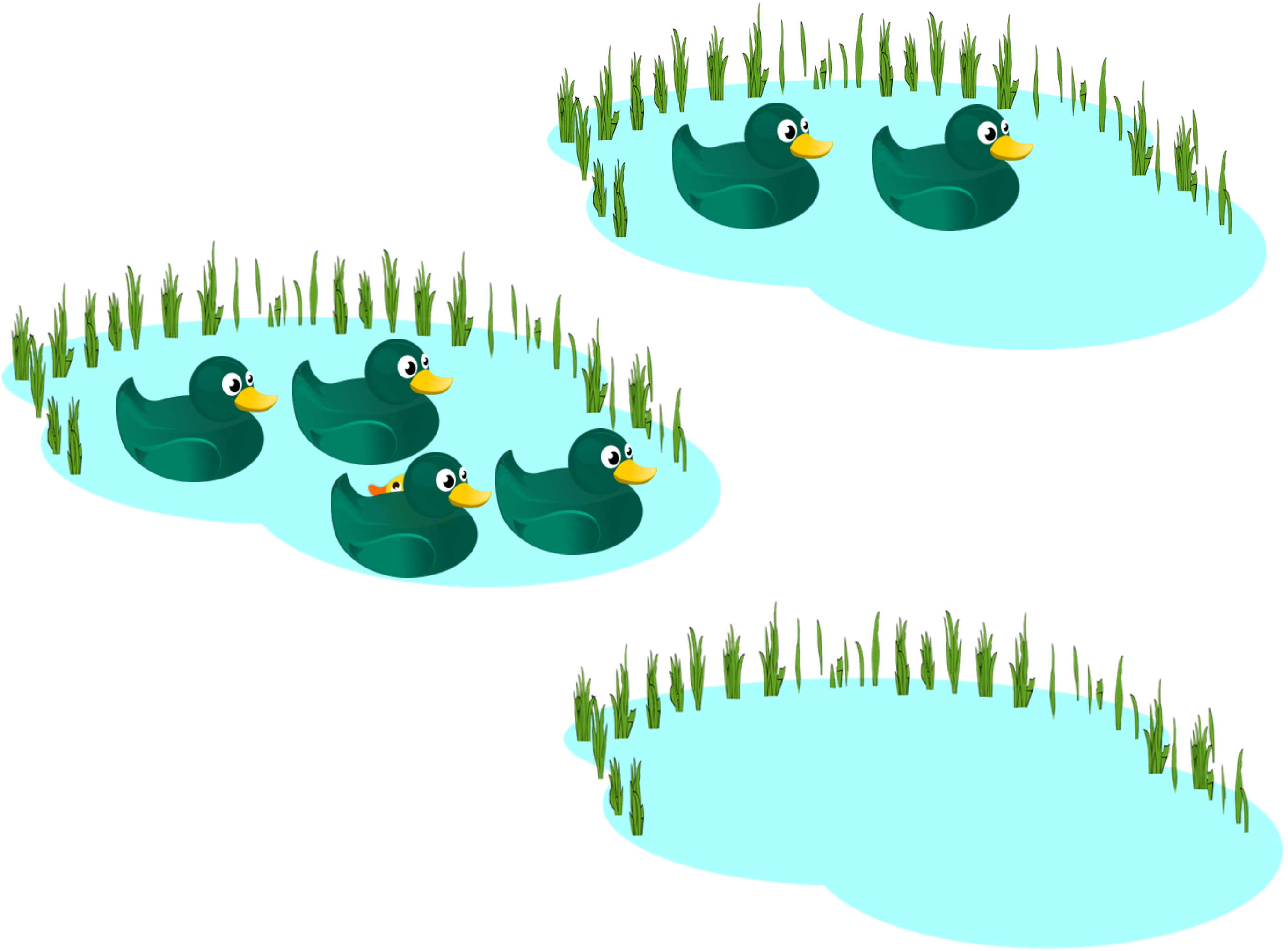
$$\Delta N = B - D + I - E$$

births — recruitment

deaths mortality — survival

immigration — settlement

emigration — departure



RMark Workshop – State Variables and Rate Parameters

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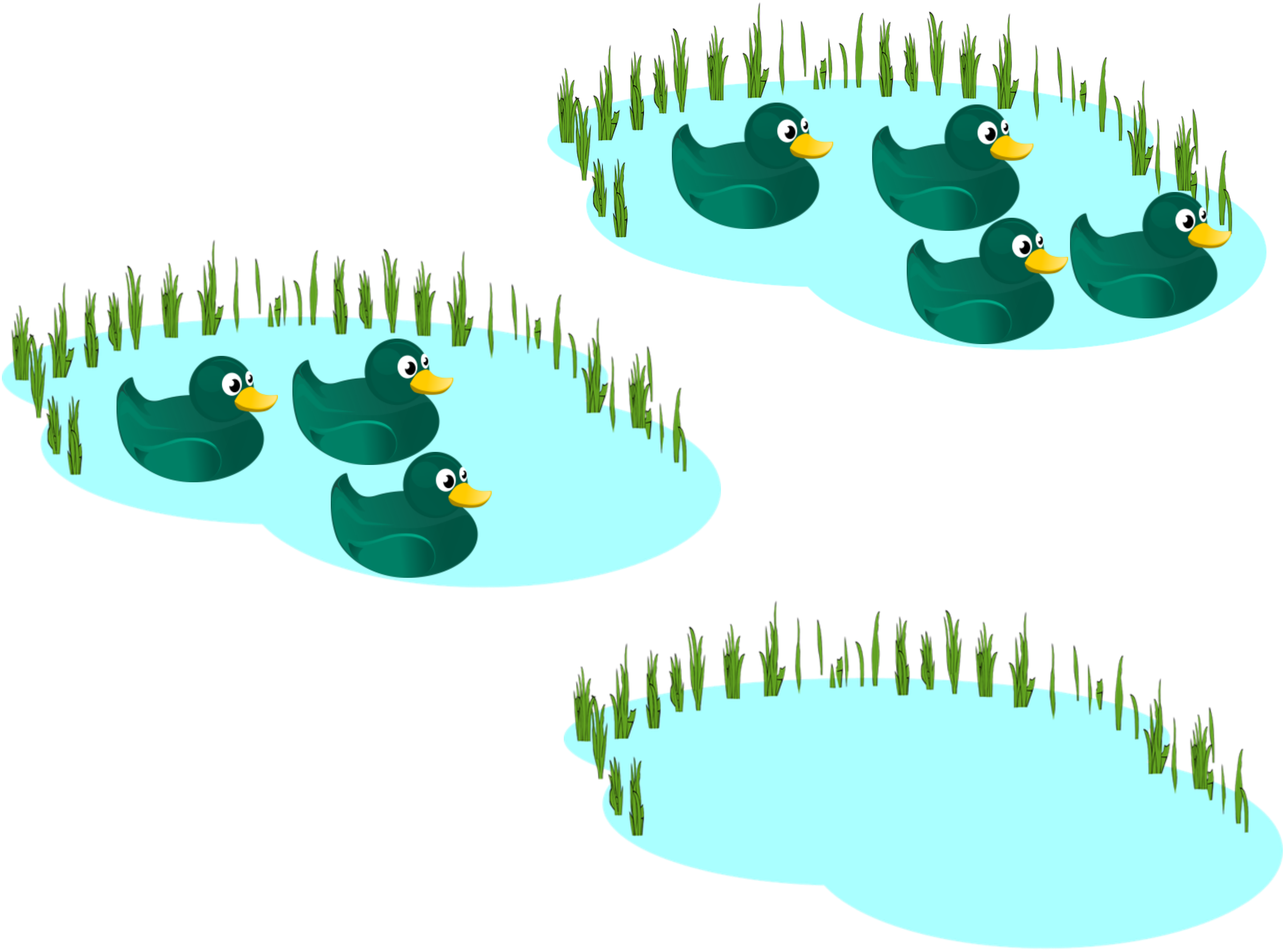

RMark Workshop – State Variables and Rate Parameters

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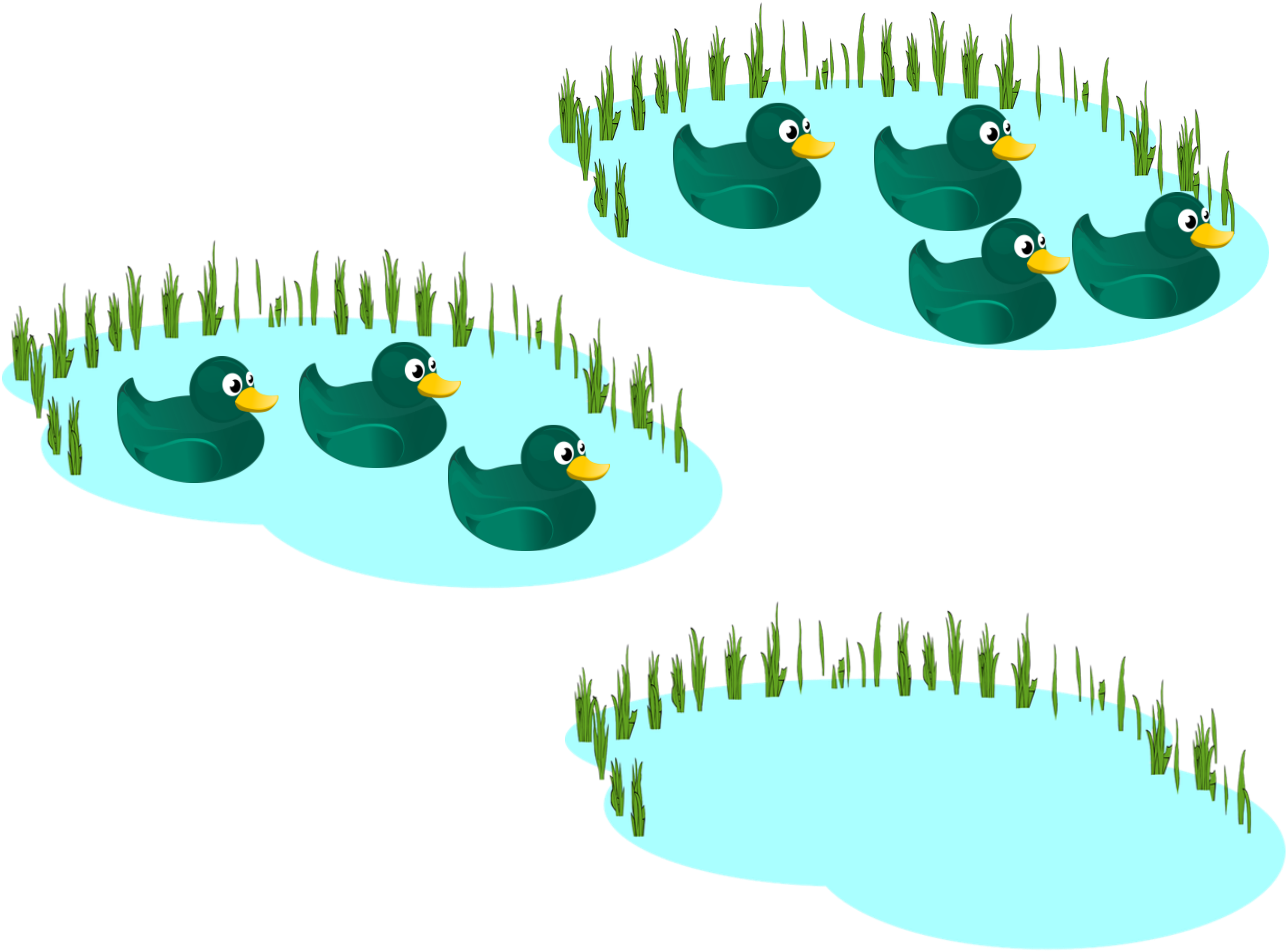

Distribution

RMark Workshop – State Variables and Rate Parameters

Abundance

dispersal

$$\Delta N = B - D + I - E$$

births | deaths mortality | immigration | emigration

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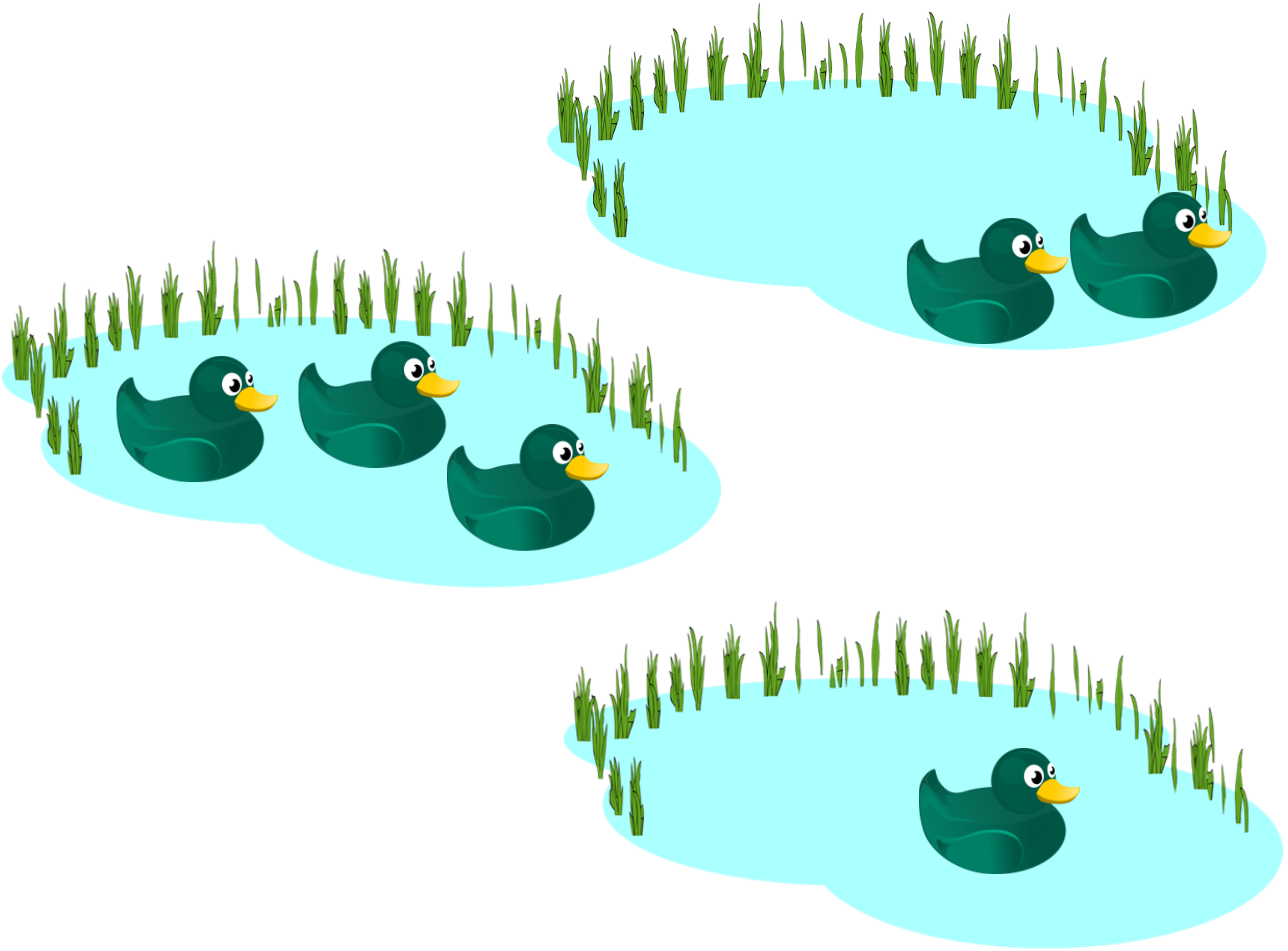
Occupancy

Occupied Site → Remain Occupied: Persistence

Occupied Site → Local Extinction: Extinction

Unoccupied Site → Remain Unoccupied: 1 - Colonization

Unoccupied Site → Become Colonized: Colonization



Population Analysis – Role in Ecology

Collectively, we call the study of these demographic quantities *population analysis*. Population analysis permeates a large part of ecology and of its applications such as conservation biology or fisheries and wildlife management. Indeed, it could be argued that population ecology, which we see as somewhat synonymous with population analysis, is a central pillar of the entire discipline of ecology.

Kéry and Schaub 2012

RMark Workshop – State Variables and Rate Parameters

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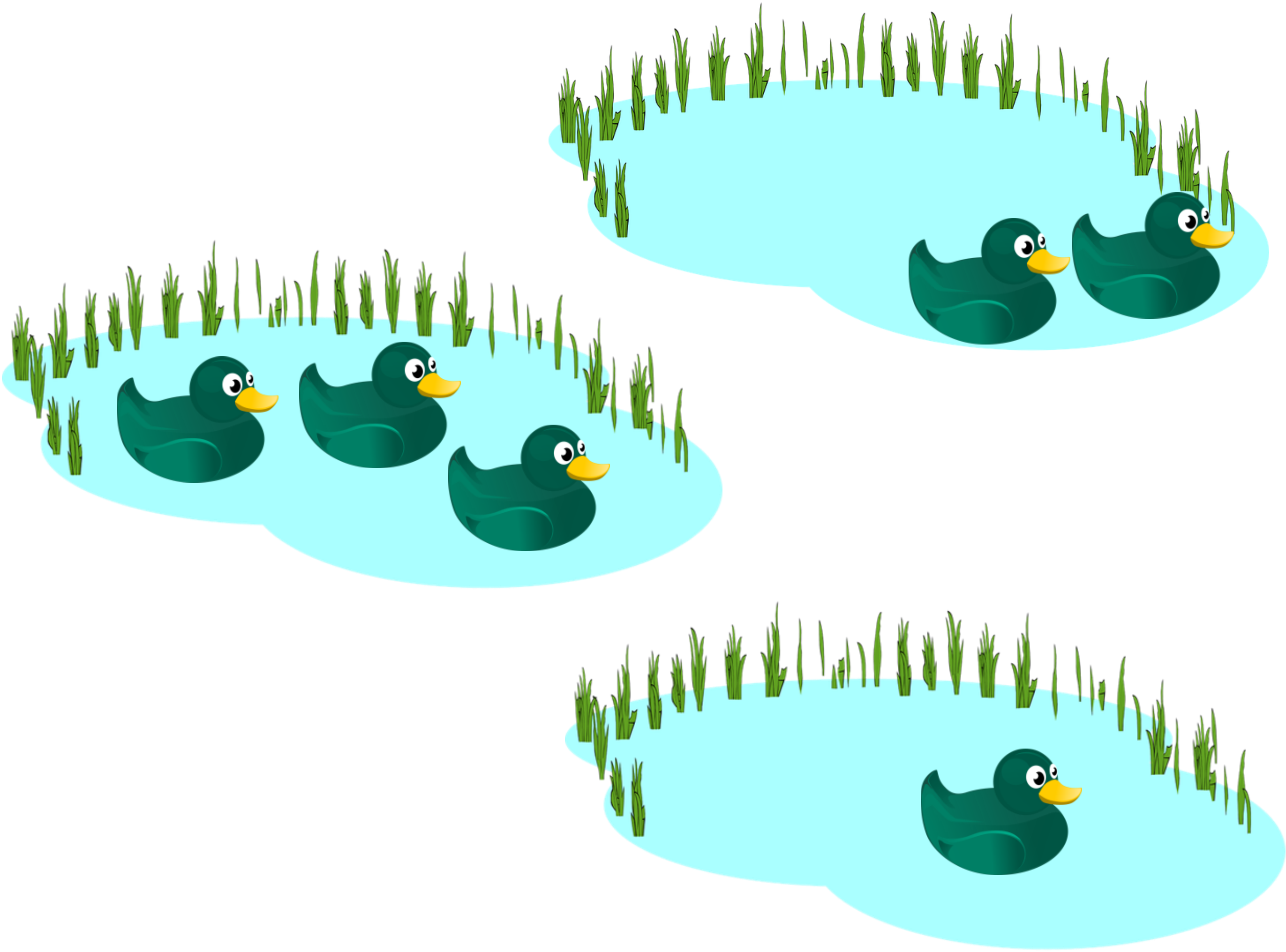

RMark Workshop – State Variables and Rate Parameters

State variables
- Occupancy
- Abundance

Vital rates
- Survival
- Recruitment
- Dispersal

-we will consider both <u>*marked*</u> and <u>*unmarked*</u> populations

-we will account for **imperfect detection** (explicitly model detection/capture probability)

RMark Workshop – Why account for detection probability?

- Animals are often not detected despite their presence
- Imperfect detection can be caused by survey methods, observers, or environmental variables

Raghu Chundawat

RMark Workshop – Why account for detection probability?

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Jialiang Gao

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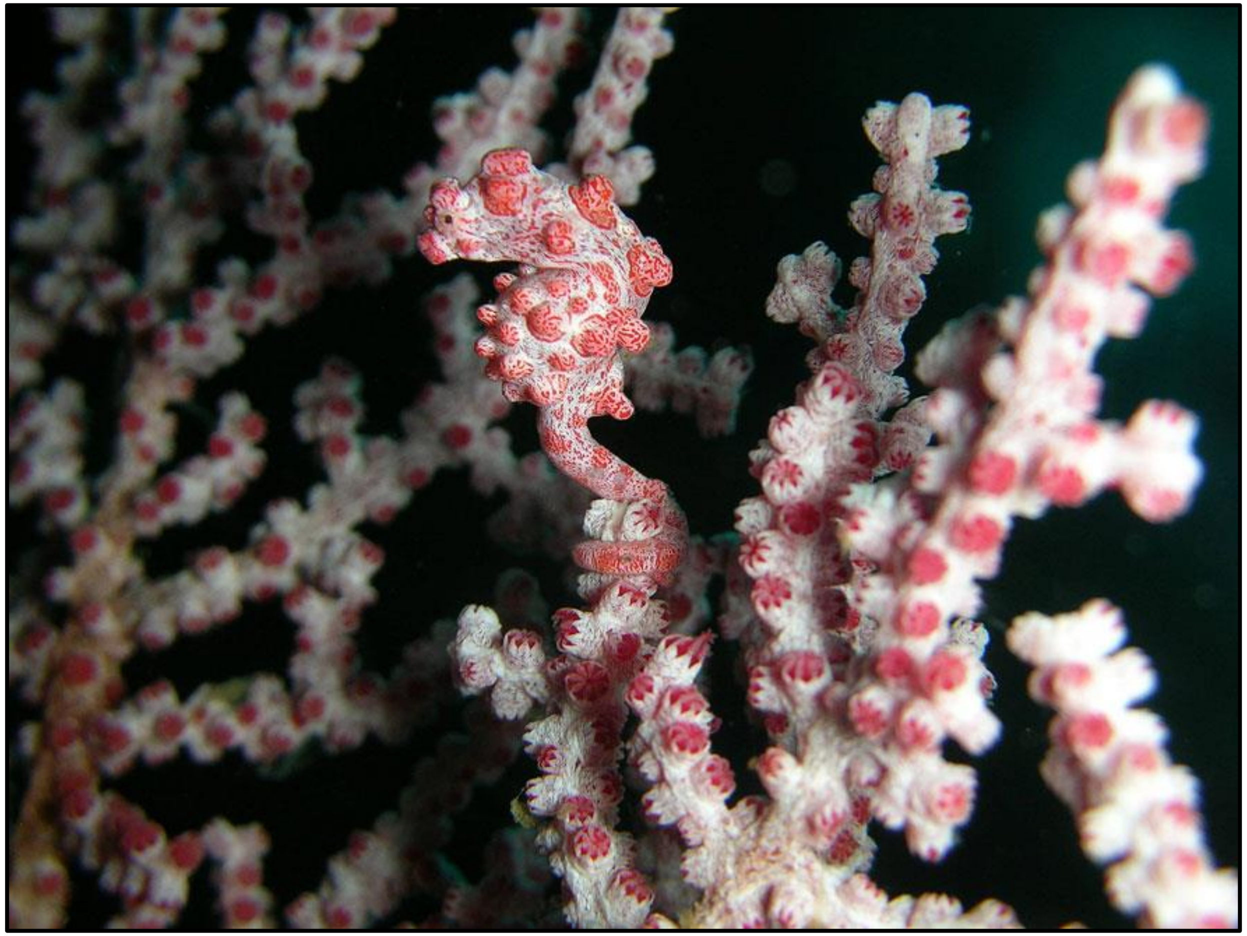

RMark Workshop – Why account for detection probability?

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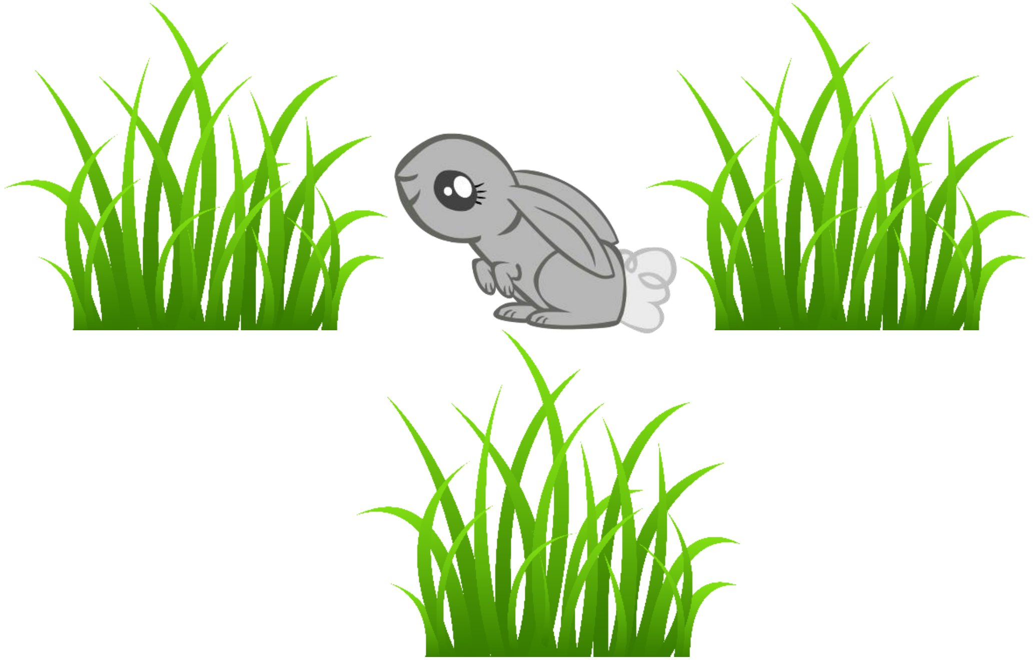
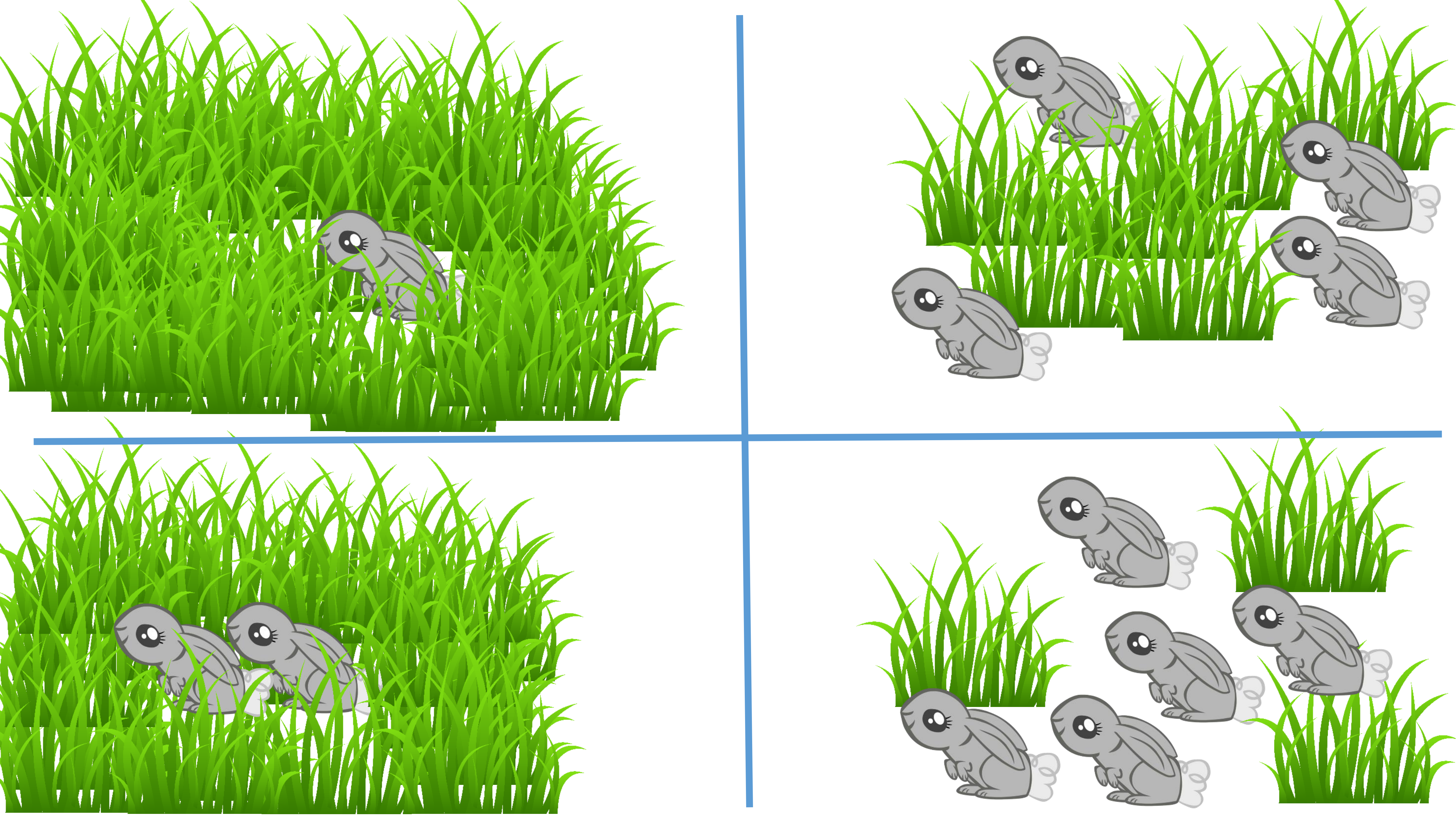
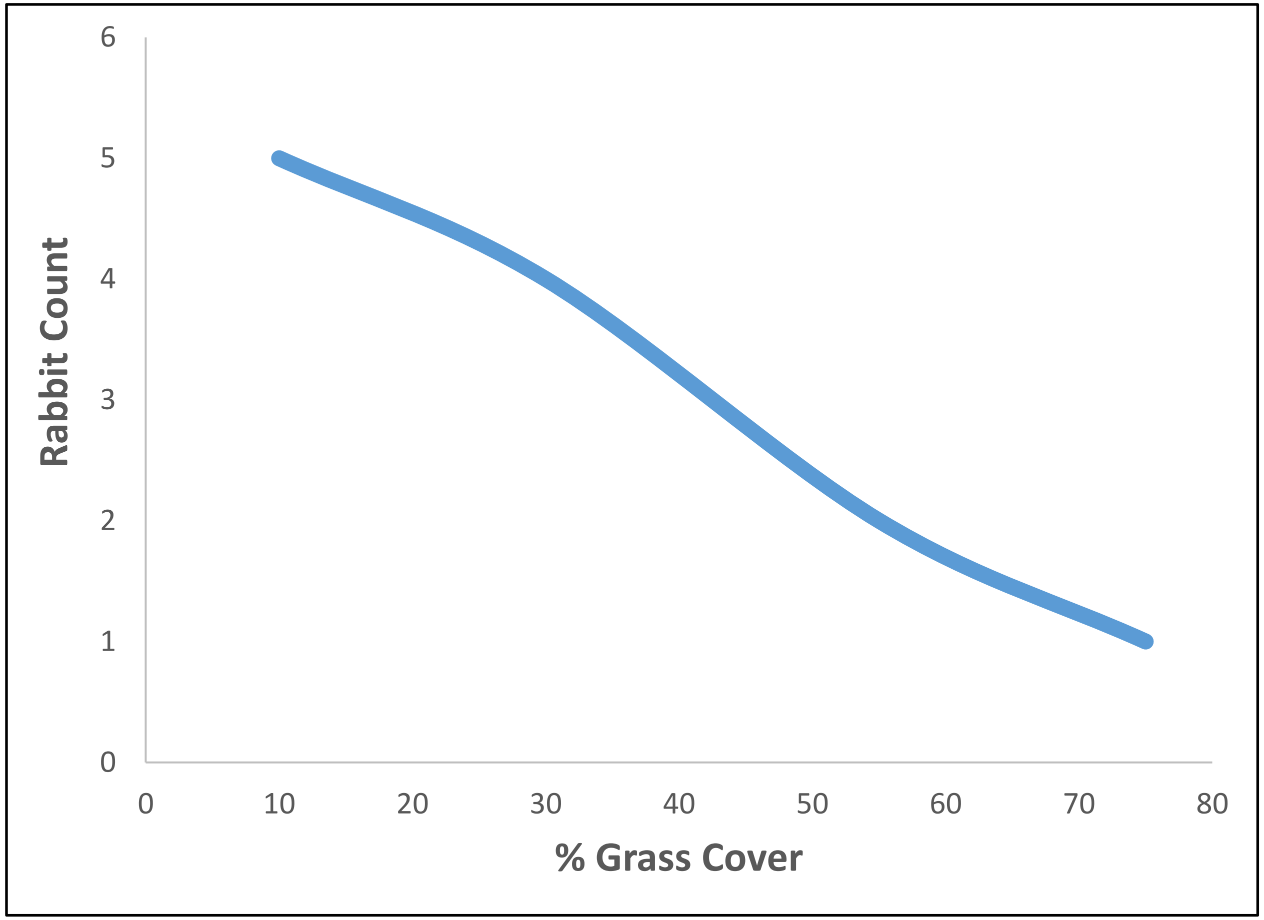
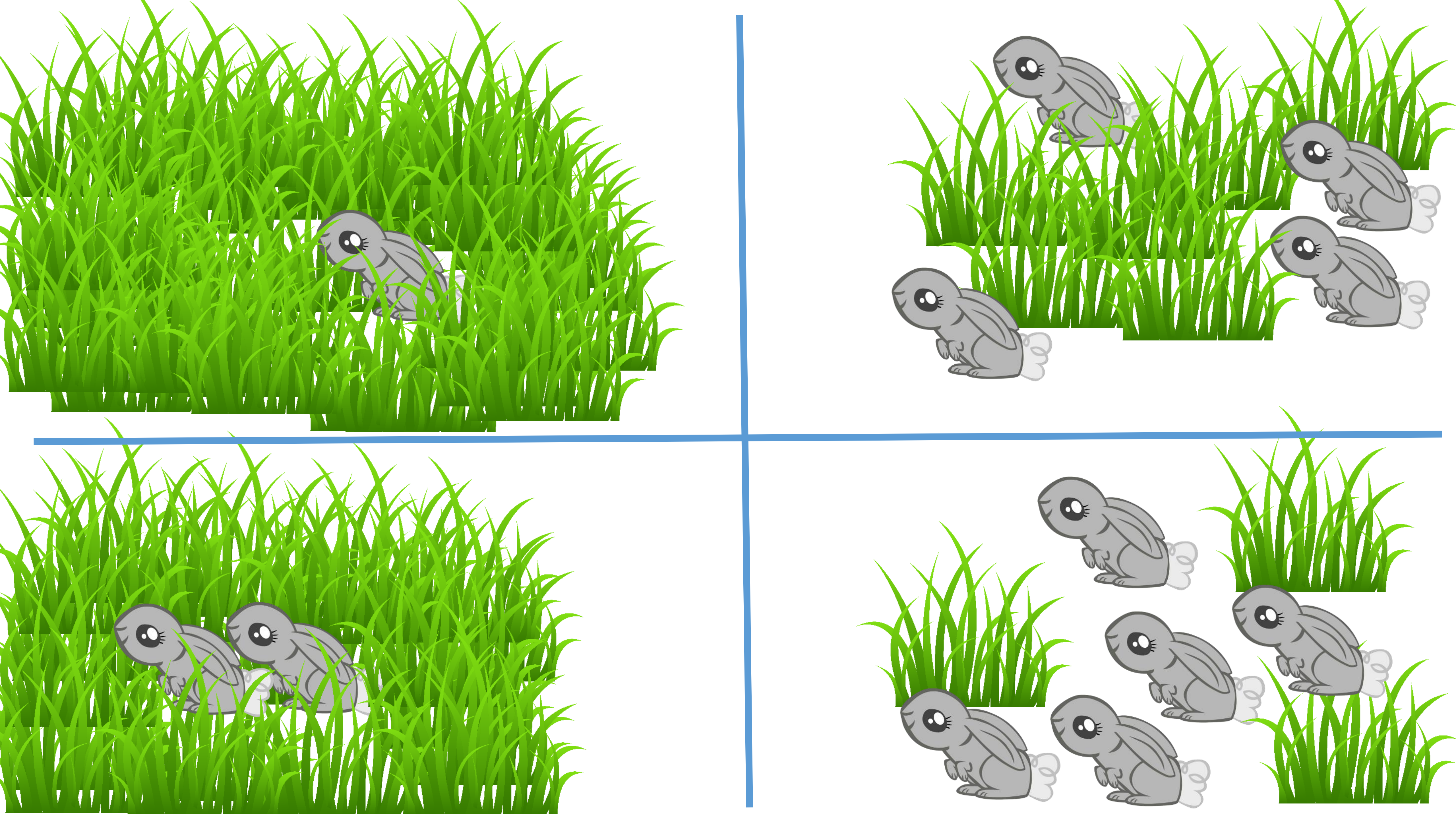
How does grass cover influence bunny rabbit **abundance**?

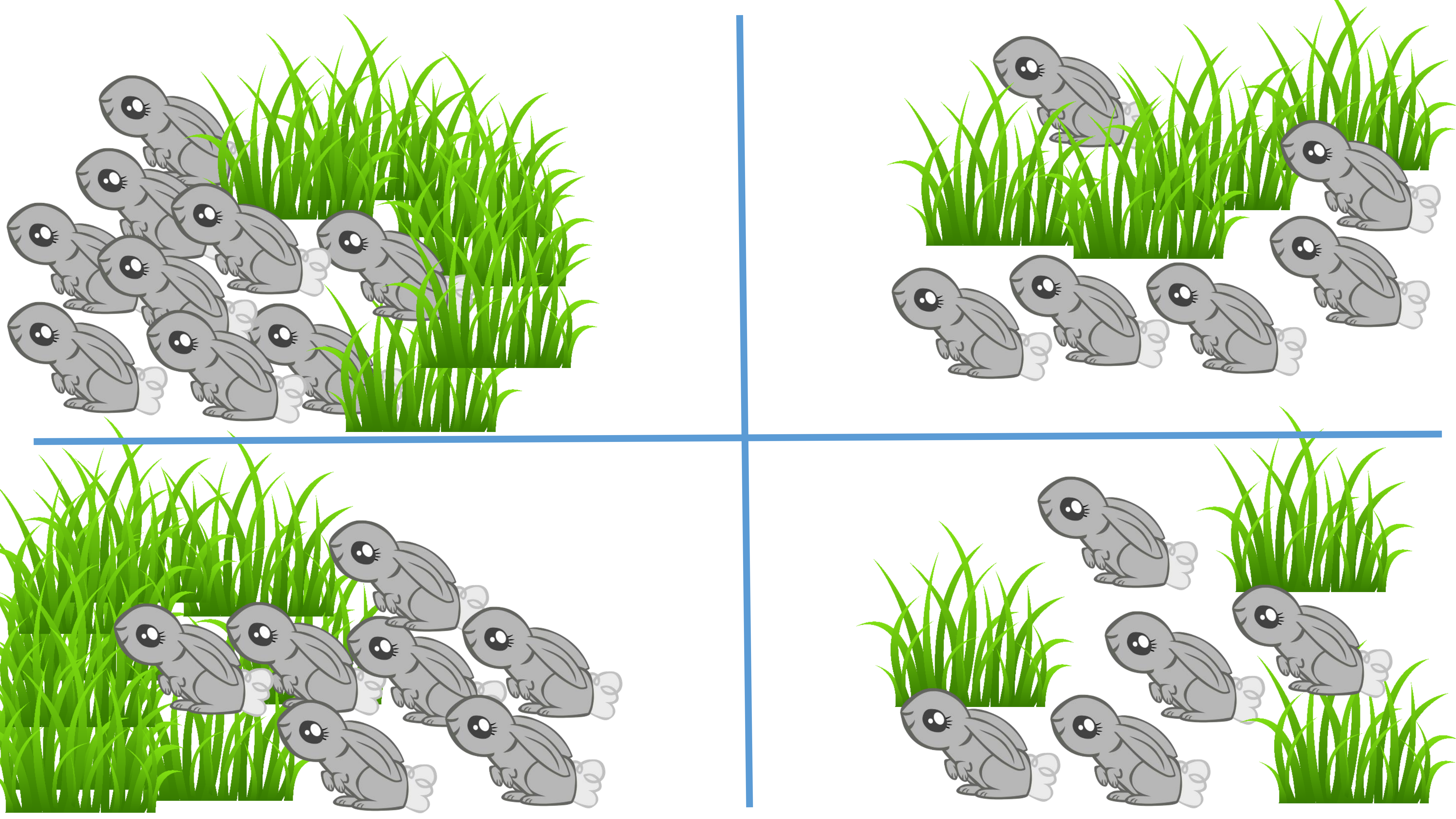






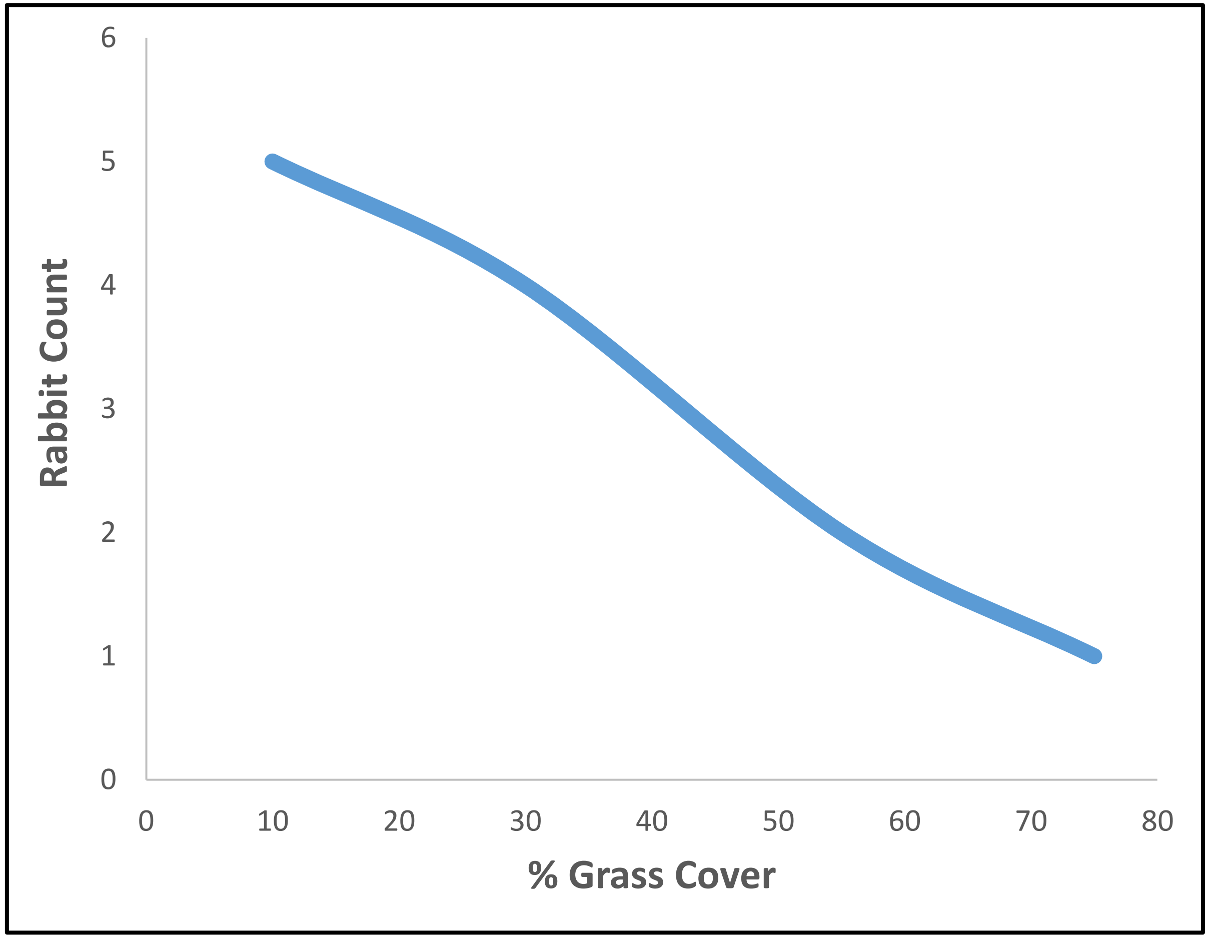
Rabbit Count
6
5
4
3
2
1
0
0
10
20
30
40
50
60
70
80
% Grass Cover



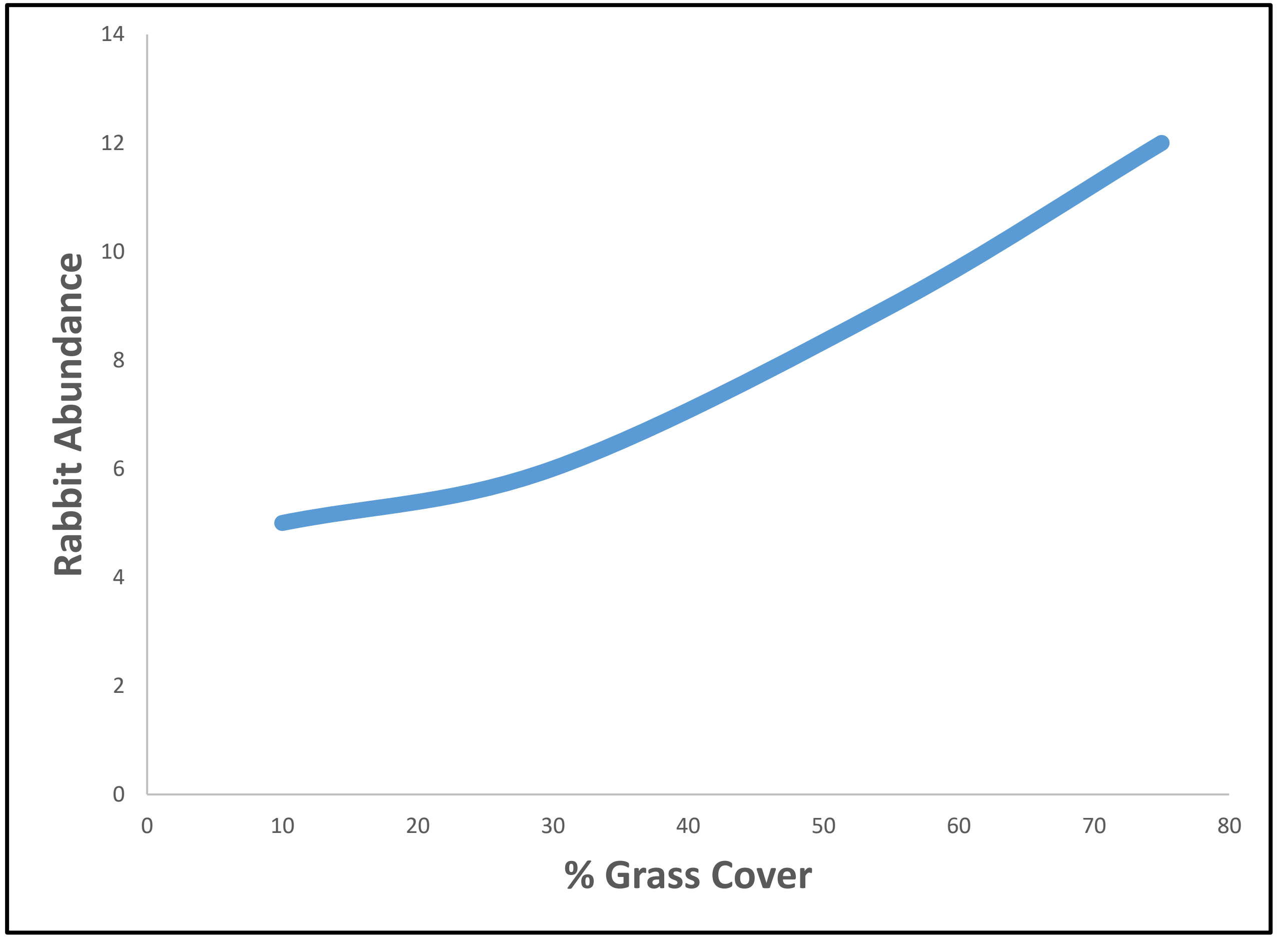


RMark Workshop – Imperfect Detection

Our Data



Reality



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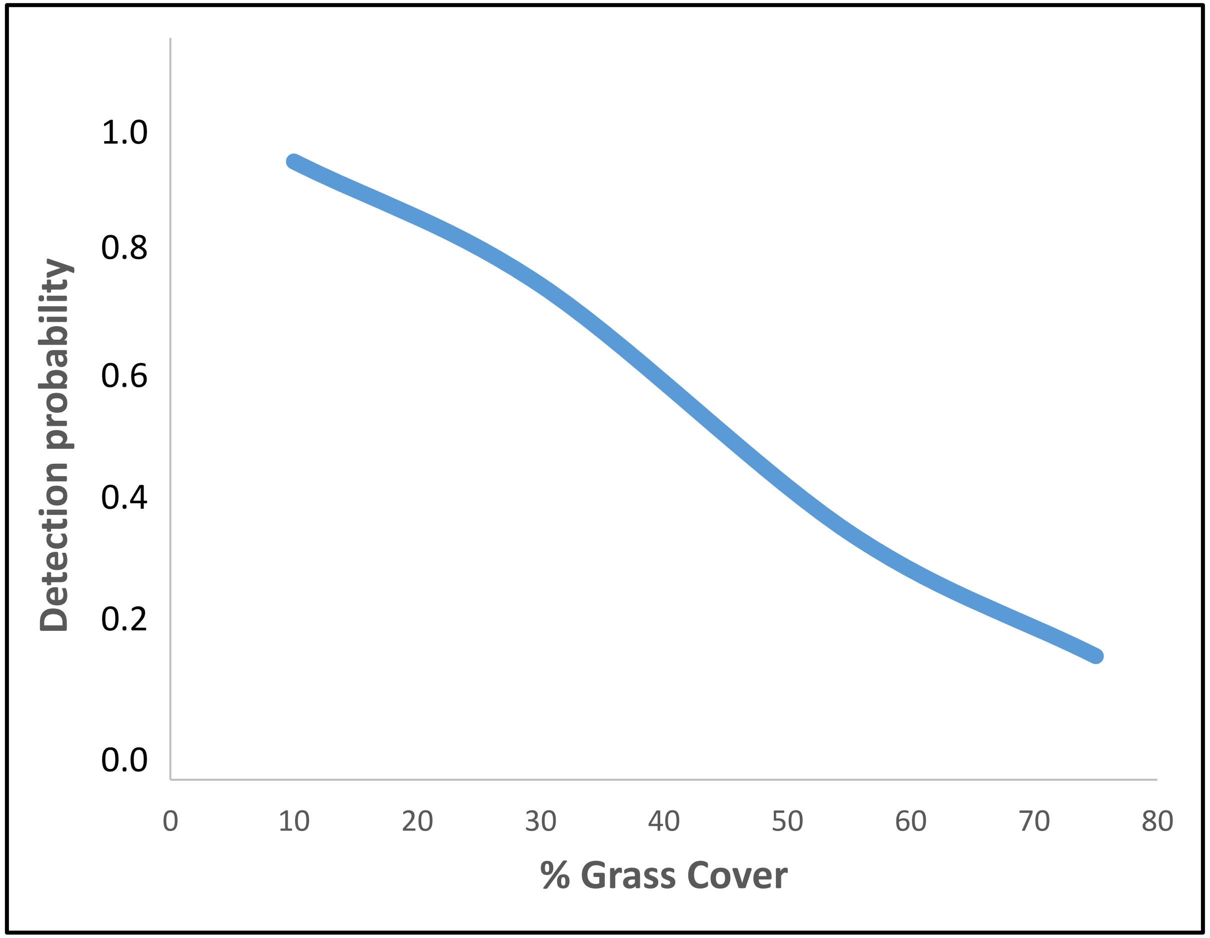

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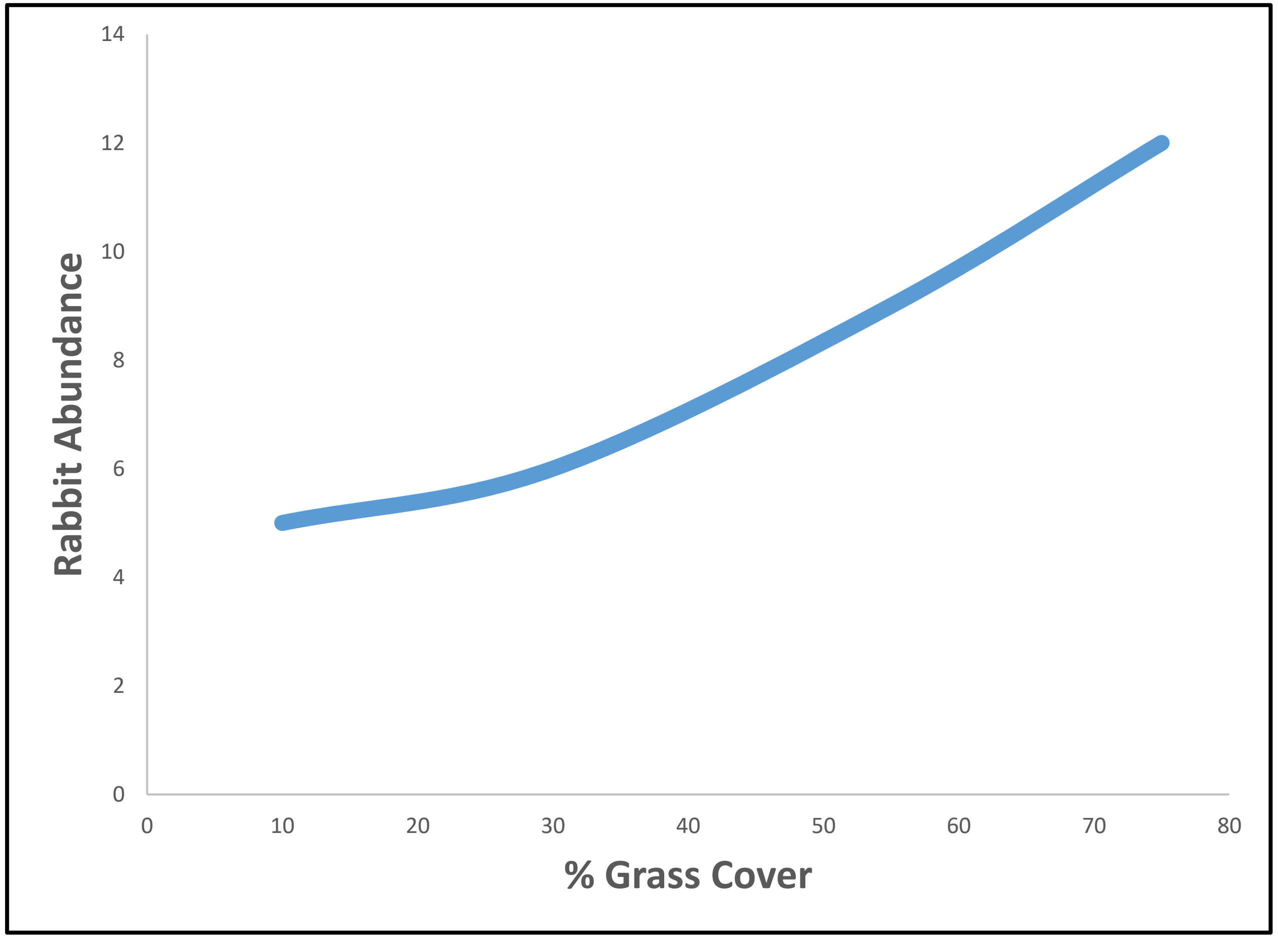

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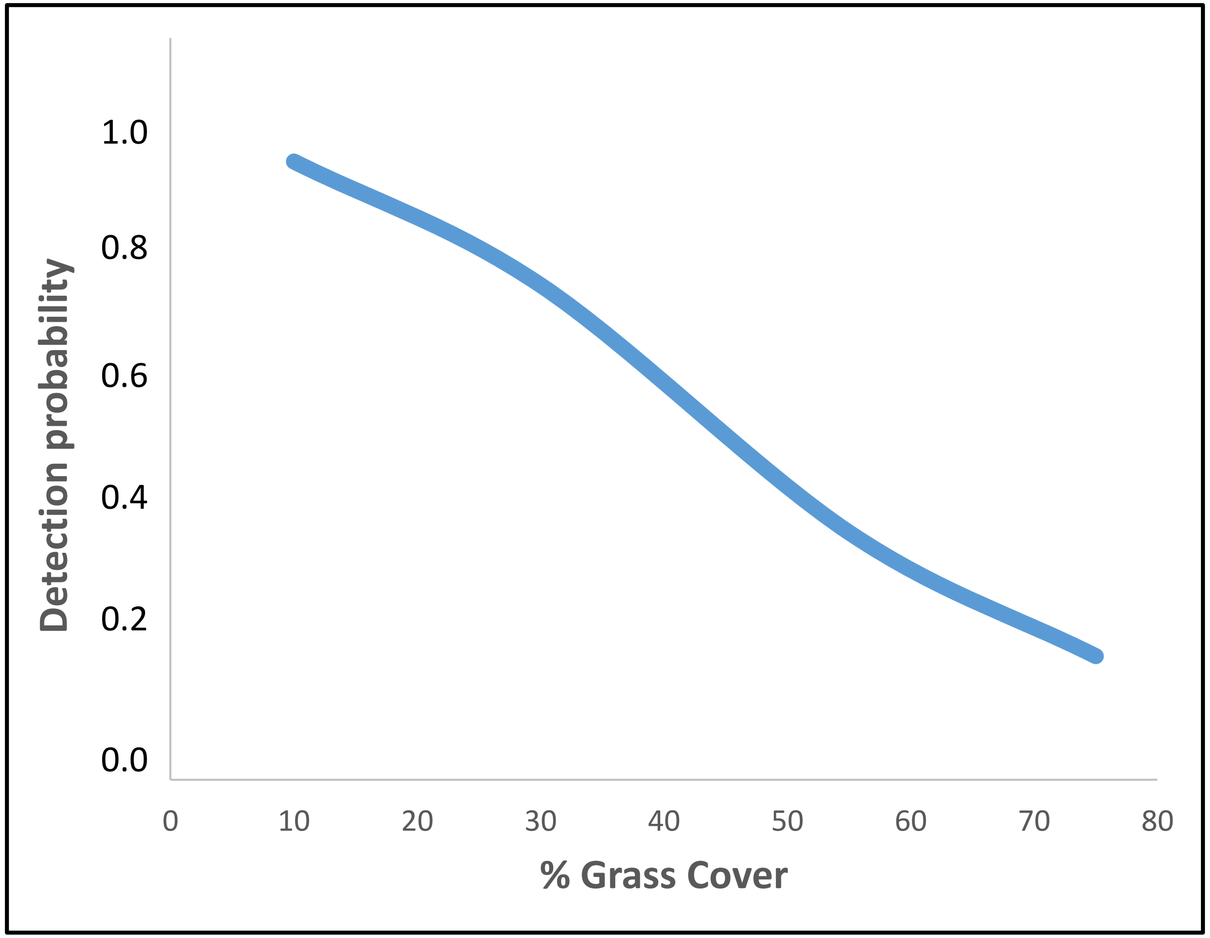

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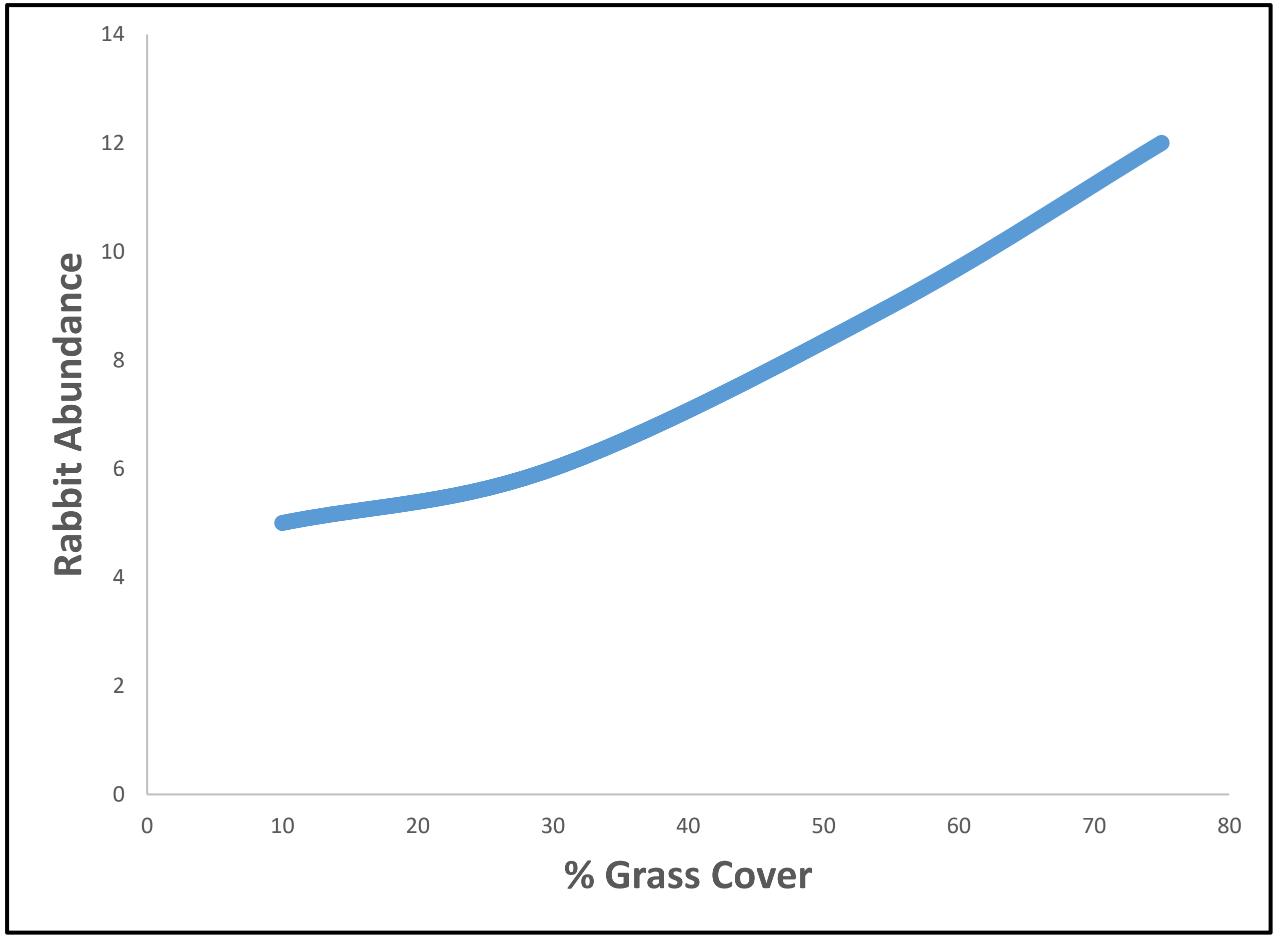
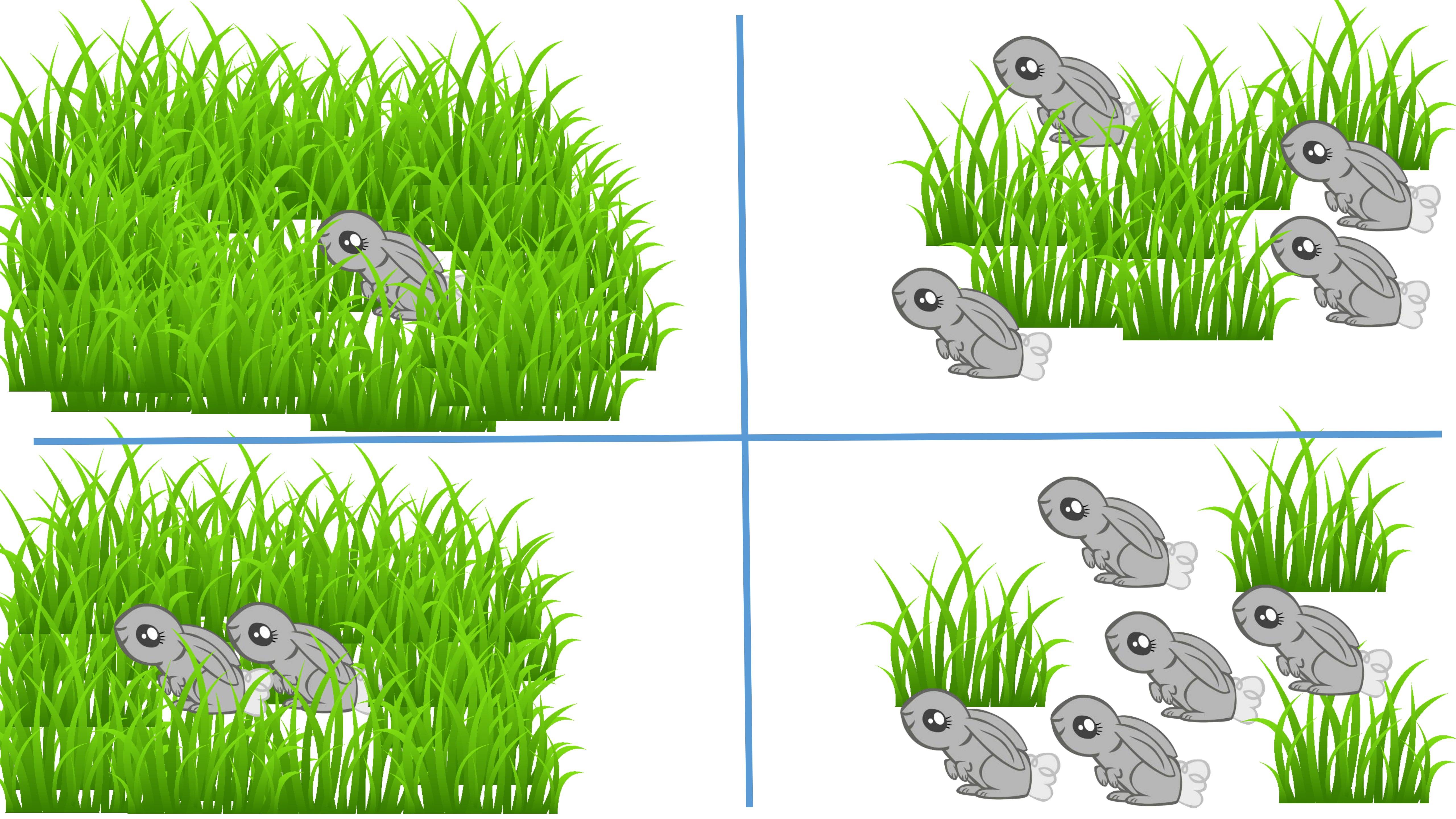
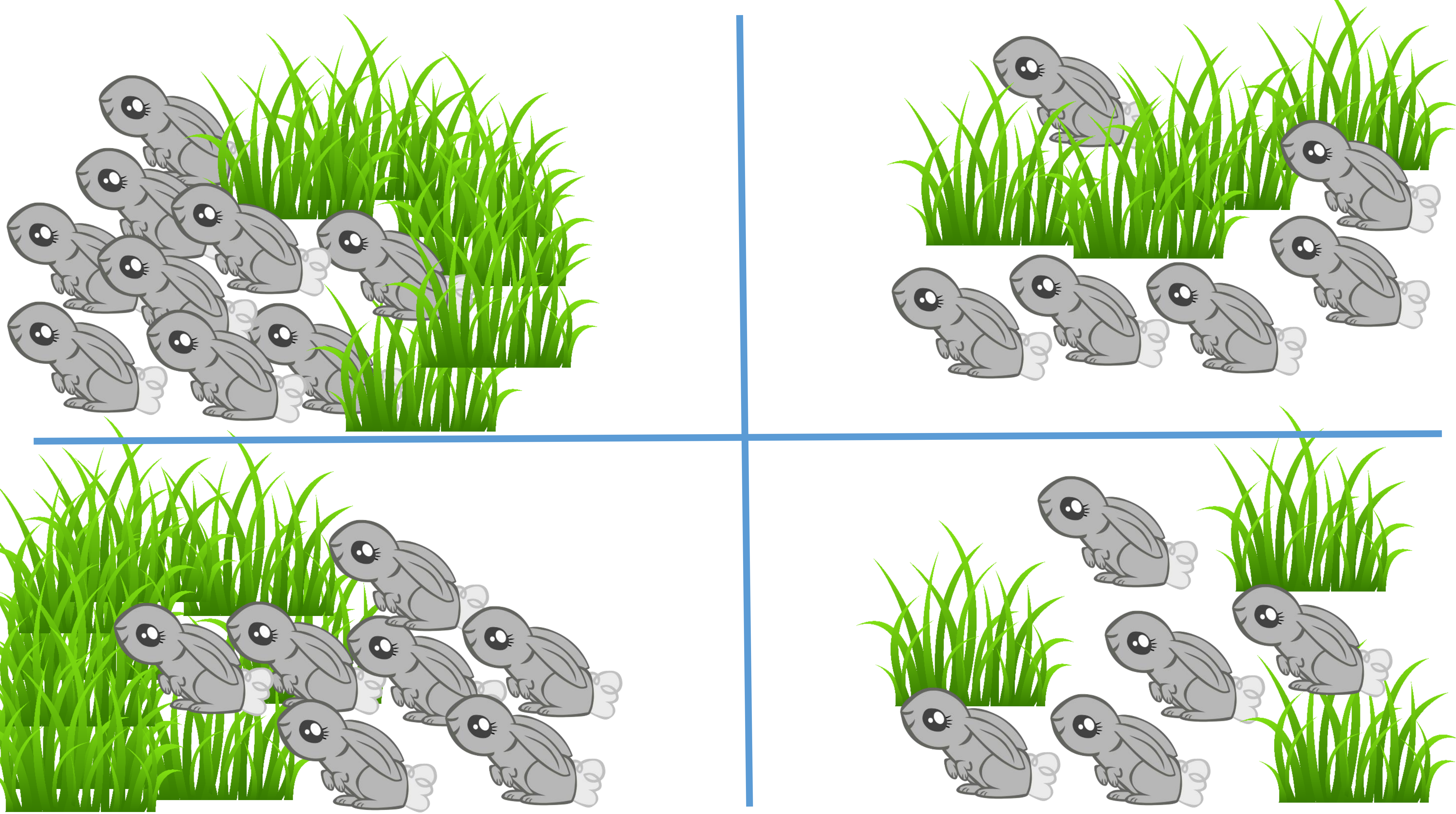


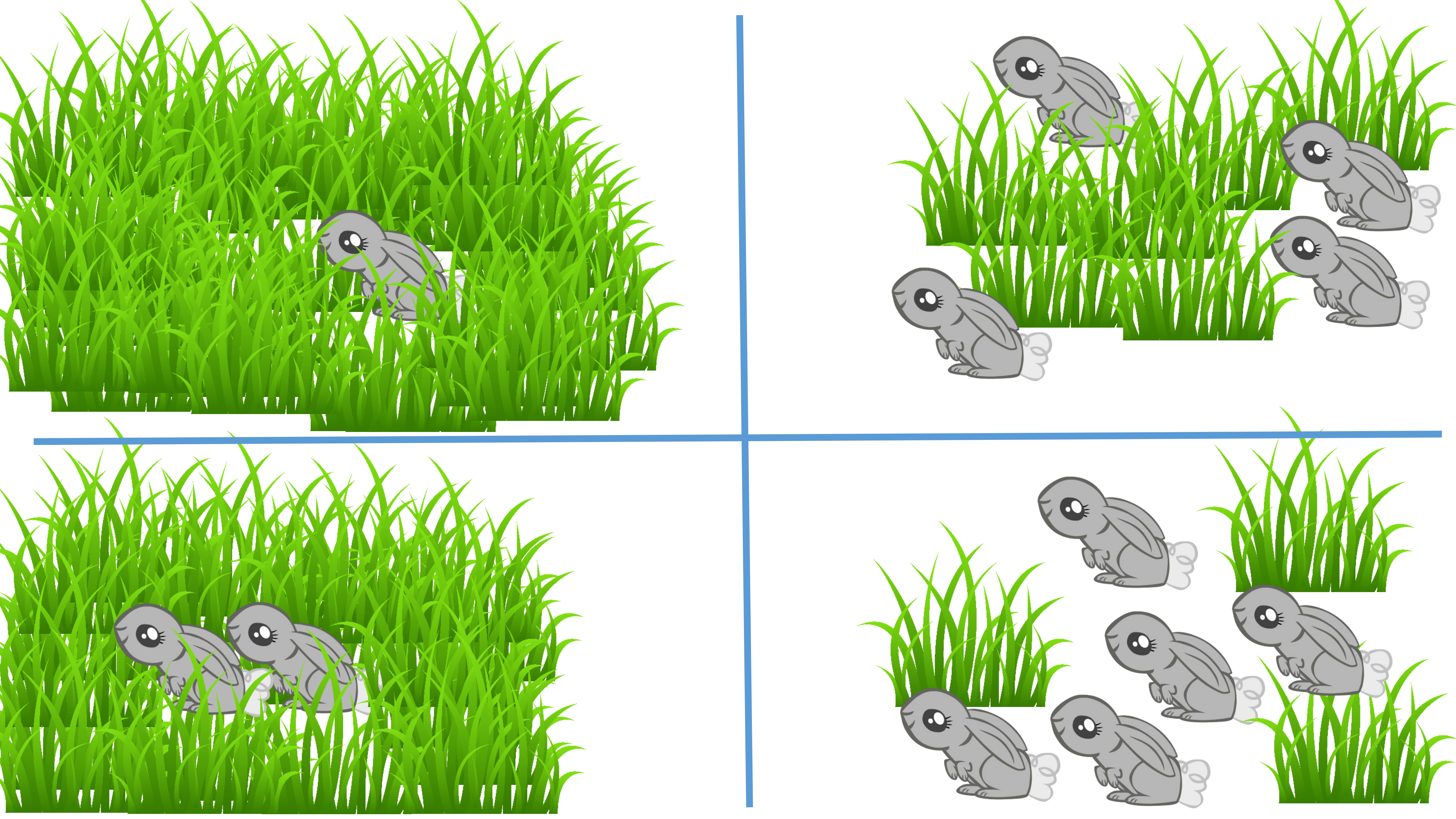
Count = true abundance * detection probability

$C = N * p$

$C / p = N$ $\quad\quad 10 / 0.5 = 20$







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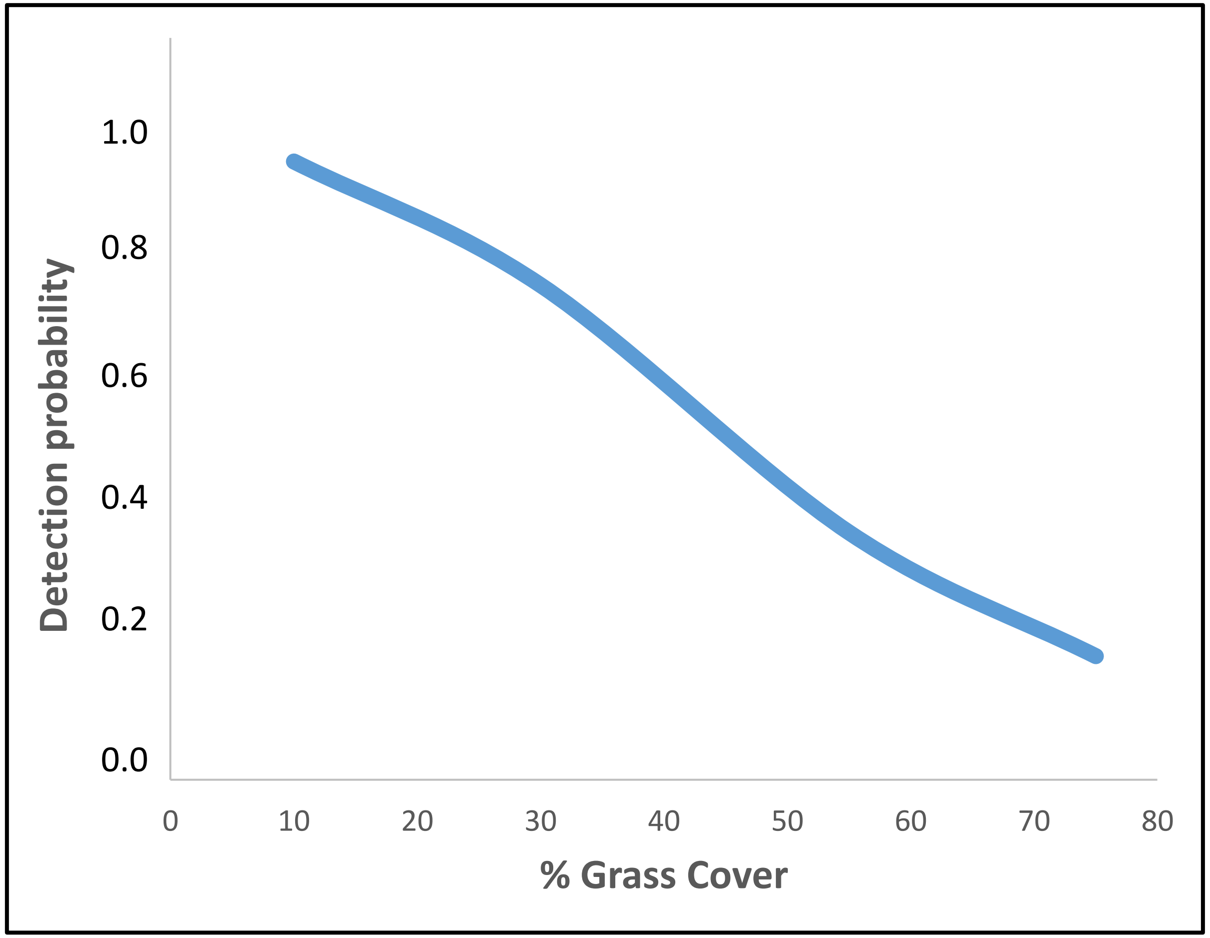

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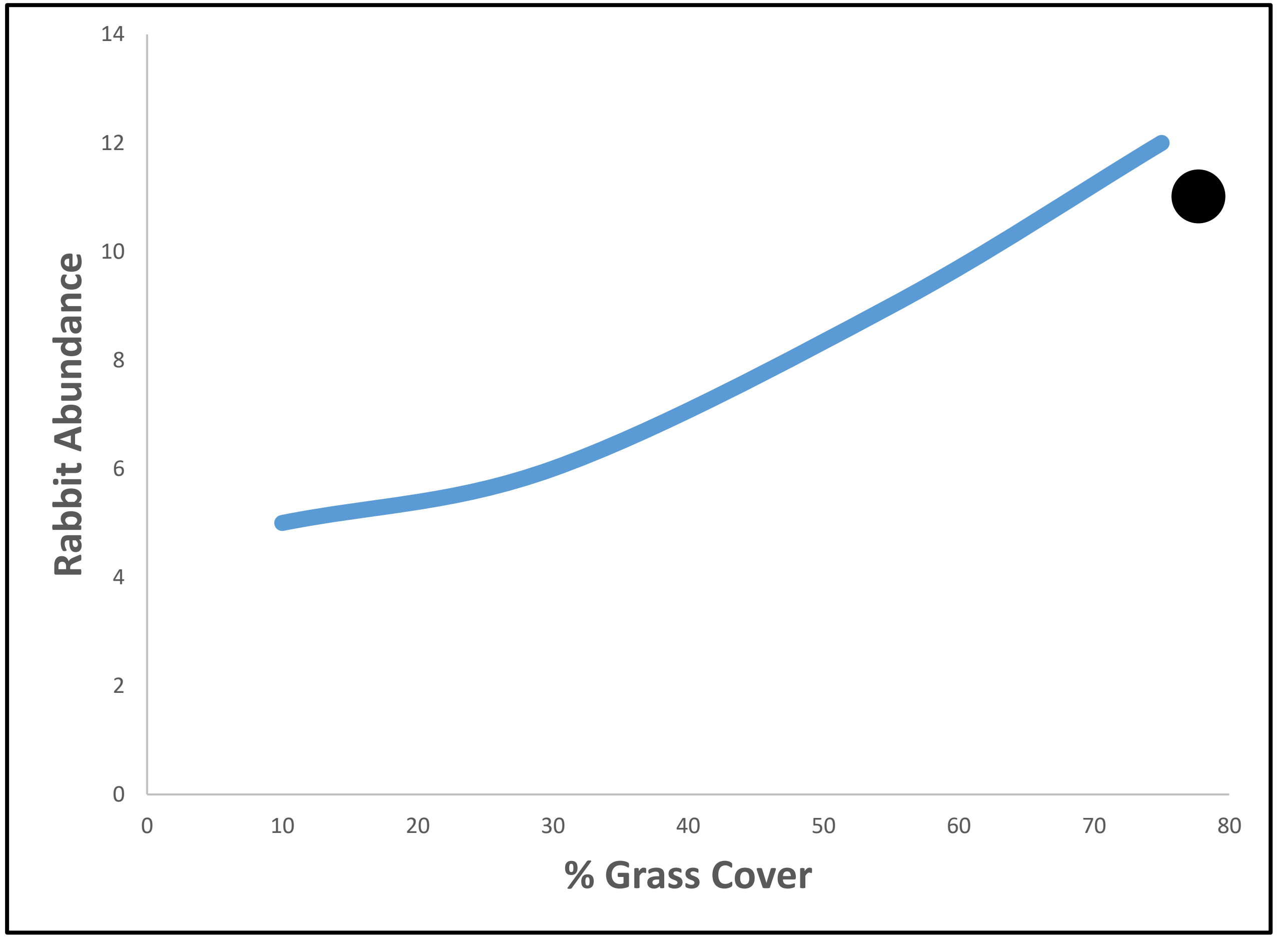
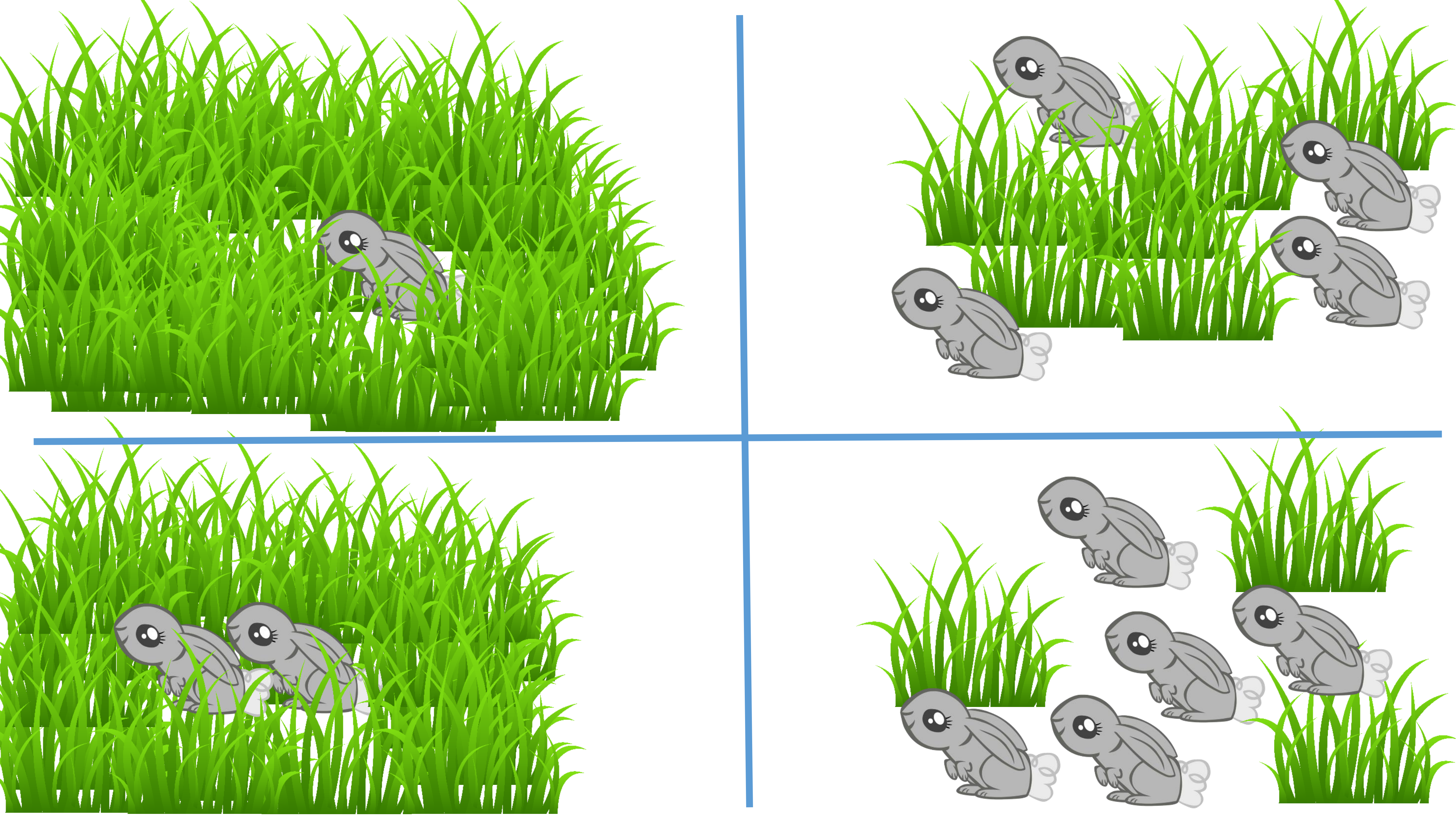


Count = true abundance * detection probability

$C = N * p$

$C / p = N$ 1 / 0.1 = **10**



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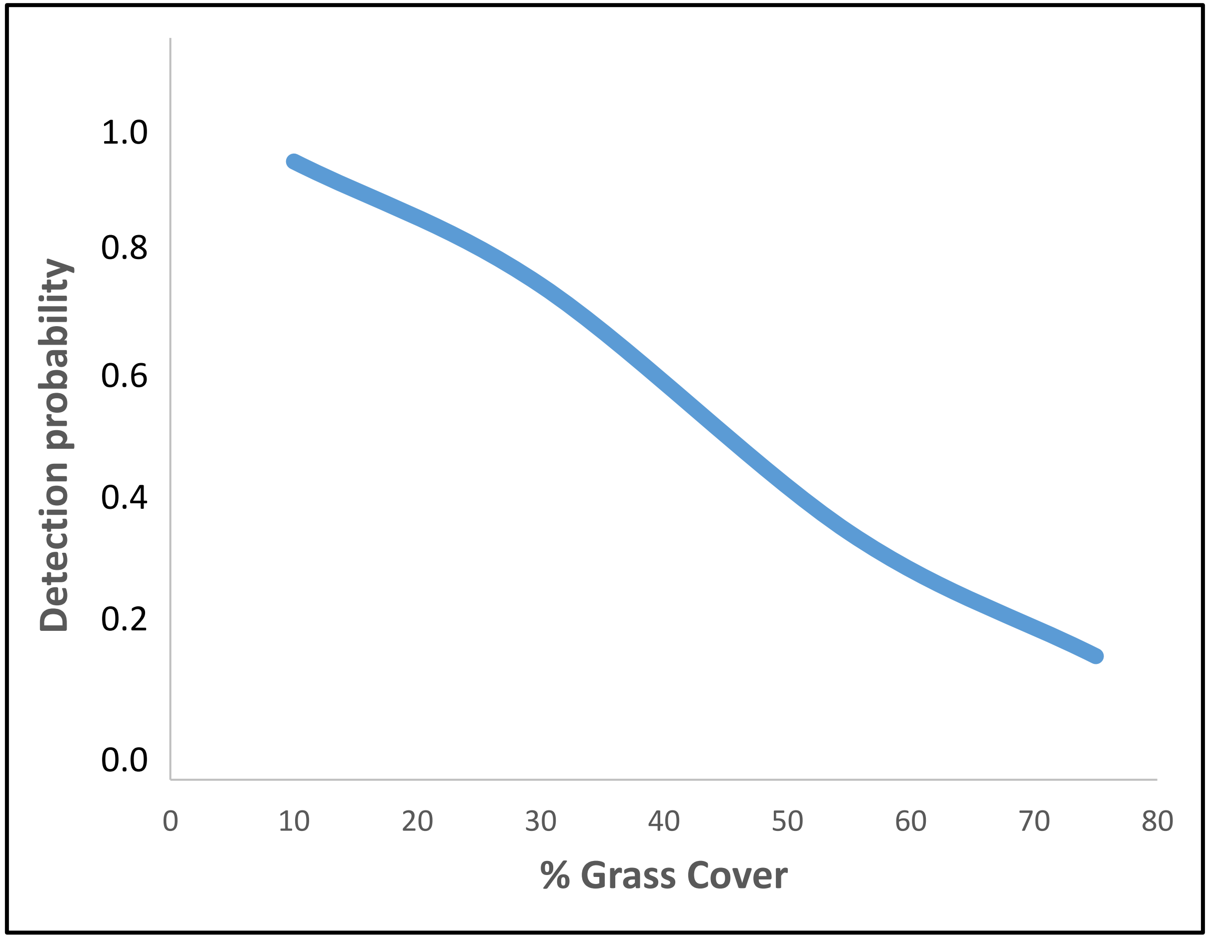

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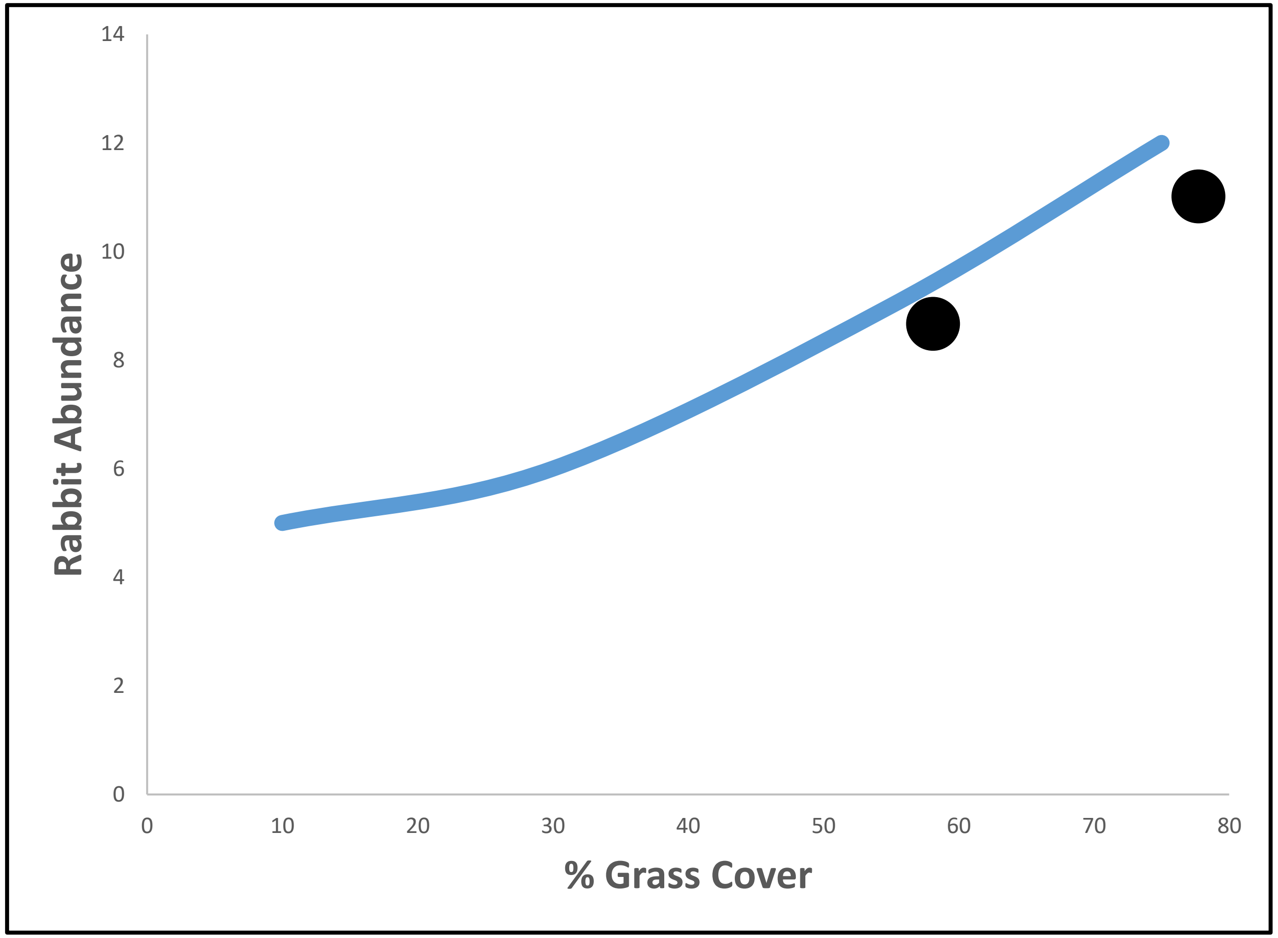
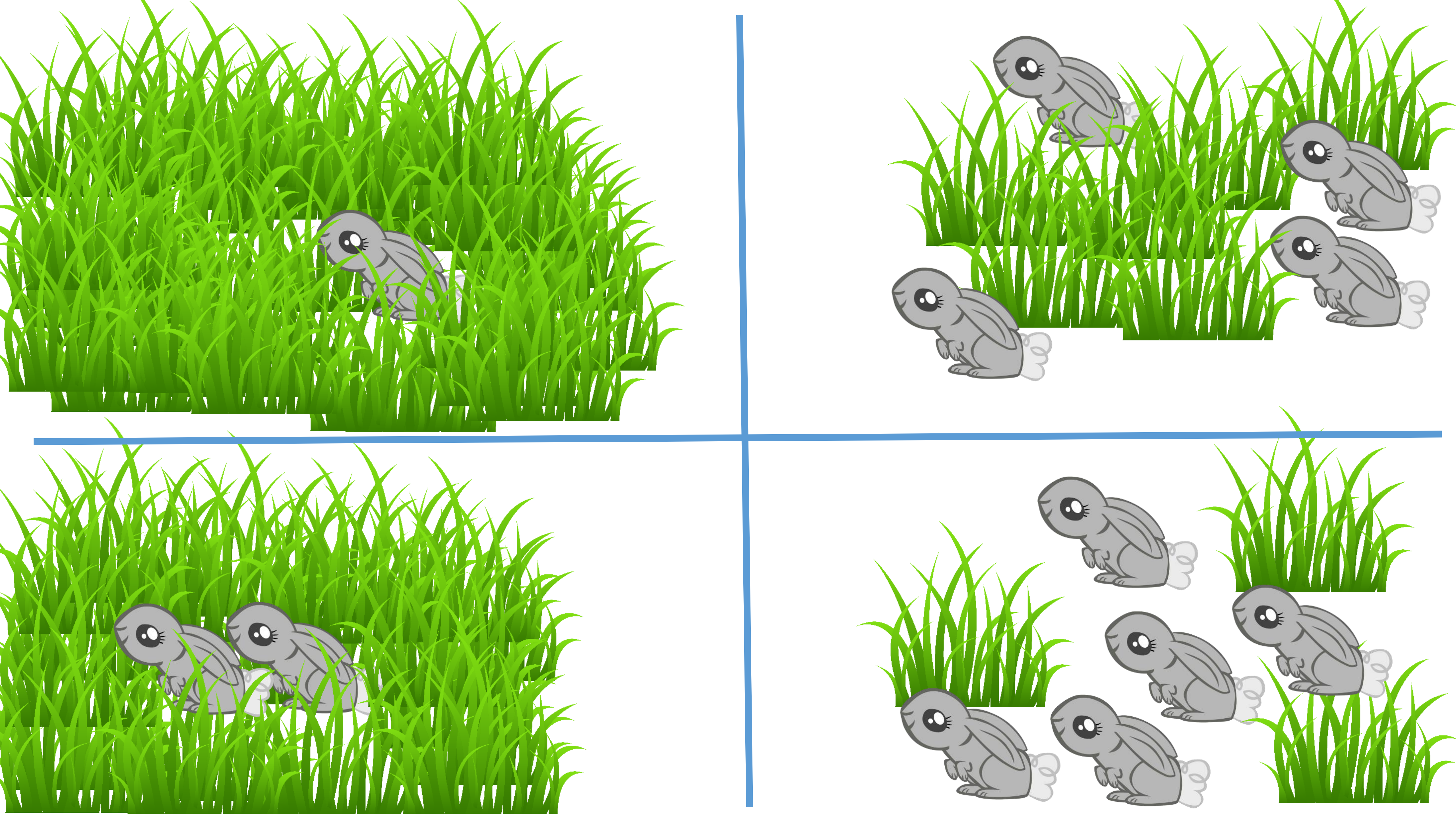


Count = true abundance * detection probability

$C = N * p$

$C / p = N$ $\quad 1 / 0.1 = \mathbf{10}$ $\quad 2 / 0.25 = \mathbf{8}$



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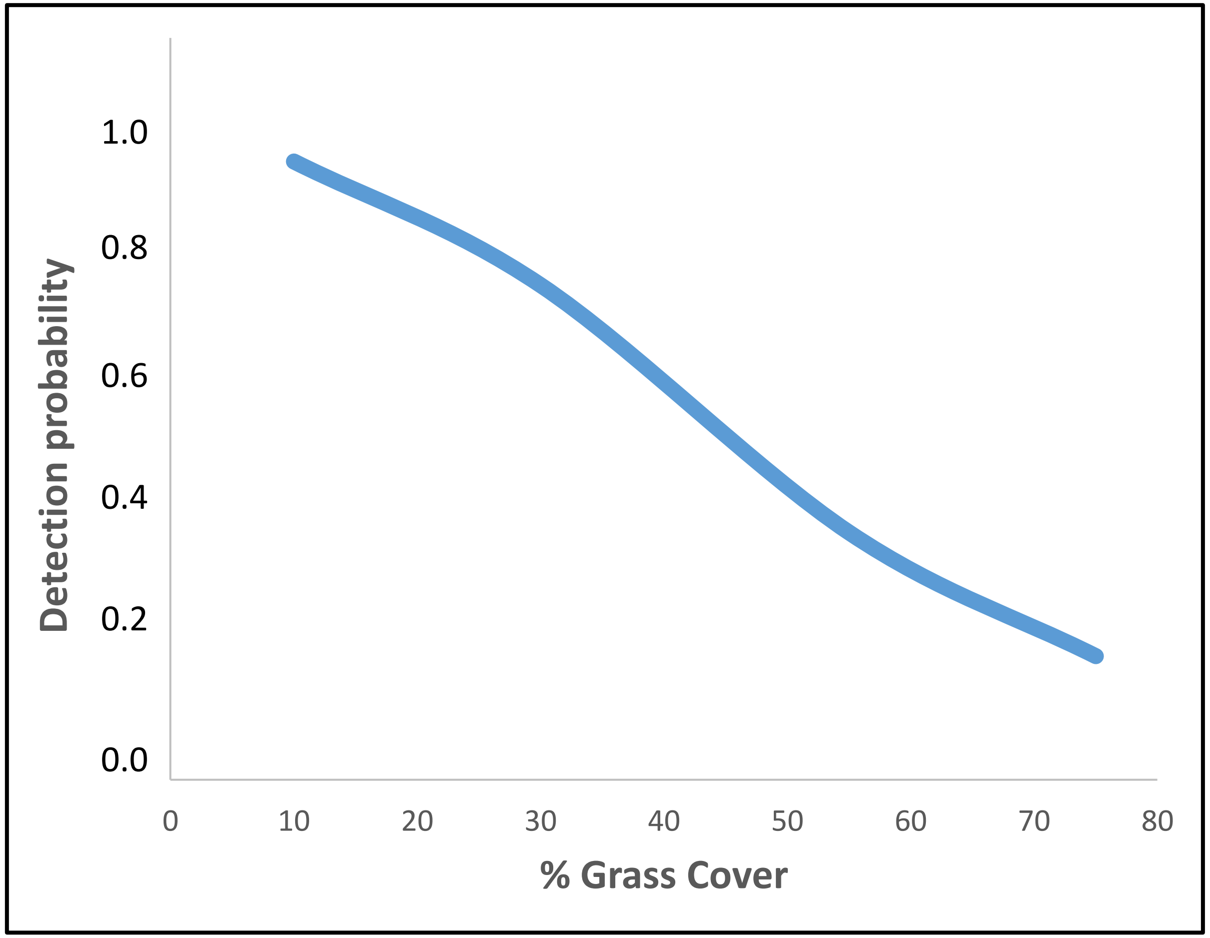

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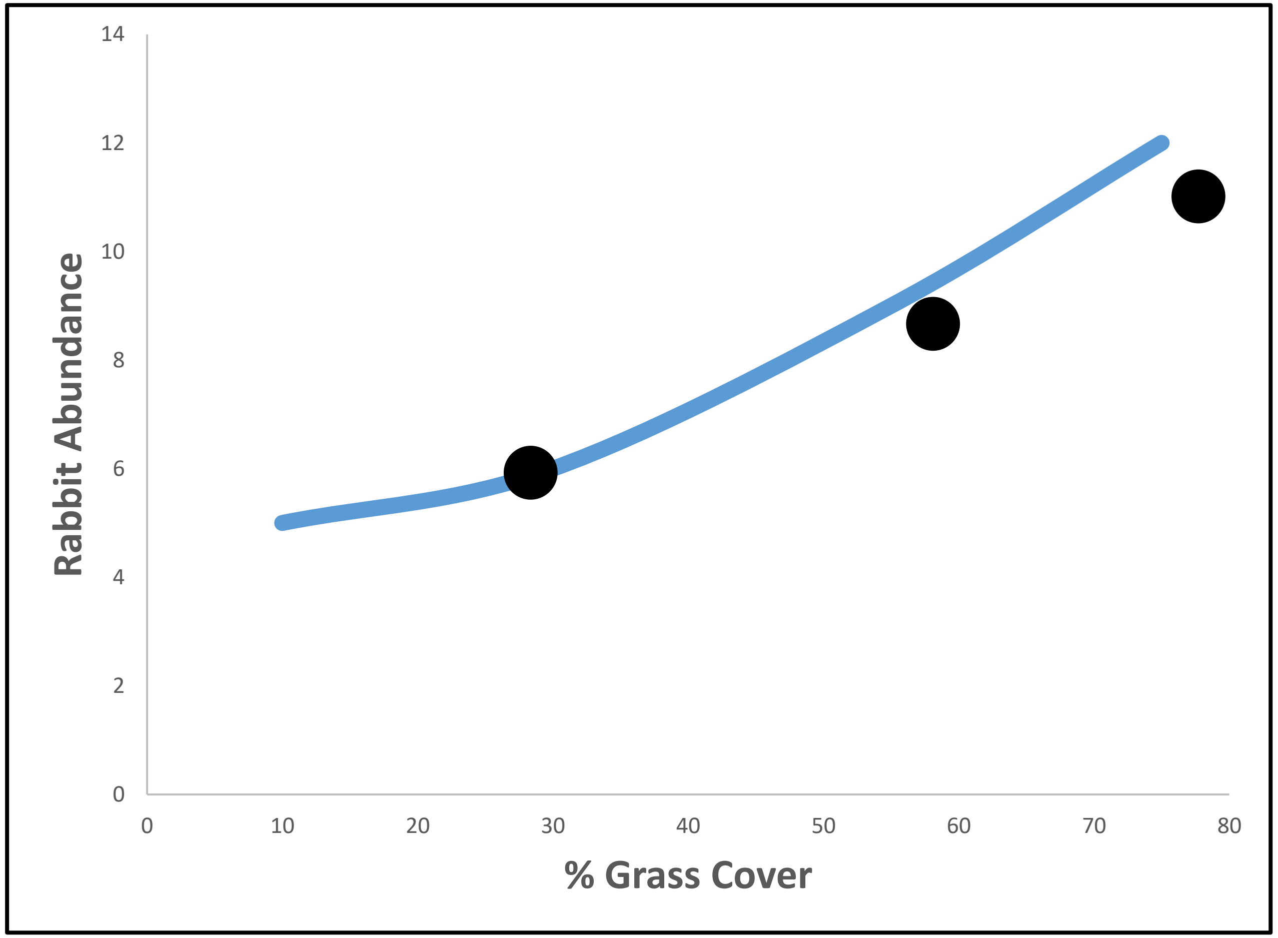
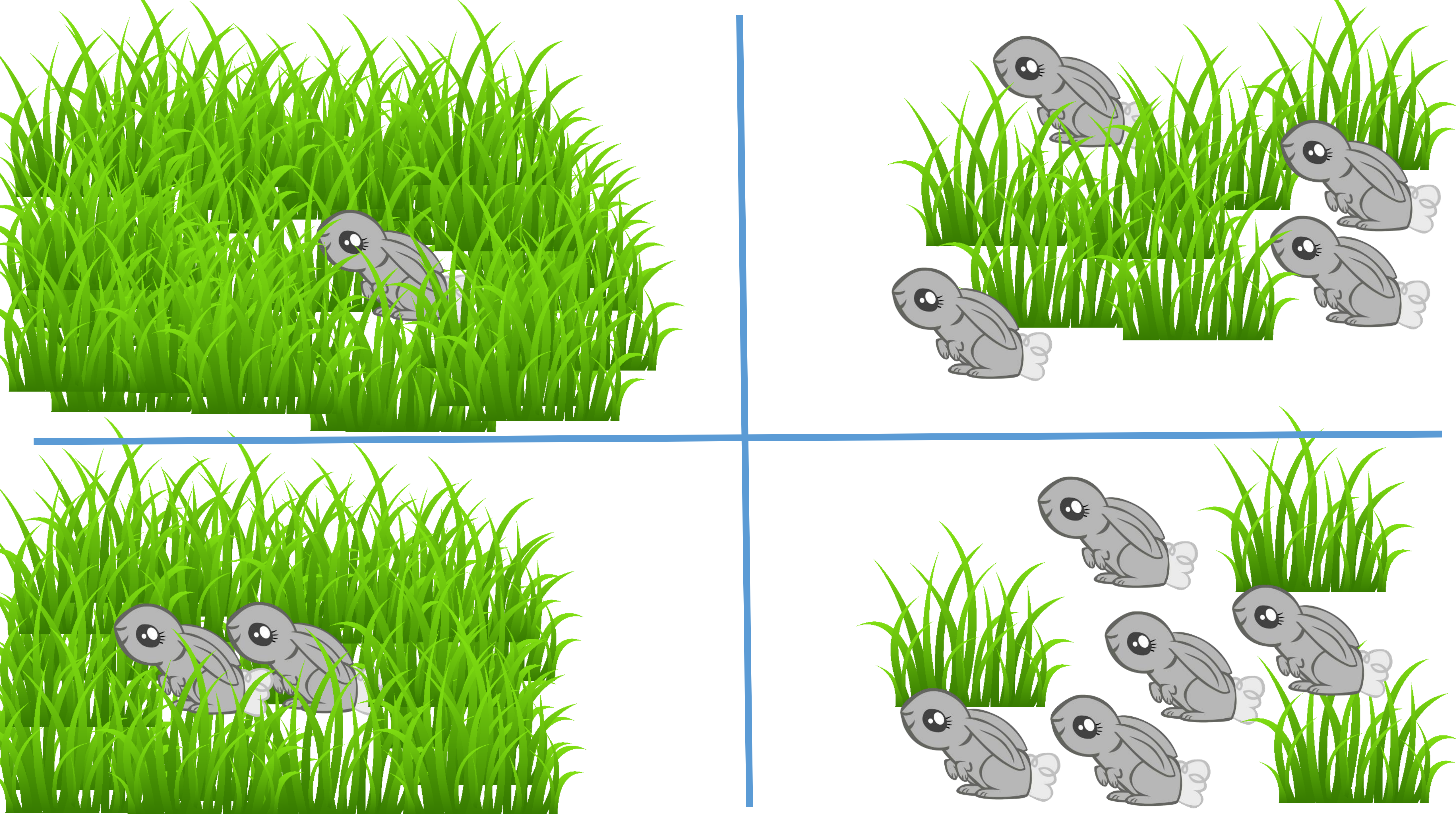


Count = true abundance * detection probability

$C = N * p$

$C / p = N$ 1 / 0.1 = **10** 2 / 0.25 = **8** 4 / 0.7 = **5.7**



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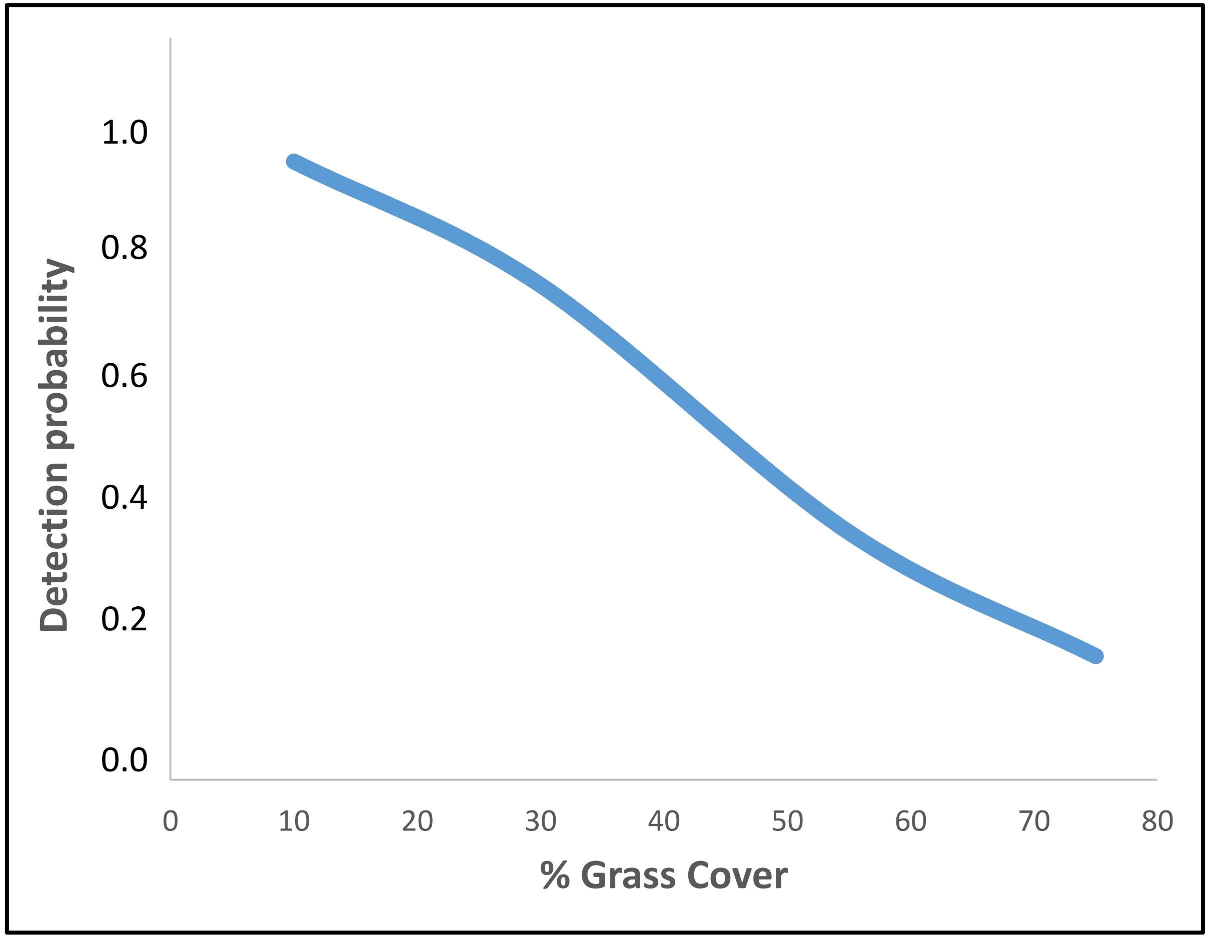

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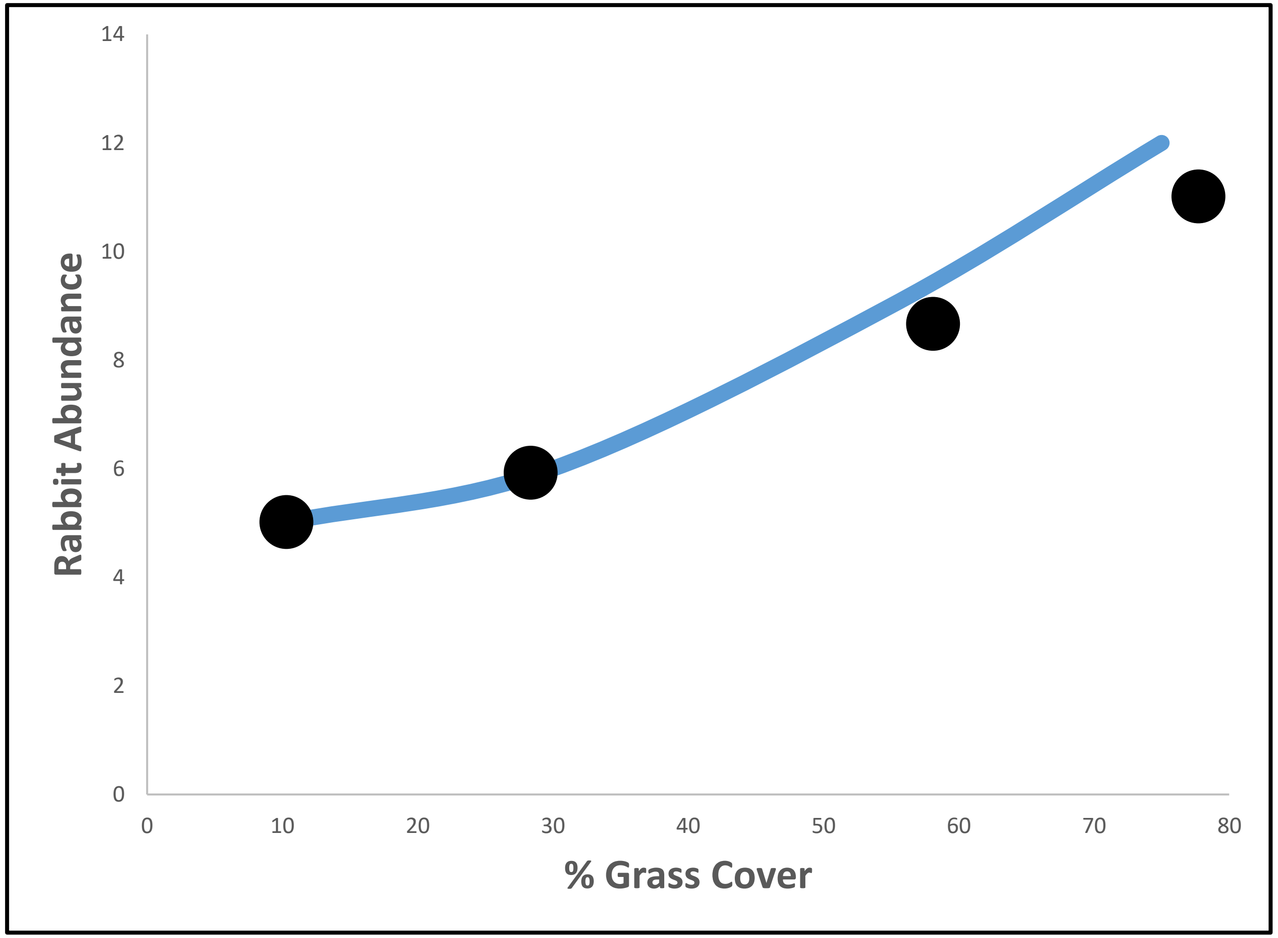


Count = true abundance * detection probability

$C = N * p$

$C / p = N$ 1 / 0.1 = **10** 2 / 0.25 = **8** 4 / 0.7 = **5.7** 5 / 0.96 = **5.2**

RMark Workshop – State and Observation Processes

1. State process (e.g., population size)
2. Observation process (e.g., population count)

For example, the **state process** describes the dynamics of **population size** over time (N_t), whereas the **observation process** describes the **error-prone population counts** (C_t).

The state-space modeling framework is very flexible and can be extended in various ways.

In this workshop, for example, we will define different state-processes.

RMark Workshop – Course Material

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

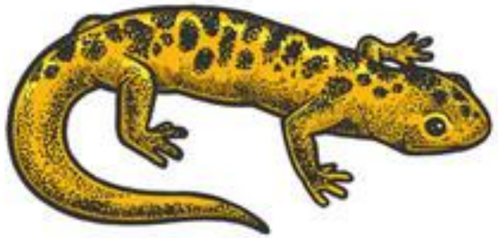
*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

RMark Workshop – Structure for each mini lesson

1. Question

How does <u>wildfire</u> influence <u>salamander abundance</u>?



RMark Workshop – Structure for each mini lesson

1. Question

How does wildfire influence salamander abundance?

2. Field Data

Site	Count	Time of Day	Date

RMark Workshop – Structure for each mini lesson

1. Question

How does <u>wildfire</u> influence <u>salamander abundance</u>?

2. Field Data

Site	Count	Time of Day	Date
1	0	5:00	5/15/2024
1	3	9:00	5/15/2024
2	4	5:30	5/19/2024
2	9	9:30	5/19/2024
3	13	6:00	5/20/2024
3	14	6:30	5/20/2024

RMark Workshop – Structure for each mini lesson

1. Question How does wildfire influence salamander abundance?
2. Field Data
3. Format Data for Analysis
4. Fit Models in RMark
5. Examine Output and Visualize Results

*steps 3-5 in Program R

RMark Workshop – Structure for each mini lesson

1. Question — How does wildfire influence salamander abundance?
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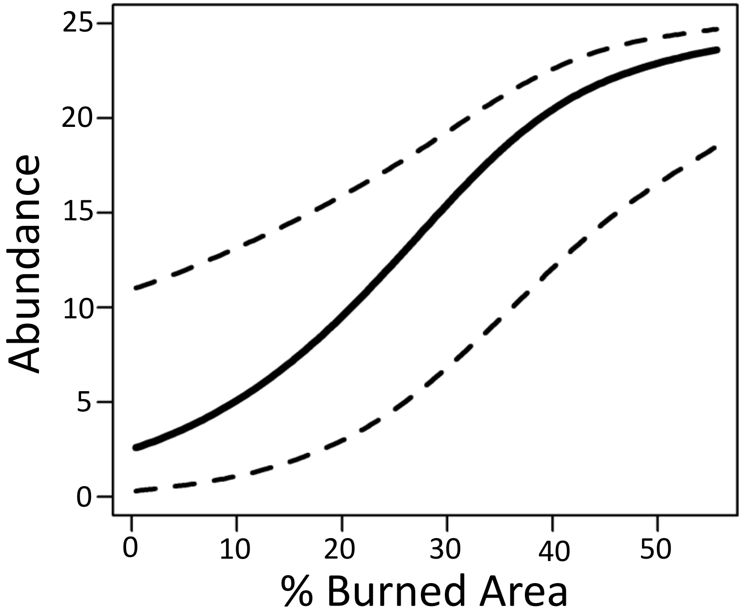

RMark Workshop – Materials (code, data, slides)

All workshop materials are hosted on GitHub:

https://github.com/gbarrile/RMark_Workshop_Sp24

RMark Workshop

Model 1 – Closed Population Estimation

RMark Workshop – Models

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Capture-Mark-Recapture

- Method used to estimate the abundance of biological populations that involves ‘**capturing**’ individuals, ‘**marking**’ them, releasing them back into the population, and then determining the ratio of marked to unmarked individuals in the population during ‘**recapture**’ surveys

- If we can estimate the abundance of organisms like salamanders and birds by counting them, why go through the trouble of capturing and marking them?

Capture-Recapture vs Count Data

$N = 100$

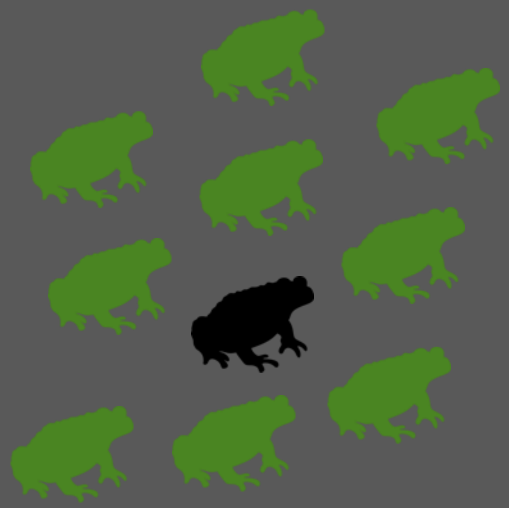
Capture-Recapture vs Count Data

N = 100

Capture-Recapture vs Count Data

$N = 100$

10



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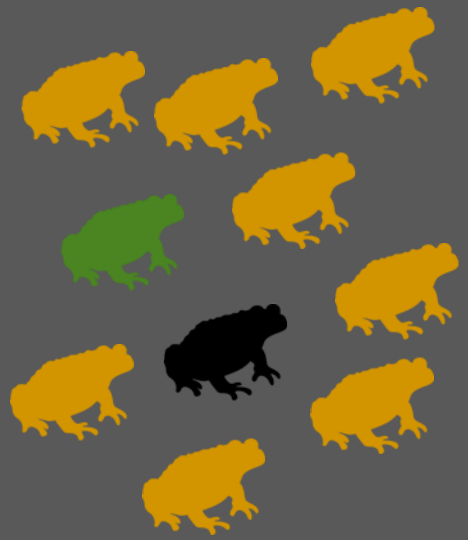

10

RMark Workshop – Closed Population Estimation

$$Population\ size = \frac{\#\ of\ individuals\ marked}{probability\ of\ capturing\ an\ individual\ at\ least\ once}$$

$$N = \frac{n}{p} \qquad N = \frac{50}{0.5} \qquad N = 100$$

RMark Workshop – Lincoln-Peterson Estimator

N = abundance (what we want to estimate)

n = number of individuals captured & marked during survey 1

m = number of individuals in survey 2 that were marked during survey 1

s = total number of individuals captured during survey 2

$\frac{n}{N} =$ $\frac{n}{N} = \frac{m}{s}$ $N = \frac{ns}{m}$ $N = \frac{n}{p}$ $p = \frac{m}{s}$ $N = \frac{n}{p} = \frac{ns}{m}$

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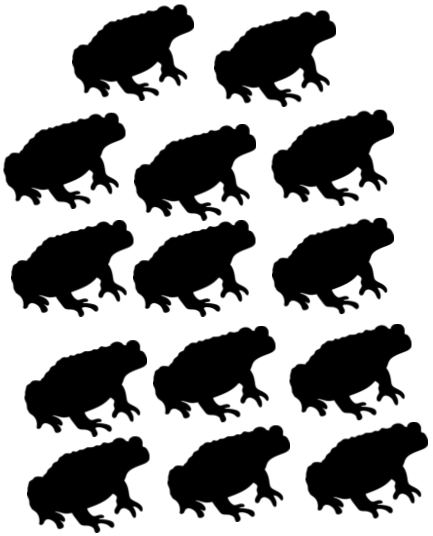

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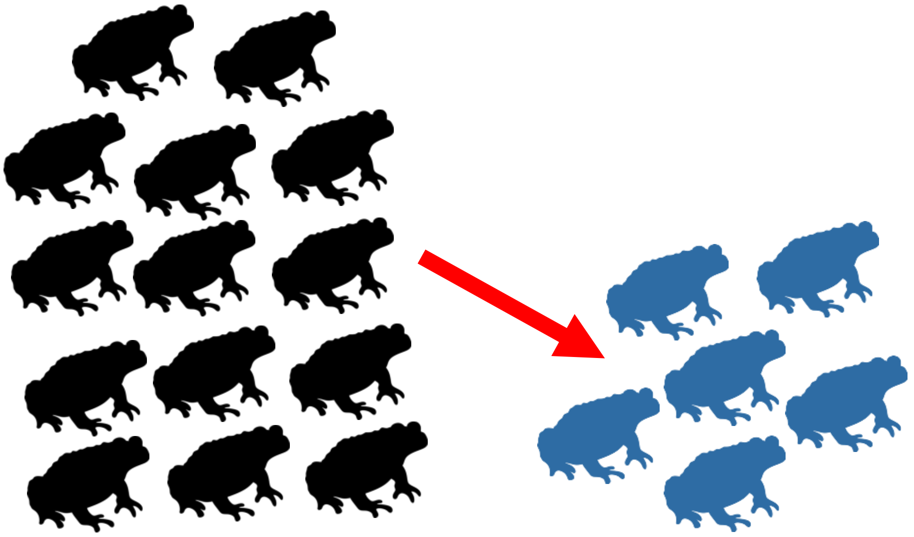

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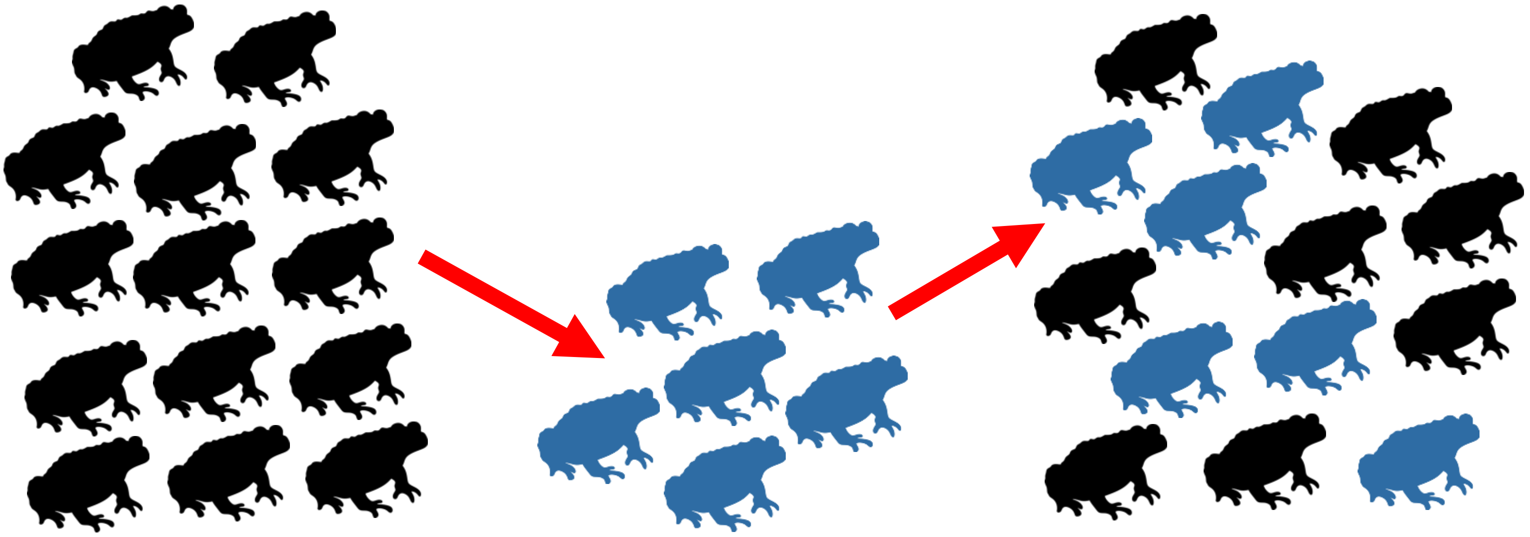

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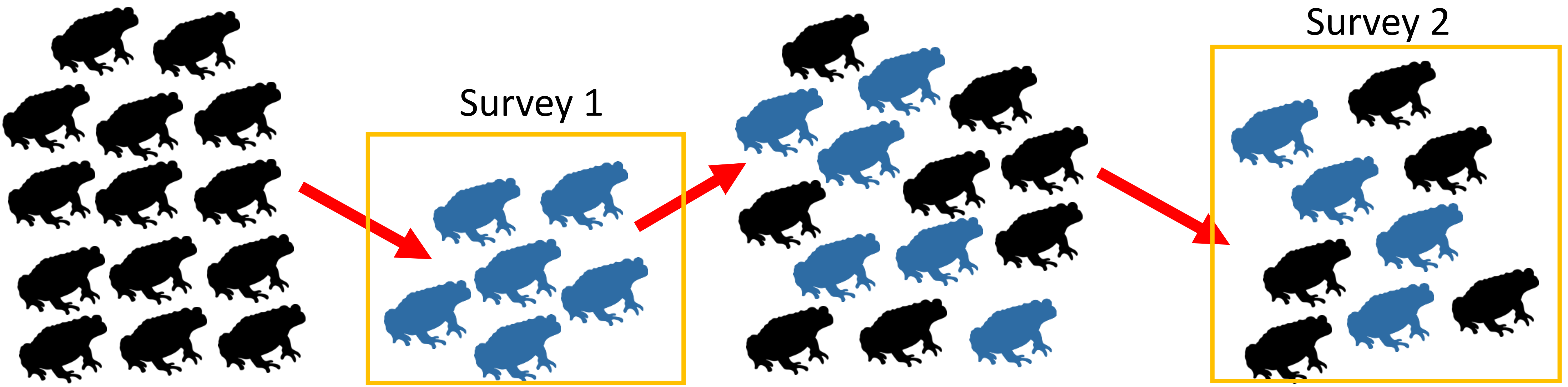
$\frac{6}{N} =$ $\quad \frac{6}{N} = \frac{4}{9}$ $\quad N = \frac{6 \: x \: 9}{4}$ $\quad N = 13.5$ $\quad p = \frac{4}{9}$ $\quad p = 0.444$ $\quad N = \frac{6}{0.444}$ $\quad N = 13.5$



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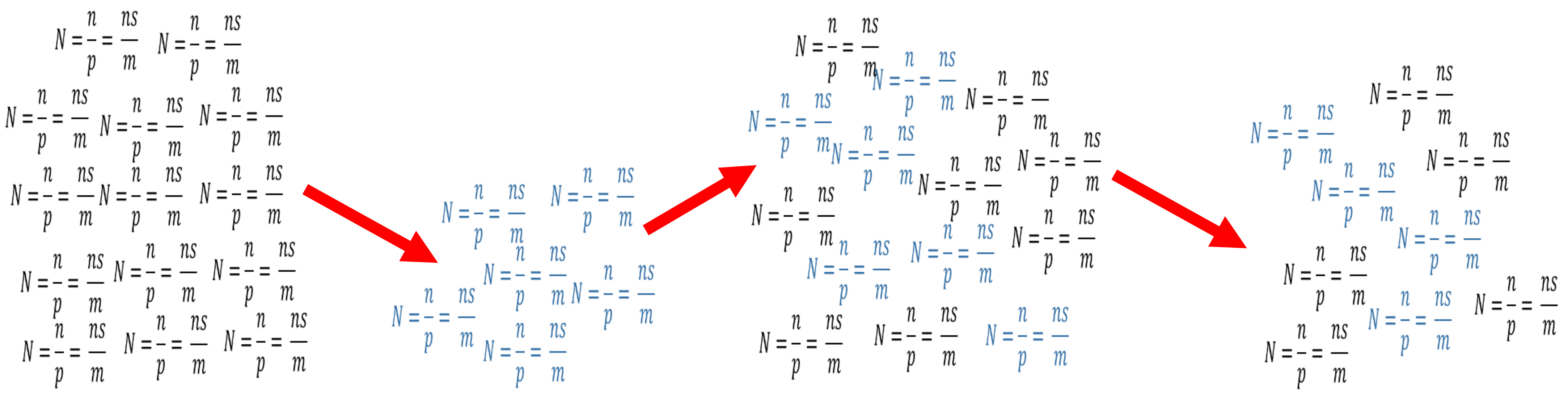


Model Parameters

p = capture probability

c = recapture probability

f0 = the number of individuals never captured

Questions

1. Differences between detection probability and capture probability?
2. Why different parameters for capture probability and recapture probability?
3. What the heck is *f0*?

$f0 = N - M$

$N = f0 + M$

Population abundance (N) is a derived parameter in these models

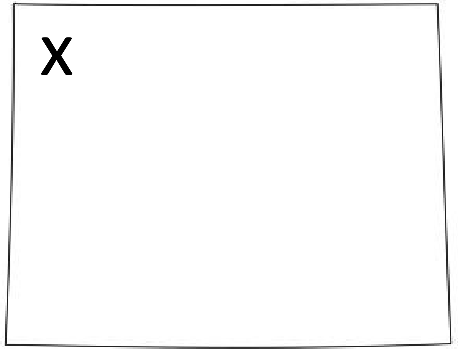
RMark Workshop – Lesson Structure

1. Question
2. Field Data
3. Format Data for Analysis
4. Fit Models in RMark
5. Examine Output and Visualize Results

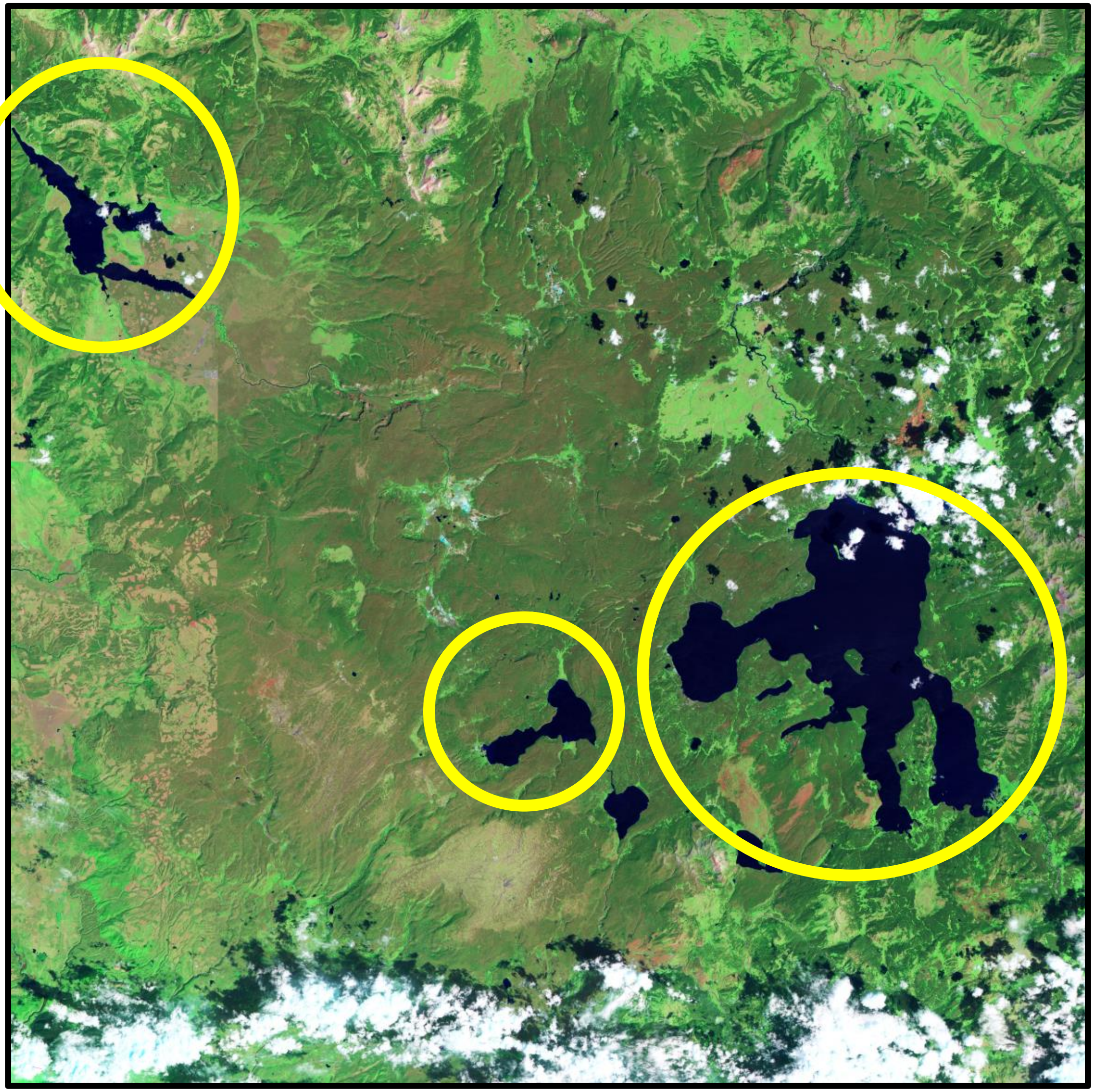
RMark Workshop – Closed Population Estimation

1. Question

How does common loon abundance vary across ponds?



C. Hagenlocher

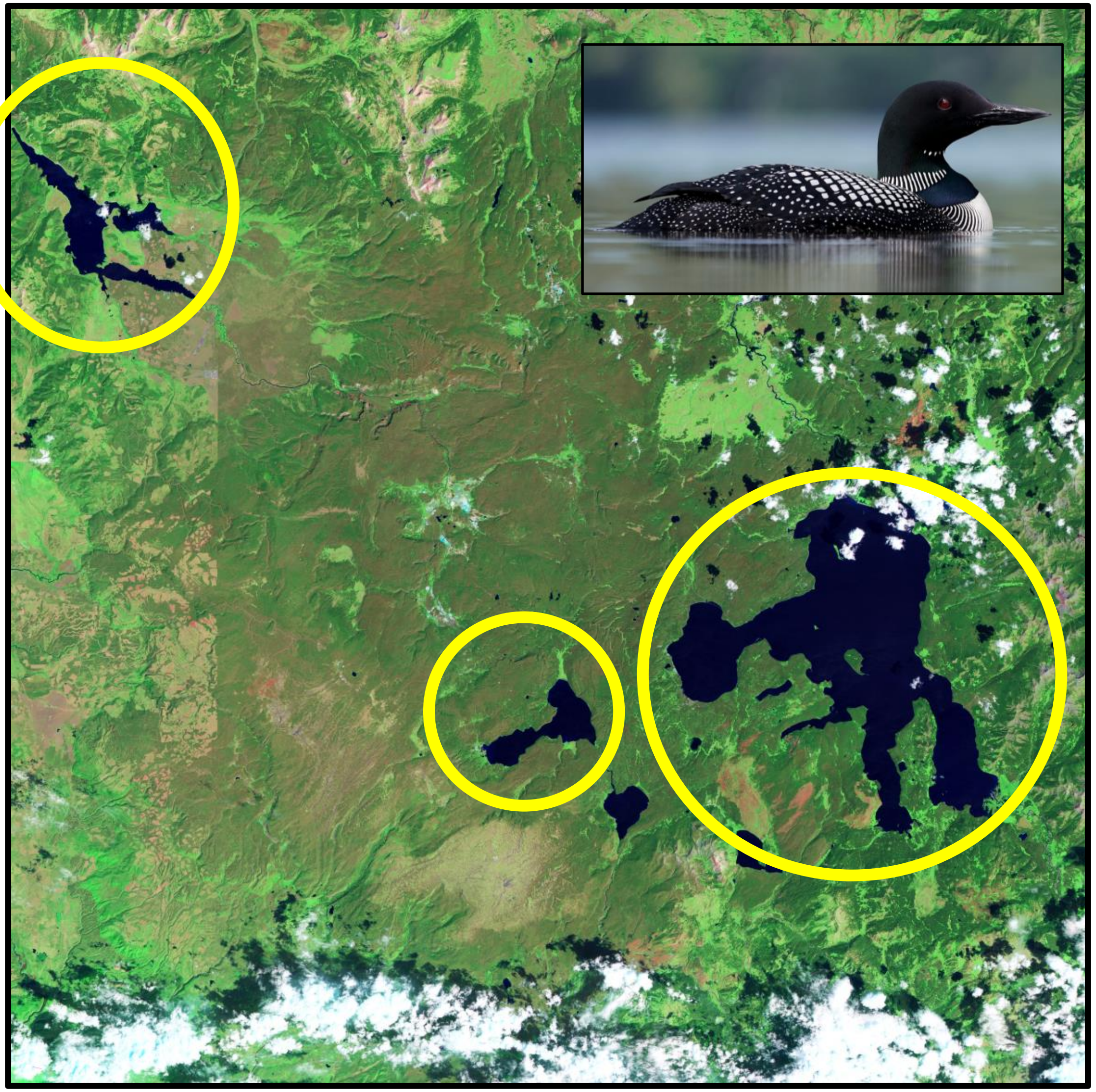


RMark Workshop – Closed Population Estimation

1. Question

How does common loon abundance vary across ponds?

Date	Pond	Survey	Size	Tag

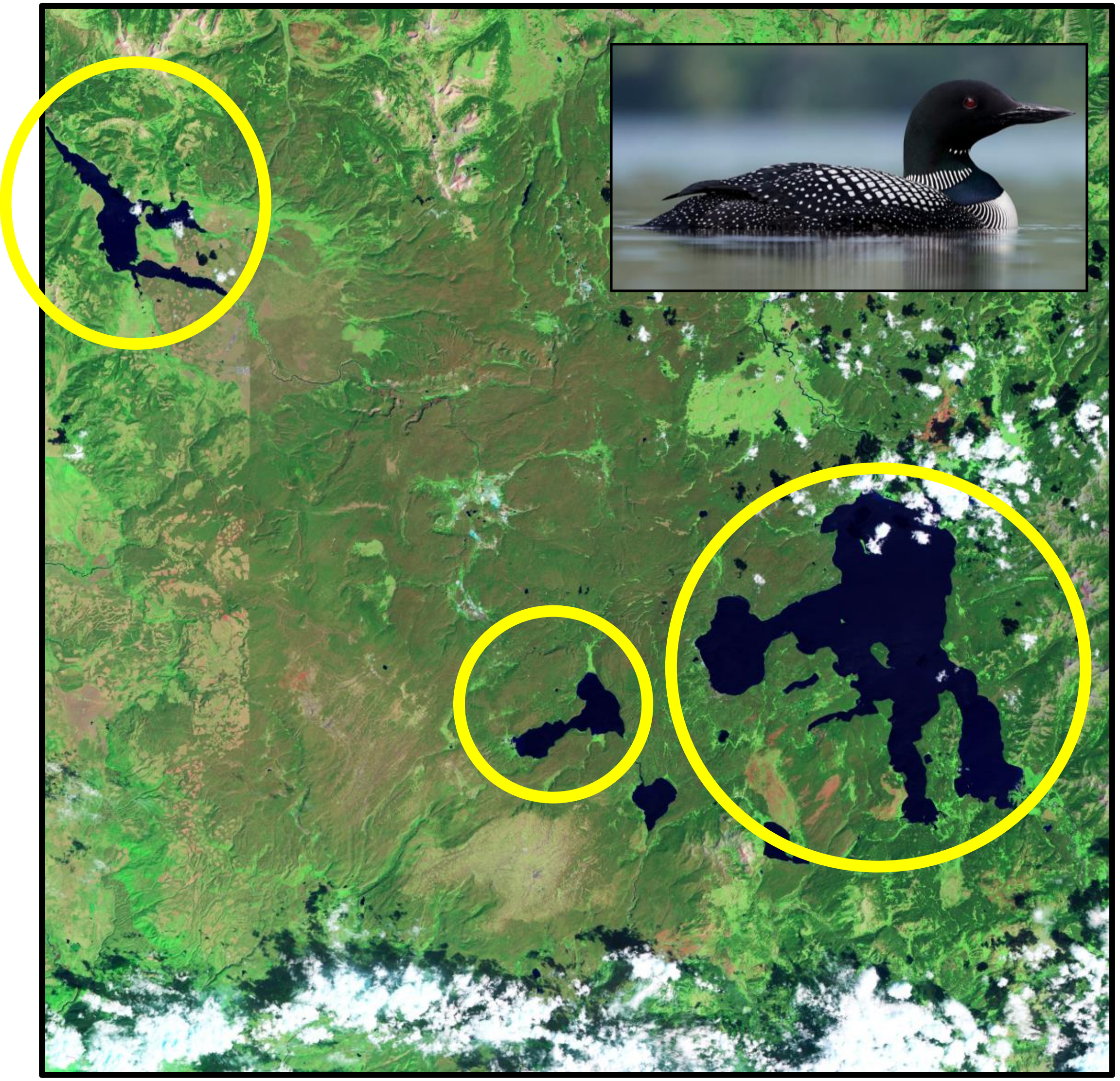


RMark Workshop – Closed Population Estimation

1. Question

How does common loon abundance vary across ponds?

Date	Pond	Survey	Size	Tag
5/29/2015	1	1		

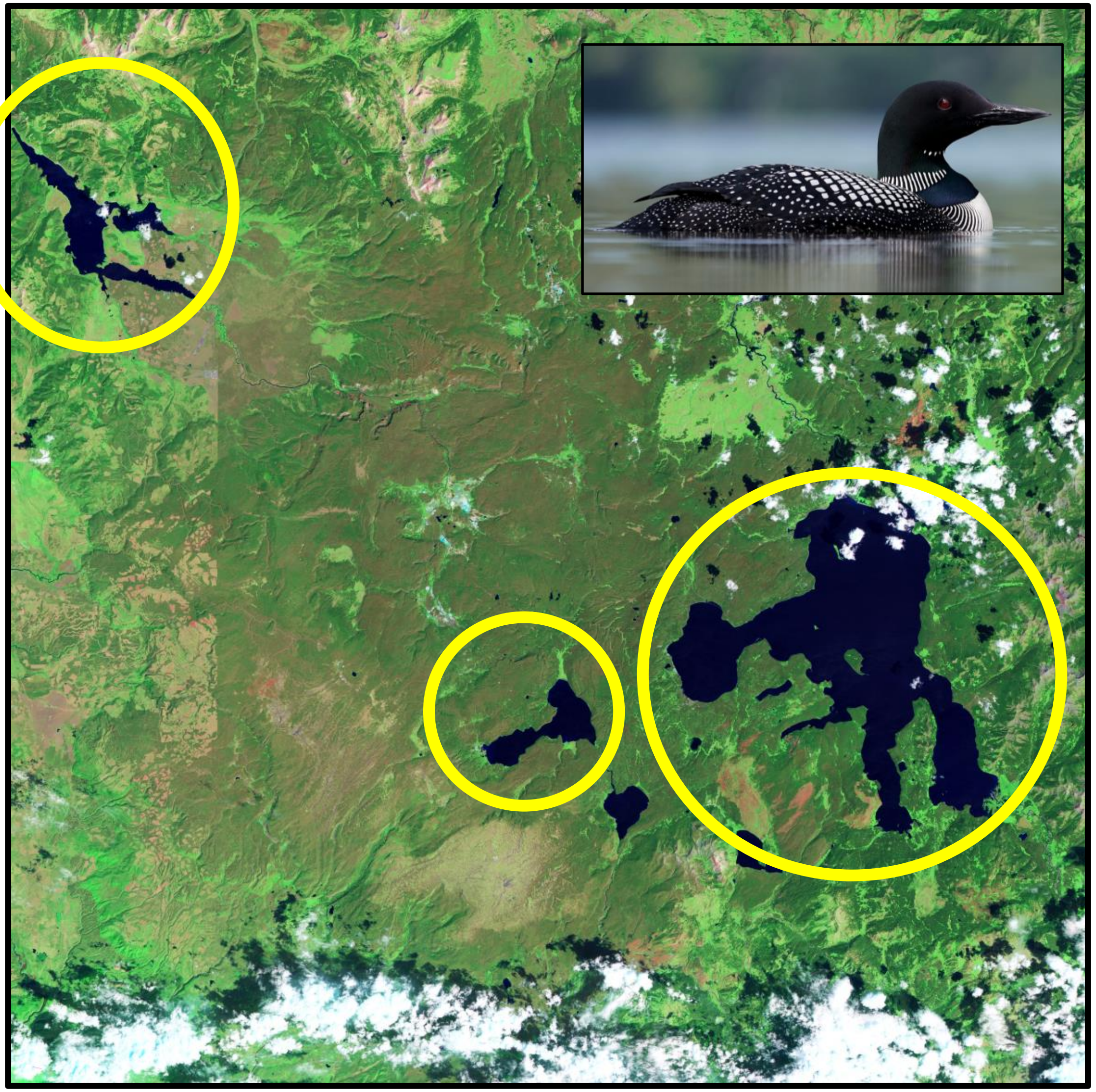


RMark Workshop – Closed Population Estimation

1. Question

How does common loon abundance vary across ponds?

Date	Pond	Survey	Size	Tag
5/29/2015	1	1	65	

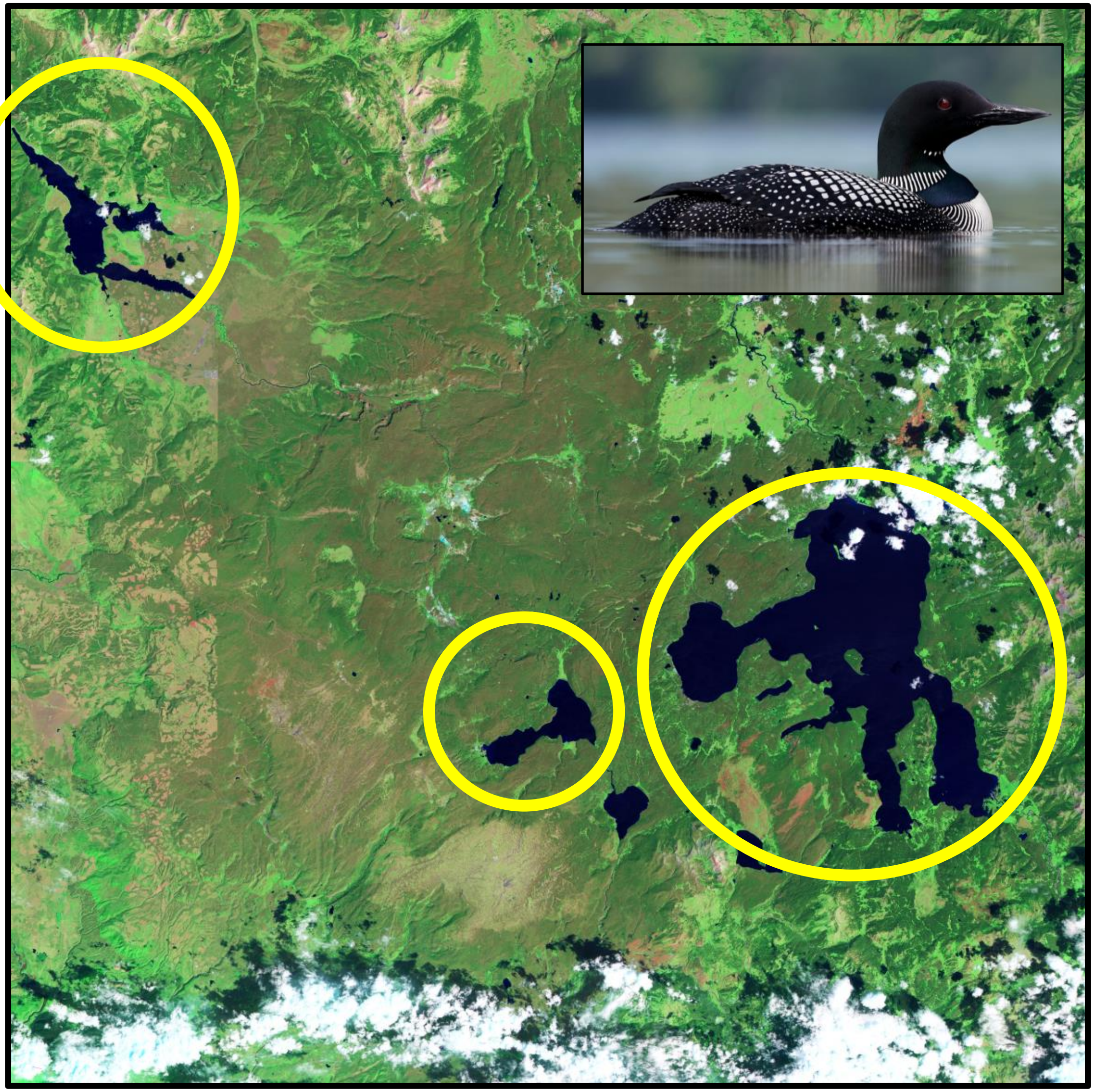


RMark Workshop – Closed Population Estimation

1. Question

How does common loon abundance vary across ponds?

Date	Pond	Survey	Size	Tag
5/29/2015	1	1	65	100

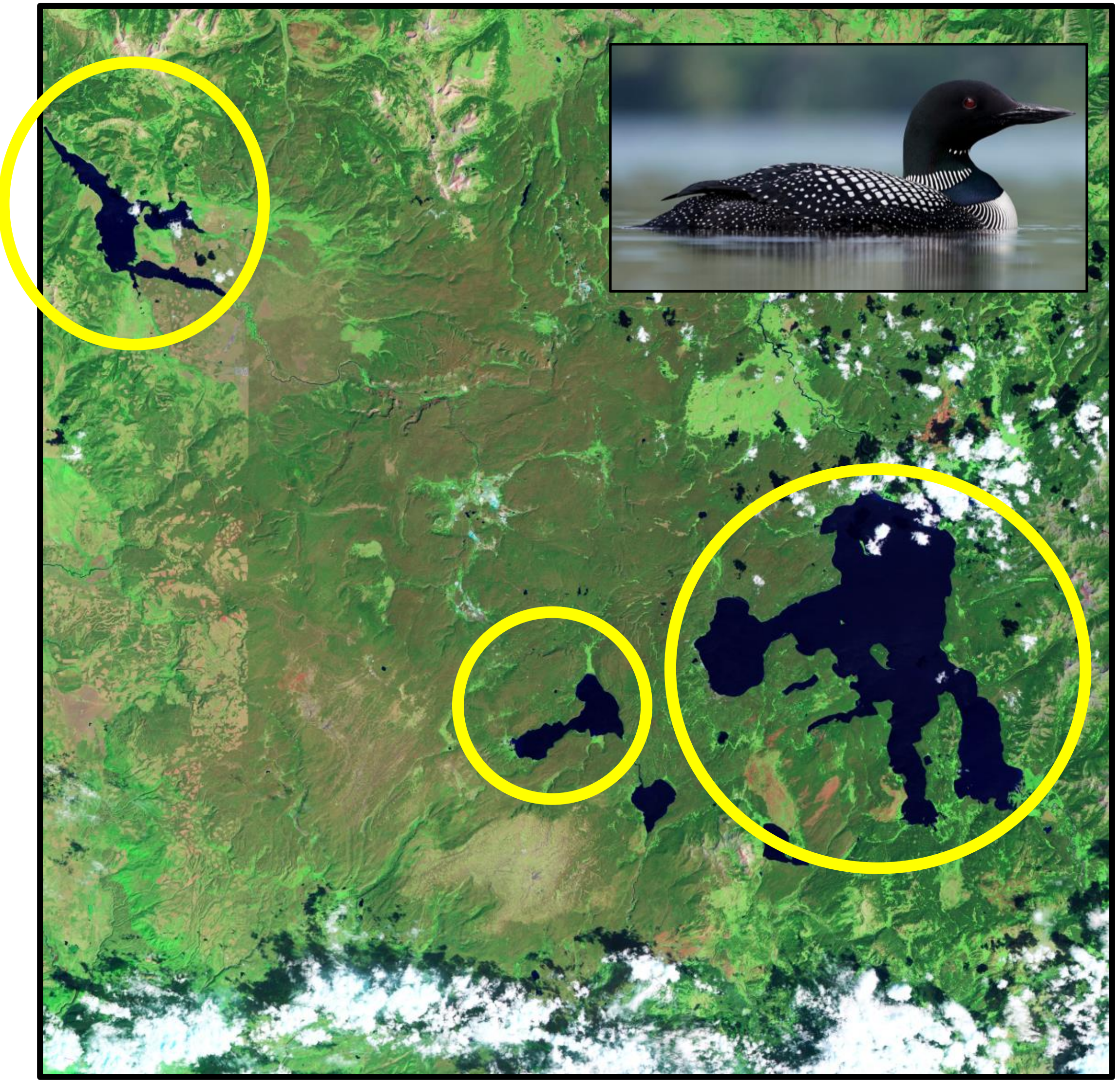


RMark Workshop – Closed Population Estimation

1. Question

How does common loon abundance vary across ponds?

Date	Pond	Survey	Size	Tag
5/29/2015	1	1	65	100
5/29/2015	1	1	75	101
5/29/2015	1	1	68	102
5/29/2015	1	1	80	103
5/29/2015	1	1	60	104
5/29/2015	1	1	89	105
5/29/2015	1	1	82	106



RMark Workshop – Closed Population Estimation

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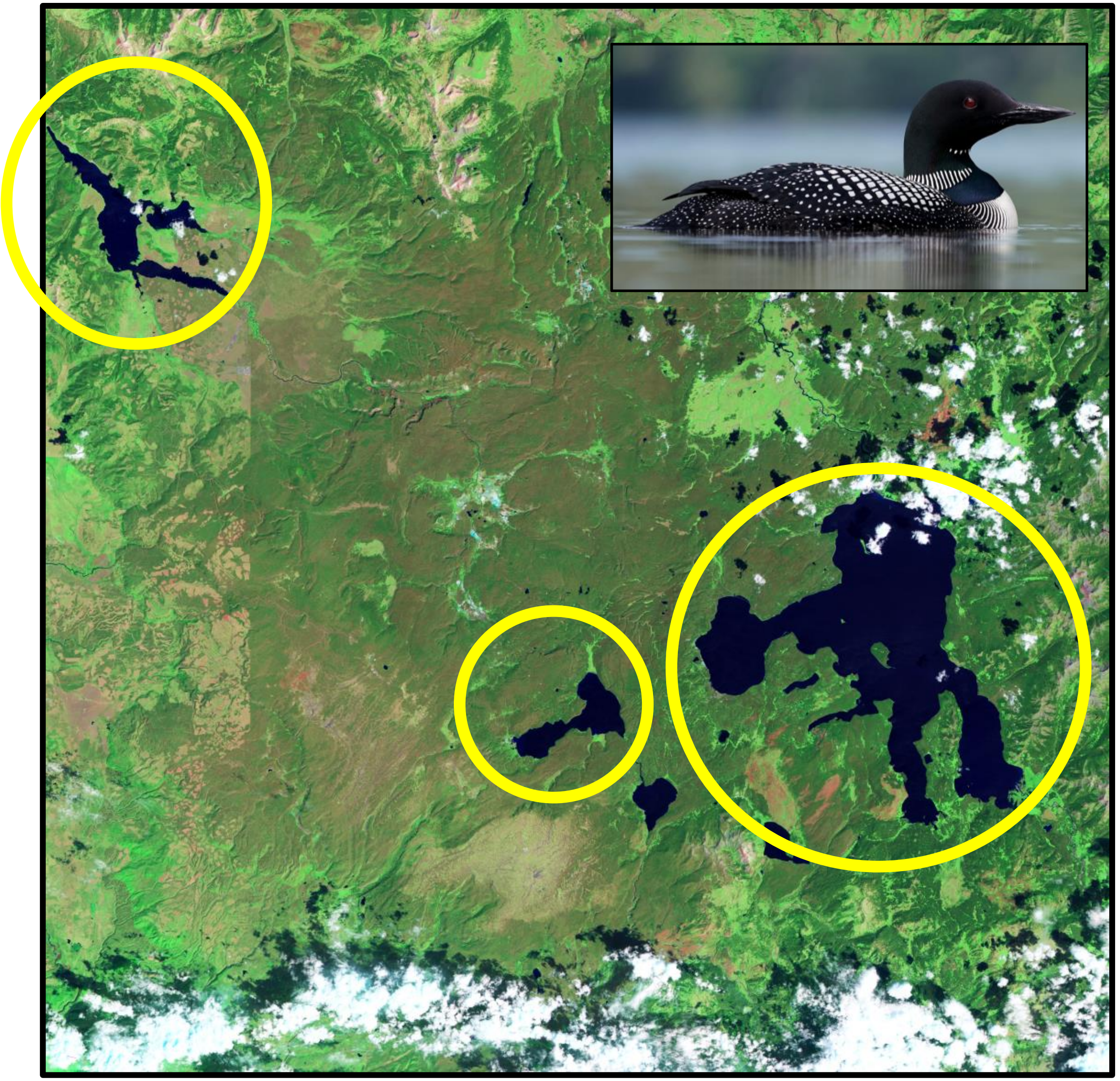
5/29/2015	1	1	60	104
5/29/2015	1	1	89	105
5/29/2015	1	1	82	106
6/1/2015	1	2		



RMark Workshop – Closed Population Estimation

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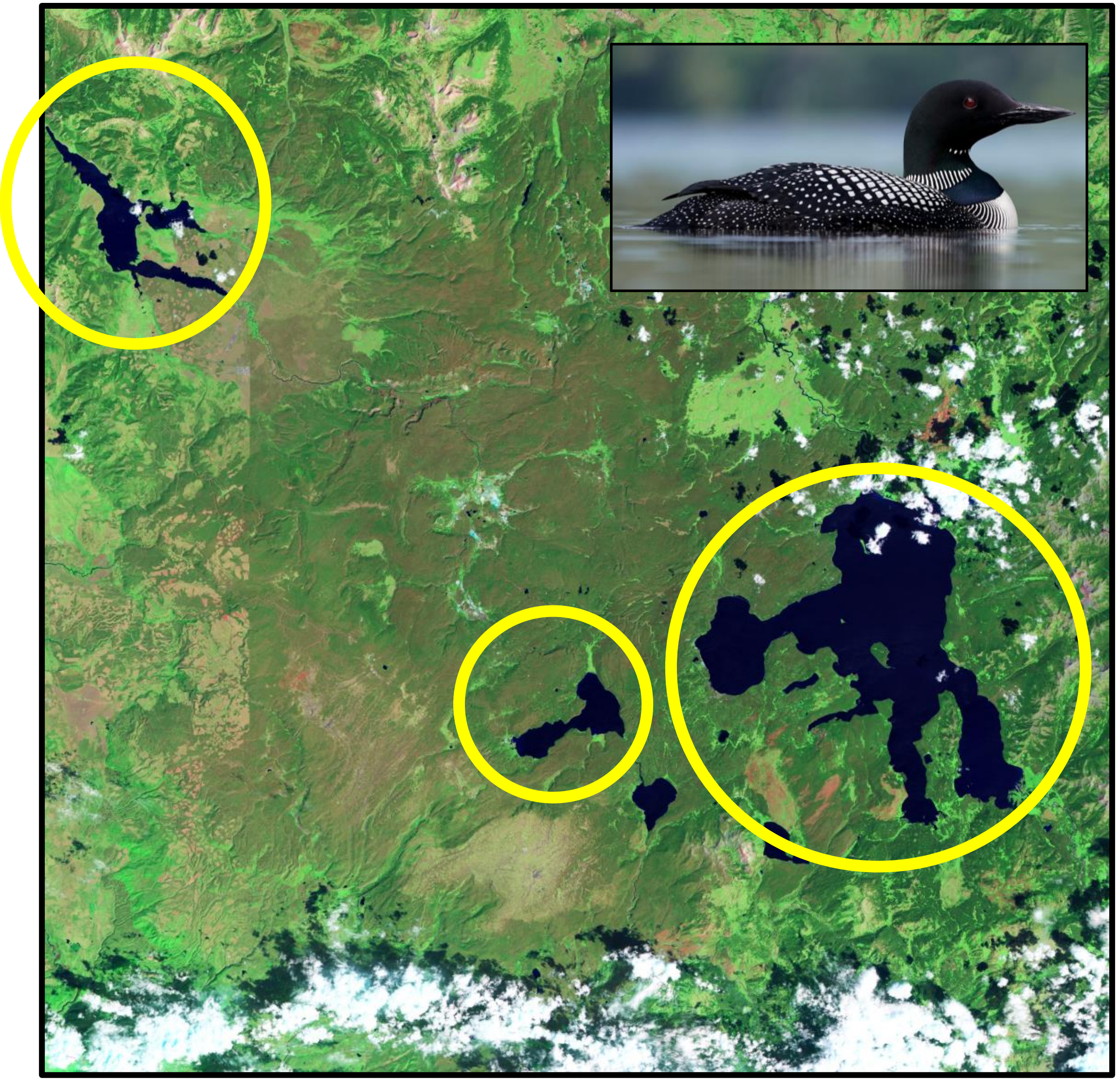
5/29/2015	1	1	60	104
5/29/2015	1	1	89	105
5/29/2015	1	1	82	106
6/1/2015	1	2	58	



RMark Workshop – Closed Population Estimation

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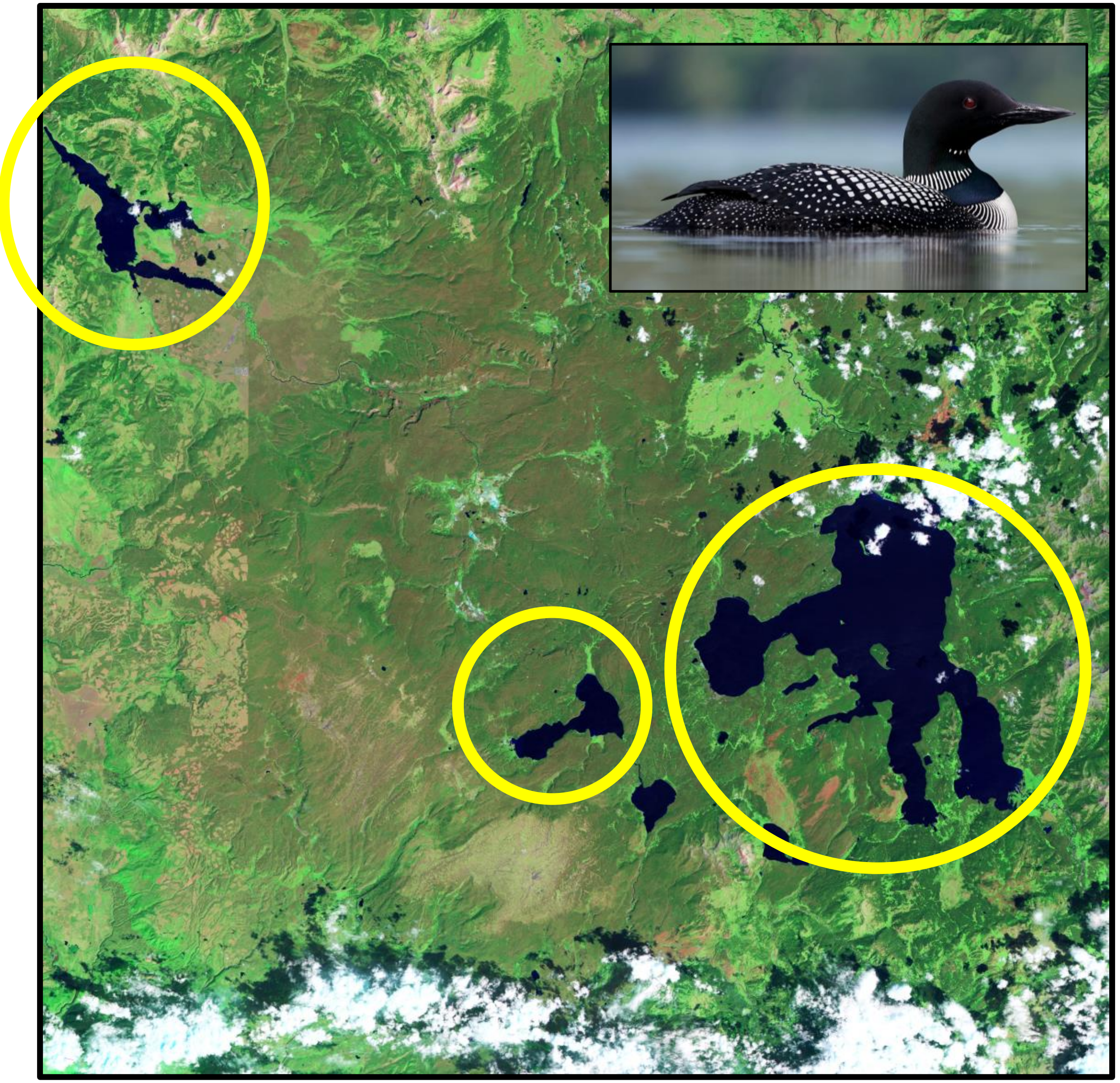

RMark Workshop – Closed Population Estimation

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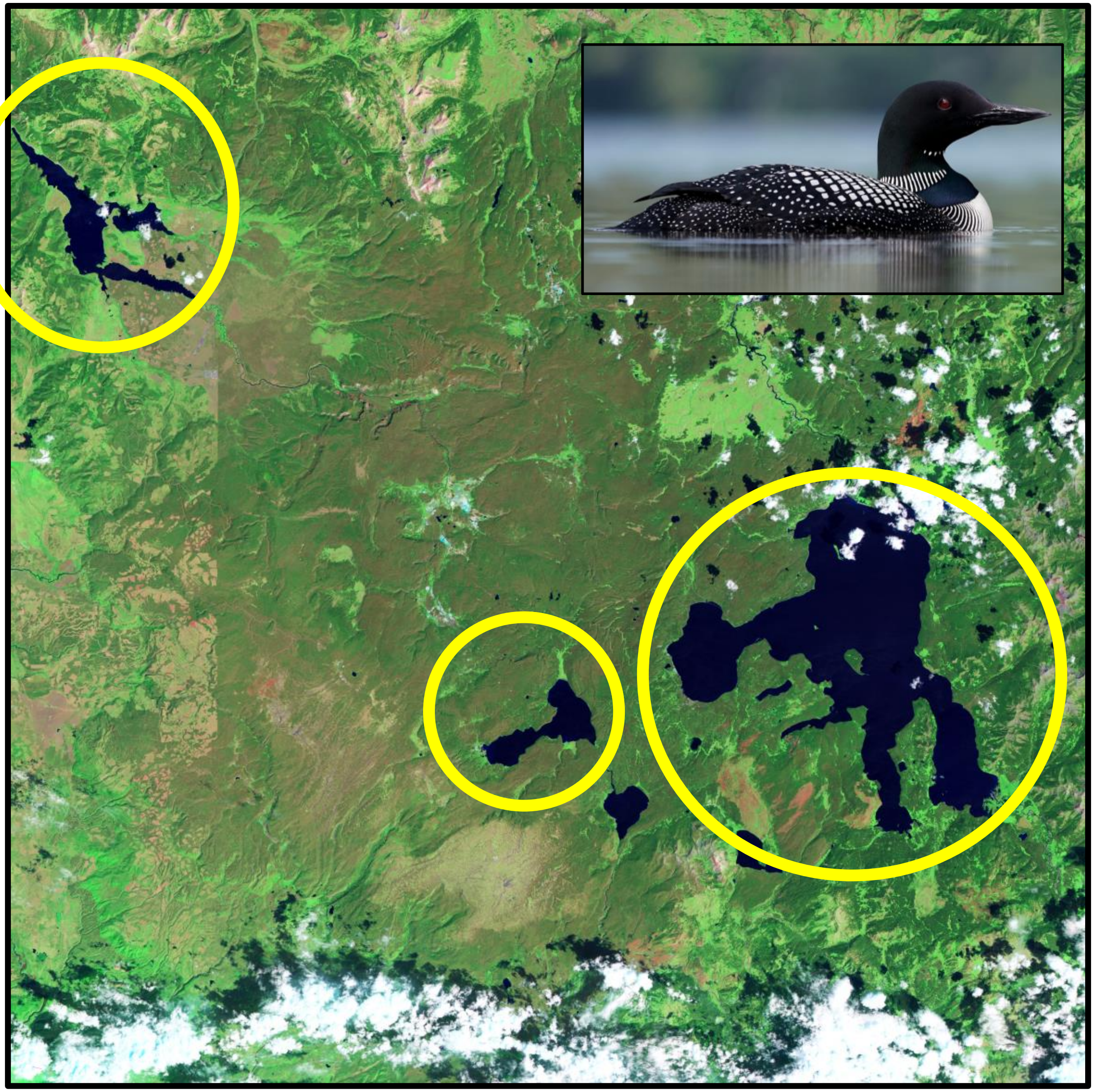
6/1/2015	1	2	68	



RMark Workshop – Closed Population Estimation

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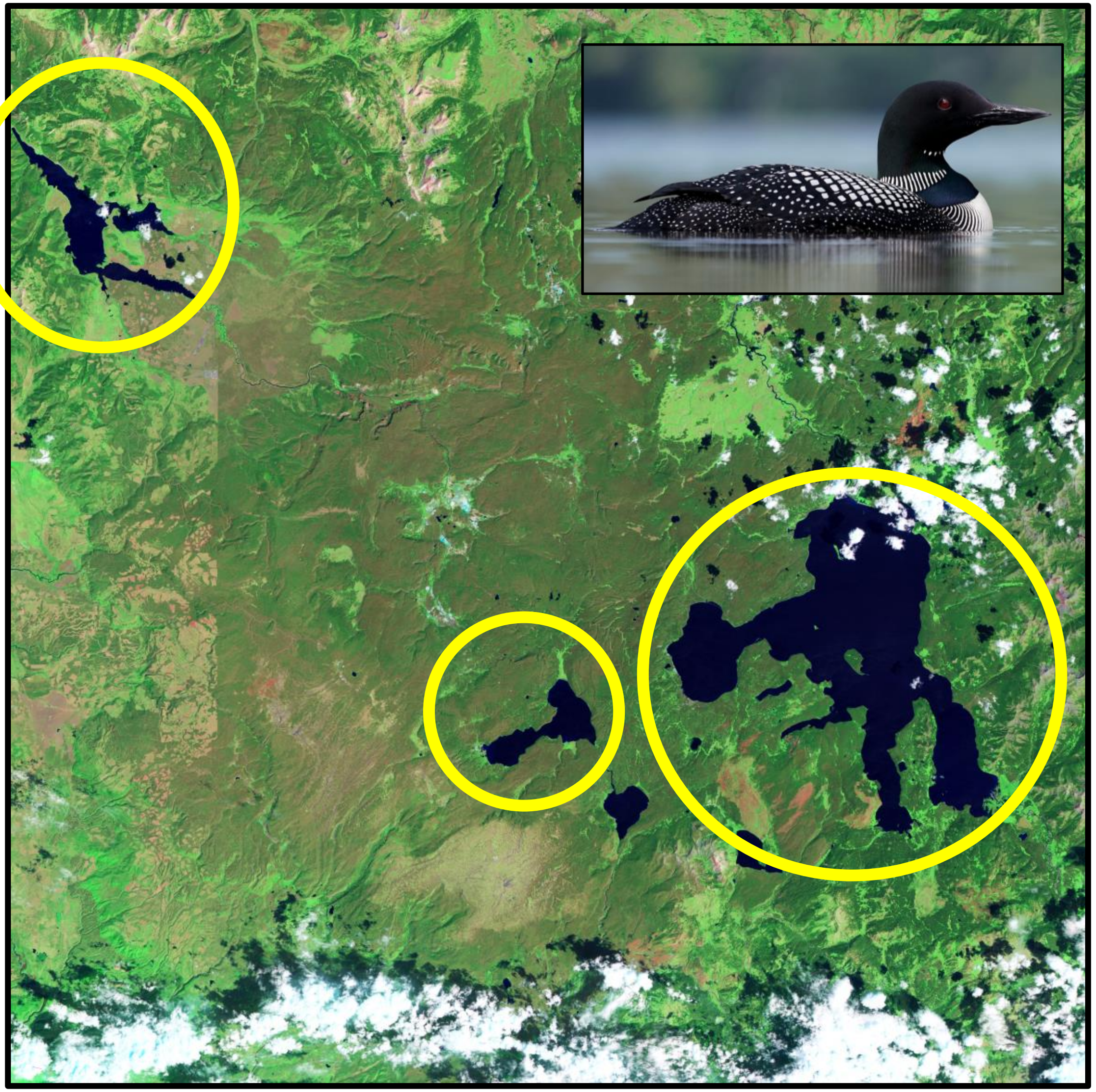
5/29/2015	1	1	89	105
5/29/2015	1	1	82	106
6/1/2015	1	2	58	107
6/1/2015	1	2	68	102



RMark Workshop – Closed Population Estimation

1. Question

How does common loon abundance vary across ponds?

Date	Pond	Survey	Size	Tag
5/29/2015	1	1	65	100
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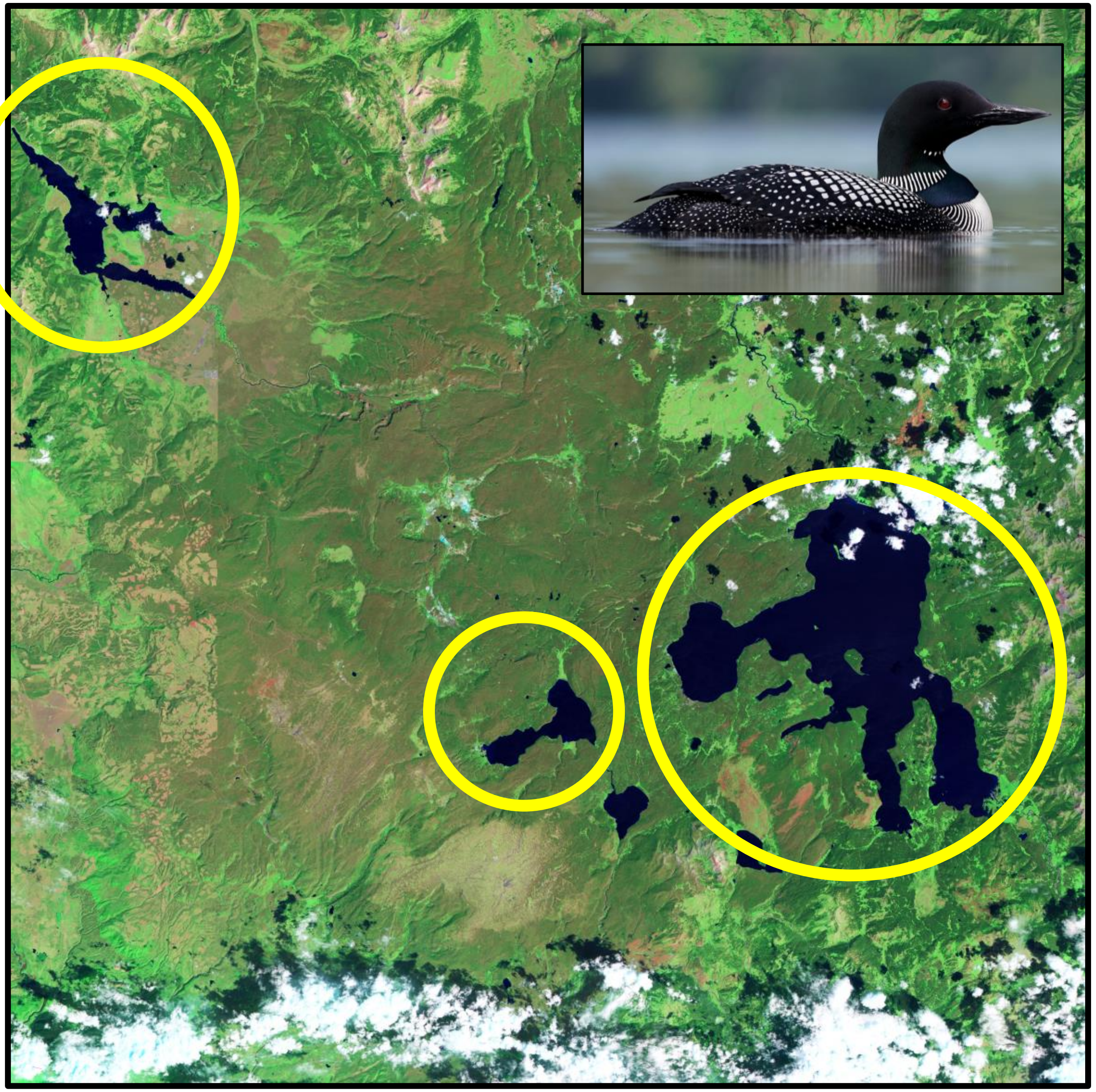
5/29/2015	1	1	82	106
6/1/2015	1	2	58	107
6/1/2015	1	2	68	102
6/1/2015	1	2	76	108
6/1/2015	1	2	75	101
6/1/2015	1	2	67	109
6/1/2015	1	2	81	110



RMark Workshop – Individual Capture Histories

Pond	Survey	Tag
1	1	100
1	2	100
1	3	100
1	4	100
1	1	101
1	3	101
1	2	102
1	4	102

Tag	Survey 1	Survey 2	Survey 3	Survey 4
100	1	1	1	1
101	1	0	1	0
102	0	1	0	1

RMark Workshop – Individual Capture Histories

Pond	Survey	Tag
1	1	100
1	2	100
1	3	100
1	4	100
1	1	101
1	3	101
1	2	102
1	4	102

Tag	Survey 1	Survey 2	Survey 3	Survey 4
100	1	1	1	1
101	1	0	1	0
102	0	1	0	1

RMark Workshop – Individual Capture Histories

Pond	Survey	Tag
1	1	100
1	2	100
1	3	100
1	4	100
1	1	101
1	3	101
1	2	102
1	4	102

Tag	Survey 1	Survey 2	Survey 3	Survey 4
100	1	1	1	1
101	1	0	1	0
102	0	1	0	1

Toad 100: **1111**

Toad 101: **1010**

Toad 102: **0101**

RMark Workshop – Closed versus Open populations

“Closed”

0 1 0 0 0 1 1 1 0

No gains and losses during the nine surveys

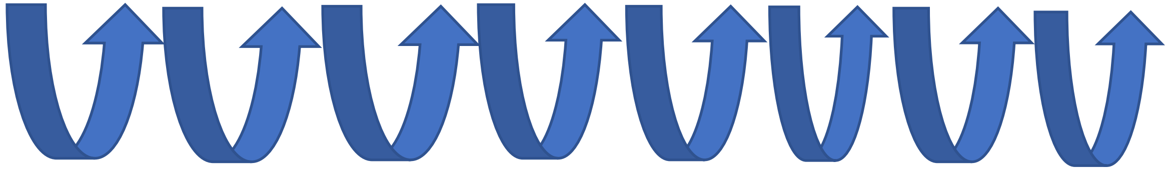
Primary periods = 1

RMark Workshop – Closed versus Open populations

“Closed” 0 1 0 0 0 1 1 1 0 Primary periods = 1

No gains and losses during the nine surveys

“CJS” 0 1 0 0 0 1 1 1 0 Primary periods = 9



Open to gains and losses between all surveys

RMark Workshop – Closed versus Open populations

"Closed" 0 1 0 0 0 1 1 1 0 Primary periods = 1

No gains and losses during the nine surveys

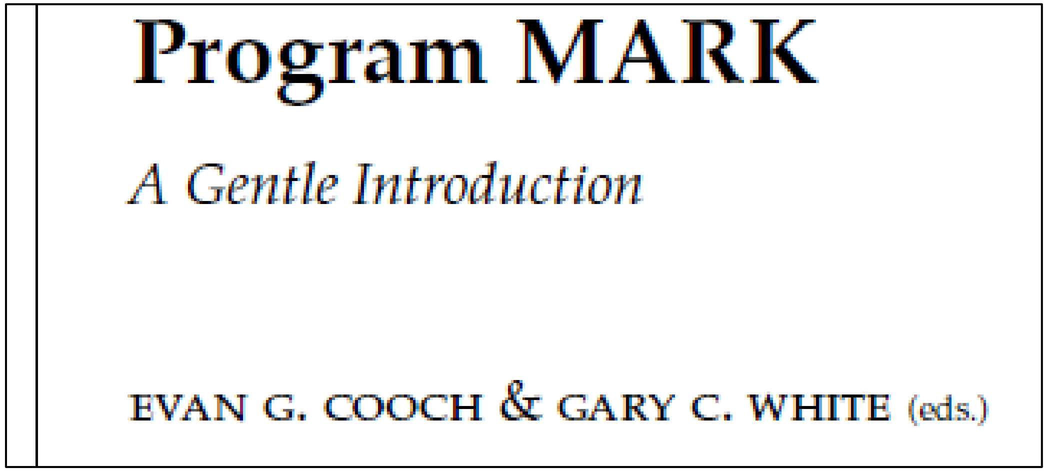
"CJS" 0 1 0 0 0 1 1 1 0 Primary periods = 9

Open to gains and losses between all surveys

"Robust" 0 1 0 0 0 1 1 1 0 Primary periods = 3

Closed within primary periods, open between primary periods

RMark Workshop – Closed Population Estimation



Chapter 14 – Closed population capture-recapture models

Appendix C – RMark, an alterative approach to building linear models in MARK

RMark Workshop – Closed Population Estimation

STATISTICAL INFERENCE FROM CAPTURE DATA ON CLOSED ANIMAL POPULATIONS

David L. Otis,[1] *Kenneth P. Burnham,*[2] *Gary C. White,*[3] *and David R. Anderson*

Utah Cooperative Wildlife Research Unit, Utah State University, Logan, Utah 84322

CONTENTS

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[3] Present address: Los Alamos Scientific Laboratory, Los Alamos, New Mexico 87545.

Biometrika (1989), 76, 1, *pp.* 133–40
Printed in Great Britain

On the statistical analysis of capture experiments

BY R. M. HUGGINS

Department of Statistics, La Trobe University, Bundoora, Victoria 3083, Australia

SUMMARY

A procedure is given for estimating the size of a closed population in the presence of heterogeneous capture probabilities using capture-recapture data when it is possible to model the capture probabilities of individuals in the population using covariates. The results include the estimation of the parameters associated with the model of the capture probabilities and the use of these estimated capture probabilities to estimate the population size. Confidence intervals for the population size using both the asymptotic normality of the estimator and a bootstrap procedure for small samples are given.

Some key words: Bootstrap; Capture experiment; Population size estimation; Variable capture probability.

1. INTRODUCTION

This work is concerned with the use of data from capture-recapture experiments to estimate the size of a closed population with heterogeneous capture probabilities modelled using covariates. Such an approach differs from those in the literature. Whilst Seber (1982) and Otis et al. (1978) give many techniques, all except the jackknife procedures of Burnham & Overton (1978), detailed by Otis et al. (1978), depend on homogeneous capture probabilities. The necessity of this homogeneity assumption when using methods based on the full likelihood is clear from its form.

Let a population consist of $i = 1, \ldots, \nu$ individuals which may be captured on occasions $j = 1, \ldots, t$ with probabilities Λ_{ij} that individual i is captured on trapping occasion j. It is crucial that the individuals behave independently. Then the full likelihood is

$$L^* = K \prod_{i=1}^{\nu} \prod_{j=1}^{t} \Lambda_{ij}^{\Delta_{ij}} (1-\Lambda_{ij})^{(1-\Delta_{ij})},$$

where $\Delta_{ij} = 1$ if individual i is captured on occasion j and 0 otherwise, and K may depend on ν but does not depend on any of the parameters which may be involved in the Λ_{ij}. Letting $i = 1, \ldots, n$ denote the captured individuals and $i = n+1, \ldots, \nu$ the individuals not captured during the course of the trapping experiment, we may write

$$L^* = K \prod_{i=1}^{n} \prod_{j=1}^{t} \Lambda_{ij}^{\Delta_{ij}} (1-\Lambda_{ij})^{(1-\Delta_{ij})} \prod_{i=n+1}^{\nu} \prod_{j=1}^{t} (1-\Lambda_{ij}).$$

It is clear from this partitioning of the likelihood that without some homogeneity assumption no expression for the contribution to the likelihood from the uncaptured individuals may be found and in general no maximum likelihood estimate of ν will be available.

To illustrate our methods we consider a linear logistic model for the capture probabilities,

$$\Lambda_{ij} = \frac{\exp(\beta_0 + \beta_1 z_i + \beta_2 x_j + \alpha z_{ij})}{1 + \exp(\beta_0 + \beta_1 z_i + \beta_2 x_j + \alpha z_{ij})},$$

RMark Workshop

Model 2 – Cormack-Jolly-Seber Model

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

RMark Workshop – Lesson Structure

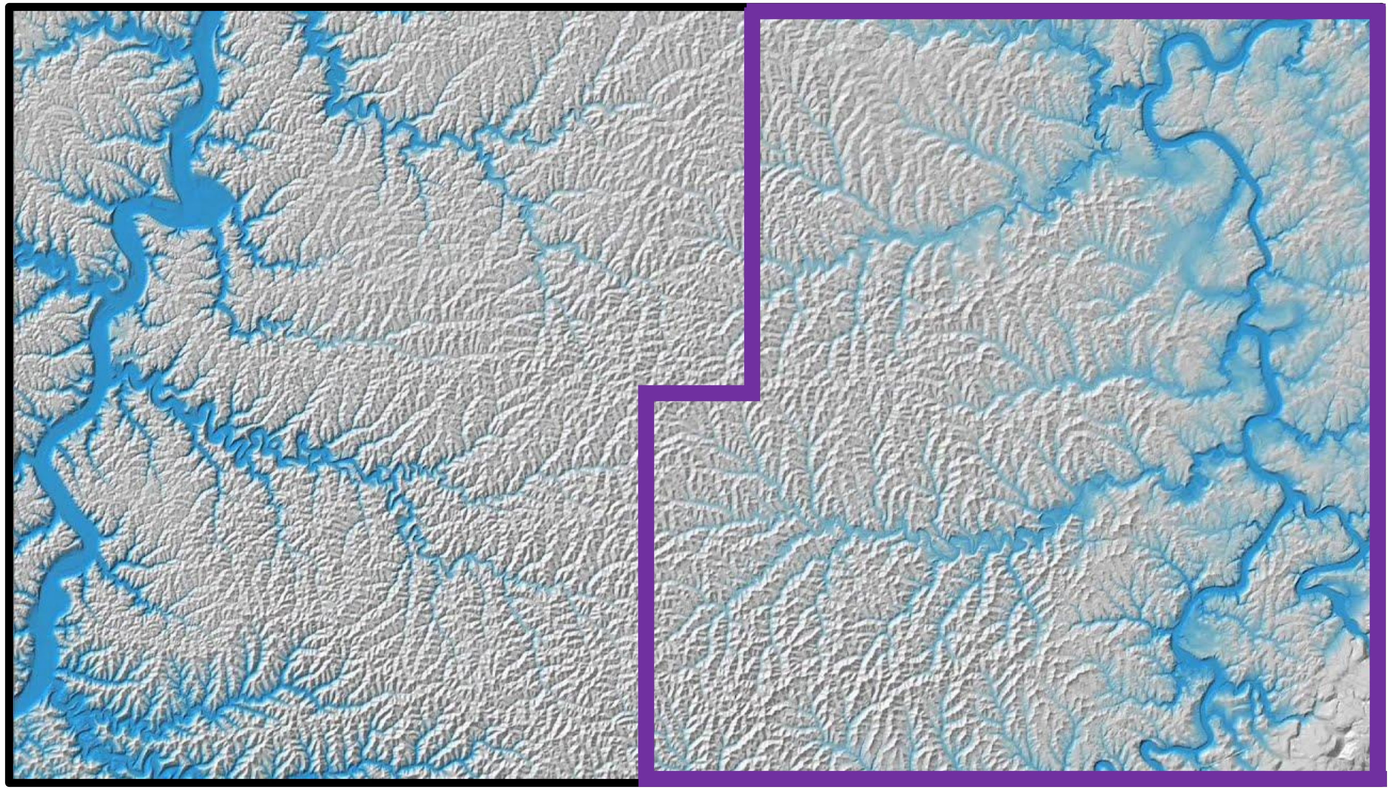
1. Question
2. Field Data
3. Format Data for Analysis
4. Fit Population Model
5. Examine Output and Visualize Results

*steps 3-5 in Program R

RMark Workshop – Cormack-Jolly-Seber Model

1. Question

Does brook trout survival differ in a national park versus land developed for energy extraction?



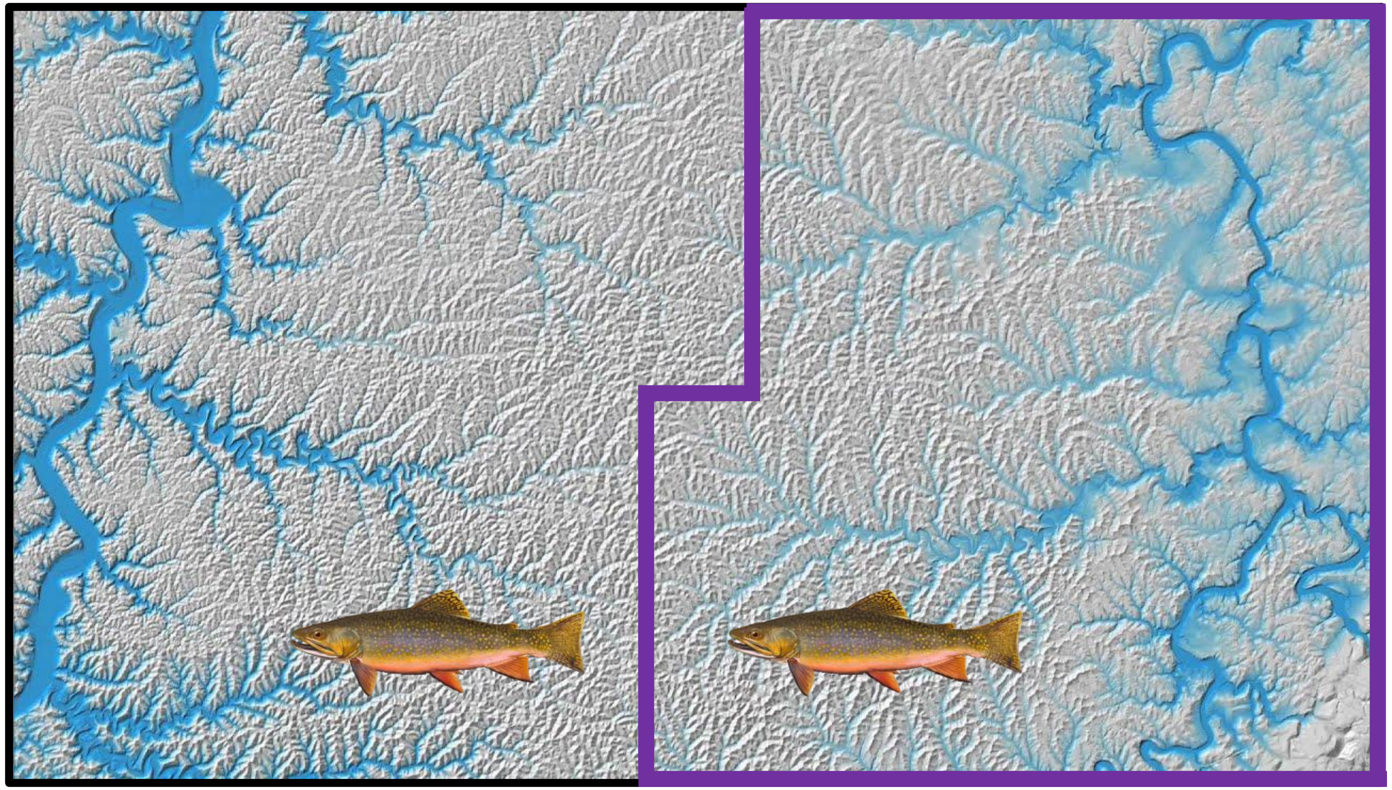
Duane Raver, USFWS

RMark Workshop – Cormack-Jolly-Seber Model

1. Question

Does brook trout survival differ in a national park versus land developed for energy extraction?

Date	Location	Survey	Tag

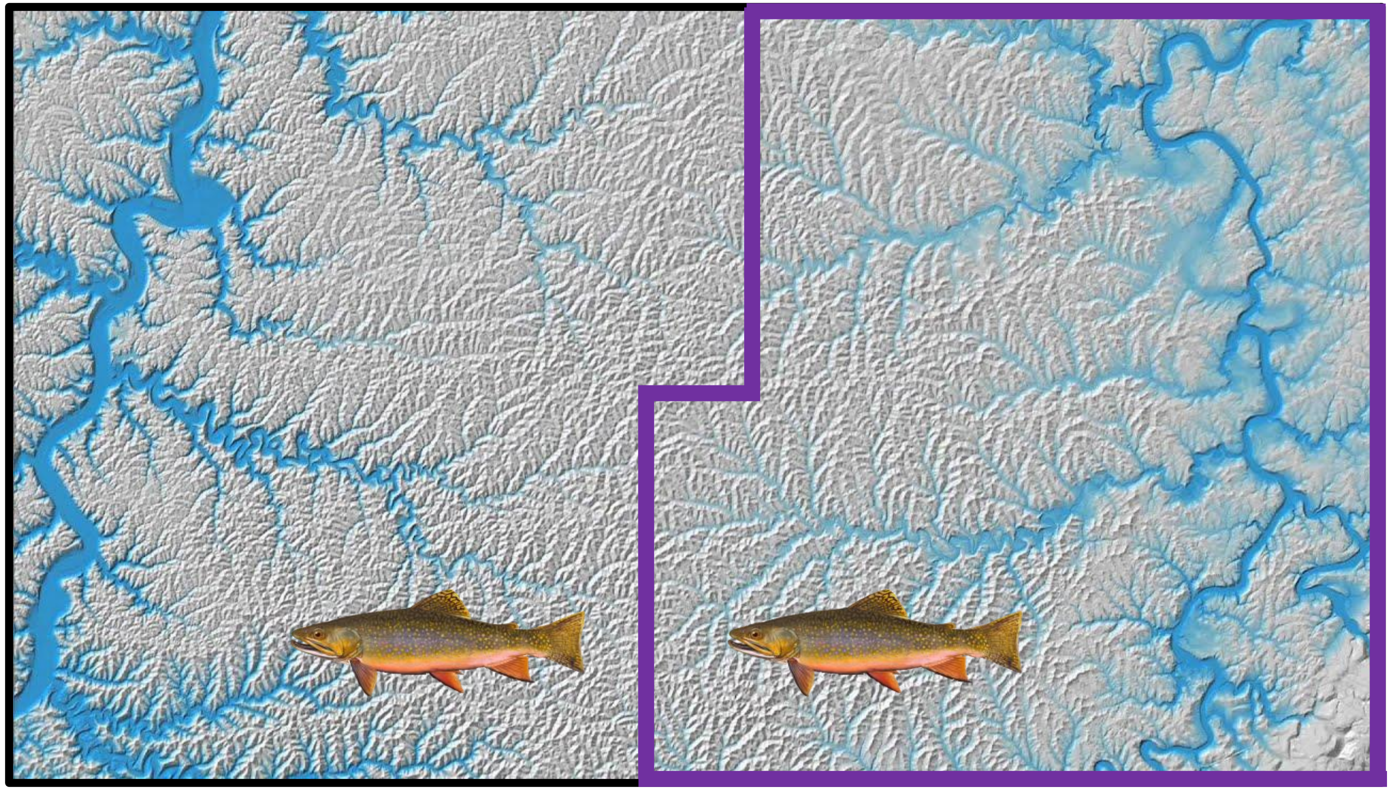


RMark Workshop – Cormack-Jolly-Seber Model

1. Question

Does brook trout survival differ in a national park versus land developed for energy extraction?

Date	Location	Survey	Tag
6/5/2015	National Park	1	

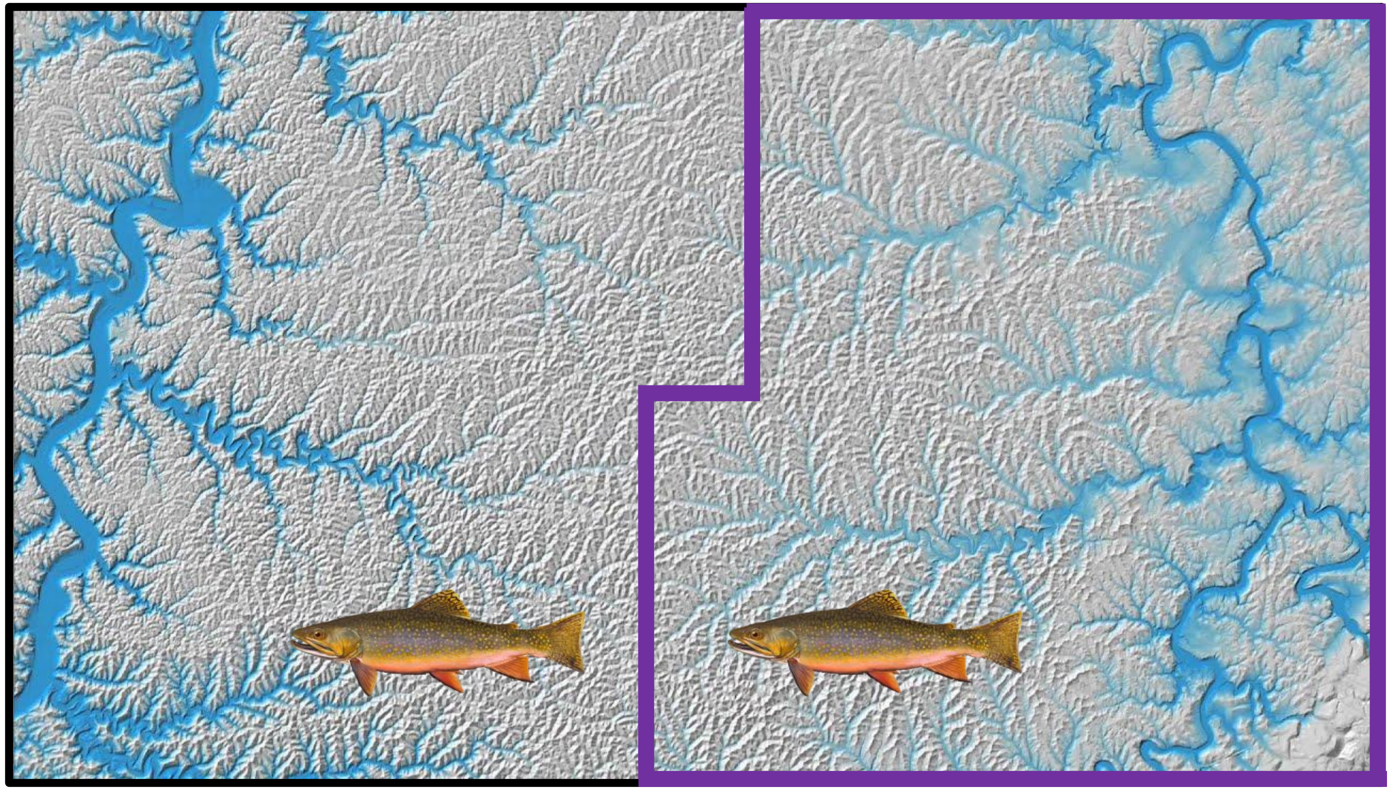


RMark Workshop – Cormack-Jolly-Seber Model

1. Question

Does brook trout survival differ in a national park versus land developed for energy extraction?

Date	Location	Survey	Tag
6/5/2015	National Park	1	100



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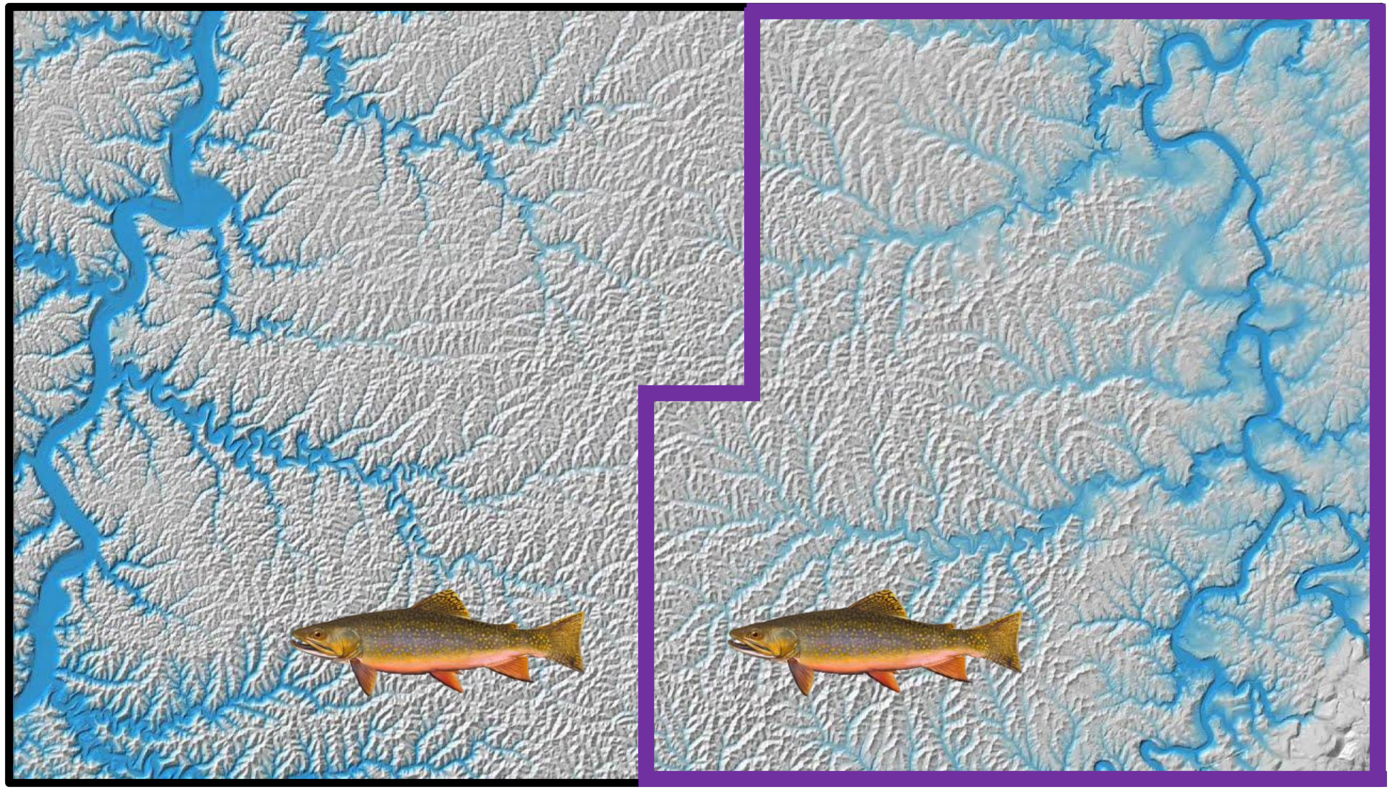
1. Question

Does brook trout survival differ in a national park versus land developed for energy extraction?

Date	Location	Survey	Tag
6/5/2015	National Park	1	100
6/5/2015	National Park	1	101
6/5/2015	National Park	1	102
6/5/2015	National Park	1	103
6/5/2015	National Park	1	104
6/5/2015	National Park	1	105
6/5/2015	National Park	1	106
6/5/2015	National Park	1	107



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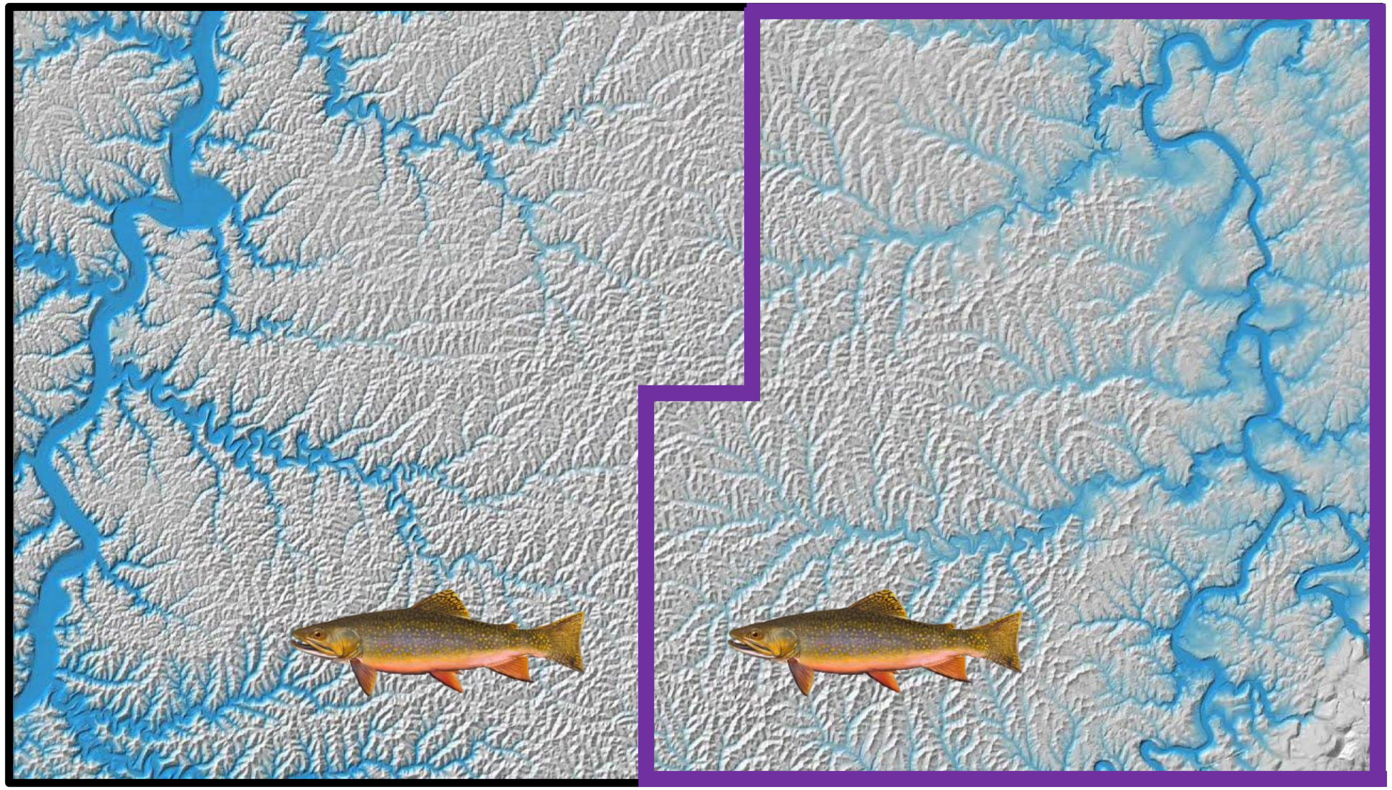
Date	Location	Survey	Tag
6/5/2015	National Park	1	100
6/5/2015	National Park	1	101
6/5/2015	National Park	1	102
6/5/2015	National Park	1	103
6/5/2015	National Park	1	104
6/5/2015	National Park	1	105
6/5/2015	National Park	1	106
6/5/2015	National Park	1	107
6/1/2016	National Park	2	



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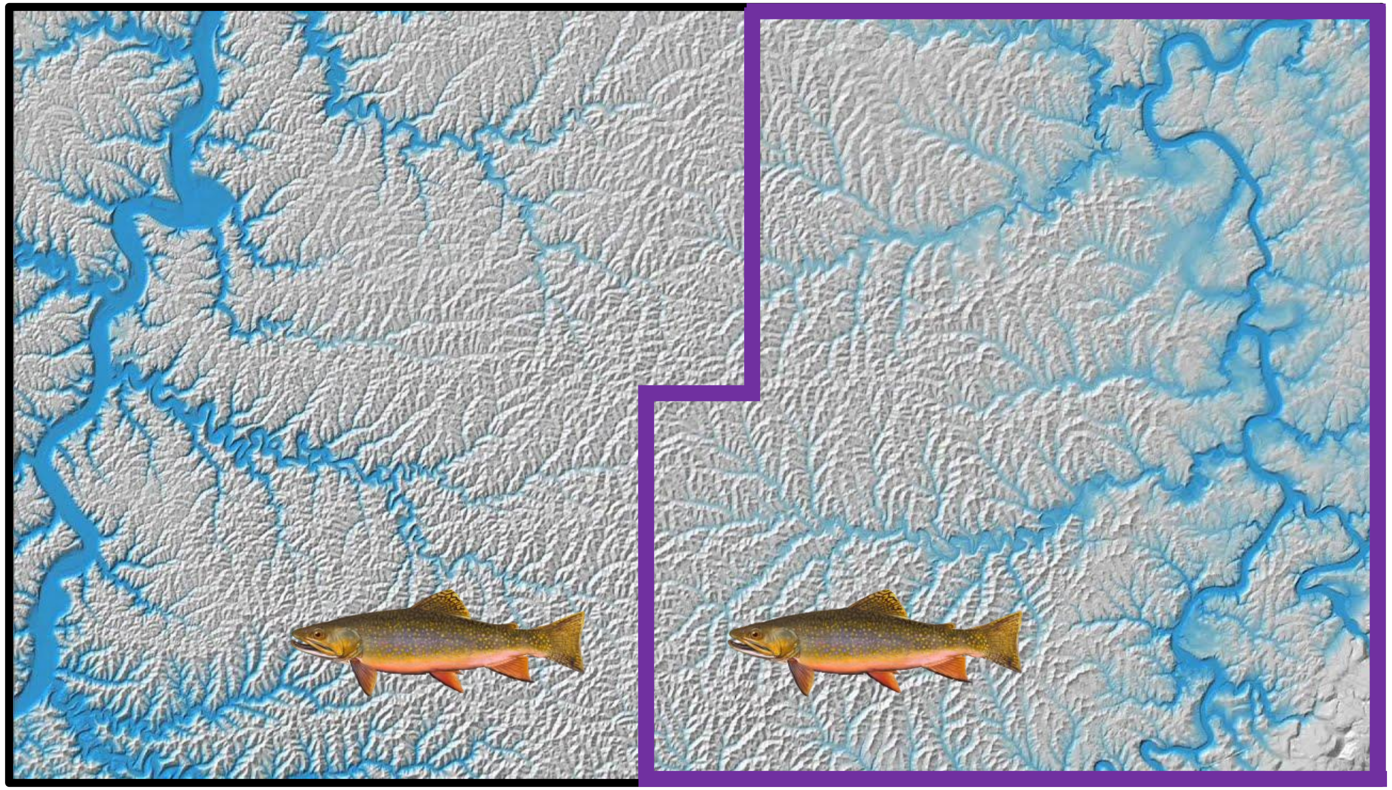
6/5/2015	National Park	1	107
6/1/2016	National Park	2	108



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6/1/2016	National Park	2	108
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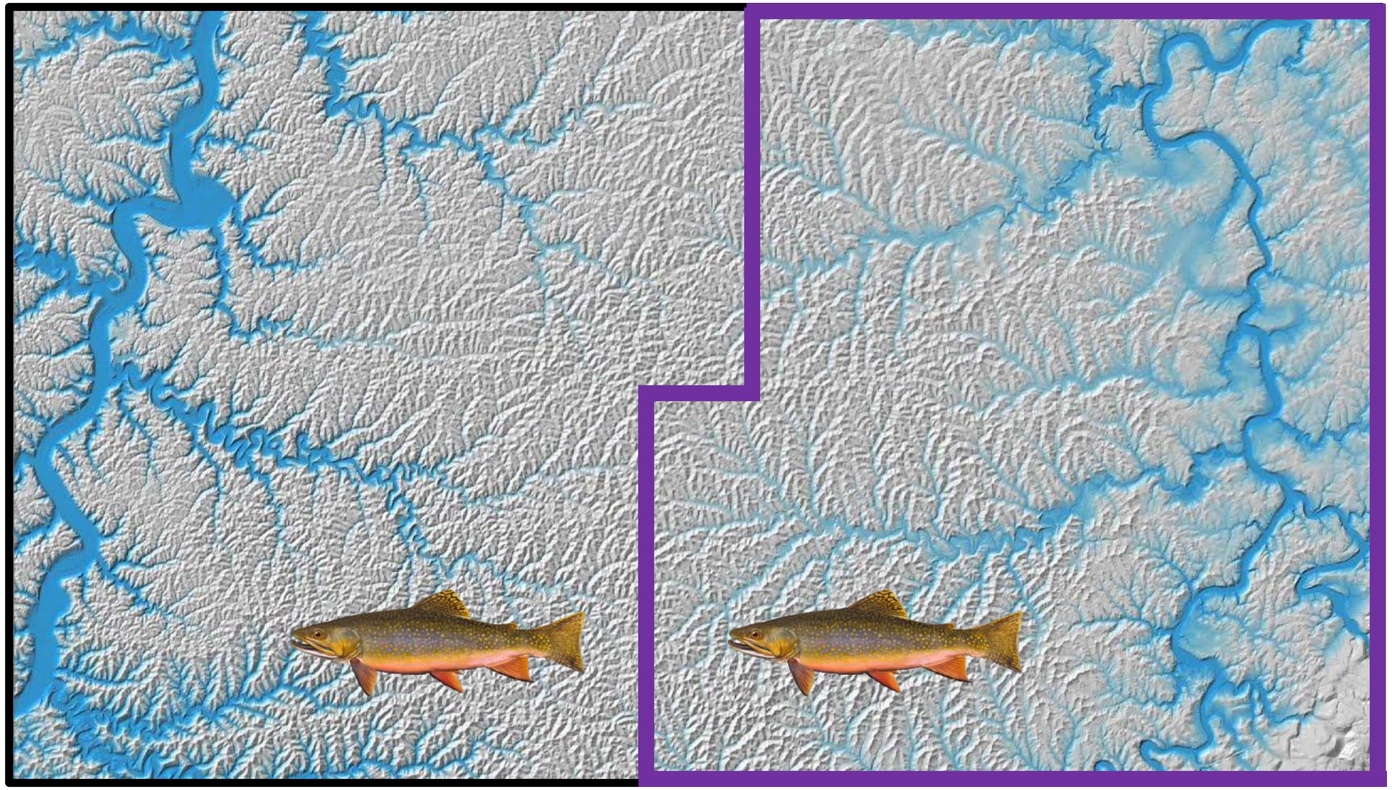
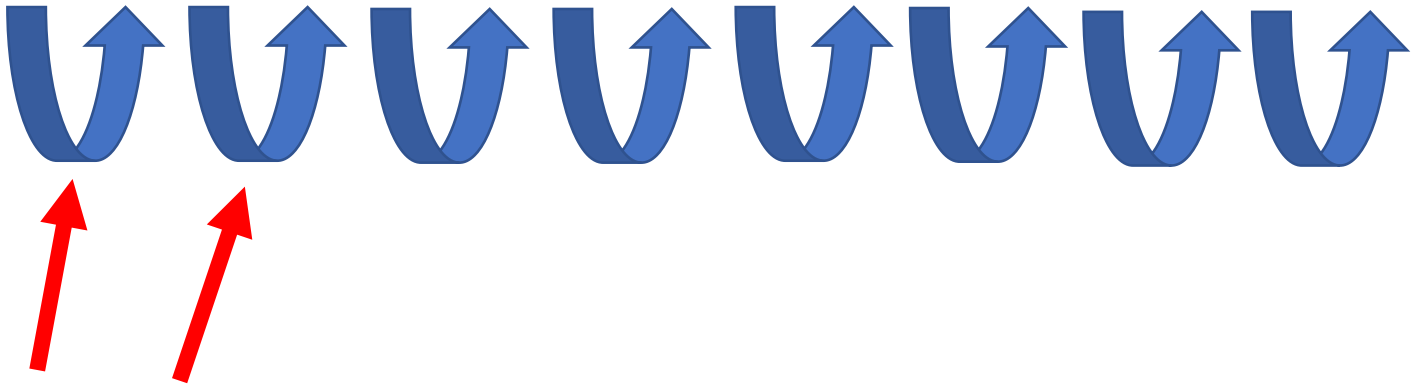
6/1/2016	National Park	2	105



Using our terminology, we can think of **CJS models** as <u>fully open models</u> (with no closed periods)

Capture History = 0 1 0 0 0 1 1 1 0



Population is open to gains and losses between every survey

RMark Workshop – Cormack-Jolly-Seber Model

<u>Two parameters:</u>

p = capture probability

Phi = apparent survival probability

apparent because we cannot separate mortality from permanent emigration (i.e., don't know if animal died or just left the study area)

So, *Phi* is the probability of surviving and remaining in the study area between t and t+1

Apparent survival is usually less than true survival:

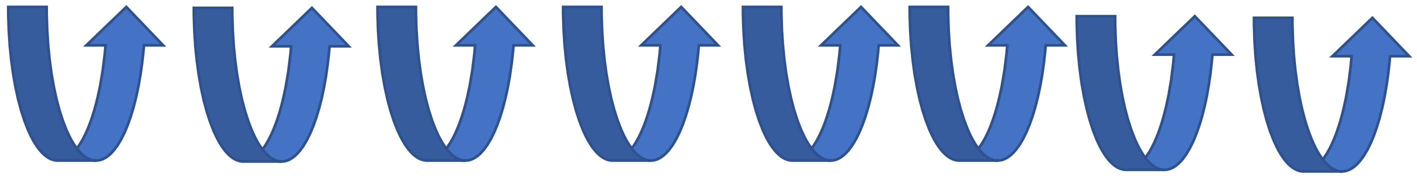
Phi = S x F

Phi = S x (1 – E)

0.90 = 0.9 x 1.0

0.45 = 0.9 x 0.5

Capture History = **0 1 0 0 0 1 1 1 0**



Population is open to gains and losses between every survey

RMark Workshop – Cormack-Jolly-Seber Model

ECOLOGICAL MONOGRAPHS
ECOLOGICAL SOCIETY OF AMERICA

Article

Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies

Jean-Dominique Lebreton, Kenneth P. Burnham, Jean Clobert, David R. Anderson

First published: 01 March 1992 | https://doi.org/10.2307/2937171 | Citations: 1,961

The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 135, 2018, pp. 299–313
DOI: 10.1642/AUK-17-91.1

RESEARCH ARTICLE

Age effects on survival of Amazon forest birds and the latitudinal gradient in bird survival

Alejandra Pizarro Muñoz,[1] Marc Kéry,[2] Pedro Vitor Martins,[3] and Gonçalo Ferraz[1]*

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[2] Swiss Ornithological Institute, Sempach, Switzerland
[3] Klamath Bird Observatory, Ashland, Oregon, USA
* Corresponding author: goncalo.ferraz@ufrgs.br

Submitted May 19, 2017; Accepted December 27, 2017; Published March 7, 2018

ABSTRACT
The search for explanations of the well-documented positive relationship between latitude and avian clutch size has created the expectation that tropical birds should balance their smaller clutch sizes with relatively high survival probabilities. So far, efforts to detect a latitudinal gradient in survival have found no statistical support, leading to the hypothesis that a gradient may be present in the survival of juveniles alone. Such a gradient could be masked by the data on adults when field records make no distinction between ages. We aimed to (1) assess the effect of age on survival of tropical birds by estimating age-specific annual apparent survival probabilities for a set of 40 passerine understory species from the central Brazilian Amazon and (2) test the hypothesis of a latitudinal gradient in adult survival with a meta-analysis of tropical and temperate-zone forest passerine survival probabilities at study areas from Peru to Alaska. We estimated age-specific survival using a hierarchical, multispecies Cormack-Jolly-Seber (CJS) model that treats species-specific parameters as random effects. To extend our analysis to data on birds of unknown age at the time of banding, we developed a novel CJS model with a mixture component for the survival of birds of unknown age. We found a strong effect of age on survival at our site, with juveniles having lower survival than adults. The meta-analysis of 342 survival estimates from 175 species and a latitude span of >60 degrees revealed a negative effect of latitude on survival, which supports the widely accepted hypothesis that, on average, tropical birds have higher annual survival than their temperate counterparts. We conclude that there is no need for an alternative latitudinal trend in juvenile survival to account for the general trend in clutch size.

RMark Workshop – Cormack-Jolly-Seber Model

Comparison of survival rates between populations of the White Stork *Ciconia ciconia* in Central Europe

S. Kanyamibwa, F. Bairlein and A. Schierer

Kanyamibwa, S., Bairlein, F. and Schierer, A. 1993. Comparison of survival rates between populations of the White Stork *Ciconia ciconia* in Central Europe. – Ornis Scand. 24: 297–302.

Many studies have shown that the decline in numbers of the White Stork populations has been stronger in the western part of its European breeding range than in the eastern. Using recent developments of capture-recapture methods to estimate survival rates, including in particular a study of relationships with environmental variables and a comparison between populations, this paper examines changes in survival rates of some European populations of the White Stork. Survival rates of all populations wintering in the Sahelian zone were positively linked to the amount of rainfall in their wintering area. However, the survival rate of the population wintering in East Africa was not significantly related to the amount of rainfall there. No significant effect of the amount of rainfall in the breeding area on survival rate was observed. Differences in survival rates were observed within western populations and between the western and eastern populations. An effect of age was only significant in the Alsacian population. No significant difference in survival rates was found between male and female storks.

S. Kanyamibwa, Wildlife Conservation International, Projet Conservation de la Foret de Nyengwe (PCFN), B.P. 363 Cyangugu, Rwanda. F. Bairlein, Institut für Vogelforschung "Vogelwarte Helgoland", An der Vogelwarte 21, 26386 Wilhelmshaven, Germany. A. Schierer, C.R.B.O., 1 Rue de Mâcon, 6700 Strasbourg, France.

Seasonal dynamic of population survival and its mechanism in Mongolian gerbils（*Meriones unguiculatus*）in the Inner Mongolia agro-pastoral ecotone

LIU Wei[1,2]，ZHONG Wenqin[1]，WANG Dehua[1,2*]

（1 *State Key Lab of Integrated Management of Pest Insects and Rodent*，*Institute of Zoology*，*Chinese Academy of Sciences*，*Beijing* 100101，*China*）

（2 *University of Chinese Academy of Science*，*Beijing* 100049，*China*）

Abstract：Understanding differential and integral effects of climate and population density on vital rates e. g. survival，helps elucidate the ecological and demographic mechanisms underlying animal population dynamics. The Mongolian gerbil（*Meriones unguiculatus*）is one of dominate rodents widely distributed in semi-arid，typical steppes，and desert grasslands in north of China. We studied population dynamics of gerbils under semi-natural conditions using monthly capture-mark-recapture methods from October 2000 to 2004 in agro-pastoral ecotone of south-central Inner Mongolia，China. We used Cormack-Jolly-Seber（CJS）models to estimate apparent survival probability，and analyzed the difference of survival between males and females，or the survival seasonal variations. Additionally，we used multistate（MS）models to test the differ-

基金项目：国家自然科学基金项目（31872232）
作者简介：刘伟（1972－），男，博士，副研究员，主要从事动物种群生态学和行为生态学研究.
收稿日期：2020－04－20；　**修回日期**：2020－05－24
＊通讯作者，Corresponding author，E－mail：wangdh@ ioz. ac. cn

RMark Workshop

Model 3 – Robust Design with Temporary Emigration

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

RMark Workshop – Lesson Structure

1. Question
2. Field Data
3. Format Data for Analysis
4. Fit Population Model
5. Examine Output and Visualize Results

*steps 3-5 in Program R

RMark Workshop – Robust Design with Temporary Emigration

1. Question

Does annual precipitation influence the survival of black-footed ferrets at reintroduction sites?

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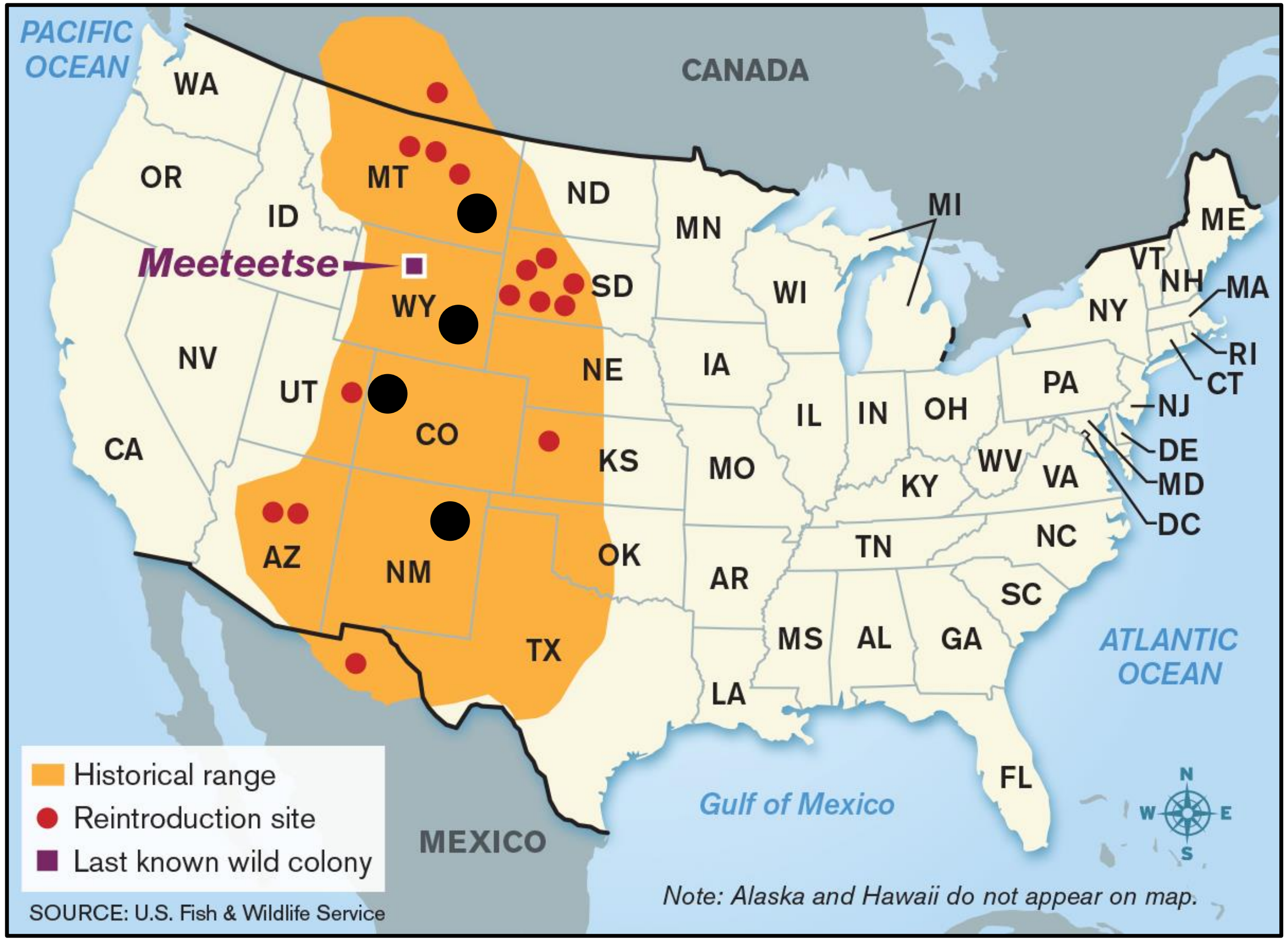


RMark Workshop – Robust Design with Temporary Emigration

1. Question

Does annual precipitation influence the survival of black-footed ferrets at reintroduction sites?

Year	Site	Primary	Secondary	Tag	Precipitation

RMark Workshop – Robust Design with Temporary Emigration

1. Question

Does annual precipitation influence the survival of black-footed ferrets at reintroduction sites?

Year	Site	Primary	Secondary	Tag	Precipitation
2015	MT	1	1	200	990

RMark Workshop – Robust Design with Temporary Emigration

1. Question

Does annual precipitation influence the survival of black-footed ferrets at reintroduction sites?

Year	Site	Primary	Secondary	Tag	Precipitation
2015	MT	1	1	200	990
2015	MT	1	1	201	990
2015	MT	1	1	202	990
2015	MT	1	1	203	990

RMark Workshop – Robust Design with Temporary Emigration

1. Question

Does annual precipitation influence the survival of black-footed ferrets at reintroduction sites?

Year	Site	Primary	Secondary	Tag	Precipitation
2015	MT	1	1	200	990
2015	MT	1	1	201	990
2015	MT	1	1	202	990
2015	MT	1	1	203	990
2015	MT	1	2	204	990
2015	MT	1	2	205	990
2015	MT	1	2	**201**	990
2015	MT	1	2	206	990
2015	MT	1	2	**203**	990

RMark Workshop – Robust Design with Temporary Emigration

1. Question

Does annual precipitation influence the survival of black-footed ferrets at reintroduction sites?

Year	Site	Primary	Secondary	Tag	Precipitation
2015	MT	1	1	200	990
2015	MT	1	1	201	990
2015	MT	1	1	202	990
2015	MT	1	1	203	990
2015	MT	1	2	204	990
2015	MT	1	2	205	990
2015	MT	1	2	**201**	990
2015	MT	1	2	206	990
2015	MT	1	2	**203**	990
2015	MT	1	3	207	990
2015	MT	1	3	208	990
2015	MT	1	3	**200**	990
2015	MT	1	3	209	990

RMark Workshop – Robust Design with Temporary Emigration

Example capture history: **111 000 101 010 011**

Primary periods

2015	2016	2017	2018	2019
111	$\boxed{\textbf{000}}$	**101**	**010**	**011**

Secondary periods

1. Ferret is alive and in the study area, but we just did not capture it

OR

2. Ferret temporarily emigrated from study area, thus was unavailable for capture

*Modeling temporary emigration helps account for differences in capture probability between individuals inside and temporarily outside the study area, which results in less-biased capture probabilities and less bias in estimates of survival probability (Fujiwara & Caswell, 2002).

Correctly Specifying **Time Intervals** for Robust Design in *Rmark* is important!

Capture History = **010001110**

2015			2016			2017		
0	1	0	0	0	1	1	1	0

0 0 1 0 0 1 0 0

Time Intervals = **00100100** (number of surveys minus 1)

Question

What would time intervals be for capture history:

0110100101010

If using robust design and conducted
4 surveys in 2015, 6 in 2016, and 3 in 2018

Capture History = 0110 100101 010

2015		2016		2018
0 1 1 0		1 0 0 1 0 1		0 1 0
0 0 0	1	0 0 0 0 0	2	0 0

Time Intervals = 000100000200 (number of surveys minus 1)

RMark Workshop – More on temporary emigration

In the CJS model, we had apparent survival because we couldn't separate mortality from permanent emigration, so *Phi* = S x F

What we didn't say was that capture probability was actually apparent capture probability because we cannot separate missing an individual available for capture versus an individual being temporarily off the study area, so $p = (1 - y) \times p^*$

Where y is the probability of being off the study area and p* is true capture probability

For example, if $y = 0$ vs $y = 0.5$

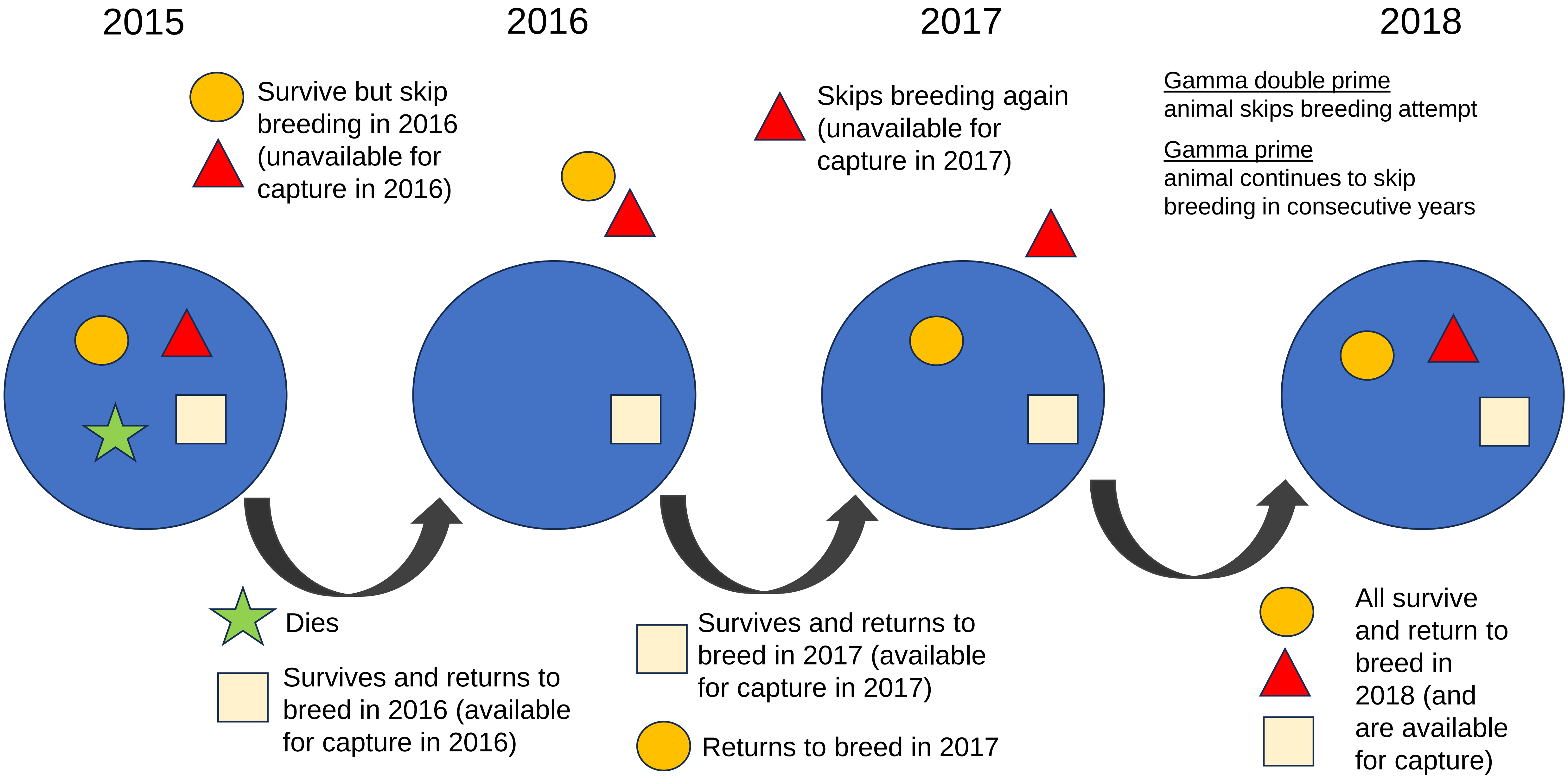
$p = (1 - y) \times p^*$

0.90 = (1 – 0.0) x 0.9 (apparent capture prob is equal to true capture prob)

0.45 = (1 – 0.5) x 0.9 (apparent capture prob is less than true capture prob)

So, let's model temporary emigration explicitly so that we can estimate true capture probability

RMark Workshop – More on temporary emigration



RMark Workshop – Robust Design with Temporary Emigration

Program MARK

A Gentle Introduction

EVAN G. COOCH & GARY C. WHITE (eds.)

CHAPTER 15

The 'robust design'

William Kendall, *USGS Colorado Cooperative Fish & Wildlife Research Unit*

Changes in population size through time are a function of births, deaths, immigration, and emigration. Population biologists have devoted a disproportionate amount of time to models that assume immigration and emigration are non-existent (or, not important). However, modern thinking suggests that these effects are potentially (perhaps generally) quite important. For example, metapopulation dynamics are not possible without immigration and emigration in the subpopulations. A model which allows the estimation of emigration and immigration to a population is therefore of considerable utility.

In this chapter, we consider Pollock's *robust design*, an approach which will allow us considerable flexibility in estimating a very large number of important demographic parameters, including estimates of emigration and immigration. As you might imagine, such a model is bound to be more complicated than most (if not all) of the models we've previously considered, but it brings more biological reality to the analysis of population dynamics.

15.1. Decomposing the probability of subsequent encounter

RMark Workshop – Robust Design with Temporary Emigration

Ecology, 78(2), 1997, pp. 563–578
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ESTIMATING TEMPORARY EMIGRATION USING CAPTURE–RECAPTURE DATA WITH POLLOCK'S ROBUST DESIGN

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Abstract. Statistical inference for capture–recapture studies of open animal populations typically relies on the assumption that all emigration from the studied population is permanent. However, there are many instances in which this assumption is unlikely to be met. We define two general models for the process of temporary emigration: completely random and Markovian. We then consider effects of these two types of temporary emigration on Jolly–Seber estimators and on estimators arising from the full-likelihood approach to robust design data.

Capture–recapture data arising from Pollock's robust design provide the basis for obtaining unbiased estimates of demographic parameters in the presence of temporary emigration, and for estimating the probability of temporary emigration. We present a likelihood-based approach to dealing with temporary emigration that permits estimation under different models of temporary emigration and yields tests for completely random and Markovian emigration. In addition, we use the relationship between capture probability estimates based on closed and open models under completely random temporary emigration to derive three ad hoc estimators for the probability of temporary emigration. Two of these should be especially useful in situations where capture probabilities are heterogeneous among individual animals. Ad hoc and full-likelihood estimators are illustrated for small-mammal capture–recapture data sets.

We believe that these models and estimators will be useful for testing hypotheses about the process of temporary emigration, for estimating demographic parameters in the presence of temporary emigration, and for estimating probabilities of temporary emigration. These latter estimates are frequently of ecological interest as indicators of animal movement and, in some sampling situations, as direct estimates of breeding probabilities and proportions.

Key words: *capture–recapture; demographic parameters;* Microtus pennsylvanicus; *models; open populations;* Peromyscus leucopus; *Pollock's robust design; statistical estimation; temporary emigration.*

Ecology, 83(12), 2002, pp. 3266–3275
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A GENERAL APPROACH TO TEMPORARY EMIGRATION IN MARK–RECAPTURE ANALYSIS

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Abstract. During mark–recapture studies of open populations, animals often temporarily emigrate from study areas. Such temporary emigration can cause biased estimates of survival probabilities. We present a new statistical method to estimate survival probability from the capture histories of marked individuals in the presence of temporary emigration. This method uses stage-structured models that include one or more stages representing the individuals that have temporarily emigrated. Although not all parameters can be estimated in such stage structures, some important parameters are still estimable. Here, we determined the estimability of parameter values from the rank of the Jacobian of the likelihood function. We applied the temporary-emigration mark–recapture method to artificial data, representing various life histories and demonstrated consistency between actual and estimated values. As an example, we used the method to analyze data on reproductive female North Atlantic right whales. The method presented in this paper will be especially useful for studies of seabird, sea turtle, and marine-mammal populations where individuals are sampled only on their breeding grounds.

Key words: *capture–recapture studies; multi-stage mark–recapture method; North Atlantic right whale; stage-structured models; survival probability; temporary emigration; transition probability.*

RMark Workshop – Robust Design with Temporary Emigration

ESTIMATING DETECTION PROBABILITY PARAMETERS FOR PLETHODON SALAMANDERS USING THE ROBUST CAPTURE–RECAPTURE DESIGN

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THEODORE R. SIMONS, Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695-7617, USA
KENNETH H. POLLOCK, Department of Statistics, Biomathematics, and Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695-7617, USA

Abstract: Recent concern over global amphibian population declines has highlighted a need for more extensive, rigorous monitoring programs. Two sources of variation, spatial variation and variation in detection probability, make the design and implementation of effective monitoring programs difficult. We used Pollock's robust design in a 3-year capture–recapture study to estimate detection probability and temporary emigration for Plethodon salamanders in Great Smoky Mountains National Park (Tennessee/North Carolina), USA. We used 12 competing models to determine the importance of temporary emigration, and we explored temporal and behavioral effects on conditional capture probabilities. The top 4 models all included random temporary emigration, and Akaike model weights indicated that this parameter was the most important. Models that contained behavioral effects in capture probabilities were selected more often than models with equal capture probabilities for marked and previously unmarked individuals. The "best" model contained random emigration and behavioral effects and was selected 4 times as often as any other model. When we included Markovian emigration, the probability of emigrating from the surface usually was less than the probability of remaining an emigrant (73% of site-years). Markovian emigration estimates often were similar and always had overlapping confidence intervals, thus the Markovian model rarely was chosen over the random emigration models (only 9.6% of site-years). Our study is the first to formally estimate temporary emigration in terrestrial salamander populations, and our results verify that significant proportions of terrestrial salamander populations are subterranean. We determined that the probability of capturing salamanders on the surface may also vary temporally within a sampling season. Therefore, we caution against using unadjusted count indices to compare salamander populations over time or space unless detection probabilities are estimated. Temporary emigration models will improve abundance estimates when a large proportion of the population is unavailable for capture during a given sampling period.

JOURNAL OF WILDLIFE MANAGEMENT 68(1):1–13

Key words: capture–recapture, detection probability, Great Smoky Mountains National Park, model selection, plethodontid salamanders, Pollock's robust design, population monitoring, program MARK, temporary emigration.

Ecology, 87(4), 2006, pp. 1048–1056
© 2006 by the Ecological Society of America

ESTIMATION OF TEMPORARY EMIGRATION IN MALE TOADS

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[2]*Colorado State University, Department of Fishery and Wildlife Biology, Wagar Building Rm. 136, Fort Collins, Colorado 80523 USA*
[3]*USGS, Northern Rocky Mountain Science Center, Aldo Leopold Wilderness Research Institute, 790 E. Beckwith Avenue, Missoula, Montana 59801 USA*
[4]*Colorado Natural Heritage Program, Colorado State University, Campus Delivery 8002, Fort Collins, Colorado 80523 USA*

Abstract. Male boreal toads (*Bufo boreas*) are thought to return to the breeding site every year but, if absent in a particular year, will be more likely to return the following year. Using Pollock's robust design we estimated temporary emigration (the probability a male toad is absent from a breeding site in a given year) at three locations in Colorado, USA: two in Rocky Mountain National Park and one in Chaffee County. We present data that suggest that not all male toads return to the breeding site every year. Our analyses indicate that temporary emigration varies by site and time (for example, from 1992 to 1998, the probability of temporary emigration ranged from 10% to 29% and from 3% to 95% at Lost Lake and Kettle Tarn, respectively). Although the results provide weak evidence that males are more likely to return after a year's hiatus, a general pattern of state-dependent temporary emigration was not supported. We also hypothesized relationships between temporary emigration and a number of weather variables. While some competitive models included weather covariates, imprecise and variable estimates of the effects of these covariates precluded fully defining their impact on temporary emigration.

Key words: amphibian; boreal toad; Bufo boreas; *capture–recapture; Colorado, USA; robust design; temporary emigration.*

RMark Workshop

Model 5 – Multi-state models

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

RMark Workshop – Lesson Structure

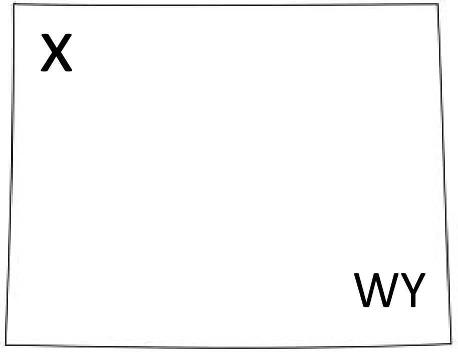
1. Question
2. Field Data
3. Format Data for Analysis
4. Fit Population Model
5. Examine Output and Visualize Results

*steps 3-5 in Program R

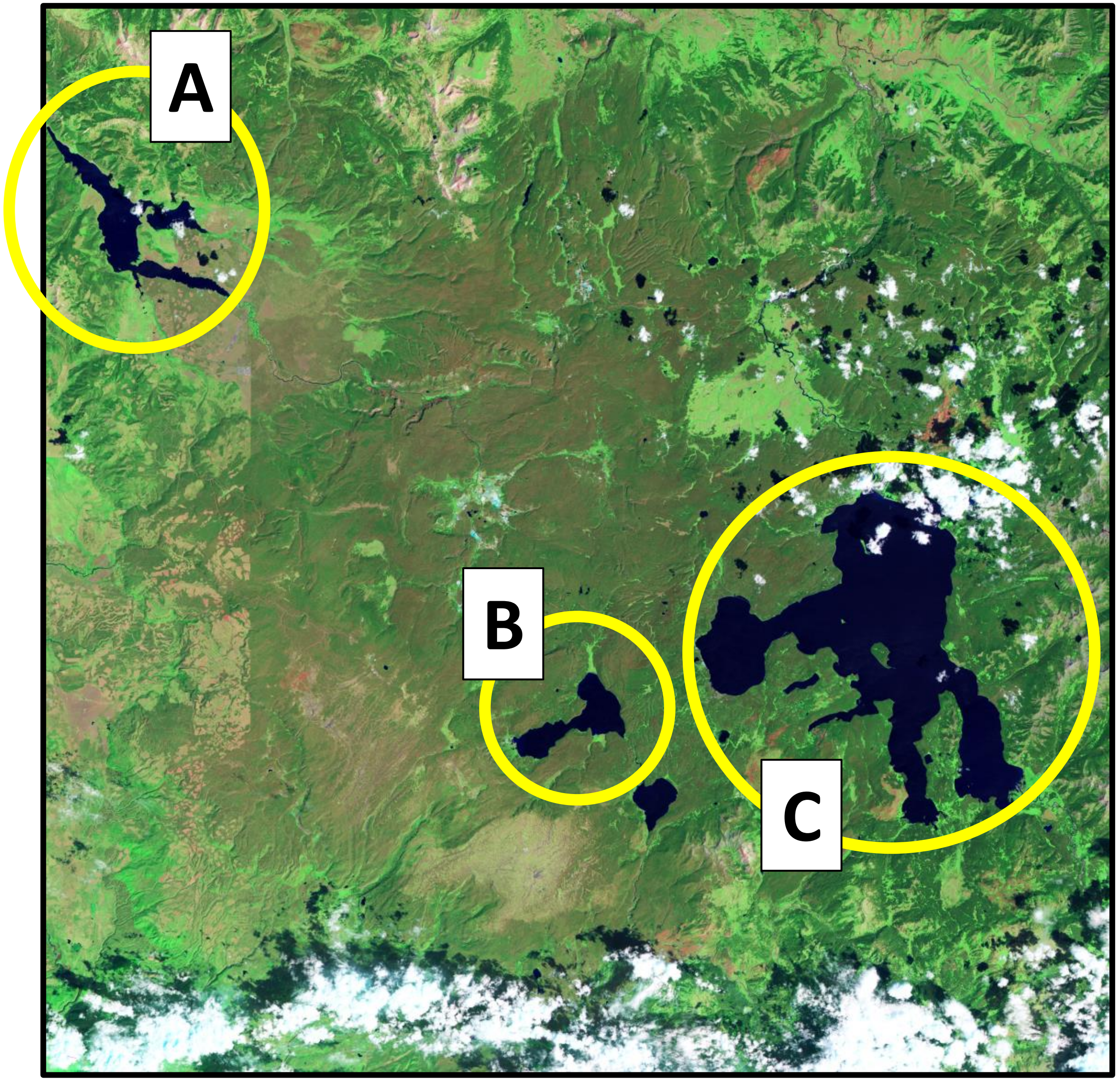
RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?



J. Grant

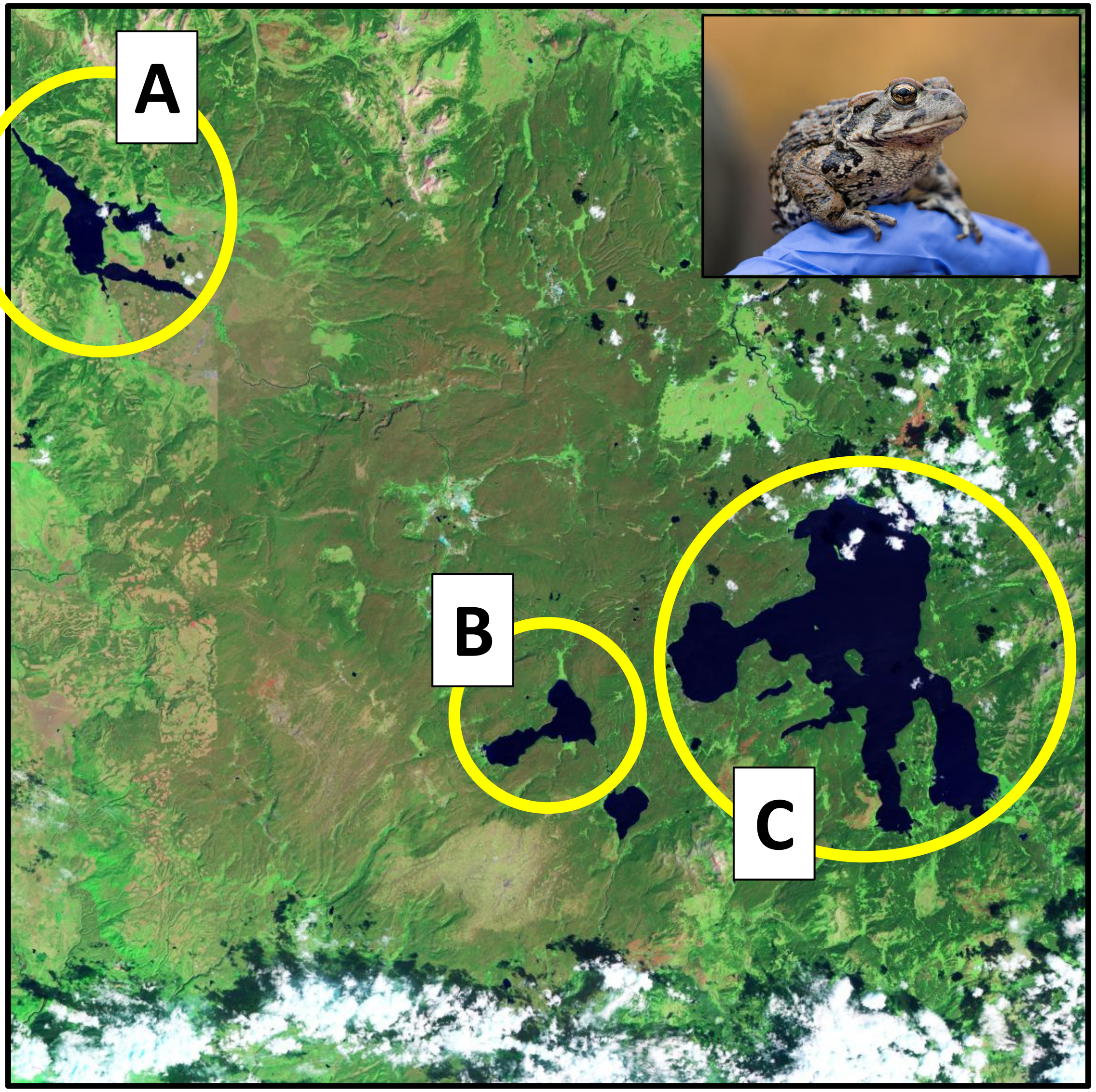


RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?

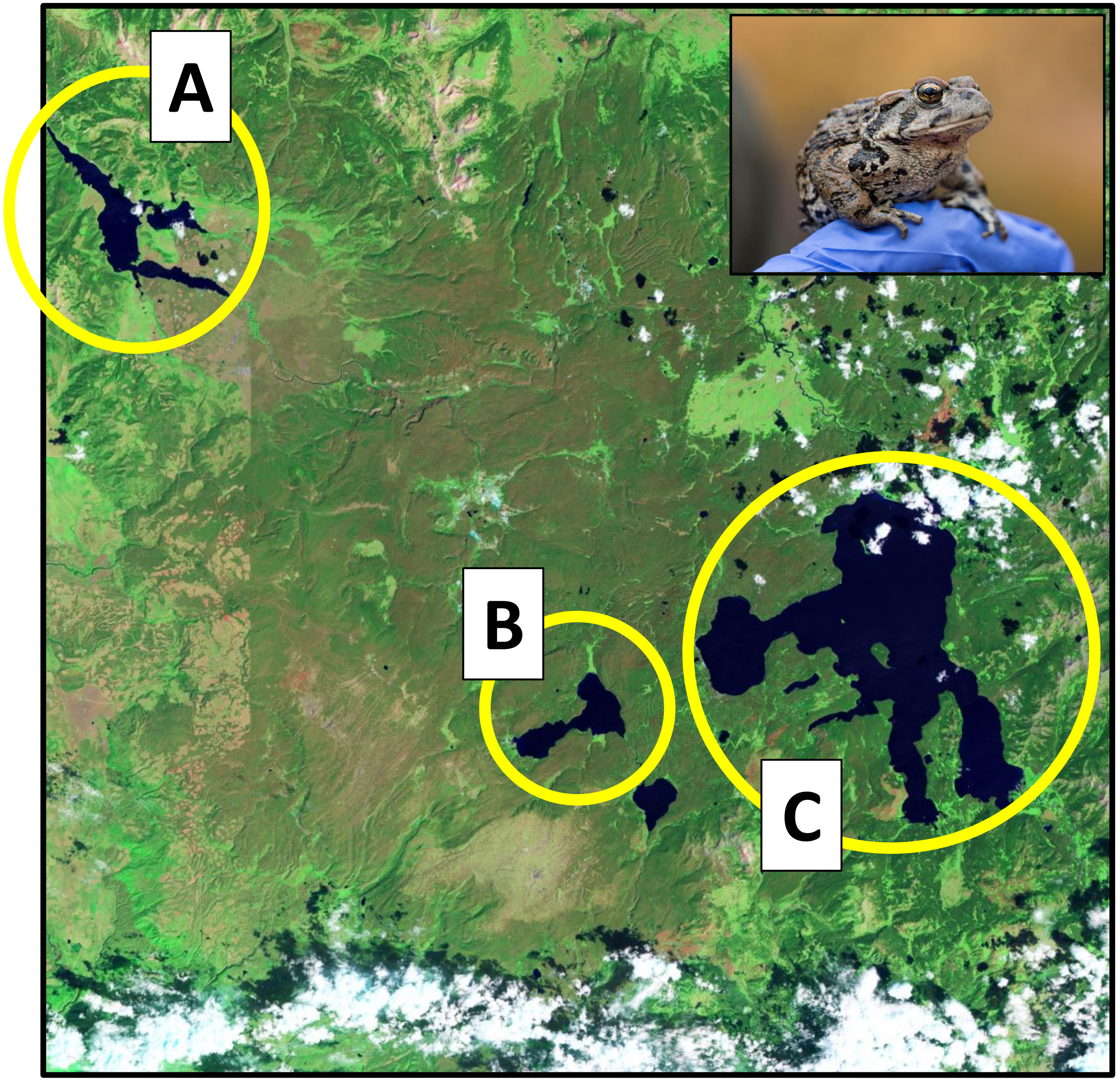
Date	Pond	Survey	Tag



RMark Workshop – Multi-state capture-recapture model

1. Question How does boreal toad dispersal vary among three study ponds?

Date	Pond	Survey	Tag
5/25/2016	A	1	100

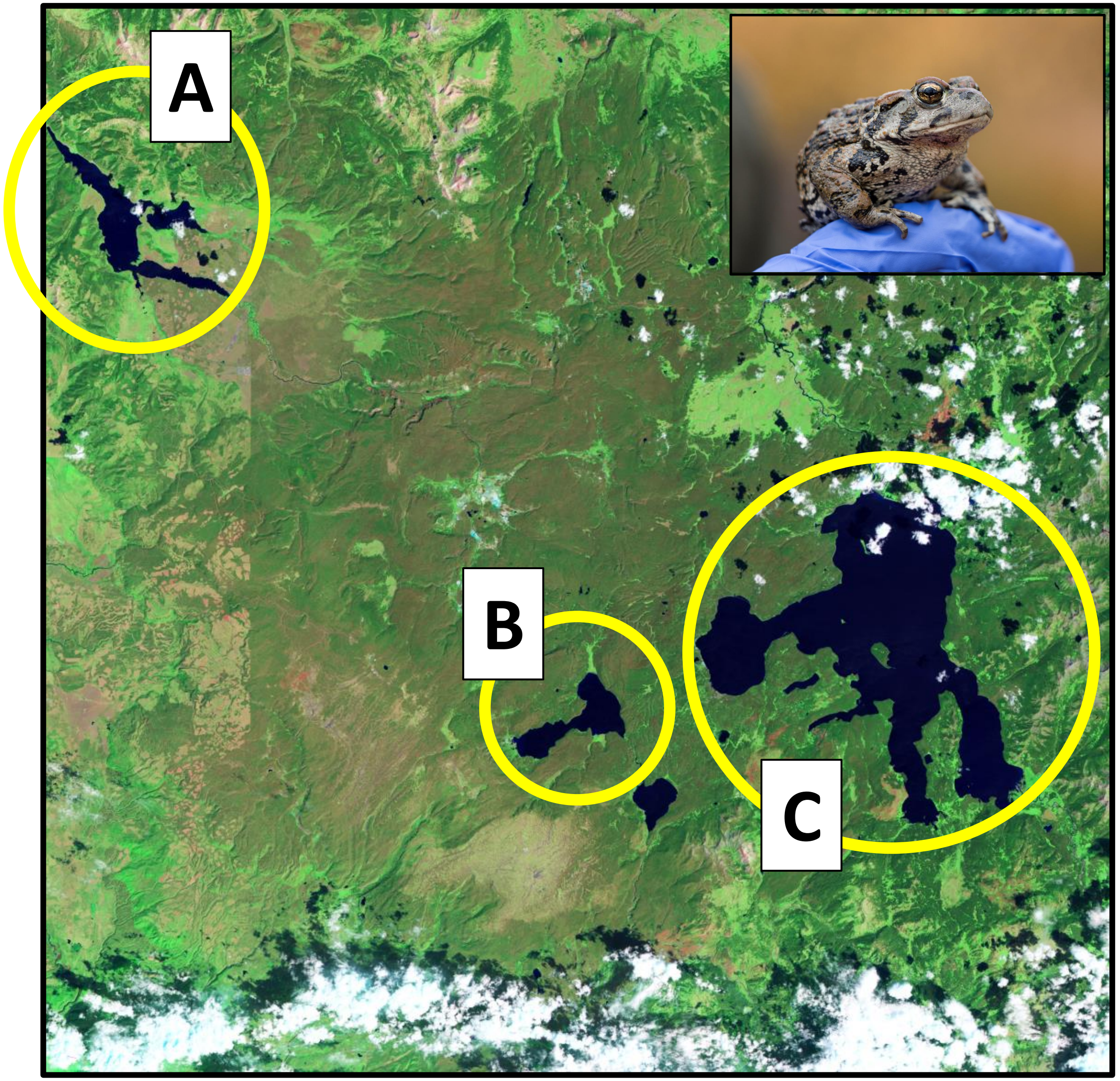


RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?

Date	Pond	Survey	Tag
5/25/2016	A	1	100
5/25/2016	A	1	101
5/25/2016	A	1	102

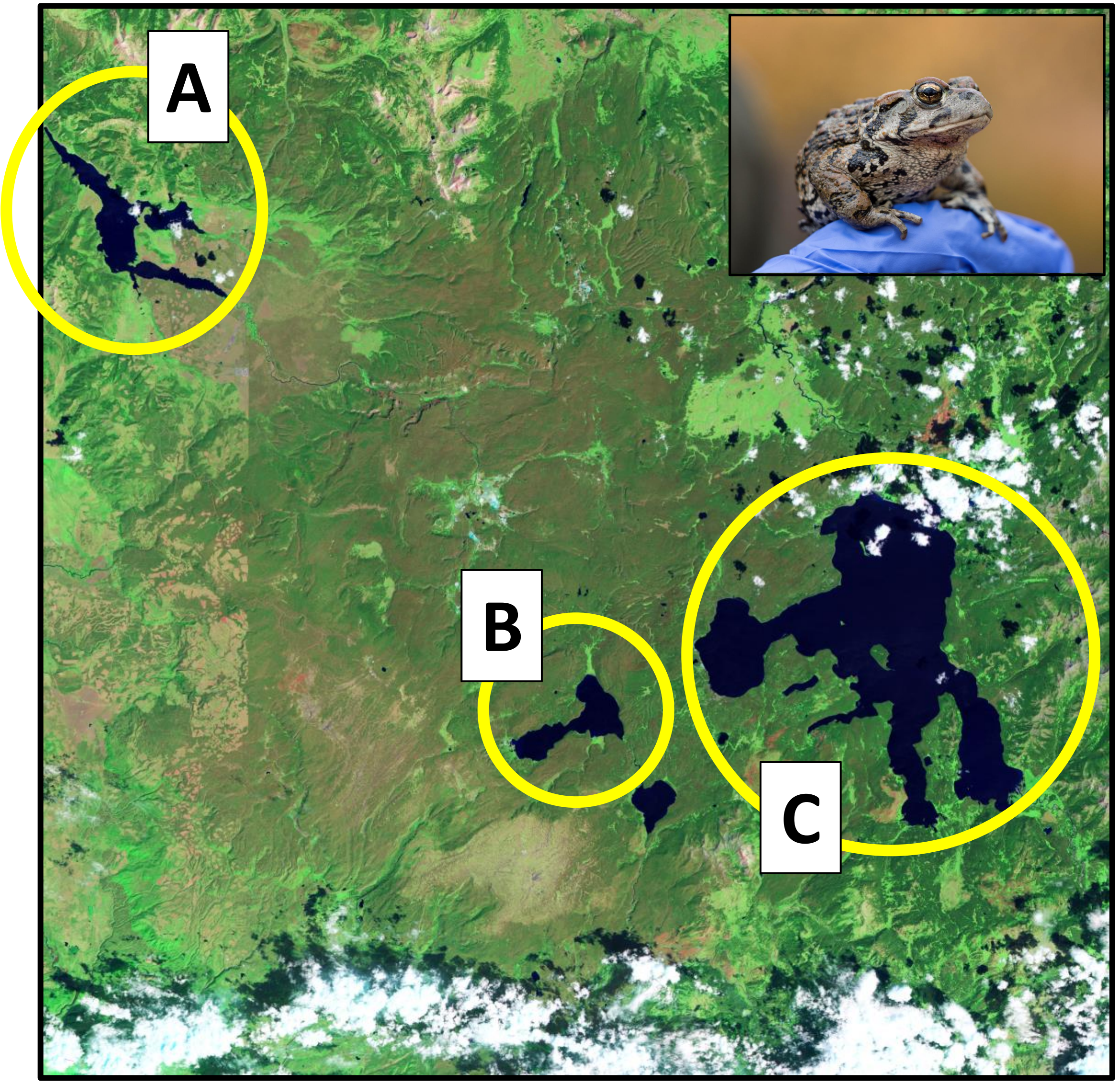


RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?

Date	**Pond**	**Survey**	**Tag**
5/25/2016	A	1	100
5/25/2016	A	1	101
5/25/2016	A	1	102
6/2/2016	A	2	103
6/2/2016	A	2	104
6/2/2016	A	2	**101**
6/2/2016	A	2	105

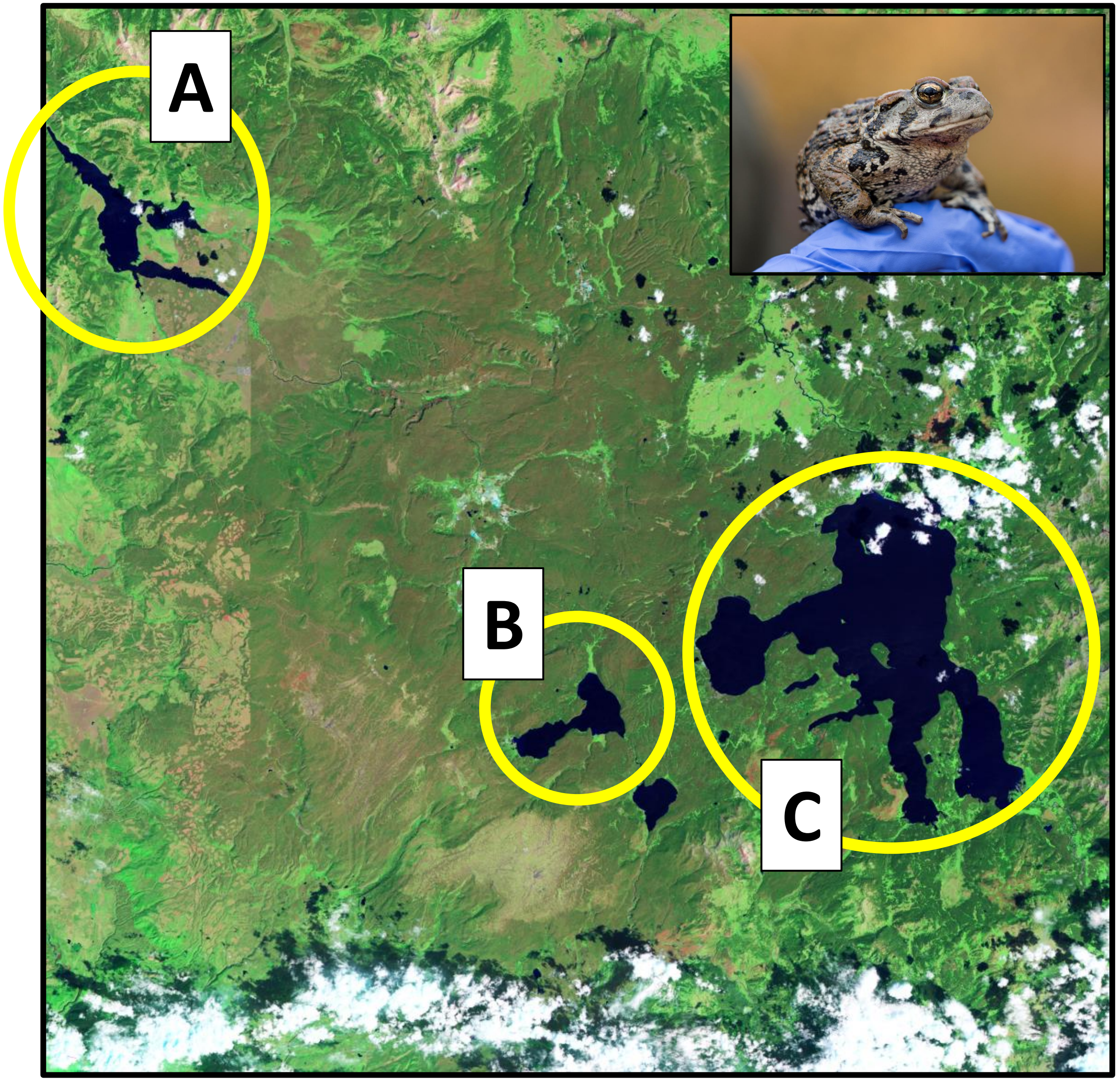


RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?

Date	Pond	Survey	Tag
5/25/2016	A	1	100
5/25/2016	A	1	101
5/25/2016	A	1	102
6/2/2016	A	2	103
6/2/2016	A	2	104
6/2/2016	A	2	**101**
6/2/2016	A	2	105
6/1/**2017**	**B**	3	

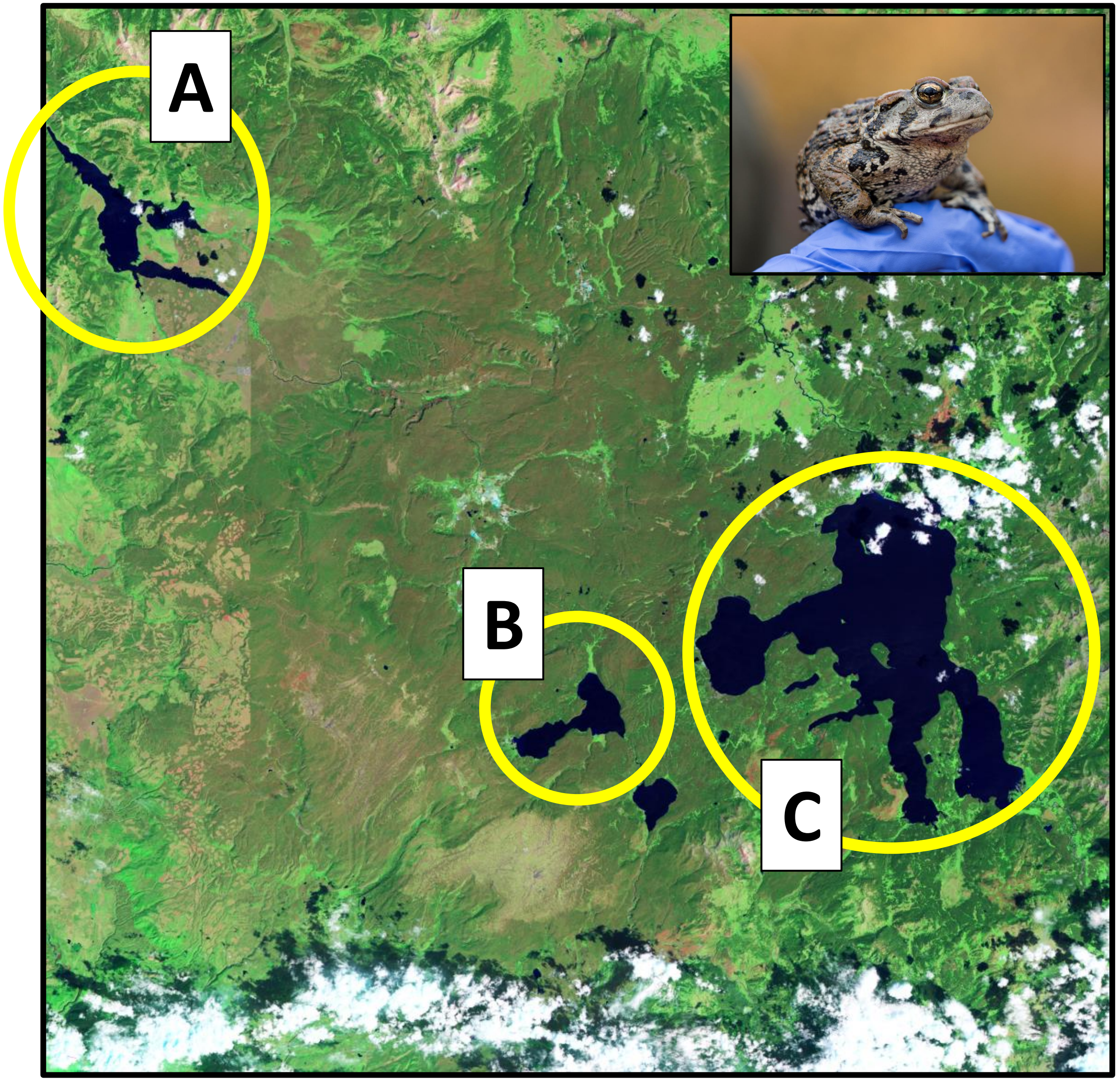


RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?

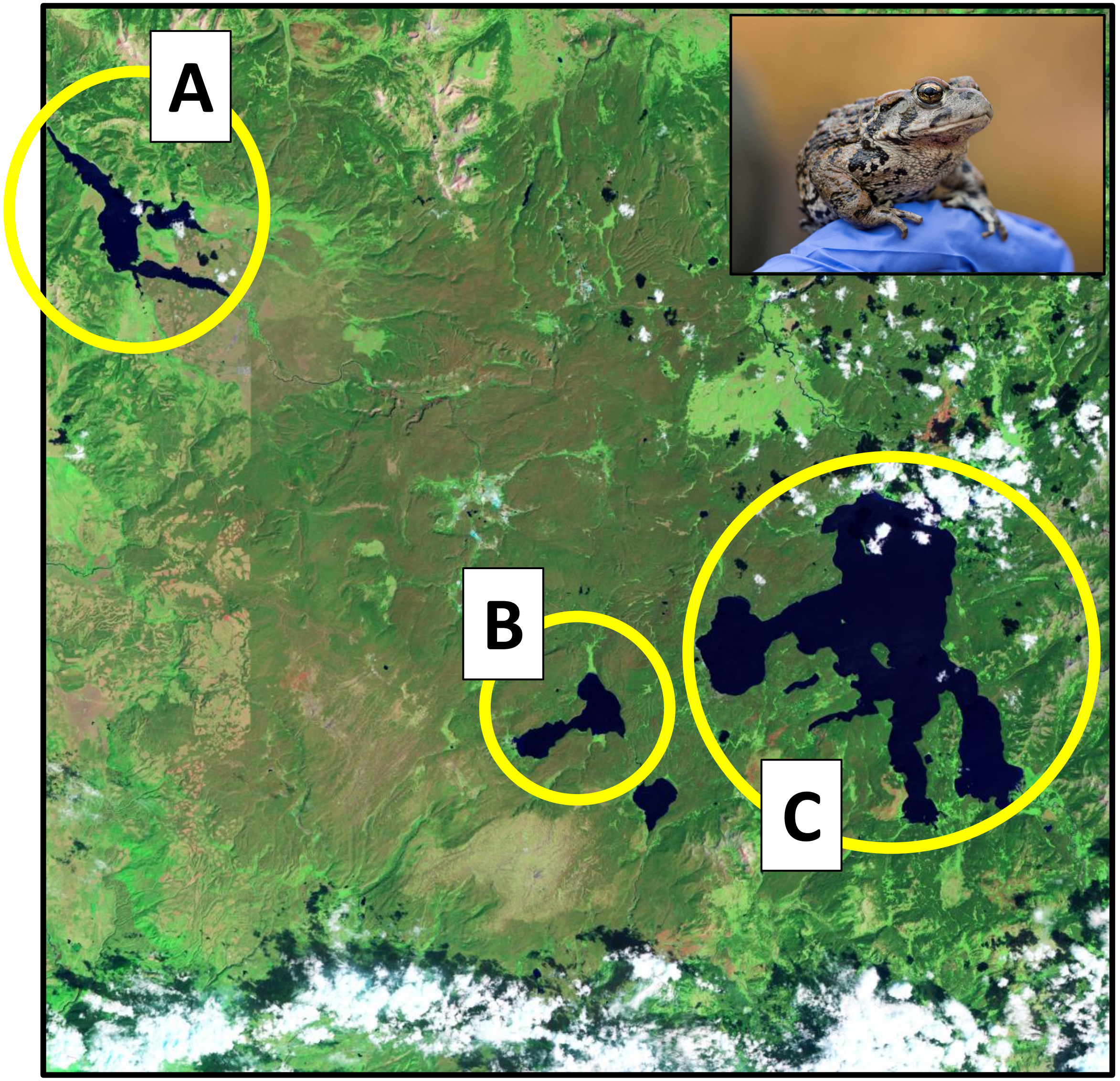
Date	Pond	Survey	Tag
5/25/2016	A	1	100
5/25/2016	A	1	101
5/25/2016	A	1	102
6/2/2016	A	2	103
6/2/2016	A	2	104
6/2/2016	A	2	101
6/2/2016	A	2	105
6/1/2017	B	3	205
6/1/2017	B	3	207
6/1/2017	B	3	216
6/1/2017	B	3	
6/1/2017	B	3	
6/1/2017	B	3	



RMark Workshop – Multi-state capture-recapture model

1. Question How does boreal toad dispersal vary among three study ponds?

Date	Pond	Survey	Tag
5/25/2016	A	1	100
5/25/2016	A	1	101
5/25/2016	A	1	**102**
6/2/2016	A	2	103
6/2/2016	A	2	104
6/2/2016	A	2	101
6/2/2016	A	2	105
6/1/2017	B	3	205
6/1/2017	B	3	207
6/1/2017	B	3	216
6/1/2017	B	3	**102**
6/1/2017	B	3	211
6/1/2017	B	3	218



RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?

Date	Pond	Survey	Tag
5/25/2016	A	1	100
5/25/2016	A	1	101
5/25/2016	A	1	102
6/2/2016	A	2	103
6/2/2016	A	2	104
6/2/2016	A	2	101
6/2/2016	A	2	105
6/1/2017	B	3	205
6/1/2017	B	3	207
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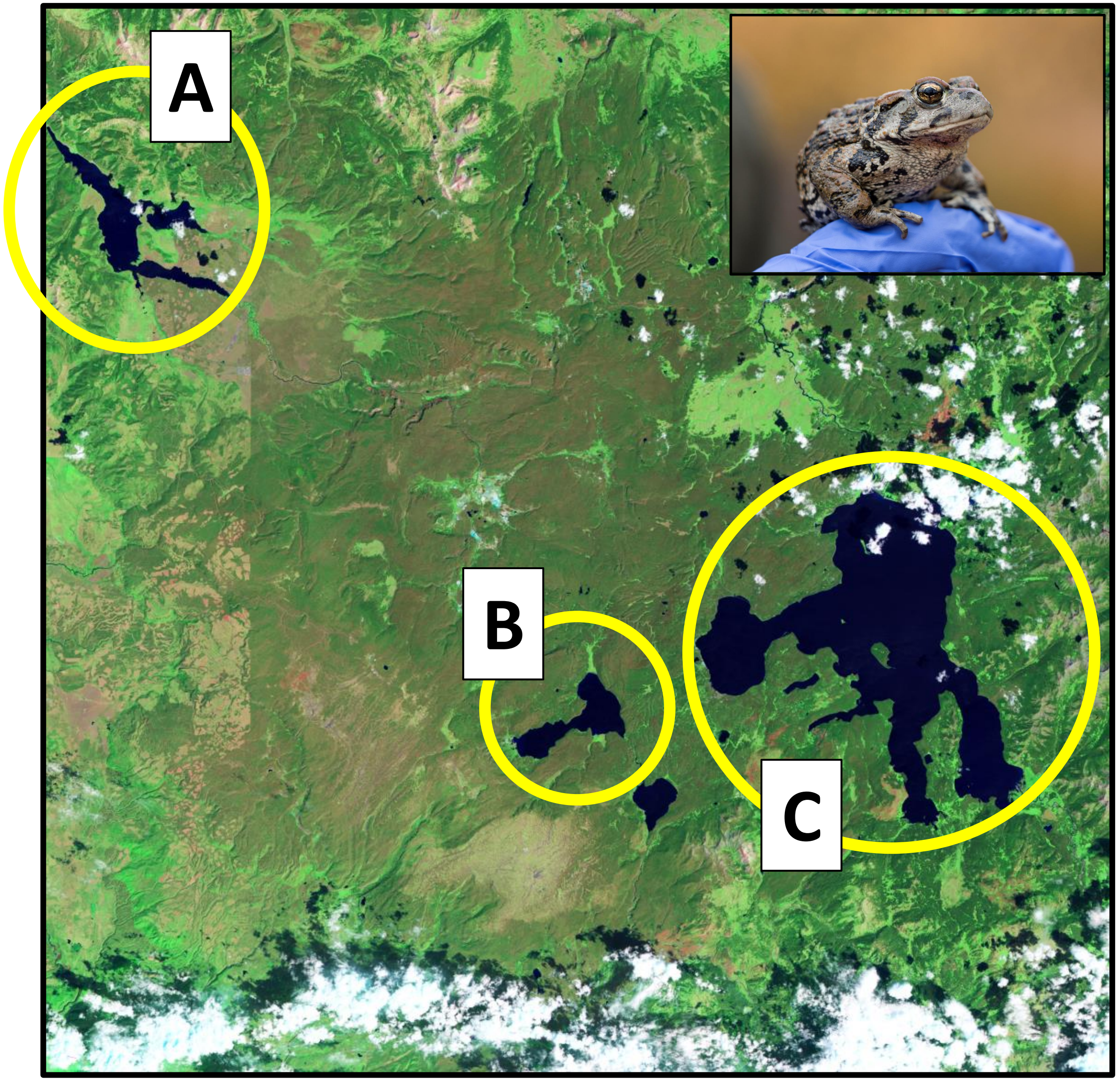
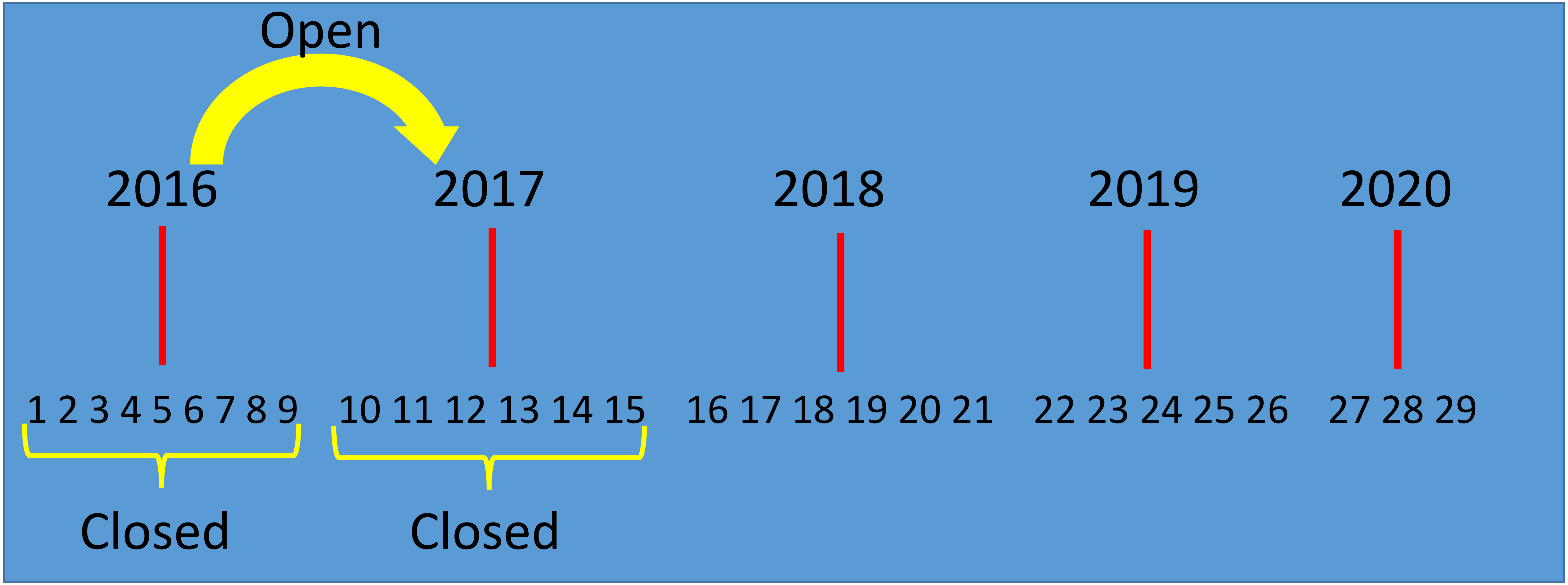
6/1/2017	B	3	211
6/1/2017	B	3	218



RMark Workshop – Multi-state capture-recapture model

1. Question How does boreal toad dispersal vary among three study ponds?



RMark Workshop – Multi-state capture-recapture model

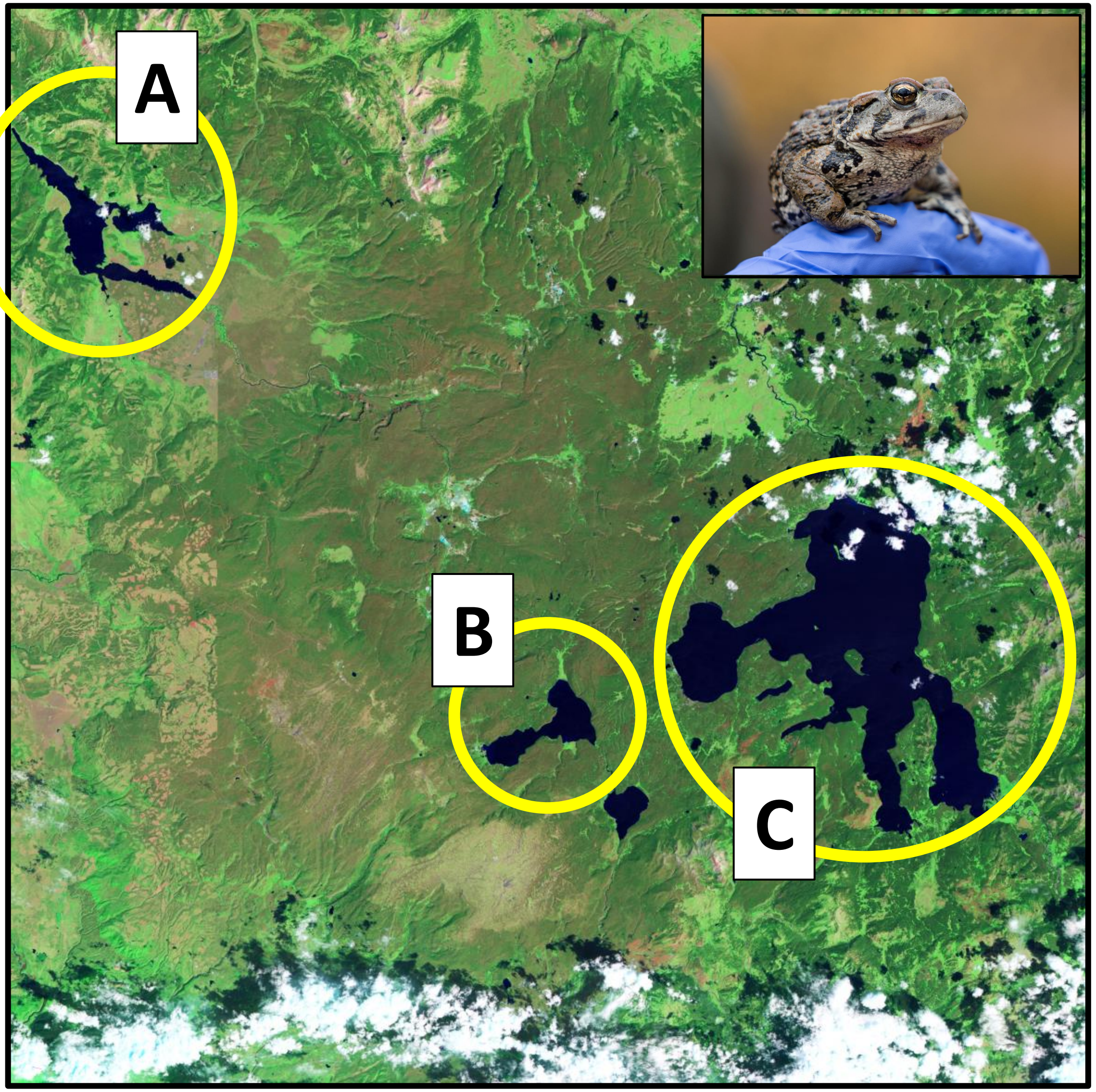
1. Question

How does boreal toad dispersal vary among three study ponds?

Encounter History

10110

A0BB0



RMark Workshop – Multi-state capture-recapture model

1. Question

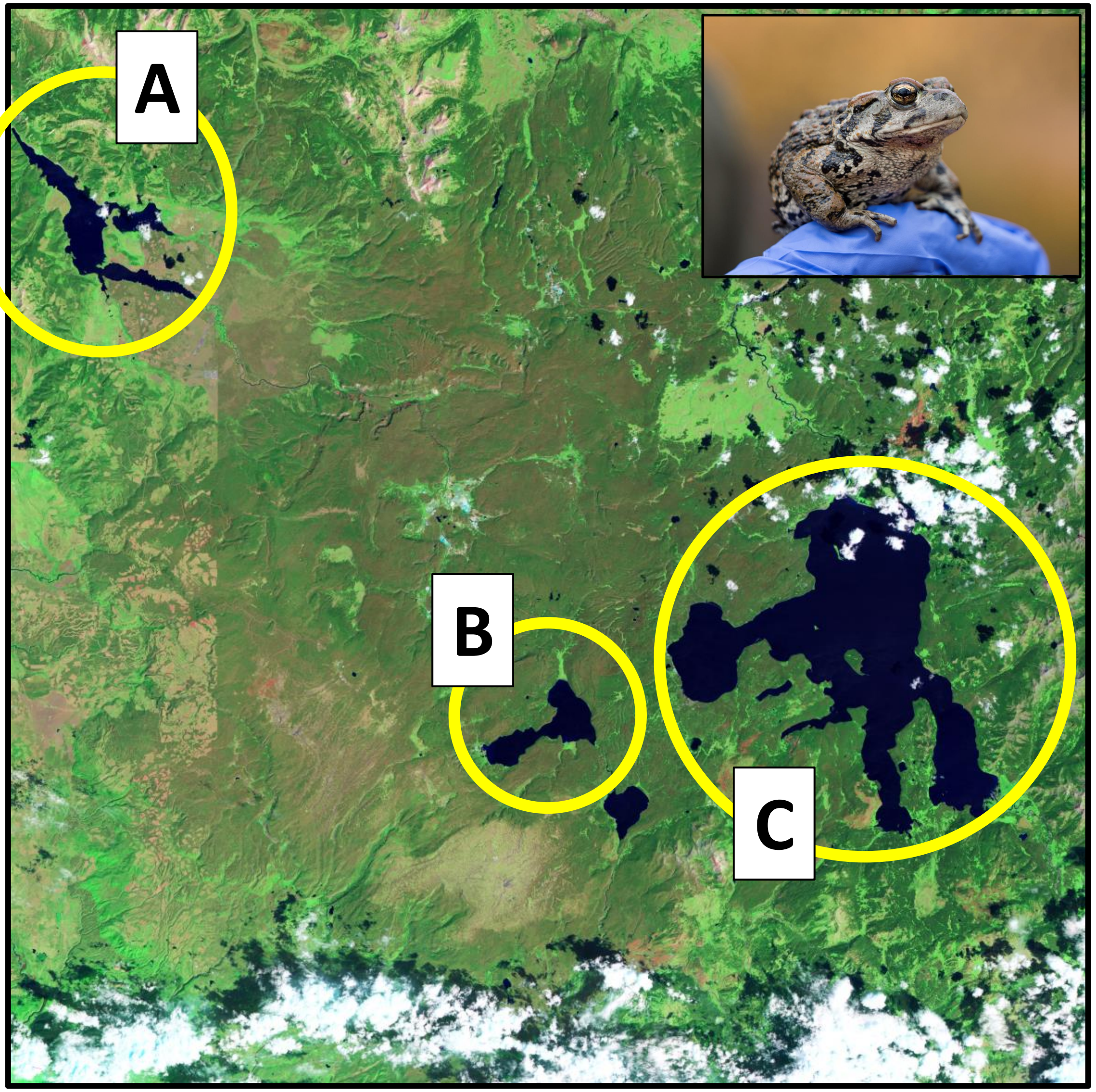
How does boreal toad dispersal vary among three study ponds?

Probability of encountering an individual:

probability that the animal was alive and in the sampling area (φ)

and

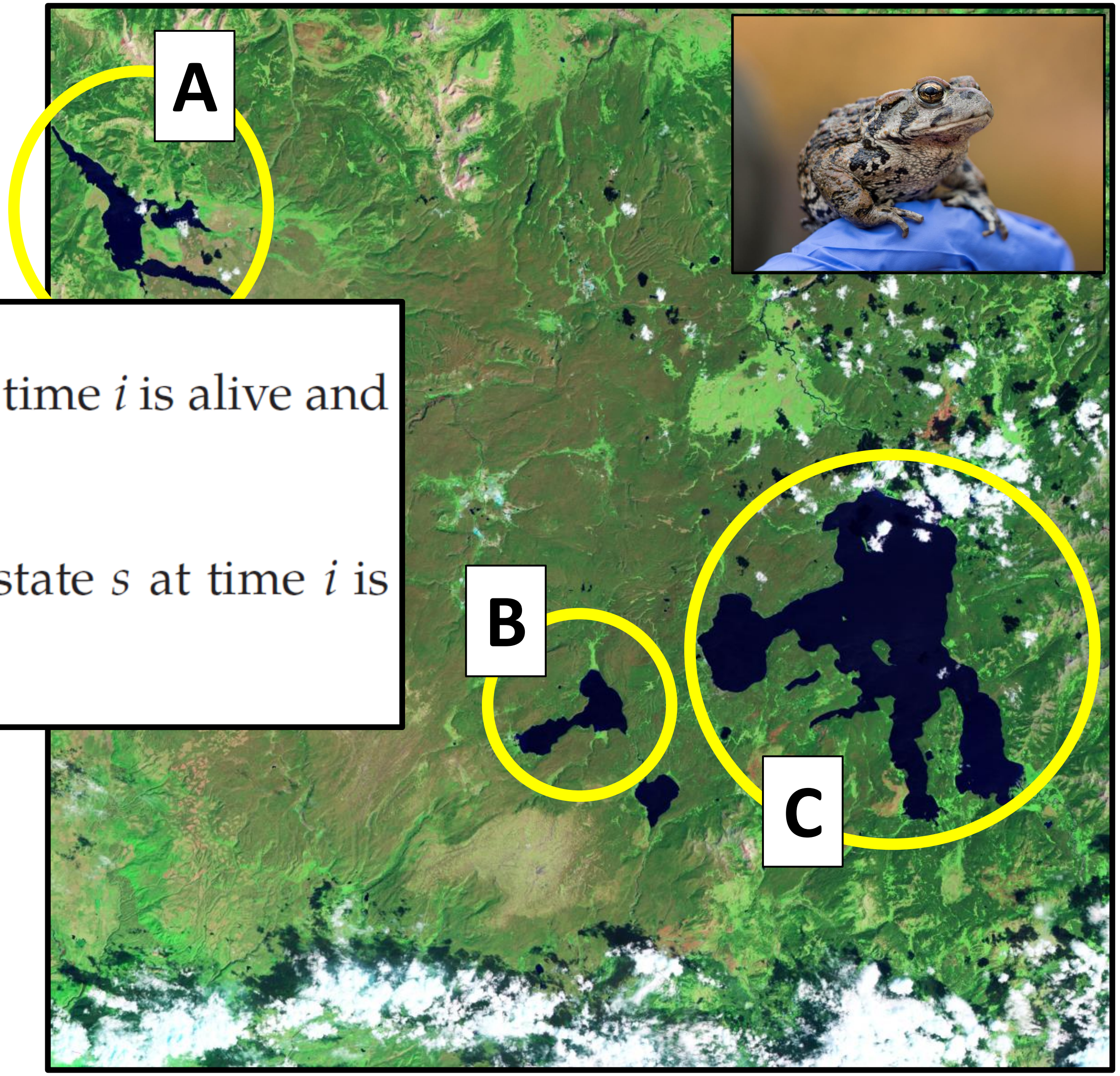
probability of encounter conditional on being alive and in the sample area (*p*)



RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?



φ_i^{rs} = the probability that an animal alive in state r at time i is alive and in state s at time i+1

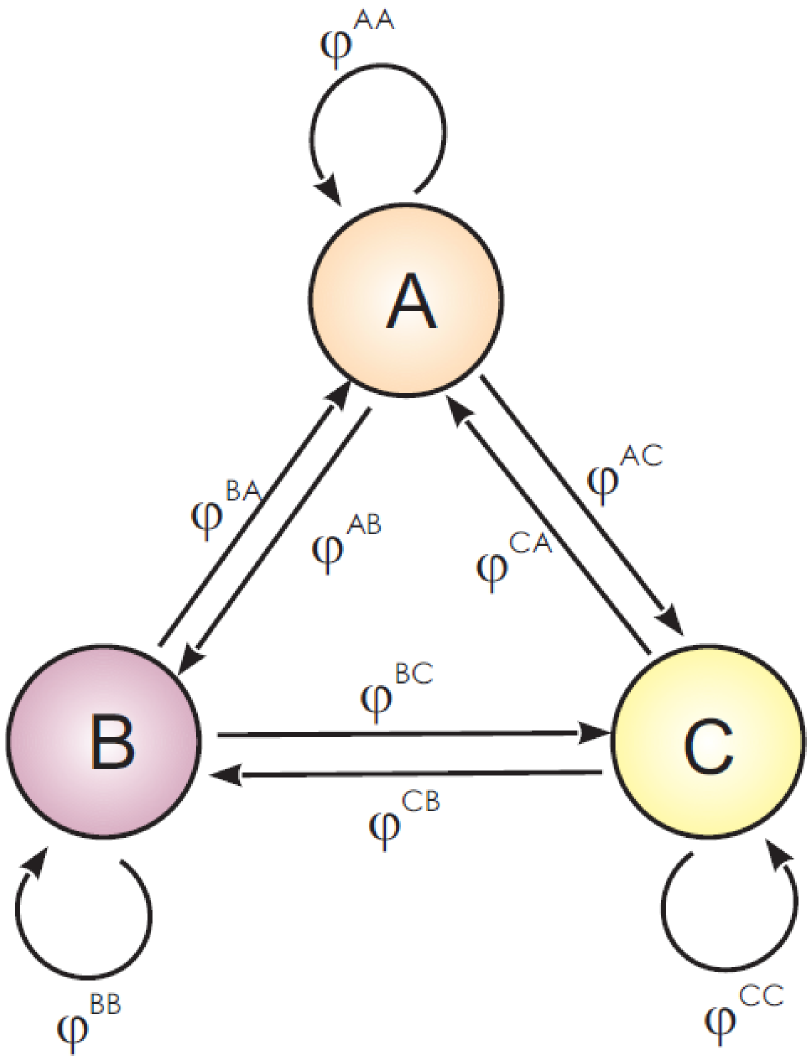
p_i^s = the probability that a marked animal alive in state s at time i is recaptured or resighted at time i.

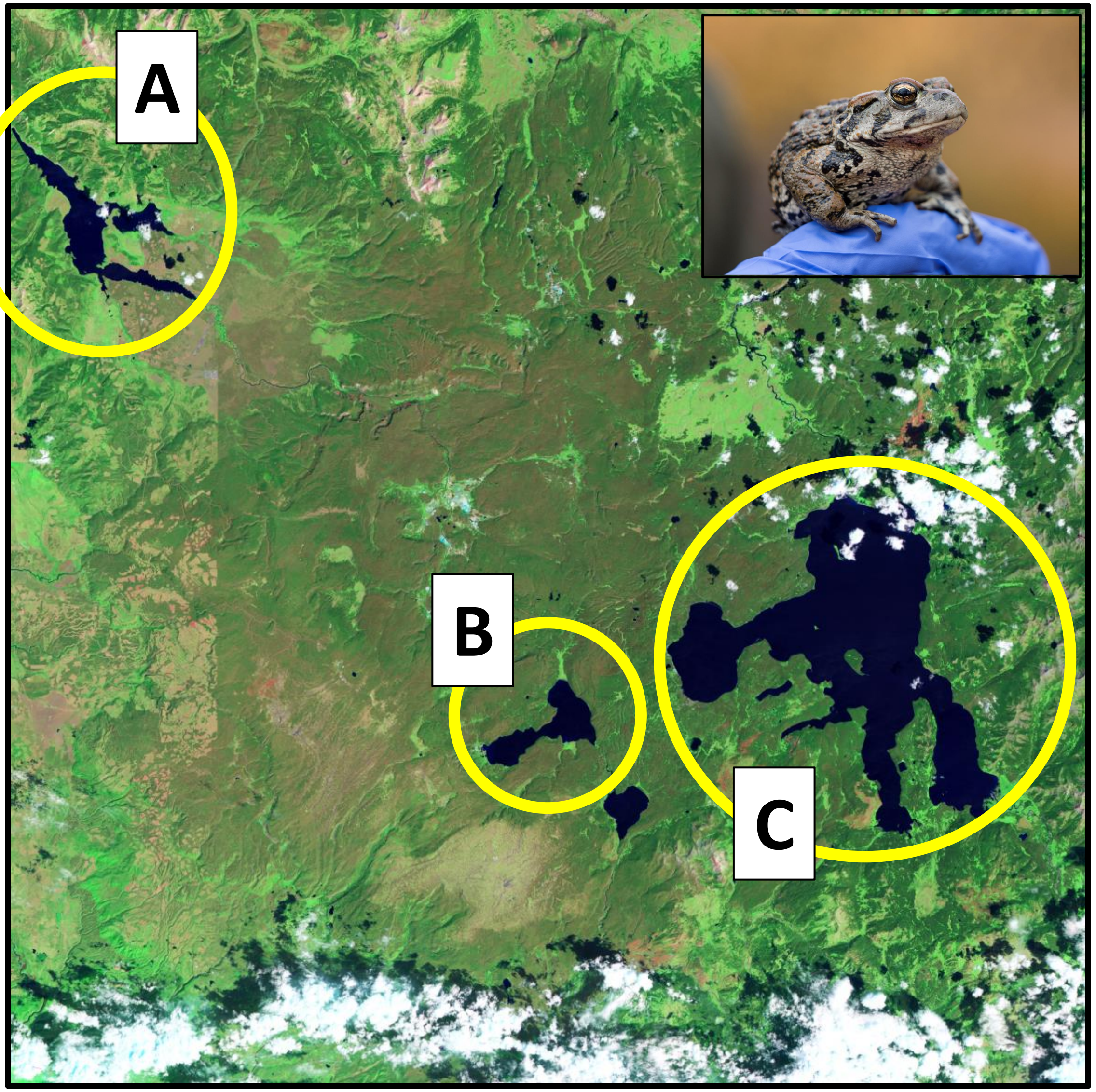
Program MARK Book: Chapter 10; page 10 - 2

RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?



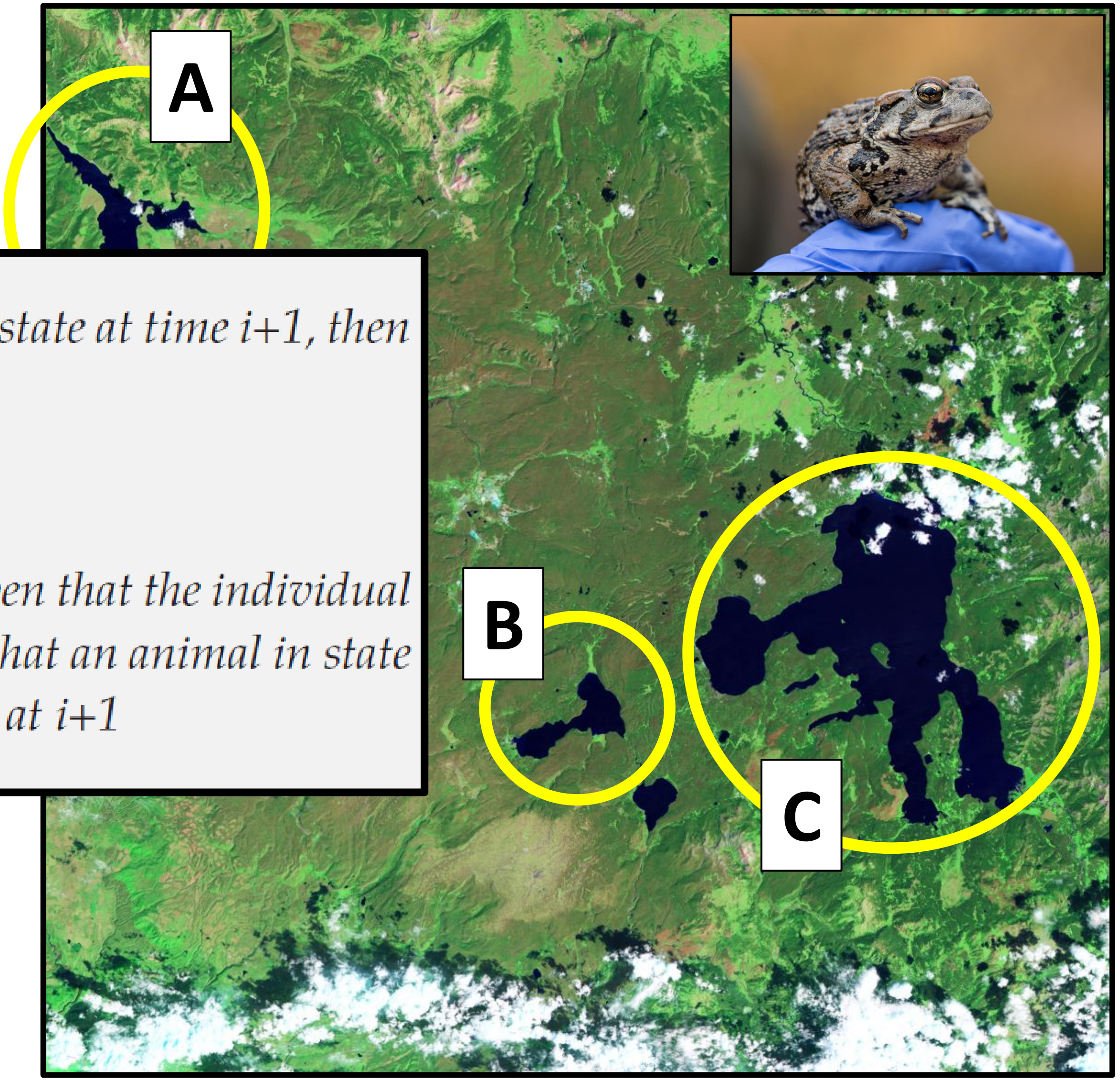


Program MARK Book: Chapter 10; page 10 - 2

RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?



If we assume that survival from time i to i+1 does not depend on state at time i+1, then we can write

$$\varphi_i^{rs} = S_i^r \psi_i^{rs}$$

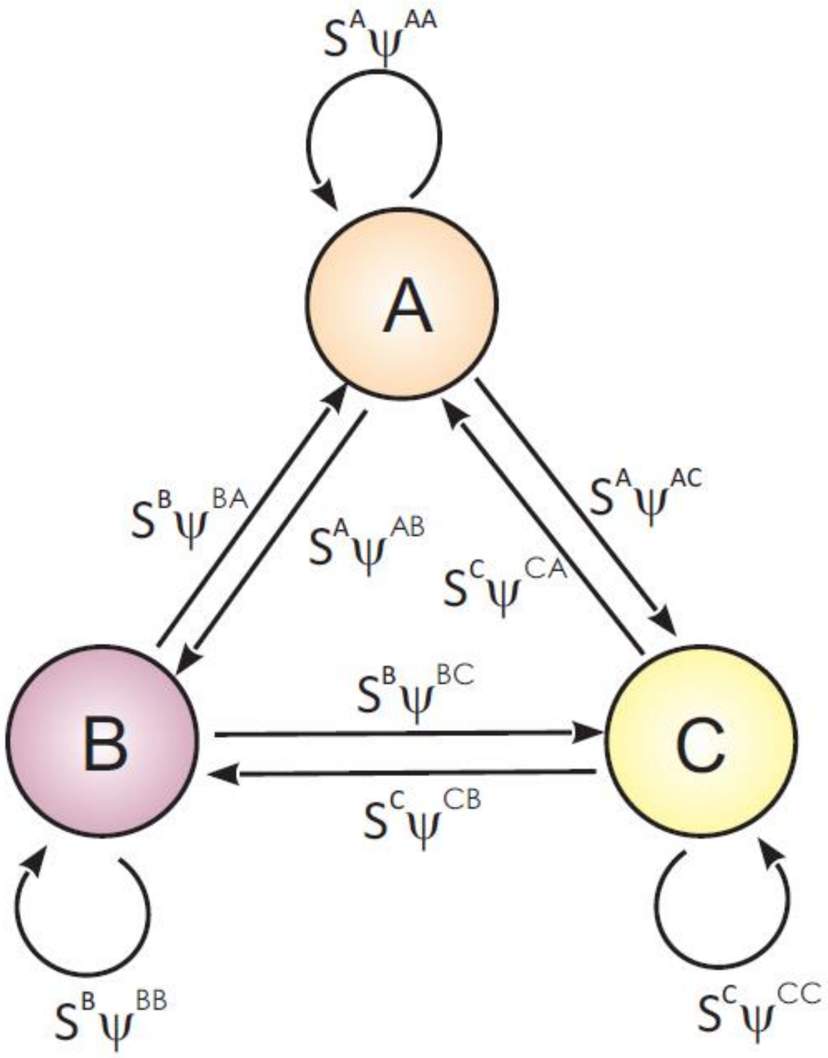
where (i) S_i^r *is the probability of survival from time i to i + 1, given that the individual is in state r at time i , and (ii)* ψ^{rs} *is the conditional probability that an animal in state r at time i is in state s at time i+1, given that the animal is alive at i+1*

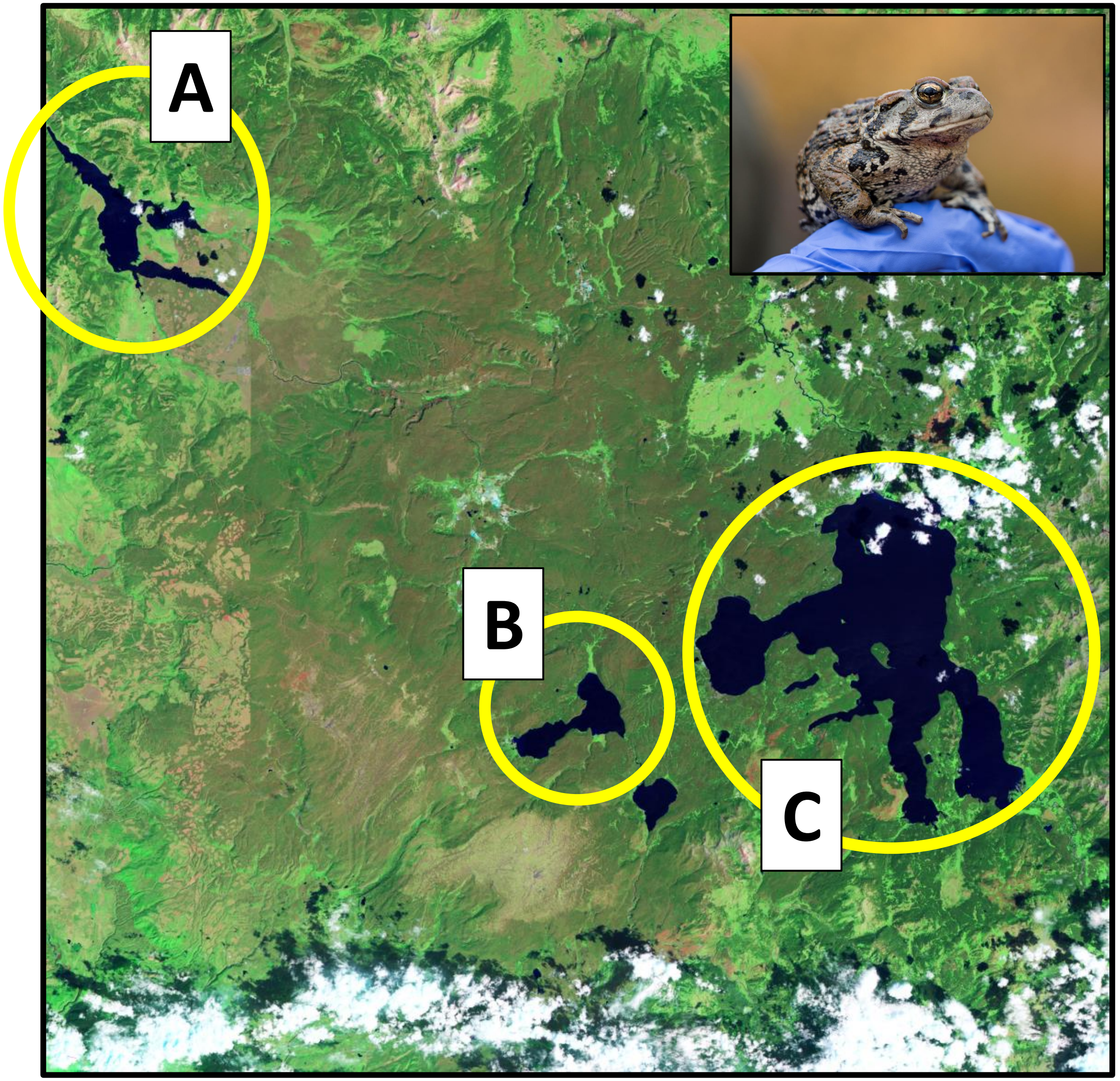
Program MARK Book: Chapter 10; page 10 - 4

RMark Workshop – Multi-state capture-recapture model

1. Question

How does boreal toad dispersal vary among three study ponds?





Program MARK Book: Chapter 10; page 10 - 5

RMark Workshop – Multi-state capture-recapture model

CHAPTER 10

Multi-state models...

Many of the first chapters in this book focussed on 'typical' open population mark-recapture models, where the probability of an individual being seen was defined by 2 parameters: the probability the animal survived and remained in the sample area (φ), and the probability that the animal was encountered (p), conditional on being alive and in the sample area.

In this chapter, we extend this simpler paradigm by (in effect) considering a third parameter – a 'movement' parameter (ψ). We'll defer formal definition of this parameter for a moment, since the definition changes somewhat depending on one or more assumptions. However, to foreshadow, let ψ represent the probability of moving between states in which the marked individual may potentially be encountered, conditional on being alive and in that state. The fact that there may be more than a single state (i.e., more than one location, or condition, or state) is what leads to the models we describe in this chapter being referred to generally as *multi-state models*.

Most of this chapter is a synthesis of the basic ideas behind multi-state models, with particular focus on how to implement them in **MARK**. The concepts and ideas are derived from seminal work by Neil Arnason, Carl Schwarz, Cavell Brownie, Ken Pollock, Bill Kendall, Jim Hines and Jim Nichols, who have been exploring the mechanics and application of these models. Critical in this early evolution was the advent of software to fit multi-state models, most notably program **MS-SURVIV**, created by Jim Hines. More recently, the development of programs **M/E-SURGE** by Rémi Choquet, Roger Pradel and Jean-Dominique Lebreton. Multi-state models have been shown to be an extremely rich class of models, with broad applications to many important questions in evolutionary ecology, population dynamics (especially metapopulation dynamics), and conservation biology and management. At best, we hope to provide you with the essence of multi-state models as implemented in **MARK**, sufficient to convince you of the importance of more careful study of this class of models.

Program MARK

A Gentle Introduction

EVAN G. COOCH & GARY C. WHITE (eds.)

RMark Workshop – Multi-state capture-recapture model

Methods in Ecology and Evolution

BRITISH ECOLOGICAL SOCIETY

Methods in Ecology and Evolution 2017, **8**, 1547–1557 doi: 10.1111/2041-210X.12792

Applying the multistate capture–recapture robust design to characterize metapopulation structure

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Summary

1. Population structure must be considered when developing mark–recapture (MR) study designs as the sampling of individuals from multiple populations (or subpopulations) may increase heterogeneity in individual capture probability. Conversely, the use of an appropriate MR study design which accommodates heterogeneity associated with capture occasion varying covariates due to animals moving between 'states' (i.e. geographic sites) can provide insight into how animals are distributed in a particular environment and the status and connectivity of subpopulations.

2. The multistate closed robust design (MSCRD) was chosen to investigate: (i) the demographic parameters of Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) subpopulations in coastal and estuarine waters of Perth, Western Australia; and (ii) how they are related to each other in a metapopulation. Using 4 years of year-round photo-identification surveys across three geographic sites, we accounted for heterogeneity of capture probability based on how individuals distributed themselves across geographic sites and characterized the status of subpopulations based on their abundance, survival and interconnection.

RMark Workshop – Multi-state capture-recapture model

The Auk 126(1):77–88, 2009
© The American Ornithologists' Union, 2009.
Printed in USA.

MULTISTATE MODELS FOR ESTIMATION OF SURVIVAL AND REPRODUCTION IN THE GREY-HEADED ALBATROSS (*THALASSARCHE CHRYSOSTOMA*)

Sarah J. Converse,[1,2,5] William L. Kendall,[1] Paul F. Doherty, Jr.,[3] and Peter G. Ryan[4]

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[2]*Colorado Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado 80523, USA;*
[3]*Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado 80523, USA; and*
[4]*University of Cape Town, Percy FitzPatrick Institute of African Ornithology, Rondebosch 7701, South Africa*

Abstract.—Reliable information on demography is necessary for conservation of albatrosses, the most threatened family of pelagic birds. Albatross survival has been estimated using mark–recapture data and the Cormack-Jolly-Seber (CJS) model. However, albatross exhibit skipped breeding, violating assumptions of the CJS model. Multistate modeling integrating unobservable states is a promising tool for such situations. We applied multistate models to data on Grey-headed Albatross (*Thalassarche chrysostoma*) to evaluate model performance and describe demographic patterns. These included a multistate equivalent of the CJS model (MS-2), including successful and failed breeding states and ignoring temporary emigration, and three versions of a four-state multistate model that accounts for temporary emigration by integrating unobservable states: a model (MS-4) with one sample per breeding season, a robust design model (RDMS-4) with multiple samples per season and geographic closure within the season, and an open robust design model (ORDMS-4) with multiple samples per season and staggered entry and exit of animals within the season. Survival estimates from the MS-2 model were higher than those from the MS-4 model, which resulted in apparent percent relative bias averaging 2.2%. The ORDMS-4 model was more appropriate than the RDMS-4 model, given that staggered entry and exit occurred. Annual survival probability for Grey-headed Albatross at Marion Island was 0.951 ± 0.006 (SE), and the probability of skipped breeding in a subsequent year averaged 0.938 for successful and 0.163 for failed breeders. We recommend that multistate models with unobservable states, combined with robust-design sampling, be used in studies of species that exhibit temporary emigration. *Received 13 November 2007, accepted 25 June 2008.*

esa ECOSPHERE

Estimating the probability of movement and partitioning seasonal survival in an amphibian metapopulation

Erin Muths,[1,†] Larissa L. Bailey,[2] Brad A. Lambert,[3] and Scott C. Schneider[3]

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[2]*Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, Colorado 80523 USA*
[3]*Colorado Natural Heritage Program, Colorado State University, Fort Collins, Colorado 80523-1475 USA*

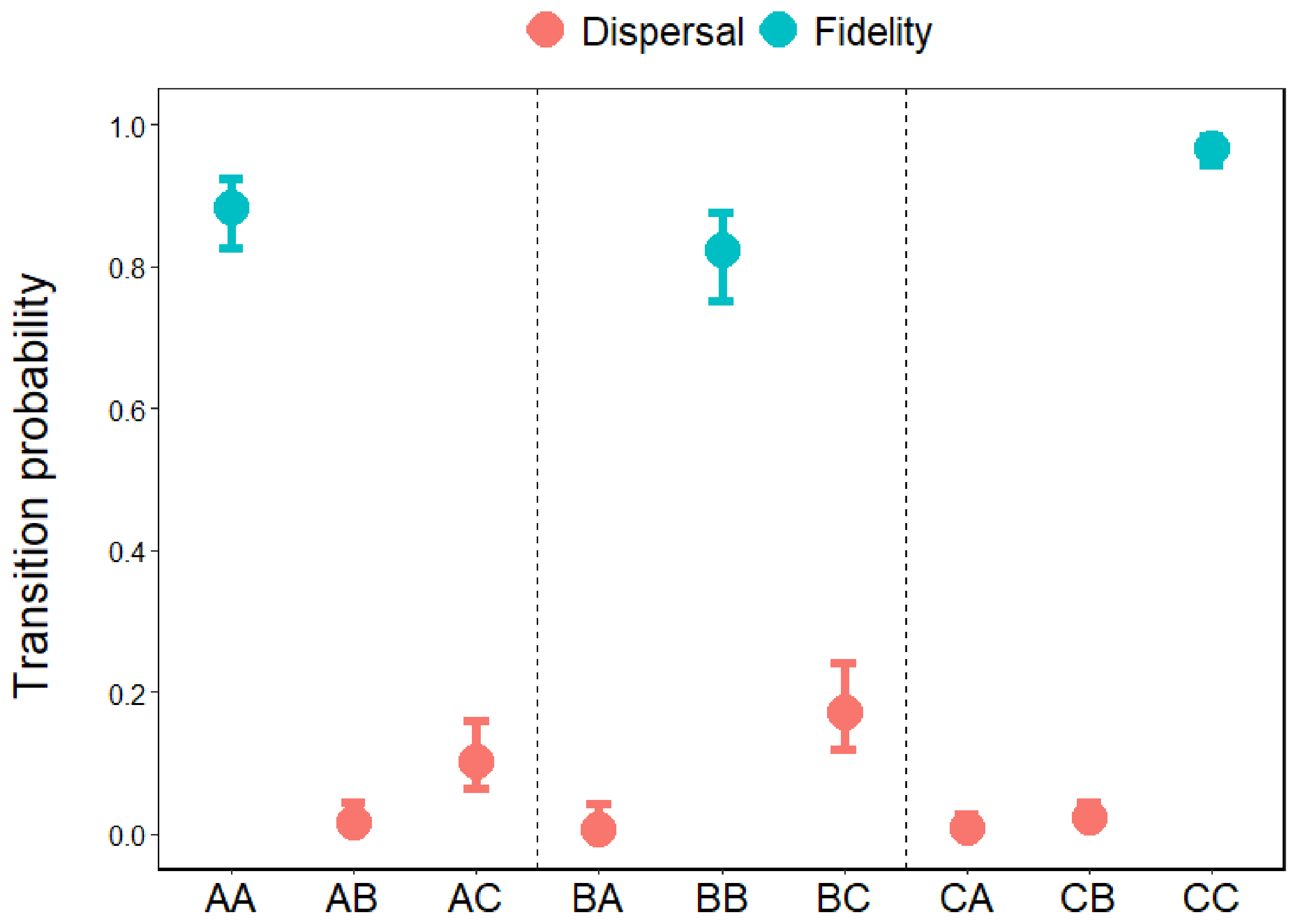
Citation: Muths, E., L. L. Bailey, B. A. Lambert, and S. C. Schneider. 2018. Estimating the probability of movement and partitioning seasonal survival in an amphibian metapopulation. Ecosphere 9(10):e02480. 10.1002/ecs2.2480

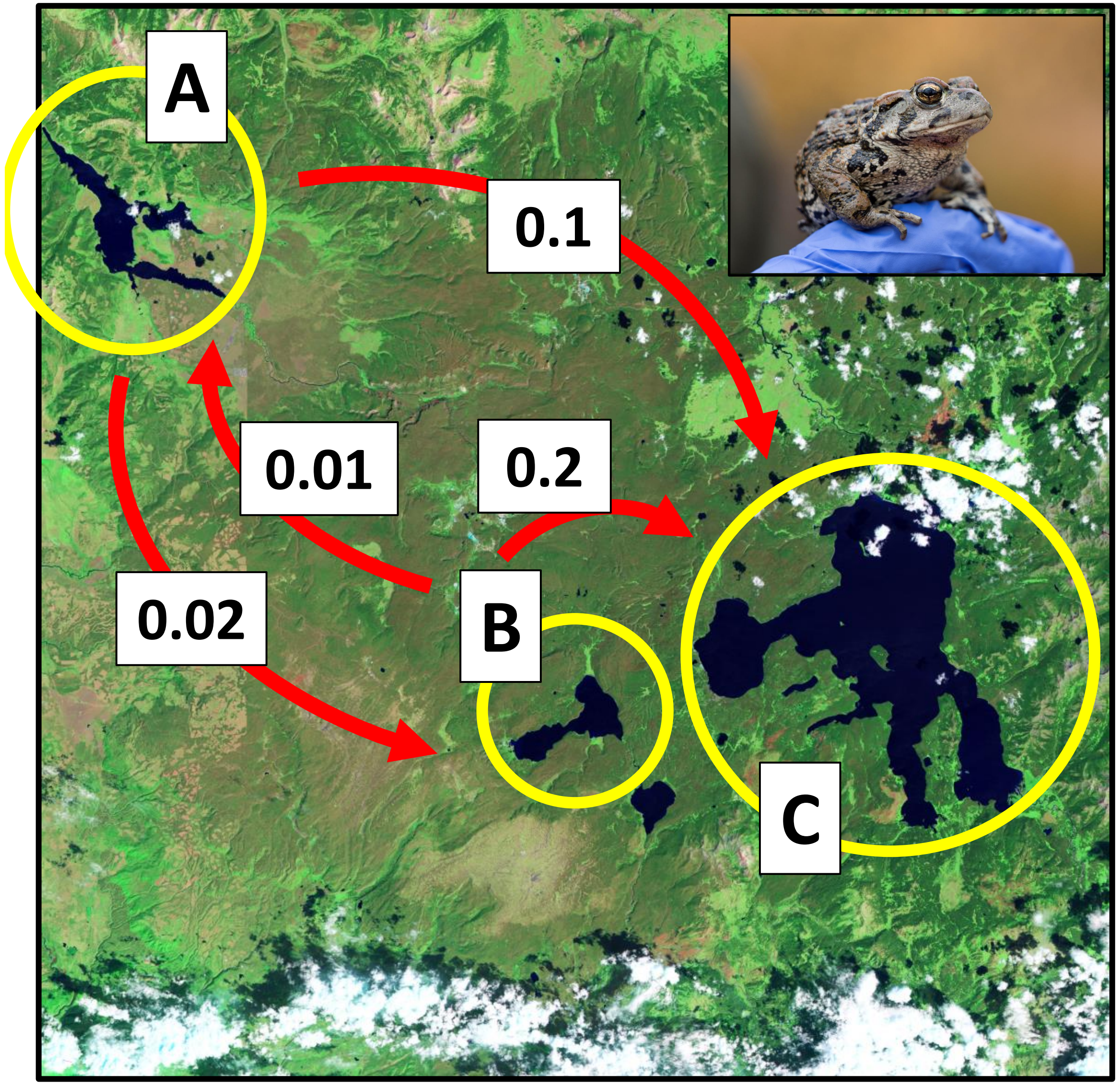
Abstract. Movement of individuals has been described as one of the best studied, but least understood concepts in ecology. The magnitude of movements, routes, and probability of movement have significant application to conservation. Information about movement can inform efforts to model species persistence and is particularly applicable in situations where specific threats (e.g., disease) may depend on the movement of hosts and potential vectors. We estimated the probability of movement (breeding dispersal and permanent emigration) in a metapopulation of 16 breeding sites for boreal toads (*Anaxyrus boreasboreas*). We used a multi-state mark–recapture approach unique in its complexity (16 sites over 18 yr) to address questions related to these movements and variation in resident survival. We found that individuals had a 1–2% probability of dispersing in a particular year and that approximately 10–20% of marked individuals were transient and observed in the metapopulation only once. Resident survival probabilities differed by season, with 71–90% survival from emergence from hibernation through early post-breeding and >97% survival from mid-/late active season through hibernation. Movement-related probabilities are needed to predict species range expansions and contractions, estimate population and metapopulation dynamics, understand host–pathogen and native–invasive species interactions, and to evaluate the relative effects of proposed management actions.

RMark Workshop – Multi-state capture-recapture model

1. Question

How do toad dispersal rates vary among three study ponds?





RMark Workshop

Model 6 – Single-season occupancy model

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

RMark Workshop – Lesson Structure

1. Question
2. Field Data
3. Format Data for Analysis
4. Fit Population Model
5. Examine Output and Visualize Results

*steps 3-5 we will do together in class on Monday

RMark Workshop – Single-Season Occupancy Model

1. Question

How does forest cover influence the occurrence of brown tree snakes on pacific islands?

Bjorn Lardner, United States Geological Survey

RMark Workshop – Single-Season Occupancy Model

1. Question

How does forest cover influence the occurrence of brown tree snakes on pacific islands?

Date	Island	Survey	BTS	Forest Cover	Prey Abundance	Temp	Region
7/2/2022	1	1					

RMark Workshop – Single-Season Occupancy Model

1. Question

How does forest cover influence the occurrence of brown tree snakes on pacific islands?

Date	Island	Survey	BTS	Forest Cover	Prey Abundance	Temp	Region
7/2/2022	1	1	0	0	94	21	N

RMark Workshop – Single-Season Occupancy Model

1. Question

How does forest cover influence the occurrence of brown tree snakes on pacific islands?

Date	Island	Survey	BTS	Forest Cover	Prey Abundance	Temp	Region
7/2/2022	1	1	0	0	94	21	N
7/6/2022	1	2	0	0	94	34	N
7/10/2022	1	3	0	0	94	38	N
7/13/2022	1	4	0	0	94	25	N
7/18/2022	1	5	0	0	94	27	N
7/23/2022	1	6	0	0	94	26	N

RMark Workshop – Single-Season Occupancy Model

1. Question

How does forest cover influence the occurrence of brown tree snakes on pacific islands?

Date	Island	Survey	BTS	Forest Cover	Prey Abundance	Temp	Region
7/2/2022	1	1	0	0	94	21	N
7/6/2022	1	2	0	0	94	34	N
7/10/2022	1	3	0	0	94	38	N
7/13/2022	1	4	0	0	94	25	N
7/18/2022	1	5	0	0	94	27	N
7/23/2022	1	6	0	0	94	26	N
7/3/2022	2	1	0	85	82	40	N
7/7/2022	2	2	1	85	82	22	N
7/11/2022	2	3	1	85	82	24	N
7/14/2022	2	4	1	85	82	27	N
7/19/2022	2	5	0	85	82	33	N
7/24/2022	2	6	1	85	82	26	N

RMark Workshop – Detection histories for each site (island)

Island	Survey	BTS
1	1	0
1	2	0
1	3	0
1	4	0
1	5	0
1	6	0
2	1	0
2	2	1
2	3	1
2	4	1
2	5	0
2	6	1

Island	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Survey 6
1	0	0	0	0	0	0
2	0	1	1	1	0	1

RMark Workshop – Detection histories for each site (island)

Island	Survey	BTS
1	1	0
1	2	0
1	3	0
1	4	0
1	5	0
1	6	0
2	1	0
2	2	1
2	3	1
2	4	1
2	5	0
2	6	1

Island	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Survey 6
1	0	0	0	0	0	0
2	0	1	1	1	0	1

RMark Workshop – Single-Season Occupancy Model

Ecology, 83(8), 2002, pp. 2248–2255
© 2002 by the Ecological Society of America

ESTIMATING SITE OCCUPANCY RATES WHEN DETECTION PROBABILITIES ARE LESS THAN ONE

DARRYL I. MACKENZIE,[1,5] JAMES D. NICHOLS,[2] GIDEON B. LACHMAN,[2,6] SAM DROEGE,[2] J. ANDREW ROYLE,[3] AND CATHERINE A. LANGTIMM[4]

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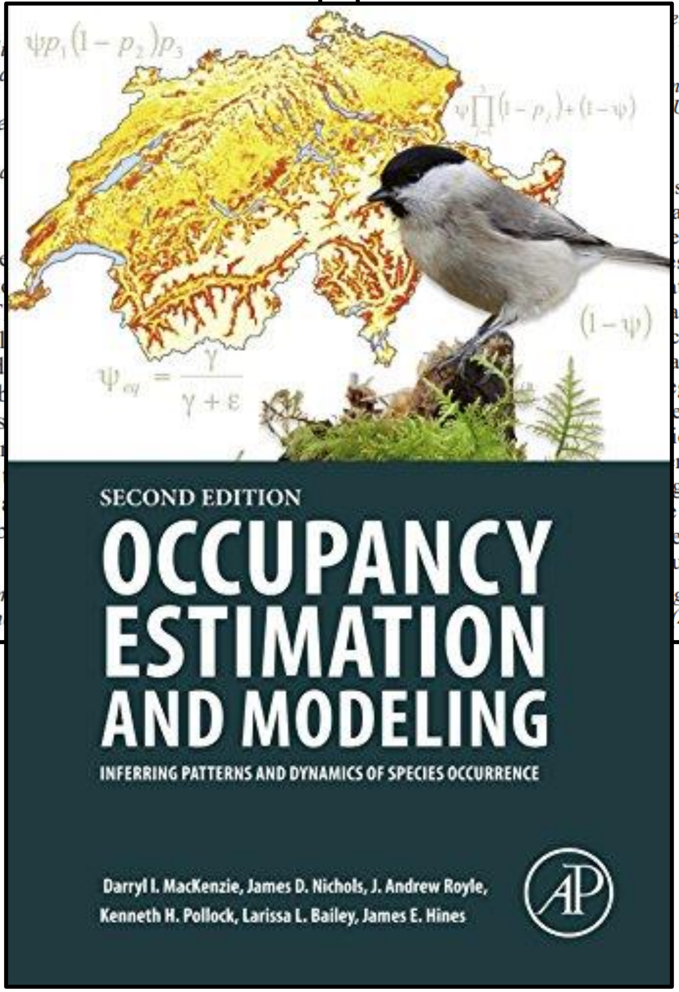
7920 NW 71st Street, Gainesville, Florida 32653 USA

Abstract. Nondetection of a species at a site does not imply that the
unless the probability of detection is 1. We propose a model and likelih
for estimating site occupancy rates when detection probabilities are <1. T
a flexible framework enabling covariate information to be included and all
observations. Via computer simulation, we found that the model provid
of the occupancy rates, generally unbiased for moderate detection probab
estimated site occupancy rates for two anuran species at 32 wetland s
USA, from data collected during 2000 as part of an amphibian monitori
watch USA. Site occupancy rates were estimated as 0.49 for American
icanus), a 44% increase over the proportion of sites at which they were
and as 0.85 for spring peepers (*Pseudacris crucifer*), slightly above the ob
of 0.83.

Key words: *anurans; bootstrap;* Bufo americanus; *detection probability;*
metapopulation; monitoring; patch occupancy; Pseudacris crucifer; *site occupan*



Ecological Applications, 13(6), 2003, pp. 1790–1801
© 2003 by the Ecological Society of America

IMPROVING PRECISION AND REDUCING BIAS IN BIOLOGICAL SURVEYS: ESTIMATING FALSE-NEGATIVE ERROR RATES

ANDREW J. TYRE,[1,5] BRIGITTE TENHUMBERG,[1] SCOTT A. FIELD,[1,2] DARREN NIEJALKE,[3] KIRSTEN PARRIS,[4] AND HUGH P. POSSINGHAM[1]

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Molecular Ecology, Waite Campus, University of Adelaide PMB 1, Glen Osmond,
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Urban Ecology, Royal Botanic Gardens Melbourne, c/o School of Botany, University of
Melbourne, Victoria 3010, Australia

se of presence/absence data in wildlife management and biological
ad. There is a growing interest in quantifying the sources of error
e data. We show that false-negative errors (failure to record a species
sent) can have a significant impact on statistical estimation of habitat
ted data. Then we introduce an extension of logistic modeling, the
l (ZIB) model that permits the estimation of the rate of false-negative
ction of estimates of the probability of occurrence for false-negative
ated visits to the same site. Our simulations show that even relatively
gatives bias statistical estimates of habitat effects. The method with
eliminates the bias, but estimates are relatively imprecise. Six repeated
ion of estimates to levels comparable to that achieved with conventional
nce of false-negative errors. In general, when error rates are ≤50%
gained by adding more sites, whereas when error rates are >50% it is
number of repeated visits. We highlight the flexibility of the method
es, clearly demonstrating the effect of false-negative errors for a range
urvey methods.

gical surveys; false-negative errors; habitat effects; presence–absence data;
ZIB) model.

RMark Workshop – Single-Season Occupancy Model

Urban Ecosyst (2017) 20:1027–1034
DOI 10.1007/s11252-017-0656-3

CrossMark

Factors determining the occupancy of Trumpeter Hornbills in urban-forest mosaics of KwaZulu-Natal, South Africa

Moses Chibesa[1] · Colleen T. Downs[1]

Published online: 16 March 2017
© Springer Science+Business Media New York 2017

Abstract Understanding the factors determining the occupancy and detection probability of birds in human dominated environments is important for their conservation. In this study we investigated various environmental variables believed to influence the site occupancy and detection probability of Trumpeter Hornbill (*Bycanistes bucinator*) in urban-forest mosaics of KwaZulu-Natal, South Africa. Presence/absence data were collected from a total of 50 point count stations established between September 2014 and March 2015 in urban-forest mosaics of Durban, Eshowe and Mtunzini. Mean occupancy rate of Trumpeter Hornbill was 0.40 ± 0.09 with a low detection probability of 0.28 ± 0.04. For Trumpeter Hornbills, large trees influenced their occupancy positively (sum AIC weight (ω_i) = 79%) while relative human abundance negatively influenced their occupancy (ω_i = 91%). Model selection suggested that housing density had a strong negative influence on detection probability of Trumpeter Hornbills (ω_i = 82 %) and availability of fruiting trees influenced their detection positively (ω_i = 29%). With continued

Keywords Point count · Trumpeter hornbill · D
probability · Occupancy · Urban-forest mosaic ·
Urbanisation

Introduction

Some of the leading causes of biodiversity los
change, habitat fragmentation due to land use cha
international trade in flora and fauna species (Trai
et al. 2012; WWF 2016). The current Living Plan
lished by World Wide Fund for Nature in colla
Global Footprint Network and Zoological Socie
indicates that global vertebrate population may d
in the year 2020 as a result of human exploitat
resources (WWF 2016). As the world populatio
grow and is projected to reach 9 billion people
2015), natural landscapes are greatly being transformed by hu-
man encroachment and this has resulted in huge pressure being

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journal homepage: www.elsevier.com/locate/ufug

URBAN FORESTRY & URBAN GREENING

Factors affecting the occupancy of forest mammals in an urban-forest mosaic in EThekwini Municipality, Durban, South Africa

Check for updates

Manqoba M. Zungu[a], Mfundo S.T. Maseko[a], Riddhika Kalle[a,b], Tharmalingam Ramesh[a,b], Colleen T. Downs[a,*]

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A R T I C L E I N F O

Handling Editor: Cecil Konijnendijk van den Bosch

Keywords:
Forest
Fragmentation
Mammal
Occupancy
Protected area
Urbanisation

A B S T R A C T

Urbanisation is one of the most rapidly expanding forms of landscape modification by humans and leads to large-scale loss and fragmentation of native habitat. This can alter the structure, composition and function of remnant habitat. Therefore, understanding the influence of both landscape and patch characteristics is important for understanding factors affecting the distribution of organisms in urbanised landscapes. Consequently, the aim of this study was to establish the responses of forest dwelling mammals to landscape and habitat structure in an urban-forest mosaic in the EThekwini Municipality Area, Durban, South Africa. Using presence and absence data of mammals from camera traps, we modelled occupancy of species using the occupancy modelling framework. The occupancy by *Philantomba monticola* was positively influenced by forest cover (%), woody cover (%), leaf litter (%) and stem density of large trees and negatively influenced by road density. For *Tragelaphus sylvaticus*, *Potamochoerus larvatus* and *Hystix africaeaustralis*, occupancy was influenced positively by forest cover (%), woody cover (%) and foliage height diversity and negatively influenced by road density. For *Genetta tigrina* and *Chlorocebus pygerythrus*, occupancy was positively influenced by leaf litter (%), woody cover (%), forest cover (%) and road density and negatively influenced by distance to road. Thus, species showed varying responses to landscape and habitat structural variables. *Genetta tigrina* and *C. pygerythrus* appeared less vulnerable to the loss of forest habitat and degradation in habitat quality whereas *T. sylvaticus*, *P. larvatus* and *H. africaeaustralis*

RMark Workshop – Single-Season Occupancy Model

Nature Conservation Research. Заповедная наука 2021. 6(1): 68–77 https://dx.doi.org/10.

RESEARCH AND TOURISM AFFECT POSITIVELY THE OCCUPANCY PATTERN OF *LOXODONTA CYCLOTIS* (ELEPH IN TAÏ NATIONAL PARK, CÔTE D'IVOIRE

Malé R. Kely[1,2], Célestin Y. Kouakou[1,2], Jean-Claude K. Béné[1], Manouhin I Abdoulaye Diarrasouba[3], Adama Tondossama[3], Hjalmar S. Kuehl[4], Matthias

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e-mail: tiedouer@gmail.com, abdoulaye.diarrassouba@oipr.ci, adama.tondossama@
[4]*Max Planck Institute for Evolutionary Anthropology, Germany*
e-mail: kuehl@eva.mpg.de
[5]*Georg-August-Universität Göttingen, Germany*
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Received: 27.01.2020. Revised: 12.12.2020. Accepted: 13.12.2020.

The decline and isolation of wild megafauna populations are increasingly recognised in Afri d'Ivoire where elephants are a national symbol, the Taï National Park (TNP) is a key remaining *Loxodonta cyclotis*. However, the interactions between *L. cyclotis* and its current environmenta are less known. This study aims at determining the factors that affect the occupancy patterns of th TNP for guiding conservation decision-making. We assessed the species occupancy probability that affect its distribution based on habitat variables and observations from 87 camera traps i 120 days within TNP. We used an occupancy model to determine the variables that significant *cyclotis* distribution and to estimate their occupancy probability by site of camera traps installati produced a predictive species distribution map by interpolating occupancy probability values sites. The key factors that drive the *L. cyclotis* distribution in the TNP were the distance to research or ecotourism areas, the distance to the periphery and the rate of poaching index of the

Original investigation | Published: 30 August 2017

Determinants of smooth-coated otter occupancy in a rapidly urbanizing coastal landscape in Southeast Asia

Anucha Kamjing, Dusit Ngoprasert, Robert Steinmetz, Wanlop Chutipong, Tommaso Savini & George A. Gale

Mammalian Biology **87**, 168–175 (2017) | Cite this article

44 Accesses | **5** Citations | **4** Altmetric | Metrics

Abstract

Urbanization often has negative impacts on wildlife, nevertheless many species can persist in heavily modified habitats. Understanding factors that promote species persistence in urbanizing landscapes is therefore important for maintaining biodiversity in changing landscapes and may inform more biodiversity-friendly development. We investigated effects of landscape-scale variables on habitat occupancy of Smooth-coated otter (*Lutrogale perspicillata*) in the Inner Gulf of Thailand. In this internationally important wetland complex, 86% of natural habitats have been altered and are now highly urbanized. We conducted track and sign surveys in 60, 25 km^2 grid cells encompassing 1,474 km^2. Within each cell, we quantified the landscape cover types including urban areas, natural habitat (predominately thin ribbons of mangrove along waterways), agriculture, aquaculture, and potential prey availability using a GIS and field surveys. We used occupancy models to identify habitat variables that affected probability of detection and occupancy. Estimated otter occupancy, based on the top model, was 0.33 ±0.07 (95% CI 0.18–0.48) and detection probability was 0.50 ± 0.05 (95% CI 0.41–0.60). Otter occupancy was positively associated with the proportion of natural habitat and the cover of traditional aquaculture ponds, but negatively associated with agriculture and urban cover. The remaining natural patches appear

RMark Workshop

Model 7 – Multi-season occupancy model

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

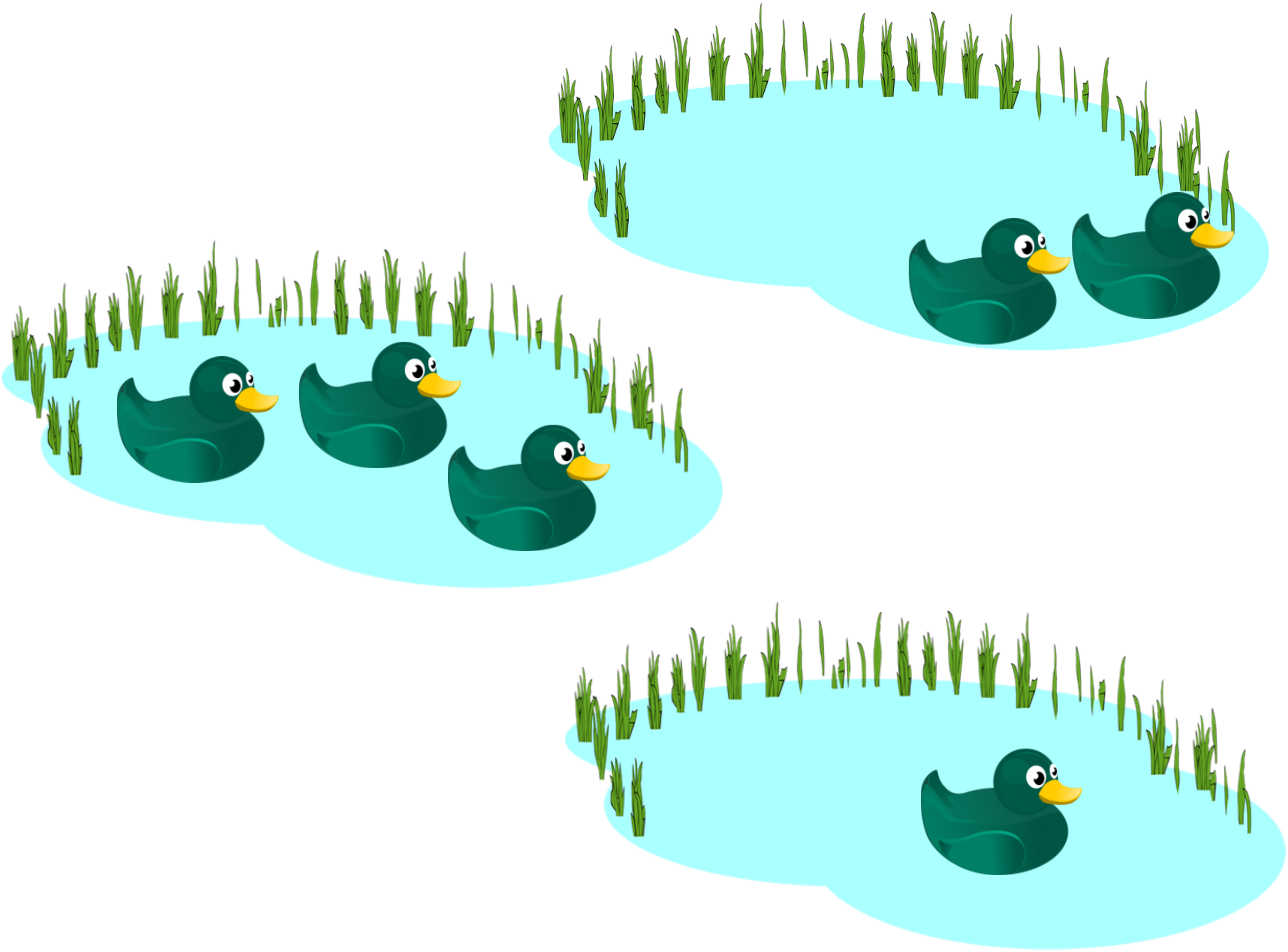
*Each model also will estimate detection/capture probability

RMark Workshop – Lesson Structure

1. Question
2. Field Data
3. Format Data for Analysis
4. Fit Population Model
5. Examine Output and Visualize Results

*steps 3-5 in Program R

RMark Workshop – State Variables and Rate Parameters



<u>**Occupancy**</u>

Occupied Site → Remain Occupied: $\boxed{\text{Persistence}}$

Occupied Site → Local Extinction: $\boxed{\text{Extinction}}$

Unoccupied Site → Remain Unoccupied: $\boxed{\text{1 - Colonization}}$

Unoccupied Site → Become Colonized: $\boxed{\text{Colonization}}$

RMark Workshop – Multi-Season Occupancy Model

Colonization Persistence Extinction

Site 000 110 011 000

Detection probability of focal species

Contracting Disease Clearing Disease

Wolf 000 110 011 000

Probability of detecting disease

RMark Workshop – Multi-Season Occupancy Model

1. Question

How does little tern breeding occurrence change over time across beaches in northern Europe?

Kevin Simmonds, BBC

RMark Workshop – Multi-Season Occupancy Model

1. Question

How does little tern breeding occurrence change over time across beaches in northern Europe?

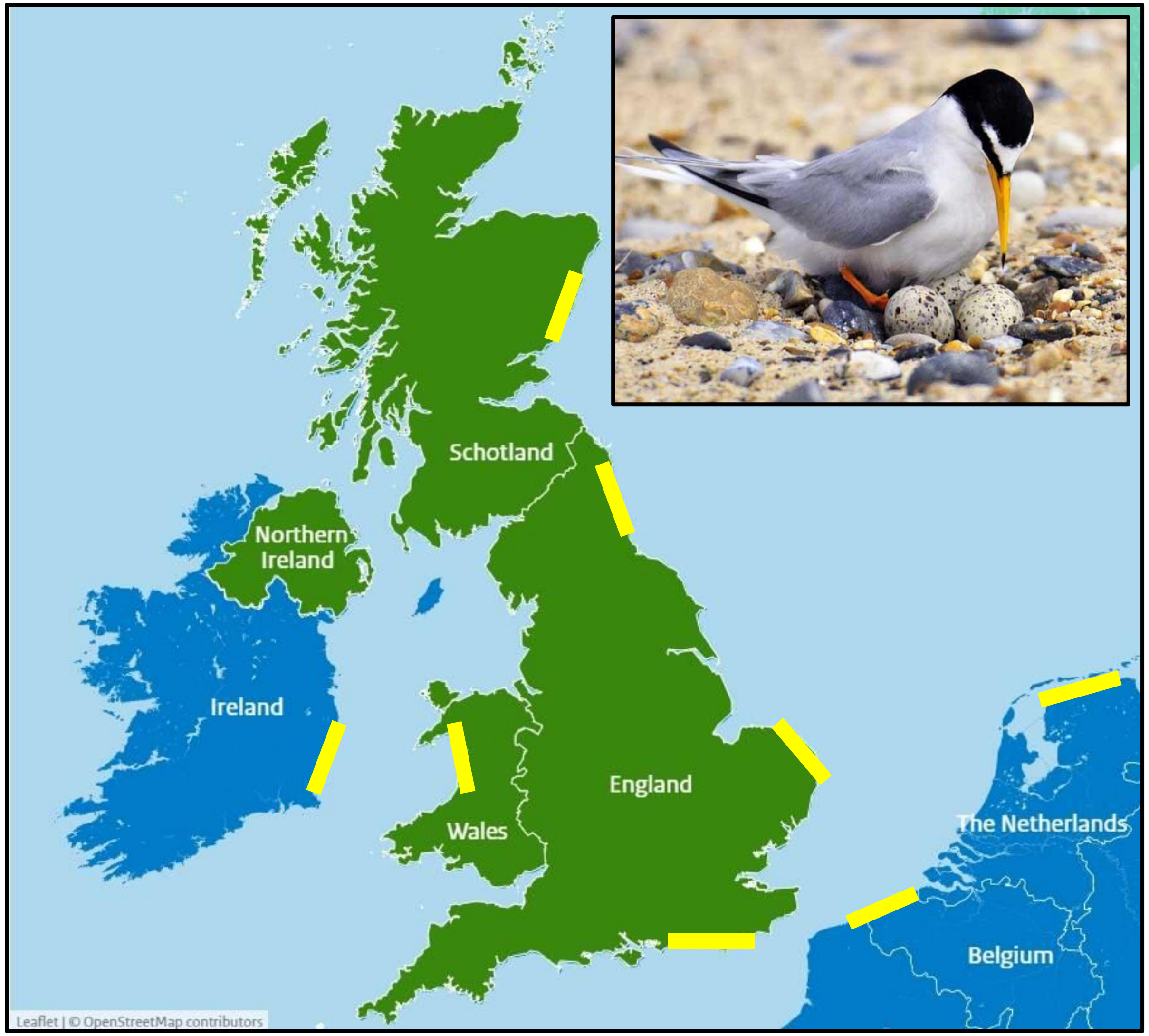
Kevin Simmonds, BBC

RMark Workshop – Multi-Season Occupancy Model

1. Question

How does little tern breeding occurrence change over time across beaches in northern Europe?

Date	Year	Primary	Secondary	Beach	Eggs

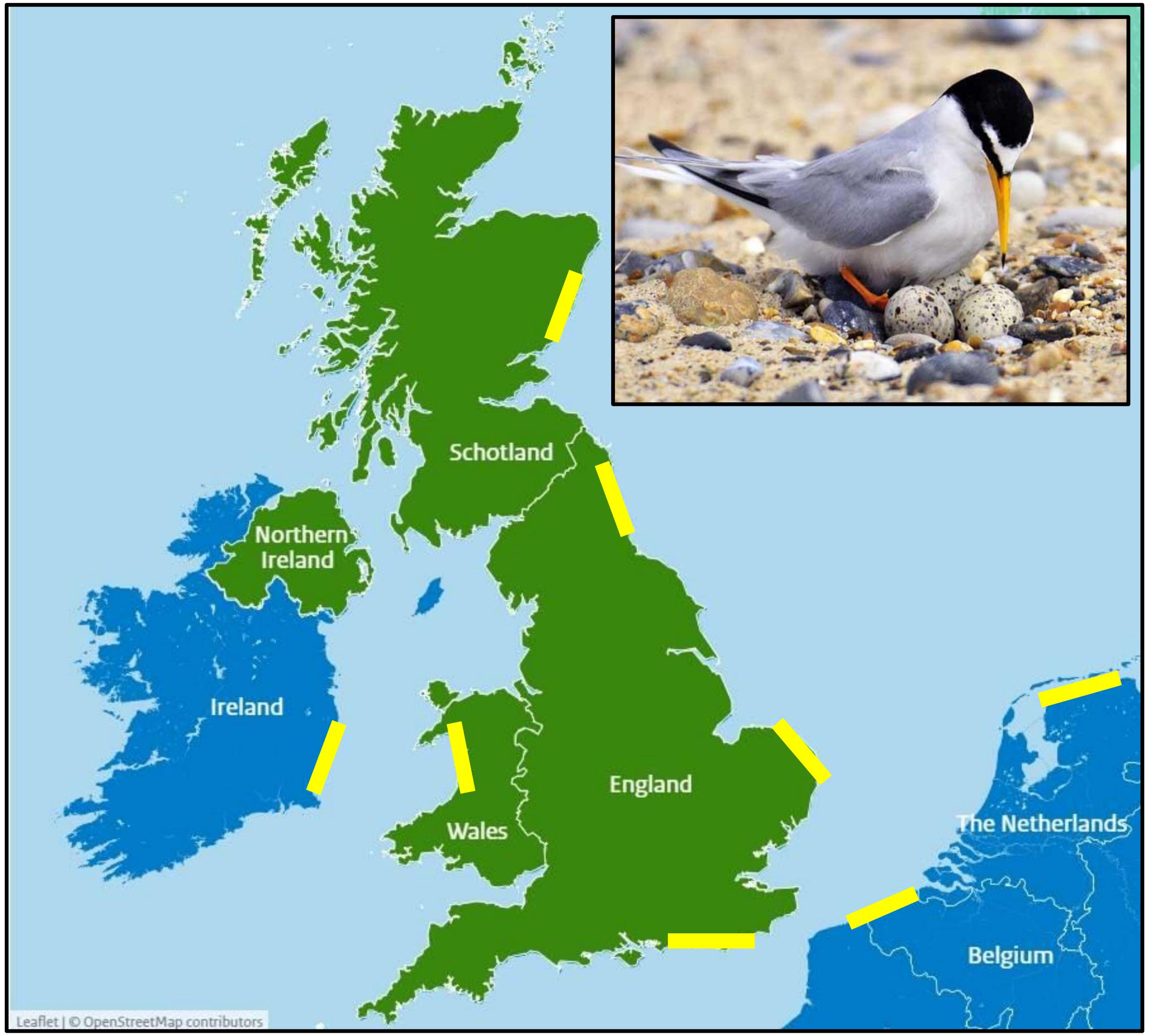


RMark Workshop – Multi-Season Occupancy Model

1. Question

How does little tern breeding occurrence change over time across beaches in northern Europe?

Date	Year	Primary	Secondary	Beach	Eggs
4/19/2015	2015	1	1	1	0

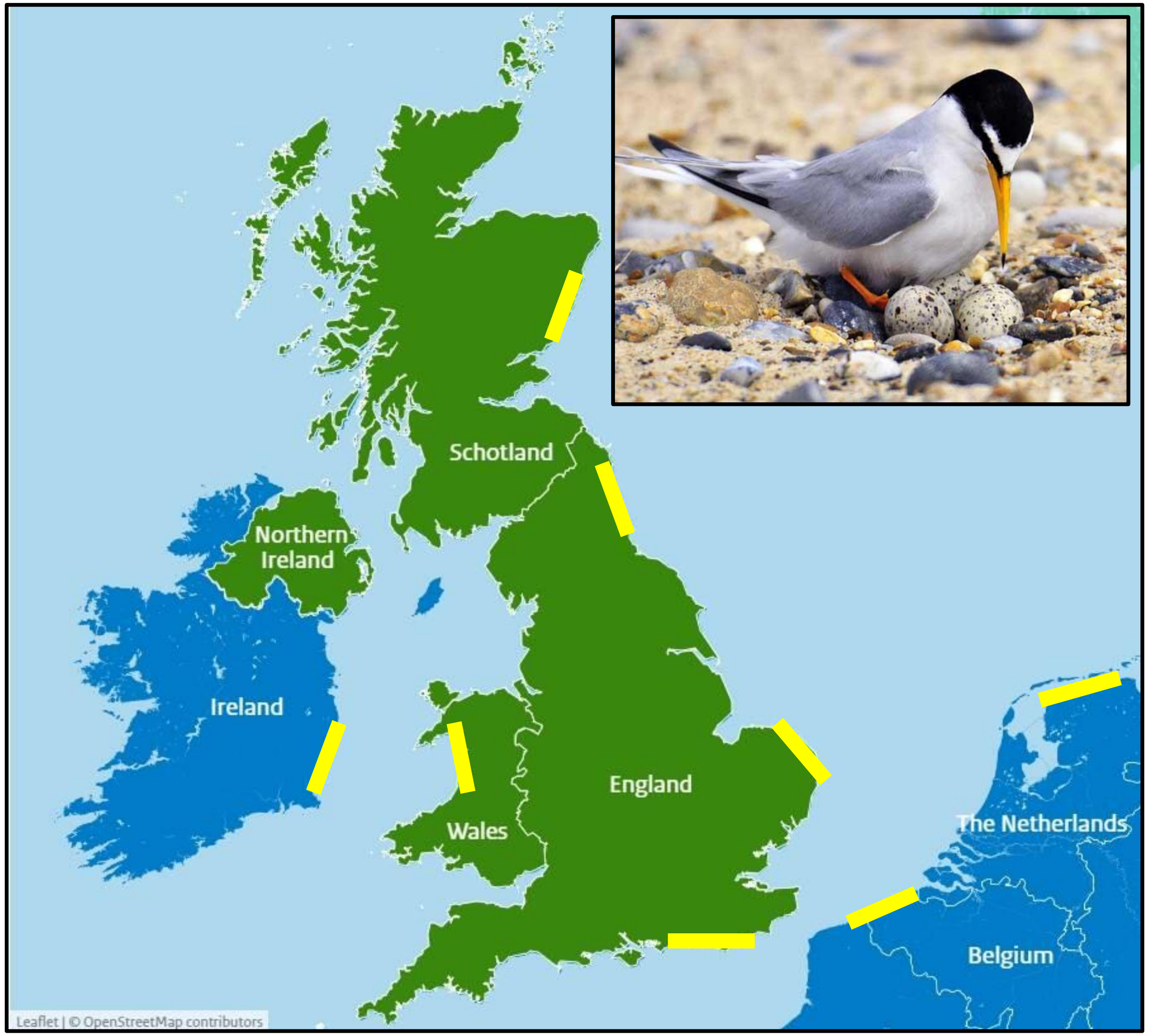


RMark Workshop – Multi-Season Occupancy Model

1. Question

How does little tern breeding occurrence change over time across beaches in northern Europe?

Date	Year	Primary	Secondary	Beach	Eggs
4/19/2015	2015	1	1	1	0
5/11/2015	2015	1	2	1	0
5/30/2015	2015	1	3	1	0

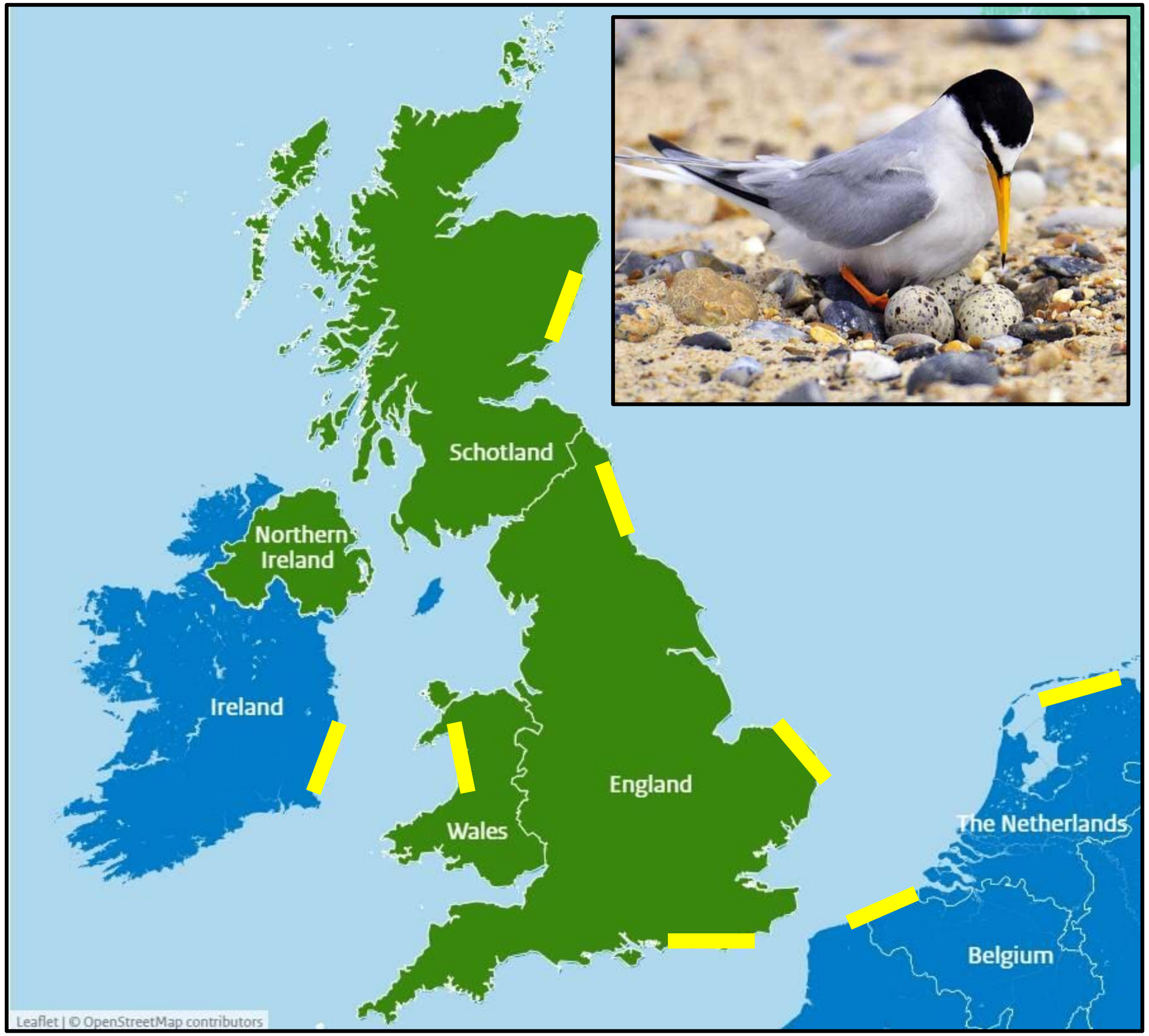


RMark Workshop – Multi-Season Occupancy Model

1. Question

How does little tern breeding occurrence change over time across beaches in northern Europe?

Date	Year	Primary	Secondary	Beach	Eggs
4/19/2015	2015	1	1	1	0
5/11/2015	2015	1	2	1	0
5/30/2015	2015	1	3	1	0
4/16/2016	2016	2	1	1	1
5/14/2016	2016	2	2	1	0
6/8/2016	2016	2	3	1	1

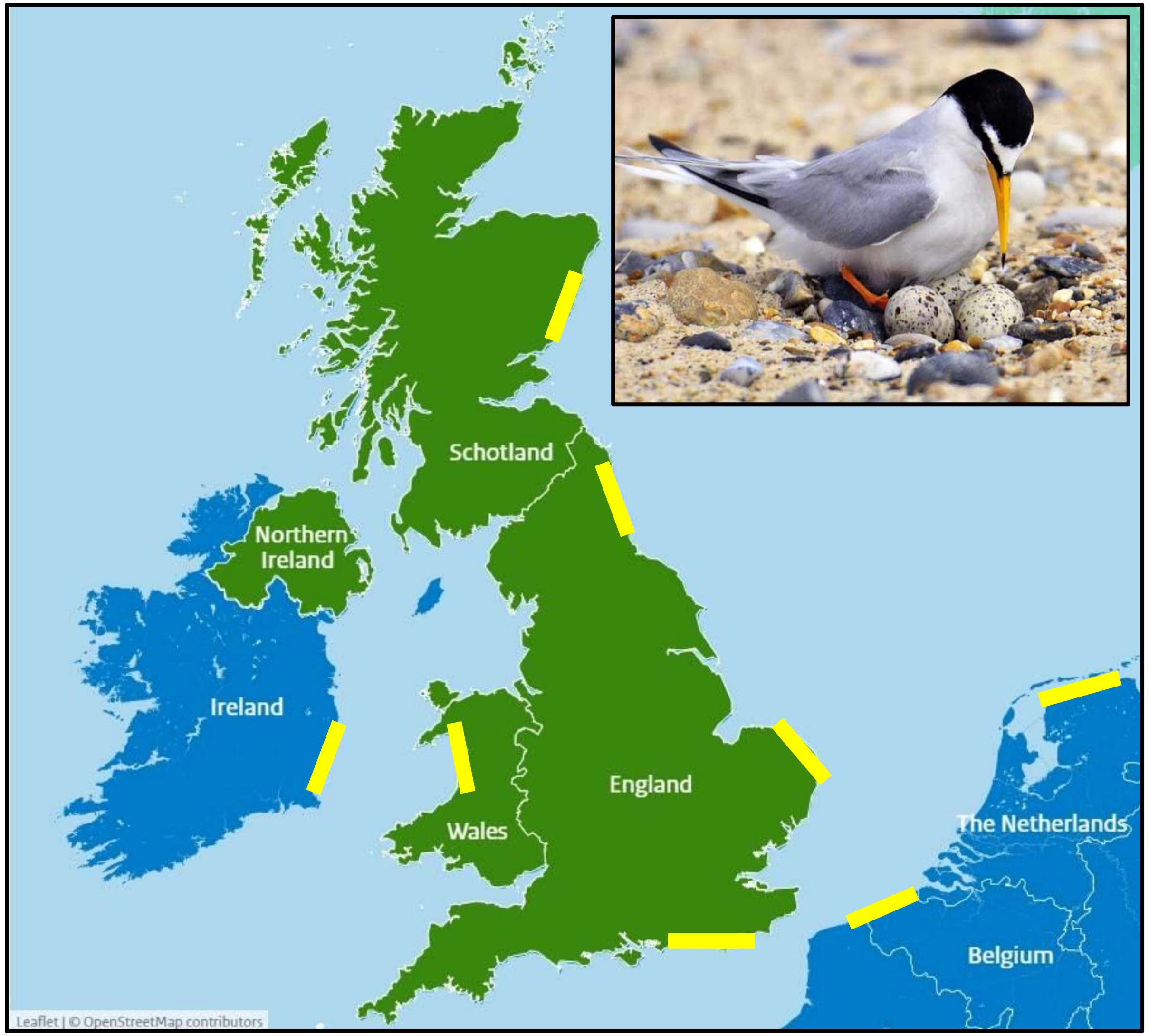


RMark Workshop – Multi-Season Occupancy Model

1. Question

How does little tern breeding occurrence change over time across beaches in northern Europe?

Date	Year	Primary	Secondary	Beach	Eggs
4/19/2015	2015	1	1	1	0
5/11/2015	2015	1	2	1	0
5/30/2015	2015	1	3	1	0
4/16/2016	2016	2	1	1	1
5/14/2016	2016	2	2	1	0
6/8/2016	2016	2	3	1	1
4/12/2017	2017	3	1	1	1
5/1/2017	2017	3	2	1	1
5/28/2017	2017	3	3	1	1
4/20/2018	2018	4	1	1	0
5/15/2018	2018	4	2	1	1
6/2/2018	2018	4	3	1	0
4/14/2019	2019	5	1	1	0
5/11/2019	2019	5	2	1	0
6/4/2019	2019	5	3	1	0



RMark Workshop – Detection histories for each site

Beach	Primary	Secondary	Eggs
1	1	1	0
1	1	2	0
1	1	3	0
1	2	1	1
1	2	2	0
1	2	3	1
1	3	1	1
1	3	2	1
1	3	3	1
1	4	1	0
1	4	2	1
1	4	3	0

Beach	2015.1	2015.2	2015.3	2016.1	2016.2	2016.3	2017.1	2017.2	2017.3	2018.1	2018.2	2018.3
1	1	1	0	1	0	0	0	0	0	0	0	0

RMark Workshop – Multi-Season Occupancy Model

Program MARK

A Gentle Introduction

EVAN G. COOCH & GARY C. WHITE (eds.)

CHAPTER 21

Occupancy models – single-species

Brian D. Gerber, Daniel Martin, Larissa Bailey, *Colorado State University*
Thierry Chambert, *Penn State University & USGS*
Brittany Mosher, *University of Vermont*

As ecologists, we are often interested in how species and communities respond to changes in available resources over space and time. Previous chapters discussed robust methods for evaluating this relationship when we are able to obtain mark-recapture information for individuals or groups. When we are unable to mark animals or when the primary interest is in patterns of species occurrence or proportion of a study area that is occupied or used by a target species, *occupancy models* provide a flexible alternative for elucidating associations between species occurrence and the environment. Our sample unit is thus no longer an individual, but rather a 'site', which is defined based on a study's objective (e.g., 1km^2 grid cell, habitat patch, camera-trap site, transect segment, point-count station).

Occupancy models enable us to estimate the probability of occurrence of a species among sampled sites, while exploring hypotheses about factors (e.g., habitat, environmental conditions, etc.) thought to influence the species' occurrence. The basic sampling design involves randomly selecting a set of independent sites and surveying each site multiple times (i.e., sample 'surveys') during a time period when the state of a site (occupied or not), does not change (see section 21.3, below). The resulting site-specific encounter histories enable us to estimate occupancy – the probability that a site is occupied – while accounting for imperfect species detection. The occupancy approach also enables us to model variation in occupancy and detection simultaneously, relative to site-specific covariates. Additional survey-specific factors can be incorporated into the detection process. The assumptions required by occupancy models share similarities with closed mark-recapture, and are discussed in detail later in this chapter. Historically, occurrence modeling used logistic or probit regression, which assumes a species was absent at sites where it was not detected, and thus inference is known to be biased when the probability of detecting a species at a site is less than one (MacKenzie *et al.* 2017).

RMark Workshop – Multi-Season Occupancy Model

Ecology, 84(8), 2003, pp. 2200–2207
© 2003 by the Ecological Society of America

ESTIMATING SITE OCCUPANCY, COLONIZATION, AND LOCAL EXTINCTION WHEN A SPECIES IS DETECTED IMPERFECTLY

DARRYL I. MACKENZIE,[1,5] JAMES D. NICHOLS,[2] JAMES E. HINES,[2] MELINDA G. KNUTSON,[3] AND ALAN B. FRANKLIN[4]

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[2]*USGS, Patuxent Wildlife Research Center, Laurel, Maryland 20708-4017 USA*
[3]*USGS, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin 54603 USA*
[4]*Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado 80523 USA*

Abstract. Few species are likely to be so evident that they will always be detected when present. Failing to allow for the possibility that a target species was present, but undetected, at a site will lead to biased estimates of site occupancy, colonization, and local extinction probabilities. These population vital rates are often of interest in long-term monitoring programs and metapopulation studies. We present a model that enables direct estimation of these parameters when the probability of detecting the species is less than 1. The model does not require any assumptions of process stationarity, as do some previous methods, but does require detection/nondetection data to be collected in a manner similar to Pollock's robust design as used in mark–recapture studies. Via simulation, we show that the model provides good estimates of parameters for most scenarios considered. We illustrate the method with data from monitoring programs of Northern Spotted Owls (*Strix occidentalis caurina*) in northern California and tiger salamanders (*Ambystoma tigrinum*) in Minnesota, USA.

Key words: *colonization; detection probability; local extinction; metapopulation; monitoring; open population; patch occupancy; robust design; site occupancy.*

Ecology, 97(1), 2016, pp. 194–204
© 2016 by the Ecological Society of America

Dynamic occupancy models for explicit colonization processes

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[1]*Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado 80523, USA*
[2]*U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Unit, Fort Collins, Colorado 80523, USA*
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[4]*National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA, 7600 Sand Point Way NE, Seattle, Washington 98115-6349, USA*
[5]*Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, Cape Town, South Africa*
[6]*African Climate and Development Initiative, University of Cape Town, Rondebosch 7701, South Africa*
[7]*School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98161-2182, USA*

Abstract. The dynamic, multi-season occupancy model framework has become a popular tool for modeling open populations with occupancies that change over time through local colonizations and extinctions. However, few versions of the model relate these probabilities to the occupancies of neighboring sites or patches. We present a modeling framework that incorporates this information and is capable of describing a wide variety of spatiotemporal colonization and extinction processes. A key feature of the model is that it is based on a simple set of small-scale rules describing how the process evolves. The result is a dynamic process that can account for complicated large-scale features. In our model, a site is more likely to be colonized if more of its neighbors were previously occupied and if it provides more appealing environmental characteristics than its neighboring sites. Additionally, a site without occupied neighbors may also become colonized through the inclusion of a long-distance dispersal process. Although similar model specifications have been developed for epidemiological applications, ours formally accounts for detectability using the well-known occupancy modeling framework. After demonstrating the viability and potential of this new form of dynamic occupancy model in a simulation study, we use it to obtain inference for the ongoing Common Myna (*Acridotheres tristis*) invasion in South Africa. Our results suggest that the Common Myna continues to enlarge its distribution and its spread via short distance movement, rather than long-distance dispersal. Overall, this new modeling framework provides a powerful tool for managers examining the drivers of colonization including short- vs. long-distance dispersal, habitat quality, and distance from source populations.

Key words: Acridotheres tristis*; citizen science; colonization; Common Myna; dynamic occupancy model; extinction; invasive species; multi-season model; Southern African Bird Atlas Project; spatiotemporal processes; species distribution maps.*

RMark Workshop – Multi-Season Occupancy Model

PeerJ

Dynamic multi-species occupancy models reveal individualistic habitat preferences in a high-altitude grassland bird community

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[1] Statistical Ecology program, South African National Biodiversity Institute, Cape Town, South Africa
[2] Department of Statistical Sciences, Statistics in Ecology, Environment and Conservation, University of Cape Town, Cape Town, South Africa
[3] Ingula Partnership Project, Blairgowrie, Randburg, BirdLife South Africa, Johannesburg, South Africa
[4] BirdLife South Africa, Johannesburg, South Africa
[5] Applied Behavioural Ecological & Ecosystem Research Unit (ABEERU), UNISA, Johannesburg, South Africa
[6] African Climate and Development Initiative, University of Cape Town, Rondebosch, Cape Town, South Africa

ABSTRACT

Moist, high-altitude grasslands of eastern South African harbour rich avian diversity and endemism. This area is also threatened by increasingly intensive agriculture and land conversion for energy production. This conflict is particularly evident at Ingula, an Important Bird and Biodiversity Area located within the least conserved high-altitude grasslands and which is also the site of a new Pumped Storage Scheme. The new management seeks to maximise biodiversity through manipulation of the key habitat variables: grass height and grass cover through burning and grazing to make habitat suitable for birds. However, different species have individual habitat preferences, which further vary through the season. We used a dynamic multi-species occupancy model to examine the seasonal occupancy dynamics of 12 common grassland bird species and their habitat preferences. We estimated monthly occupancy, colonisation and persistence in relation to grass height and grass cover throughout the summer breeding season of 2011/12. For majority of these species, at the beginning of the season occupancy increased with increasing grass height and decreased with increasing grass cover. Persistence and colonisation decreased with increasing grass height and cover. However, the 12 species varied considerably in their responses to grass height and cover. Our results suggest that management should aim to provide plots which vary in grass height and cover to maximise bird diversity. We also conclude that the decreasing occupancy with increasing grass cover and low colonisation with increasing grass height and cover is a results of little grazing on our study site. We further conclude that some of

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Alison Boyer

Additional Information and

Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2010, **47**, 621–630 doi: 10.1111/j.1365-2664.2010.01811.x

Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species

Viviana Ruiz-Gutiérrez[1,2]*, Elise F. Zipkin[3] and André A. Dhondt[1,2]

[1]Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14853; [2]Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Rd, Ithaca, NY 14850; and [3]USGS Patuxent Wildlife Research Center, 12100 Beech Forest Rd, Laurel, MD 20708, USA

Summary

1. Worldwide loss of biodiversity necessitates a clear understanding of the factors driving population declines as well as informed predictions about which species and populations are at greatest risk. The biggest threat to the long-term persistence of populations is the reduction and changes in configuration of their natural habitat.

2. Inconsistencies have been noted in the responses of populations to the combined effects of habitat loss and fragmentation. These have been widely attributed to the effects of the matrix habitats in which remnant focal habitats are typically embedded.

3. We quantified the potential effects of the inter-patch matrix by estimating occupancy and colonization of forest and surrounding non-forest matrix (NF). We estimated species-specific parameters using a dynamic, multi-species hierarchical model on a bird community in southwestern Costa Rica.

4. Overall, we found higher probabilities of occupancy and colonization of forest relative to the NF across bird species, including those previously categorized as open habitat generalists not needing forest to persist. Forest dependency was a poor predictor of occupancy dynamics in our study region, largely predicting occupancy and colonization of only non-forest habitats.

5. Our results indicate that the protection of remnant forest habitats is key for the long-term persistence of all members of the bird community in this fragmented landscape, including species typically associated with open, non-forest habitats.

RMark Workshop

Model 8 – Known fate model

RMark Workshop – Models

Response	System	Marked	Data	Model
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

Known-fate models are often used to estimate survival in wildlife studies using telemetry data

Useful if animals are monitored at equal time intervals (e.g., tracked every day or every week)

RMark Workshop – Known Fate Model

Conroy, M. J., Costanzo, G. R., & Stotts, D. B. (1989). Winter survival of female American black ducks on the Atlantic coast. *The Journal of wildlife management*, 99-109.

RMark Workshop – Known Fate Model (LDLD format)

encounter history	*probability*	*interpretation*
`10 10 10 10`	$S_1S_2S_3S_4$	tagged at occasion 1 and survived until the end of the study
`10 10 11 00`	$S_1S_2(1-S_3)$	tagged at occasion 1, known alive during the second interval, and died during the third interval
`10 11 00 00`	$S_1(1-S_2)$	tagged at occasion 1 and died during the second interval
`11 00 00 00`	$(1-S_1)$	tagged at occasion 1 and died during the first interval
`10 00 00 10`	S_1S_4	tagged at occasion 1, *censored* for interval 2 and 3 (not detected, or removed for some reason), and re-inserted into the study at occasion 4
`00 00 10 11`	$S_3(1-S_4)$	tagged at occasion 3, died during the 4th interval
`10 00 00 00`	S_1	tagged at occasion 1, known alive at the end of the first interval, but not released at occasion 2 and therefore *censored* after the first interval

RMark Workshop – Known Fate Model (LDLD format)

a. The two-digit pairs each pertain to an interval (the period of time between occasions).

b. There are only 3 possible entries for each interval:

- `10` = an animal survived the interval, given it was alive at the start of the interval
- `11` = an animal died during the interval, given it was alive at the start of the interval
- `00` = an animal was censored for this interval

c. In order to know the fate of an animal during an interval, one must have encountered it **both** at the beginning **and** the end of the interval.

RMark Workshop

Model 9 – Nest survival model

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
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**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

**Closed* may be used interchangeably with *Static*, and *Open* used interchangeably with *Dynamic*

*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

When animals are not monitored at equal time intervals, as required by known-fate models, data are termed “ragged”

Nest survival models are a special type of known-fate analysis that are especially useful if animals are monitored at irregular intervals

RMark Workshop – Nest Survival Model

If we know how many nests we found and we know the fate of every nest, why not just compare the proportion of successful nests among groups with different attributes?

Well, such an analysis is only valid if destroyed nests can be found with the same probability as active ones.

In most studies successful and unsuccessful nests are not found with equal probability, and most nests are found after egg laying has commenced.

Harold Mayfield pointed out that under these circumstances the proportion of successful nests, which he termed apparent nesting success, is biased high relative to actual nesting success, the proportion of nests that survive from initiation to completion (the above text is from Chapter 17 in the Program MARK book).

So, we want to estimate daily survival probability for only the days that nests observed, which helps to account for the fact that some nests are not under observation starting with the day of nest initiation. We can do this with Nest Survival Models.

RMark Workshop – Nest Survival Model

Rotella, J. J., Dinsmore, S. J., & Shaffer, T. L. (2004). Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal biodiversity and Conservation*, *27*(1), 187-205.

RMark Workshop

Model 4 – Pradel recruitment model (reverse-time model)

*Moved this model to the end of the workshop

RMark Workshop – Models

Response	**System**	**Marked**	**Data**	**Model**
Abundance	Closed	Yes	Capture-Mark-Recapture	Closed Population Estimation
Survival	Open	Yes	Capture-Mark-Recapture	Cormack-Jolly-Seber Model
Survival	Both	Yes	Capture-Mark-Recapture	Robust Design with Temporary Emigration
Recruitment and Population Growth	Both	Yes	Capture-Mark-Recapture	Robust Design Pradel Recruitment Model
Dispersal	Both	Yes	Capture-Mark-Recapture	Robust Design Multi-State Model
Distribution	Closed	No	Detection/Nondetection	Site-Occupancy Model (Single-Season)
Distribution (Change in Distribution)	Open	No	Detection/Nondetection	Site-Occupancy Model (Multi-Season)
Survival	Open	Yes	Biotelemetry	Known Fate Model
Survival	Open	Yes	Nest Checks	Nest Survival Model

*All models will be fit in the *RMark* package in Program R

**Abundance* may be used interchangeably with *Density*, and *Distribution* used interchangeably with *Occurrence*

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*In the **Marked** column, *Yes* indicates that individual animals are uniquely identified in the dataset

*Each model also will estimate detection/capture probability

RMark Workshop – Lesson Structure

1. Question
2. Field Data
3. Format Data for Analysis
4. Fit Population Model
5. Examine Output and Visualize Results

*steps 3-5 in Program R

RMark Workshop – Reverse-Time Pradel Recruitment Model

1. Question

Does annual precipitation & rangeland health influence the survival & recruitment of black-footed ferrets at reintroduction sites?

Year	Site	Primary	Secondary	Tag	Precipitation
2015	MT	1	1	200	990
2015	MT	1	1	201	990
2015	MT	1	1	202	990
2015	MT	1	1	203	990
2015	MT	1	2	204	990
2015	MT	1	2	205	990
2015	MT	1	2	**201**	990
2015	MT	1	2	206	990
2015	MT	1	2	**203**	990
2015	MT	1	3	207	990
2015	MT	1	3	208	990
2015	MT	1	3	**200**	990
2015	MT	1	3	209	990

So far, we have focused on animals **leaving** the population, both permanently and temporarily.

However, if we are interested in modeling the dynamics of a population…

We are likely to be as interested in the probability of **entry** into the population as we are with the probability of exit

RMark Workshop – Reverse-Time Pradel Recruitment Model

λ = 1 stable
λ < 1 decreasing
λ > 1 increasing

$$\lambda = \frac{N_{t+1}}{N_t}$$

$$\Delta N = additions - subtractions$$

$$\varphi_t = S_t F_t$$

$$N_{t+1} = N_t \varphi_t + B_t$$

$$\lambda_t = \frac{B_t}{N_t} + \varphi_t$$

$$\lambda_t = f_t + \varphi_t$$

RMark Workshop – Reverse-Time Pradel Recruitment Model

BIOMETRICS 52, 703–709
June 1996

Utilization of Capture–Mark–Recapture for the Study of Recruitment and Population Growth Rate

R. Pradel[1]

Cooperative Fish and Wildlife Research Unit, University of Florida,
Gainesville, Florida 32611, U.S.A.

SUMMARY

Capture–mark–recapture data has been extensively used for the study of survival. However, recruitment and population growth rate can be investigated as well. The study of recruitment is shown to be equivalent to the study of survival in reverse and can be carried out by inverting capture histories. The natural parameter in this approach—here called seniority probability—is, at each occasion, the probability of being previously in the population. An overall likelihood is then presented that describes the gains and losses to the population by means of survival and seniority probabilities. This likelihood can be easily modified for the direct study of population growth rates between occasions.

RMark Workshop – Reverse-Time Pradel Recruitment Model

CHAPTER 13

Time-symmetric open models: recruitment, survival, and population growth rate

So far, we have concentrated on estimation related to the general question ‘what is the probability of leaving the population?’. Clearly, death marks permanent departure from the population. Absence from the population can be permanent (like death), or temporary (a subject we’ll discuss more fully in a later chapter on something known as the ‘robust design’). However, if we’re interested in modeling the dynamics of a population, then we’re likely to be as interested in the probability of entry into the population as we are the probability of exit from the population. So, where to begin. We’ll start with the fundamental model of population dynamics. Usually, the assumption (based on even a casual glance at a typical textbook on the subject) is that population dynamics models are based entirely on high-level mathematics. However, while it isn’t difficult to find examples of such models, the fundamental model is quite simple:

population dynamics has to do with the change in abundance over space and/or time (ΔN)

$$\Delta N = \text{'additions'} - \text{'subtractions'}$$

Program MARK

A Gentle Introduction

EVAN G. COOCH & GARY C. WHITE (eds.)

RMark Workshop – Reverse-Time Pradel Recruitment Model

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Utilization of Capture–Mark–Recapture for the Study of Recruitment and Population Growth Rate

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SUMMARY

Capture–mark–recapture data has been extensively used for the study of survival. However, recruitment and population growth rate can be investigated as well. The study of recruitment is shown to be equivalent to the study of survival in reverse and can be carried out by inverting capture histories. The natural parameter in this approach—here called seniority probability—is, at each occasion, the probability of being previously in the population. An overall likelihood is then presented that describes the gains and losses to the population by means of survival and seniority probabilities. This likelihood can be easily modified for the direct study of population growth rates between occasions.

Forward in time

101110

$$\varphi_1(1-p_2)\varphi_2 p_3 \varphi_3 p_4 \varphi_4 p_5 (1-\varphi_5 p_6)$$

Backward in time

011101

$$\gamma_5 p_4 \gamma_4 p_3 \gamma_3 (1-p_2)\gamma_2 p_1$$

forward in time	φ_i	probability that if alive and in the population at time *i* (e.g., this year), the you will be alive and in the population at time *i*+1 (e.g., next year)
backward in time	γ_i	probability that if alive and in the population at time *i* (e.g., this year), that you *were* also alive and in the population at time *i*-1 (e.g., last year)

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λ = 1 stable
λ < 1 decreasing
λ > 1 increasing

$$\lambda = \frac{N_{t+1}}{N_t}$$

$$\Delta N = additions - subtractions$$

$$\lambda_t = \frac{\varphi_t}{\gamma_{t+1}}$$

$$\lambda_t = f_t + \varphi_t$$

$$f_t = \varphi_t\left(\frac{1-\gamma_{t+1}}{\gamma_{t+1}}\right)$$

Relationship between key parameters in Pradel temporal symmetry model

Time index i =1 , …, k primary occasions

Parameters we are interested in

- Apparent survival Phi ϕ_i
- "Seniority" Gamma γ_i
- Population growth rate λ_i
- Recruitment rate f_i

The standard Pradel parameterization provides estimates of ϕ_i and γ_i , but λ_i and f_i can be derived as follows:

- $\lambda_i = \dfrac{\phi_i}{\gamma_{i+1}}$
- $f_i = \lambda_i - \phi_i$

The usual procedure is to estimate ϕ_i and γ_i from the Pradel model and plug the resulting estimates into the above formulas, e.g.

- $\hat{\lambda}_i = \dfrac{\hat{\phi}_i}{\hat{\gamma}_{i+1}}$

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Compensatory effects of recruitment and survival when amphibian populations are perturbed by disease

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Summary

1. The need to increase our understanding of factors that regulate animal population dynamics has been catalysed by recent, observed declines in wildlife populations worldwide. Reliable estimates of demographic parameters are critical for addressing basic and applied ecological questions and understanding the response of parameters to perturbations (e.g. disease, habitat loss, climate change). However, to fully assess the impact of perturbation on population dynamics, all parameters contributing to the response of the target population must be estimated.

2. We applied the reverse-time model of Pradel in Program MARK to 6 years of capture–recapture data from two populations of *Anaxyrus boreas* (boreal toad) populations, one with disease and one without. We then assessed a priori hypotheses about differences in survival and recruitment relative to local environmental conditions and the presence of disease.

3. We further explored the relative contribution of survival probability and recruitment rate to population growth and investigated how shifts in these parameters can alter population dynamics when a population is perturbed.

4. High recruitment rates (0·41) are probably compensating for low survival probability (range 0·51–0·54) in the population challenged by an emerging pathogen, resulting in a relatively slow rate of decline. In contrast, the population with no evidence of disease had high survival probability (range 0·75–0·78) but lower recruitment rates (0·25).

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On valuing patches: estimating contributions to metapopulation growth with reverse-time capture–recapture modelling

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Metapopulation ecology has historically been rich in theory, yet analytical approaches for inferring demographic relationships among local populations have been few. We show how reverse-time multi-state capture–recapture models can be used to estimate the importance of local recruitment and interpopulation dispersal to metapopulation growth. We use 'contribution metrics' to infer demographic connectedness among eight local populations of banner-tailed kangaroo rats, to assess their demographic closure, and to investigate sources of variation in these contributions. Using a 7 year dataset, we show that: (i) local populations are relatively independent demographically, and contributions to local population growth via dispersal within the system decline with distance; (ii) growth contributions via local survival and recruitment are greater for adults than juveniles, while contributions involving dispersal are greater for juveniles; (iii) central populations rely more on local recruitment and survival than peripheral populations; (iv) contributions involving dispersal are not clearly related to overall metapopulation density; and (v) estimated contributions from outside the system are unexpectedly large. Our analytical framework can classify metapopulations on a continuum between demographic independence and panmixia, detect hidden population growth contributions, and make inference about other population linkage forms, including rescue effects and source–sink structures. Finally, we discuss differences between demographic and genetic population linkage patterns for our system.

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Long-term demographic consequences of habitat fragmentation to a tropical understory bird community

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Abstract. Tropical deforestation continues to cause population declines and local extinctions in centers of avian diversity and endemism. Although local species extinctions stem from reductions in demographic rates, little is known about how habitat fragmentation influences survival of tropical bird populations or the relative importance of survival and fecundity in ultimately shaping communities. We analyzed 22 years of mark–recapture data to assess how fragmentation influenced apparent survival, recruitment, and realized population growth rate within 22 forest understory bird species in the Usambara Mountains, Tanzania. This represents the first such effort, in either tropical or temperate systems, to characterize the effect of deforestation on avian survival across such a broad suite of species. Long-term demographic analysis of this suite of species experiencing the same fragmented environment revealed considerable variability in species' responses to fragmentation, in addition to general patterns that emerged from comparison among species. Across the understory bird community as a whole, we found significantly lower apparent survival and realized population growth rate in small fragments relative to large, demonstrating fragmentation effects to demographic rates long after habitat loss. Demographic rates were depressed across five feeding guilds, suggesting that fragmentation sensitivity was not limited to insectivores. Seniority analyses, together with a positive effect of fragmentation on recruitment, indicated that depressed apparent survival was the primary driver of population declines and observed extinctions. We also found a landscape effect, with lower vital rates in one mountain range relative to another, suggesting that fragmentation effects may add to other large-scale drivers of population decline. Overall, realized population growth rate (λ) estimates were <1 for most species, suggesting that future population persistence, even within large forest fragments, is uncertain in this biodiversity hotspot.

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The End