

# Estimating wolf occupancy with R

Olivier Gimenez



# Lecture 1

## Introduction

Estimating wolf occupancy with R

# Occupancy to map species distribution

**Occupancy:** proportion of an area occupied by a species

- Species range dynamics
- Habitat preferences
- Metapopulation dynamics
- ...

0	0	1	0	0
0	1	0	0	0
0	1	1	0	0
0	0	1	0	0
1	0	1	0	0
0	1	0	0	0
0	0	0	0	1
0	0	0	0	1

$$10/40 = 0.25$$

# Issue of detectability < 1

0	0	1	0	0
0	1	0	0	0
0	1	1	0	0
0	0	1	0	0
1	0	1	0	0
0	1	0	0	0
0	0	0	0	1
0	0	0	0	1

True occupancy = 25%

# Issue of detectability < 1

0	0	1	0	0
0	1	0	0	0
0	1	1	0	0
0	0	1	0	0
1	0	1	0	0
0	1	0	0	0
0	0	0	0	1
0	0	0	0	1

True occupancy = 25%

0	0	1	0	0
0	1	0	0	0
0	1	1	0	0
0	0	1	0	0
1	0	1	0	0
0	1	0	0	0
0	0	0	0	1
0	0	0	0	1

Species detected in 6 occupied sites

# Occupancy underestimation

0	0	1	0	0
0	1	0	0	0
0	1	1	0	0
0	0	1	0	0
1	0	1	0	0
0	1	0	0	0
0	0	0	0	1
0	0	0	0	1

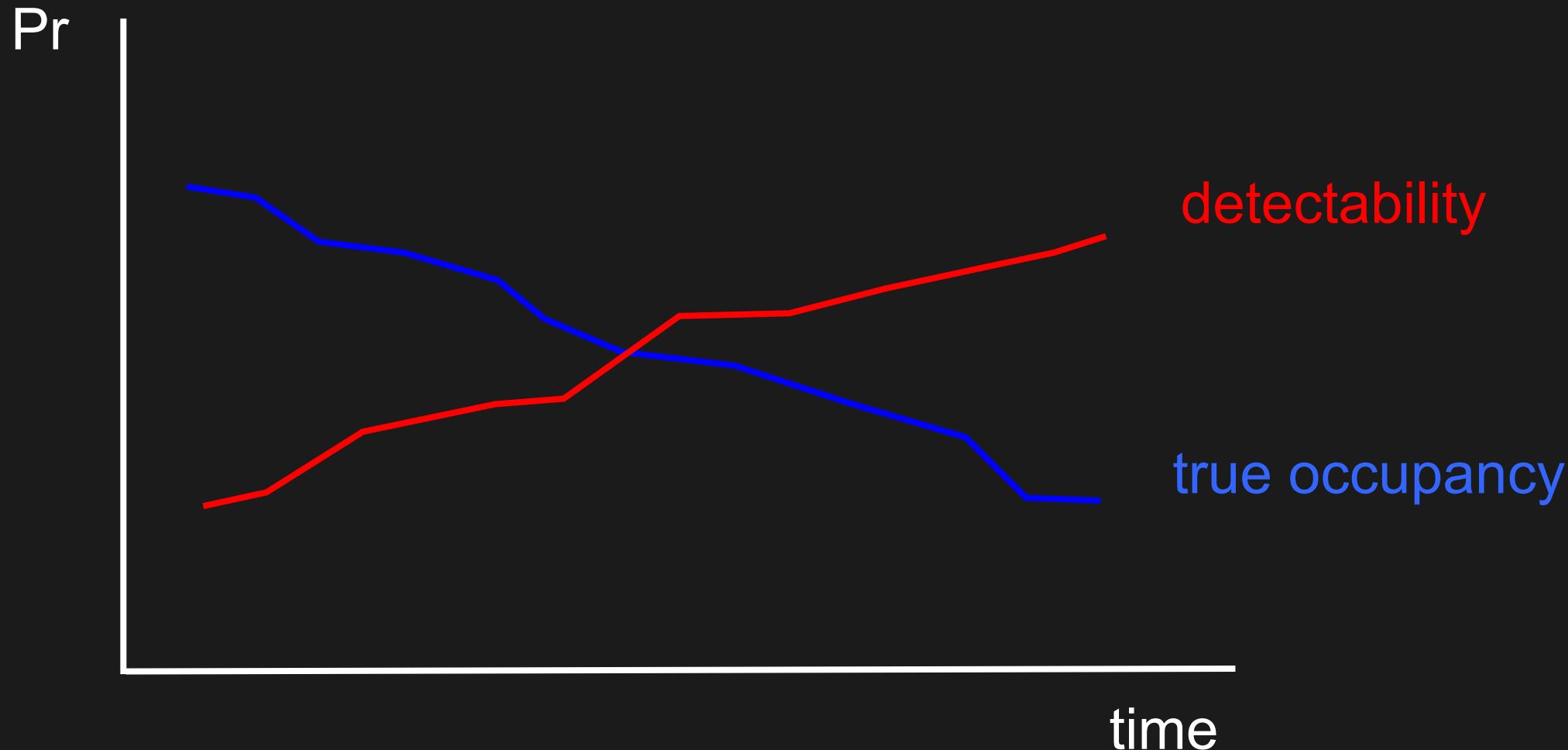
True occupancy = 25%

0	0	1	0	0
0	1	0	0	0
0	1	1	0	0
0	0	1	0	0
1	0	1	0	0
0	1	0	0	0
0	0	0	0	1
0	0	0	0	1

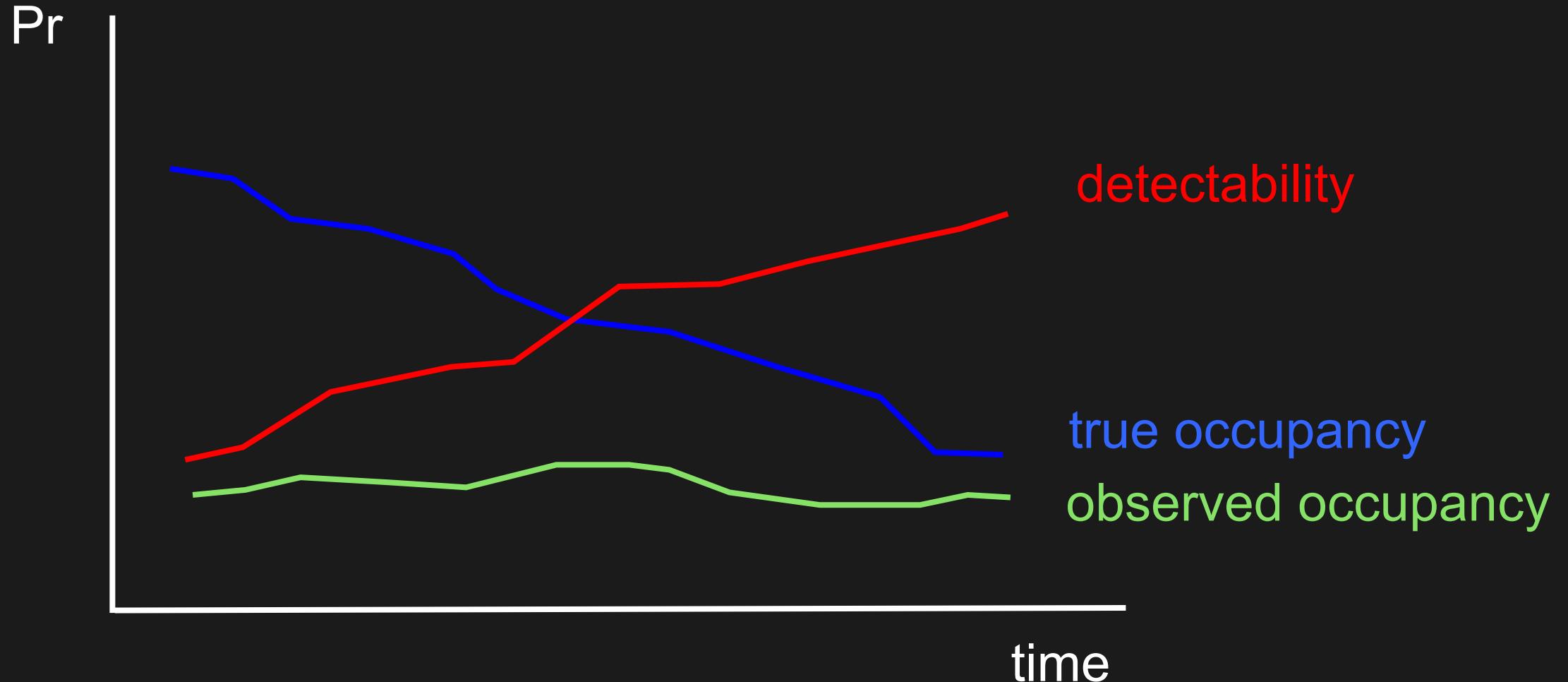
Species detected in 6 occupied sites

Naive occupancy estimate = 6/40 = 15%

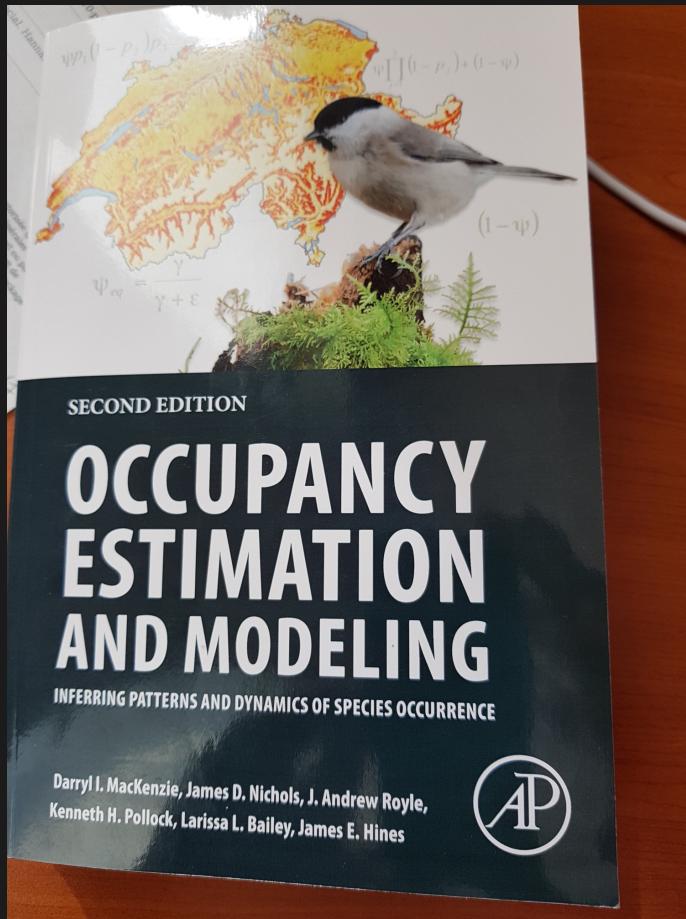
# Issue of detectability < 1



# Bias in occupancy trends



# Occupancy models



**ECOGRAPHY**

A JOURNAL OF SPACE AND TIME IN ECOLOGY

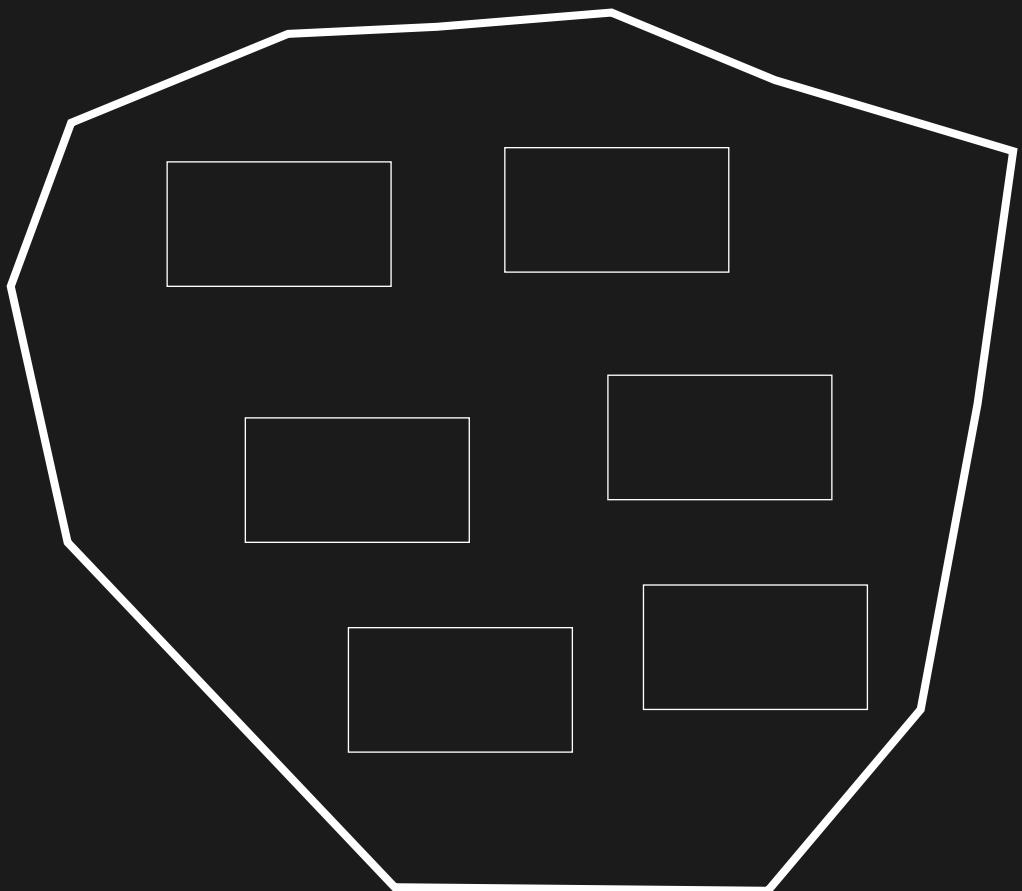
Review & synthesis | Free Access |

**Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities**

Gurutzeta Guillera-Arroita

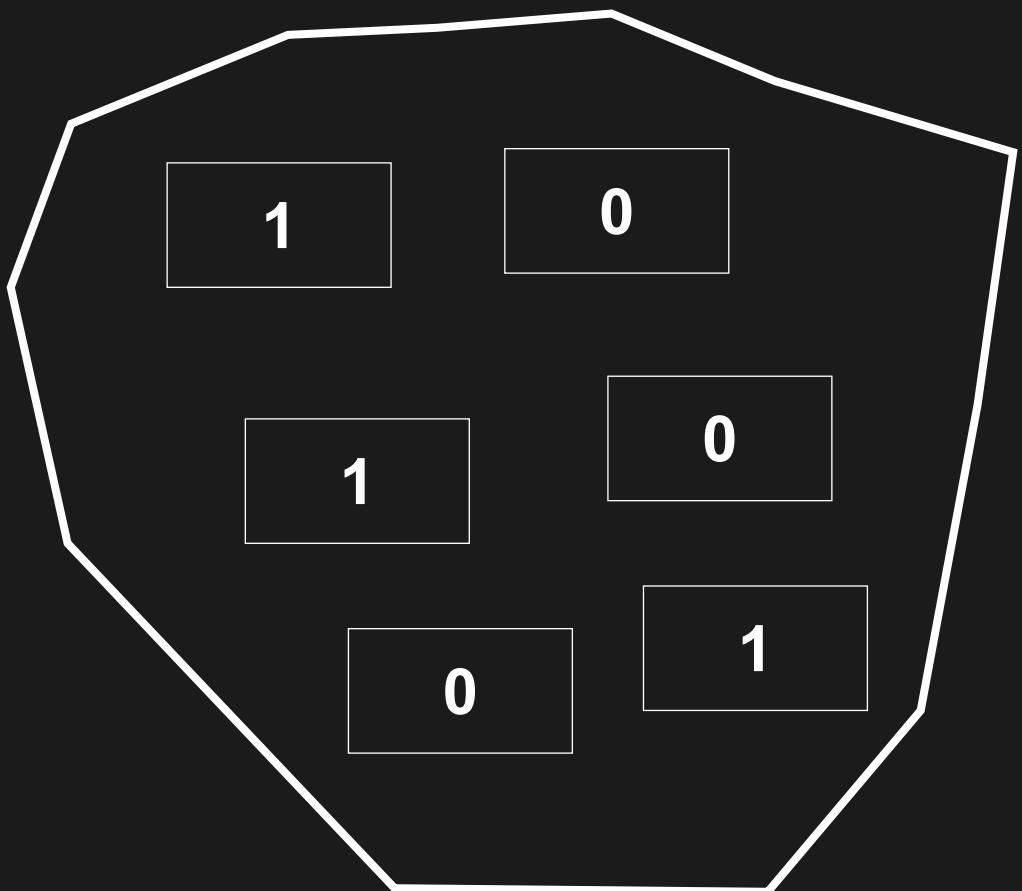
First published: 20 June 2016 | <https://doi.org/10.1111/ecog.02445> | Citations: 134

# Occupancy protocol



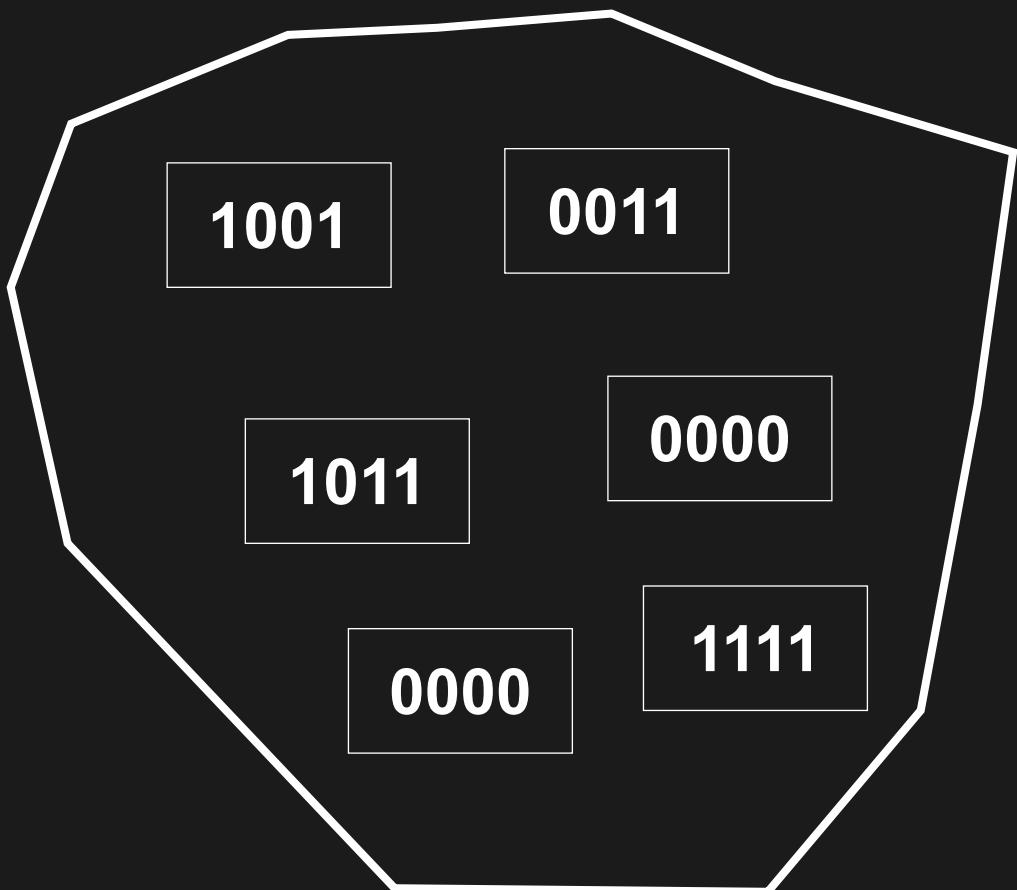
- Several sampling units surveyed

# Occupancy protocol



- Several sampling units surveyed
- Collection of detection/non-detection

# Occupancy protocol



- Several sampling units surveyed
- Collection of detection/non-detection
- Replicate surveys in each unit

# True or false absence?



reality

# True or false absence?



# True or false absence?



reality



observation

# True or false absence?



reality



observation

# Lecture 2

Static aka single-season occupancy models

Estimating wolf occupancy with R

# Single-season occupancy model likelihood

---

$\psi_1$  = prob. a site is initially occupied - **occupancy**

$p$  = prob. species is detected (given presence) – **detection**

# Single-season occupancy model likelihood

---

$\psi_1$  = prob. a site is initially occupied - **occupancy**

$p$  = prob. species is detected (given presence) – **detection**

Assuming closure, and independence of surveys:

$\Pr(1001) = ?$

# Single-season occupancy model likelihood

---

$\psi_1$  = prob. a site is initially occupied - **occupancy**

$p$  = prob. species is detected (given presence) – **detection**

Assuming closure, and independence of surveys:

$$\Pr(1001) = \psi_1 p (1 - p) (1 - p) p$$

# Single-season occupancy model likelihood

---

$\psi_1$  = prob. a site is initially occupied - **occupancy**

$p$  = prob. species is detected (given presence) – **detection**

Assuming closure, and independence of surveys:

$\Pr(0000) = ?$

# Single-season occupancy model likelihood

---

$\psi_1$  = prob. a site is initially occupied - **occupancy**

$p$  = prob. species is detected (given presence) – **detection**

Assuming closure, and independence of surveys:

$$\Pr(0000) = \psi_1 (1 - p) (1 - p) (1 - p) (1 - p) + (1 - \psi_1)$$

# Single-season occupancy model

## Initial states

$$\begin{matrix} U & O \\ (1 - \psi_1) & \psi_1 \end{matrix}$$

O = occupied; U = unoccupied

$\psi_1$  = occupancy,  $p$  = detection

# Single-season occupancy model

Initial states

$$\begin{matrix} U & O \\ (1 - \psi_1) & \psi_1 \end{matrix}$$

State process

$$t \begin{matrix} U & O \\ O & U \end{matrix} \left( \begin{matrix} 1 & 0 \\ 0 & 1 \end{matrix} \right)^{t+1}$$

Markov model

O = occupied; U = unoccupied

$\psi_1$  = occupancy,  $p$  = detection

# Single-season occupancy model

Initial states

$$\begin{matrix} U & O \\ (1 - \psi_1) & \psi_1 \end{matrix}$$

State process

$$t \begin{matrix} U & O \\ O & U \end{matrix} \left( \begin{matrix} 1 & 0 \\ 0 & 1 \end{matrix} \right)^{t+1}$$

Markov model

Observation process

$$t \begin{matrix} U & O \\ O & U \end{matrix} \left( \begin{matrix} 1 & 0 \\ 1 - p & p \end{matrix} \right)$$

hidden

O = occupied; U = unoccupied

$\psi_1$  = occupancy,  $p$  = detection

# Key occupancy model assumptions

---

- Independent detections
- No unmodelled heterogeneity
- No false positives

# Live demo

Estimating wolf occupancy with R

# ECOGRAPHY

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## Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data

Julie Louvier , Christophe Duchamp, Valentin Lauret, Eric Marboutin, Sarah Cubaynes, Rémi Choquet, Christian Miquel, Olivier Gimenez

# Covariates

---

blabla

blabla

# Lecture 3

Dynamic aka multiple-season occupancy models

Estimating wolf occupancy with R

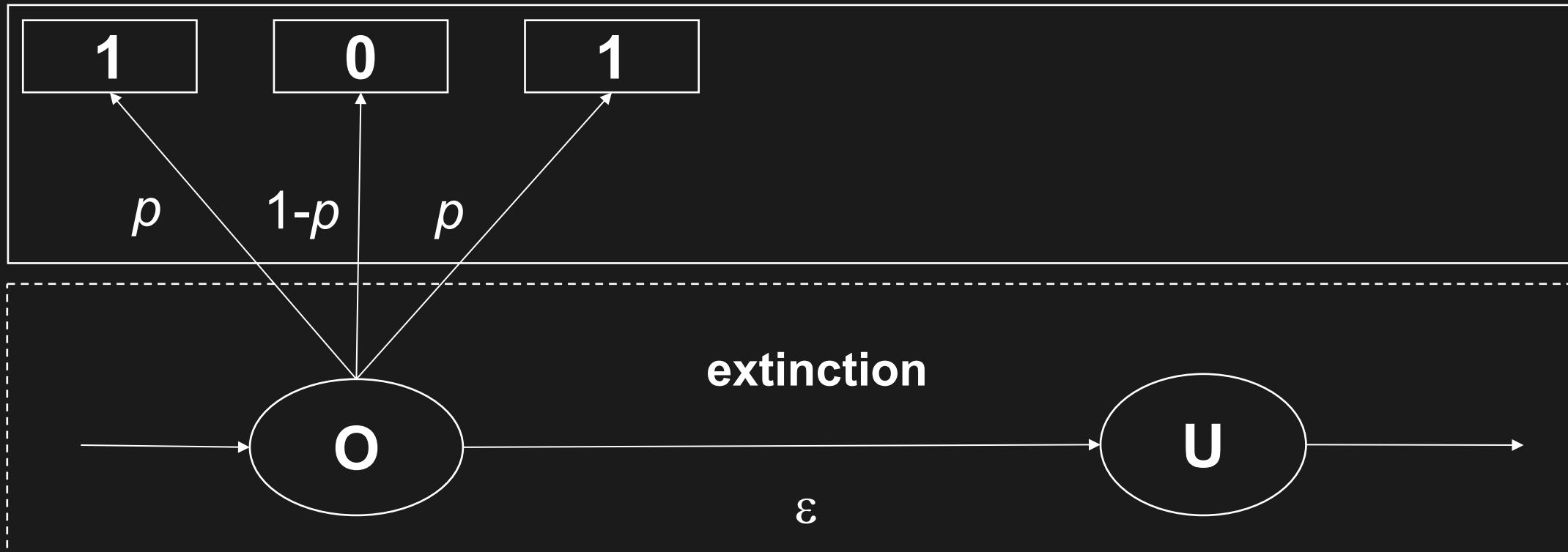
# Dynamic (multi-season) occupancy models



O = occupied; U = unoccupied

# Dynamic (multi-season) occupancy models

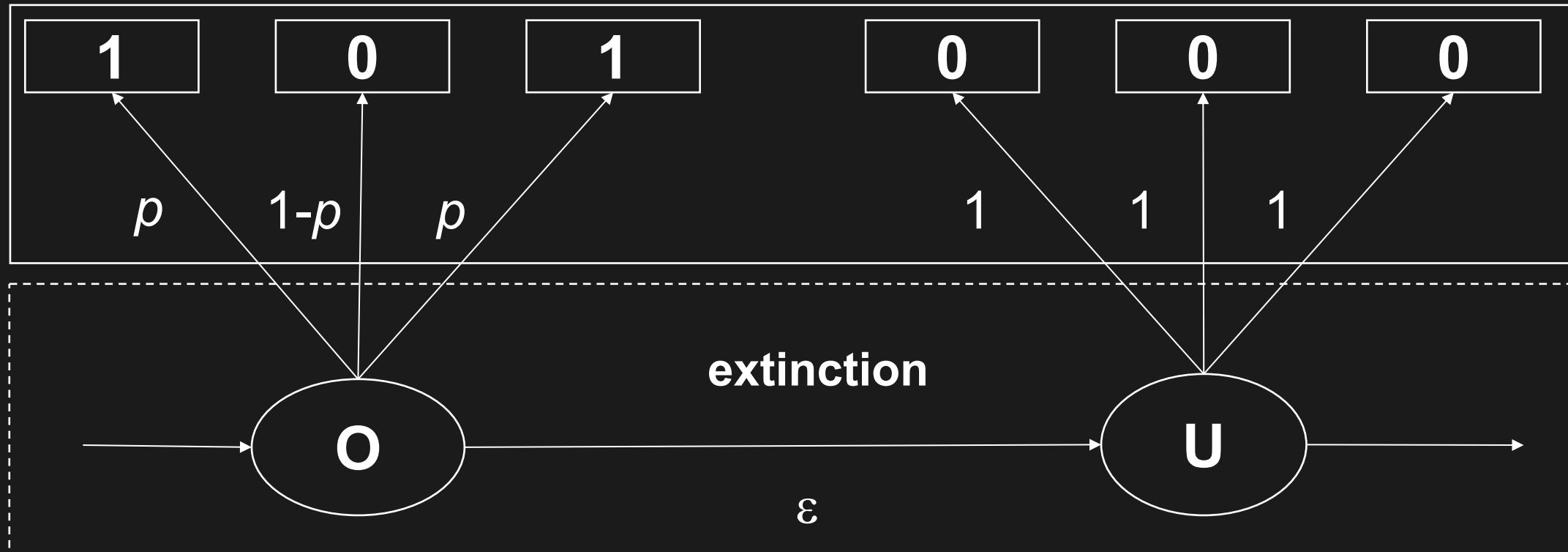
1 = species detected; 0 = species undetected



O = occupied; U = unoccupied

# Dynamic (multi-season) occupancy models

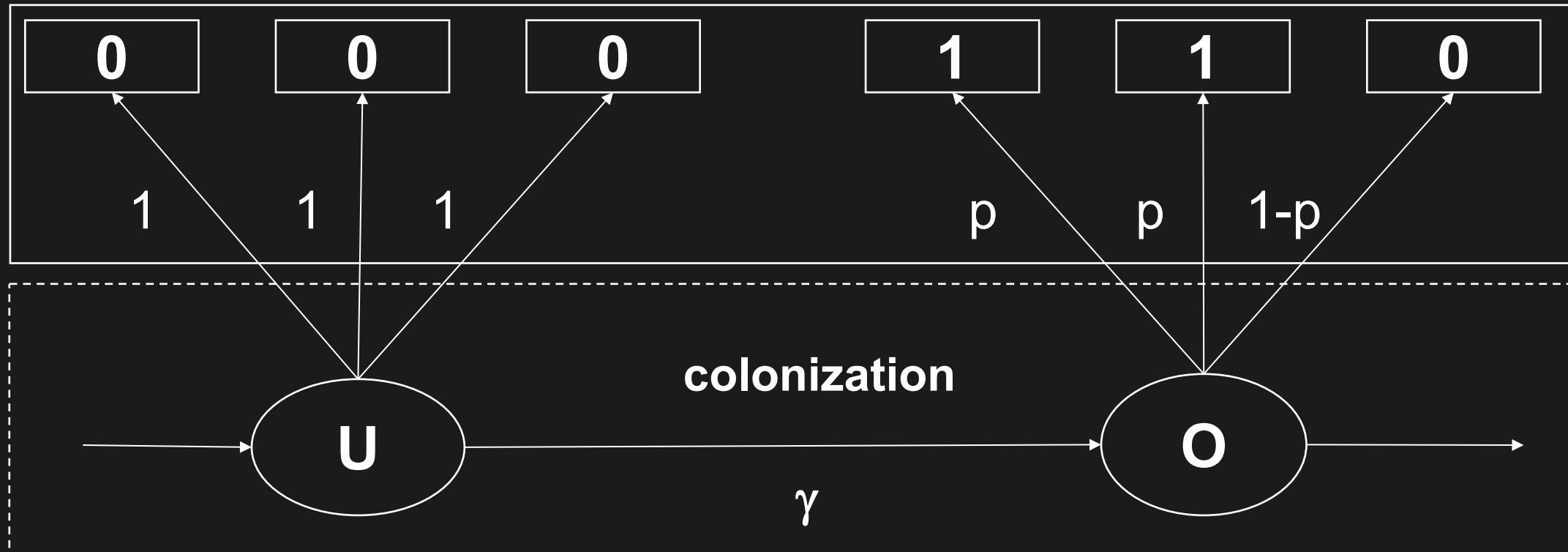
1 = species detected; 0 = species undetected



O = occupied; U = unoccupied

# Dynamic (multi-season) occupancy models

1 = species detected; 0 = species undetected



O = occupied; U = unoccupied

# Dynamic (multi-season) occupancy models

---

$\psi_1$  = prob. a site is occupied - **occupancy**

$p$  = prob. species is detected (given presence) – **detection**

$\gamma$  = prob. unoccupied site becomes occupied – **colonisation**

$\varepsilon$  = prob. occupied site becomes unoccupied – **extinction**

# Dynamic occupancy model likelihood

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$$\Pr(110\ 000) = ?$$

# Dynamic occupancy model likelihood

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$\Pr(110\ 000) =$

Three replicated surveys or secondary occasions

Closure assumption

# Dynamic occupancy model likelihood

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$$\Pr(110 \ 000) = \psi_1 p p (1 - p)$$

Three replicated surveys or secondary occasions

Closure assumption

# Dynamic occupancy model likelihood

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$$\Pr(110\ 000) = \psi_1 p p (1 - p) [\varepsilon + (1 - \varepsilon) \dots]$$

# Dynamic occupancy model likelihood

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$$\Pr(110 \text{ } 000) = \psi_1 p p (1 - p) [ \varepsilon + (1 - \varepsilon) (1 - p) (1 - p) (1 - p) ]$$

# Dynamic occupancy model likelihood

---

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$$\Pr(000\ 010) = ?$$

# Dynamic occupancy model likelihood

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$$\Pr(000\ 010) = [ \psi_1 (1 - p) (1 - p) (1 - p) (1 - \varepsilon) + (1 - \psi_1) \gamma ]$$

# Dynamic occupancy model likelihood

$\psi_1$  = **occupancy**

$p$  = **detection**

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

$$\Pr(000\ 010) = [ \psi_1 (1 - p) (1 - p) (1 - p) (1 - \varepsilon) + (1 - \psi_1) \gamma ] \\ \times (1 - p) p (1 - p)$$

# Derived parameters

---

$\psi_t$  = **occupancy**

- Season-specific occupancy:

$p$  = **detection**

$$\Psi_{t+1} = \Psi_t (1 - \varepsilon_t) + (1 - \Psi_t) \gamma_t$$

$\gamma$  = **colonisation**

$\varepsilon$  = **extinction**

- Rate of change in occupancy:

$$\lambda_t = \Psi_{t+1} / \Psi_t$$

# Dynamic occupancy model

Initial states

$$\begin{pmatrix} U & O \\ 1 - \psi_1 & \psi_1 \end{pmatrix}$$

State process

$$\begin{matrix} U & O \\ O & O \end{matrix} \begin{pmatrix} 1 - \gamma & \gamma \\ \epsilon & 1 - \epsilon \end{pmatrix}$$

Markov model

Observation process

$$\begin{matrix} 0 & 1 \\ O & O \end{matrix} \begin{pmatrix} 1 & 0 \\ 1 - p & p \end{pmatrix}$$

hidden

# Single-season is a particular case of multi-season

No colonization ( $\gamma = 0$ ) and no extinction ( $\varepsilon = 0$ )

Initial states	State process	Observation process
$\begin{matrix} U & O \\ (1 - \psi_1) & \psi_1 \end{matrix}$	$\begin{matrix} U & O \\ U & \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \\ O & \end{pmatrix}$	$\begin{matrix} 0 & 1 \\ U & \begin{pmatrix} 1 & 0 \\ 1 - p & p \end{pmatrix} \\ O & \end{pmatrix}$

# Live demo

Estimating wolf occupancy with R

# ECOGRAPHY

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## Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data

Julie Louvier , Christophe Duchamp, Valentin Lauret, Eric Marboutin, Sarah Cubaynes, Rémi Choquet, Christian Miquel, Olivier Gimenez

# Lecture 4

Occupancy models with species misidentification

Estimating wolf occupancy with R

# Species misidentification

OPEN  ACCESS Freely available online 2013



## Determining Occurrence Dynamics when False Positives Occur: Estimating the Range Dynamics of Wolves from Public Survey Data

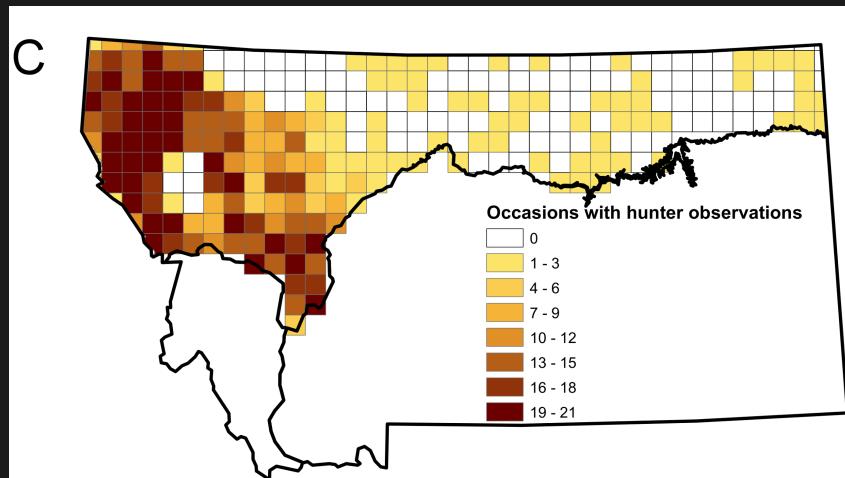
David A. W. Miller<sup>1,2\*</sup>, James D. Nichols<sup>1</sup>, Justin A. Gude<sup>3</sup>, Lindsey N. Rich<sup>4</sup>, Kevin M. Podruzny<sup>3</sup>, James E. Hines<sup>1</sup>, Michael S. Mitchell<sup>4</sup>

- How to account for false positives due to species misidentification?

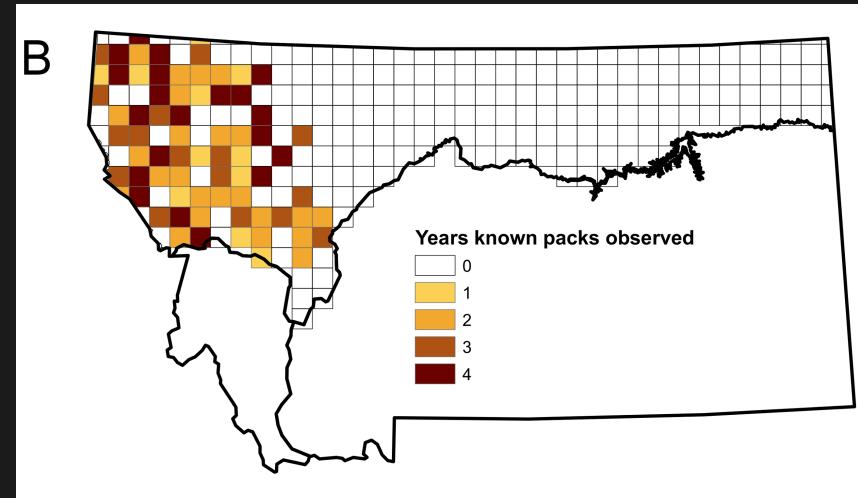


# Data

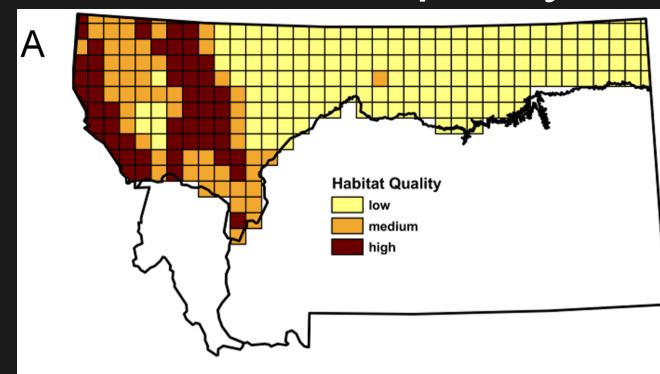
Observations by hunters (phone interviews);  
*uncertainty* in species identification



Telemetry;  
*no doubt* about species



Habitat quality



# Reminder: static occupancy model

Initial states

$$\begin{pmatrix} U & O \\ (1 - \psi_1) & \psi_1 \end{pmatrix}$$

State process

$$\begin{matrix} U & O \\ O & \left( \begin{matrix} 1 & 0 \\ 0 & 1 \end{matrix} \right) \end{matrix}$$

Observation process

$$\begin{matrix} 0 & 1 \\ U & \left( \begin{matrix} 1 & 0 \\ 1 - p & p \end{matrix} \right) \end{matrix}$$

# Model allowing for false positives

## Observation process

0

1

2

Uncertain  
detection

Detection with no doubt  
about the species

# Model allowing for false positives

## Observation process

$$U \begin{pmatrix} 1 - p_{10} & p_{10} & 0 \end{pmatrix}$$

$p_{10}$  = probability of false positive detection

# Model allowing for false positives

## Observation process

$$U \begin{pmatrix} 0 & 1 & 2 \\ 1 - p_{10} & p_{10} & 0 \\ 1 - p_{11} & (1 - b)p_{11} & bp_{11} \end{pmatrix}$$

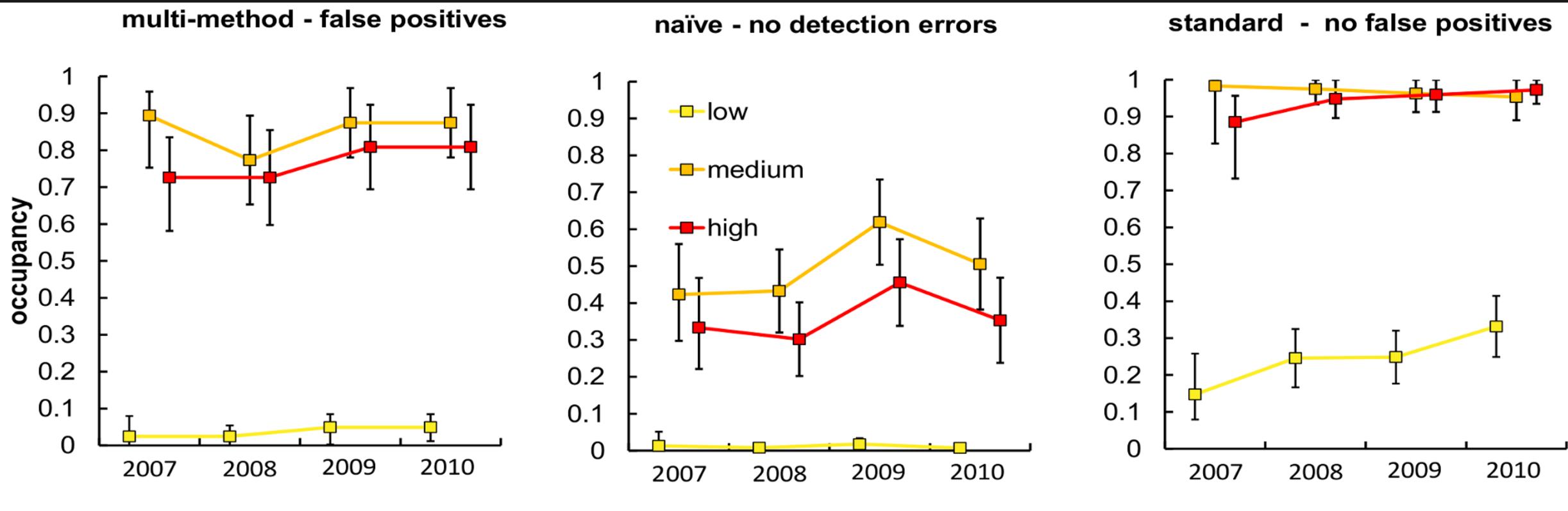
$p_{11}$  = probability of detection

$b$  = probability that a detection is classified as unambiguous

# Estimates of occupancy for gray wolves in northern Montana from 2007–2010



# Estimates of occupancy for gray wolves in northern Montana from 2007–2010



# Live demo

Estimating wolf occupancy with R

# Lecture 5

Estimating co-occurrence of interacting species

Estimating wolf occupancy with R

# Rationale

---

- Several (say 2) different species on a site
- Interactions affect occupancy probabilities
- Detection of a species affected by presence of another one: blurred interactions
- Examples: predation, mutualism, competition, ...
- Occupancy of a species when other species is present?

# States

---

U = site unoccupied

A = site occupied by species A only

B = site occupied by species B only

AB = site occupied by both species

# State process

---

$\psi^A$  = prob. a site is occupied by species A

$\psi^B$  = prob. a site is occupied by species B

$\psi^{AB}$  = prob. a site is occupied by species A and B

# Venn diagram



Occupied by  
species A only

$$\psi^A - \psi^{AB}$$



Occupied by  
both species

$$\psi^{AB}$$



Occupied by  
species B only

$$\psi^B - \psi^{AB}$$

Site unoccupied with prob.:  $1 - \psi^A - \psi^B + \psi^{AB}$

# Events

---

0 = species undetected

1 = A detected

2 = B detected

3 = both species detected

# Observation process

---

$p^A$  = prob. detecting species A given only species A is present

$p^B$  = prob. detecting species B given only species B is present

$r^{AB}$  = prob. detecting both species A and B when both present

$r^{Ab}$  = prob. detecting species A but not B when both present

$r^{aB}$  = prob. detecting species B but not A when both present

$r^{ab}$  = prob. detecting neither species when both present

# Initial states

## Initial states

$$\begin{matrix} \text{U} & \text{A} & \text{B} & \text{AB} \\ \left[ \begin{array}{cccc} 1 - \Sigma & \psi^A - \psi^{AB} & \psi^B - \psi^{AB} & \psi^{AB} \end{array} \right] \end{matrix}$$

# State process

## State process

$$\begin{array}{ccccc} & U & A & B & AB \\ U & \left[ \begin{array}{cccc} 1 & 0 & 0 & 0 \end{array} \right] \\ A & \left[ \begin{array}{cccc} 0 & 1 & 0 & 0 \end{array} \right] \\ B & \left[ \begin{array}{cccc} 0 & 0 & 1 & 0 \end{array} \right] \\ AB & \left[ \begin{array}{cccc} 0 & 0 & 0 & 1 \end{array} \right] \end{array}$$

# Observation process

## Observation process

$$\begin{array}{ccccc} & 0 & 1 & 2 & 3 \\ \text{U} & 1 & 0 & 0 & 0 \\ \text{A} & 1 - p^A & p^A & 0 & 0 \\ \text{B} & 1 - p^B & 0 & p^B & 0 \\ \text{AB} & 1 - \Sigma & r^{Ab} & r^{aB} & r^{AB} \end{array}$$

# Quantifying interactions

---

Interaction estimated by:  $\eta = \psi^{AB} / (\psi^A \psi^B)$

$\eta < 1$  – avoidance (less frequent than expected)

$\eta > 1$  – convergence (more frequent than expected)

$\eta = 1$  – independence ( $\psi^{AB} = \psi^A \psi^B$ )

# Alternative parameterization

- Introduce conditional probabilities

$\psi^{A|B}$  = prob. a site is occupied by A given presence of B

$\psi^{A|\bar{B}}$  = prob. a site is occupied by A given absence of B

$\psi^B$  = prob. a site is occupied by B

# Initial states

## Initial states, in 2 steps

$$\begin{matrix} & & \text{U} & \text{A} & \text{B} & \text{AB} \\ \text{no-B} & \text{B} & \left[ \begin{array}{cc} 1 - \psi^B & \psi^B \end{array} \right] & \left[ \begin{array}{cccc} 1 - \psi^{A|\bar{B}} & \psi^{A|\bar{B}} & 0 & 0 \\ 0 & 0 & 1 - \psi^{A|B} & \psi^{A|B} \end{array} \right] \end{matrix}$$

# Testing interactions

- A and B independent?

Compare:

model in which  $\psi^{A|B} \neq \psi^{A|\bar{B}}$  vs.

model in which  $\psi^{A|B} = \psi^{A|\bar{B}}$

# Live demo

Estimating wolf occupancy with R

# Lecture 6

## Conclusions

Estimating wolf occupancy with R

# Conclusions

---

## 1. We covered several occupancy models

- Single-season, dynamic models
- False-positives
- Species interactions

# Conclusions

---

## 1. We covered several occupancy models

- Single-season, dynamic models
- False-positives
- Species interactions

## 2. Implementation in R using package *unmarked*

# We did not cover...

- How to choose sites? Occasions?

- site selection
- allocation of effort
- design comparisons
- survey timing

- Goodness-of-fit testing

- A few other models...

- habitat and species occurrence dynamics, multistate, heterogeneity, ...

*Journal of Applied  
Ecology* 2005  
**42**, 1105–1114

## METHODOLOGICAL INSIGHTS

### Designing occupancy studies: general advice and allocating survey effort

DARRYL I. MACKENZIE\* and J. ANDREW ROYLE†

\**Proteus Wildlife Research Consultants, PO Box 5193, Dunedin, New Zealand; †US Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708–4017, USA*

## Assessing the Fit of Site-Occupancy Models

Darryl I. MACKENZIE and Larissa L. BAILEY

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*Journal of Agricultural, Biological, and Environmental Statistics*, Volume 9, Number 3, Pages 300–318  
DOI: 10.1198/108571104X3361