

# Occupancy and hidden Markov models

Olivier Gimenez

Occupancy crash course (OCC)

# Lecture 1

Hidden Markov models (HMM) and occupancy data

Occupancy crash course (OCC)

# 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

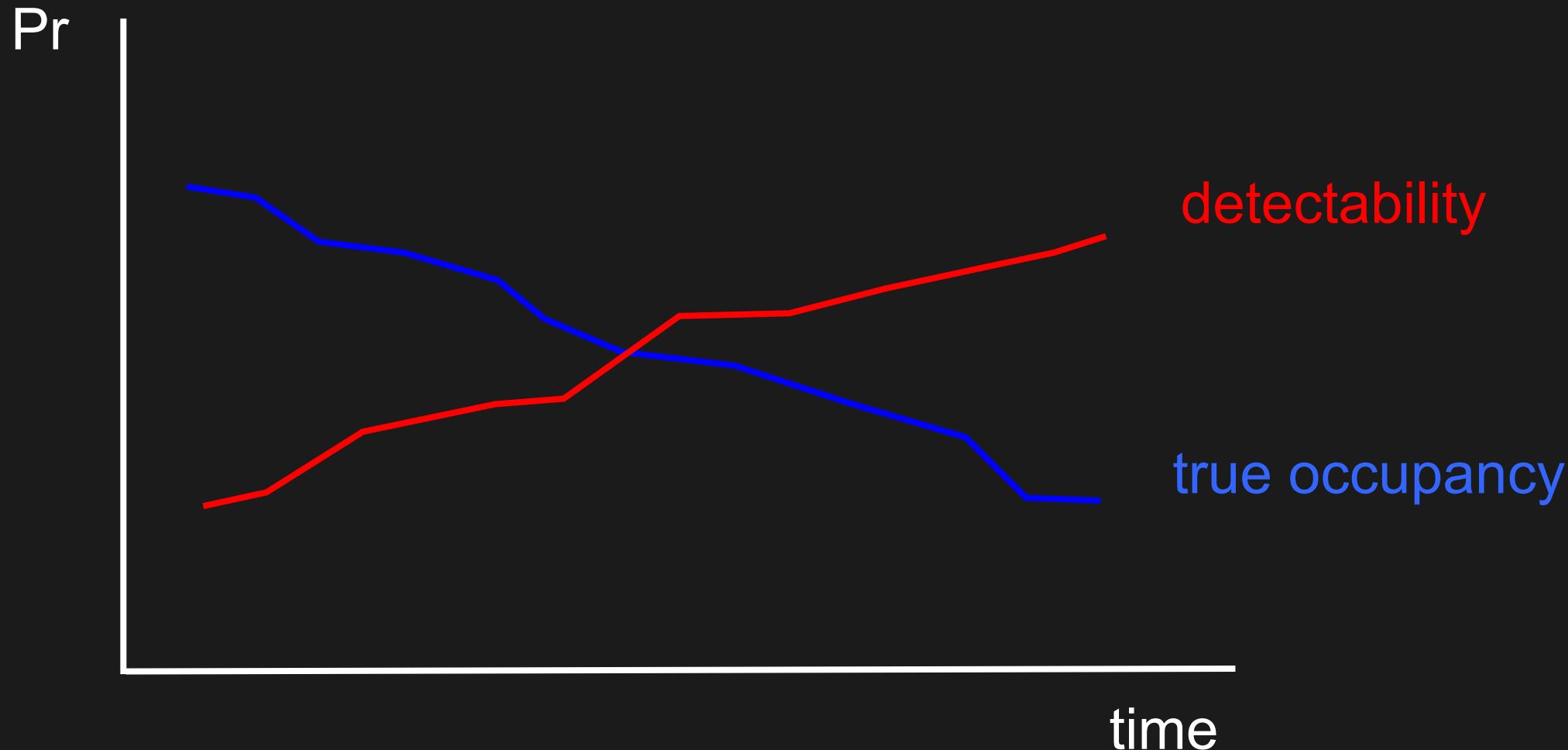
True occupancy = 25%

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

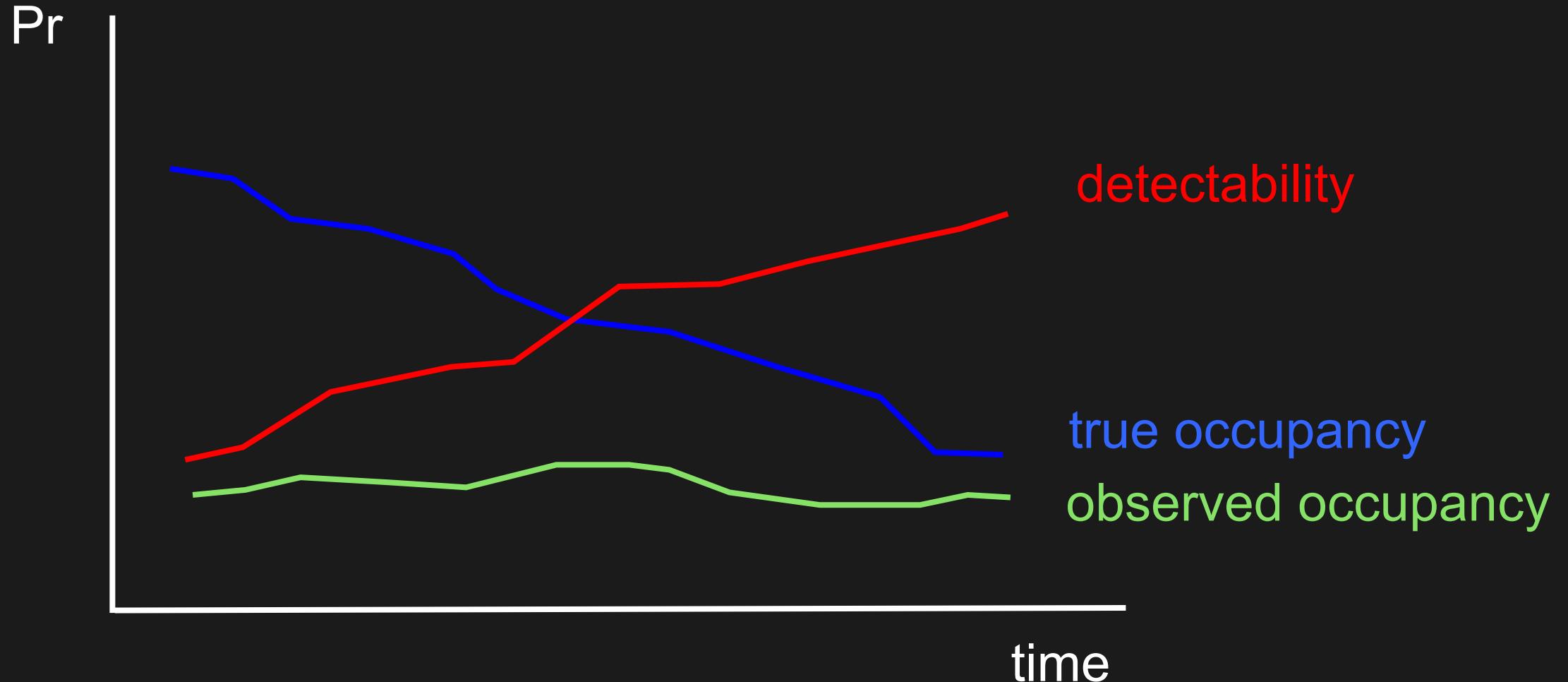
Species detected in 6 occupied sites

Naive occupancy estimate = 6/40 = 15%

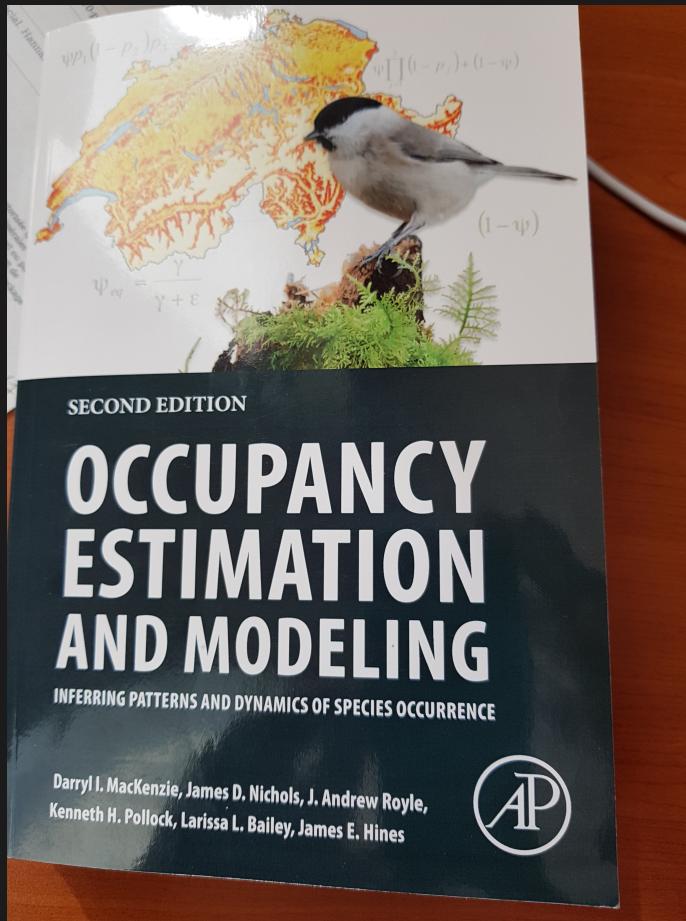
# Issue of detectability < 1



# Bias in occupancy trends



# Occupancy models



**ECOGRAPHY**

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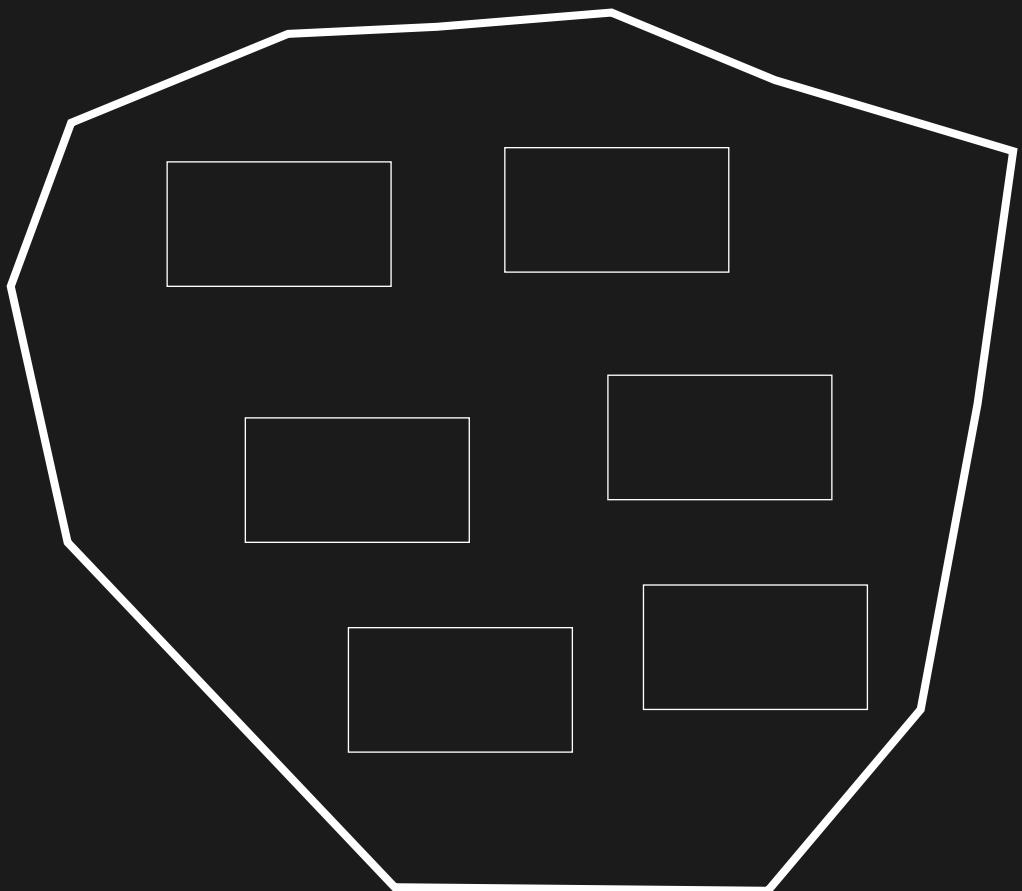
Review & synthesis | Free Access |

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

Gurutzeta Guillera-Arroita

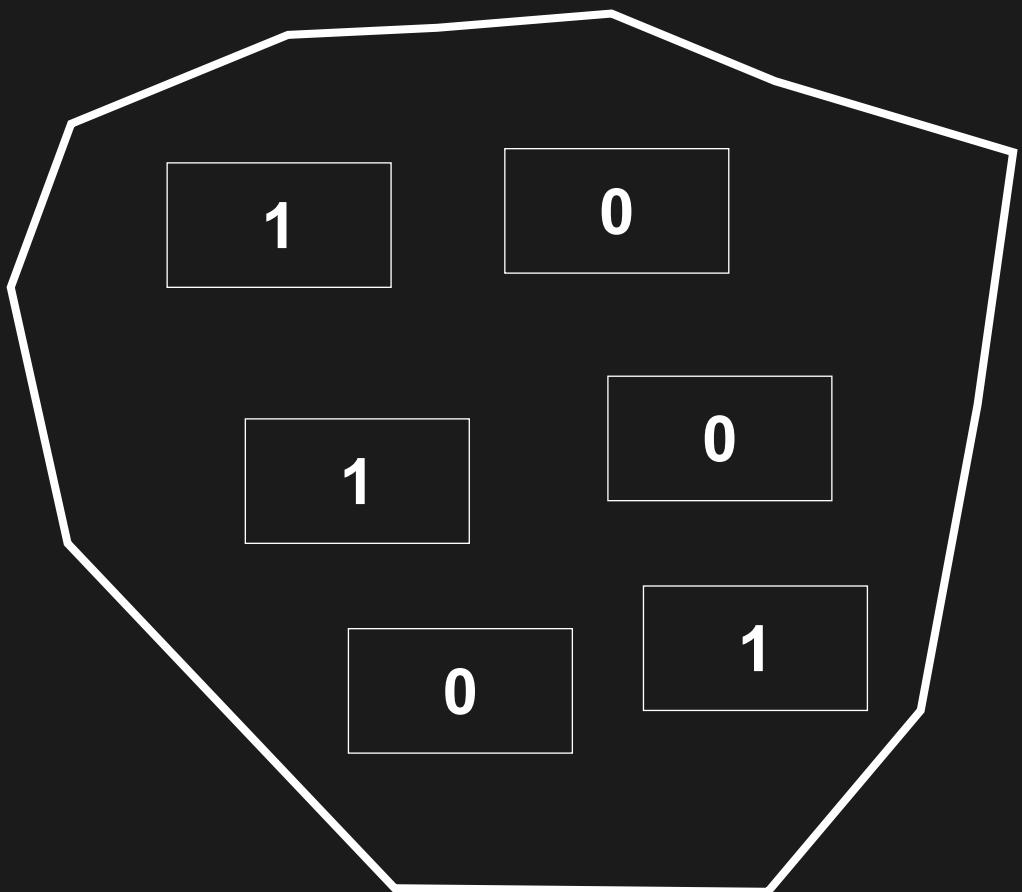
First published: 20 June 2016 | <https://doi.org/10.1111/ecog.02445> | Citations: 134

# Occupancy protocol



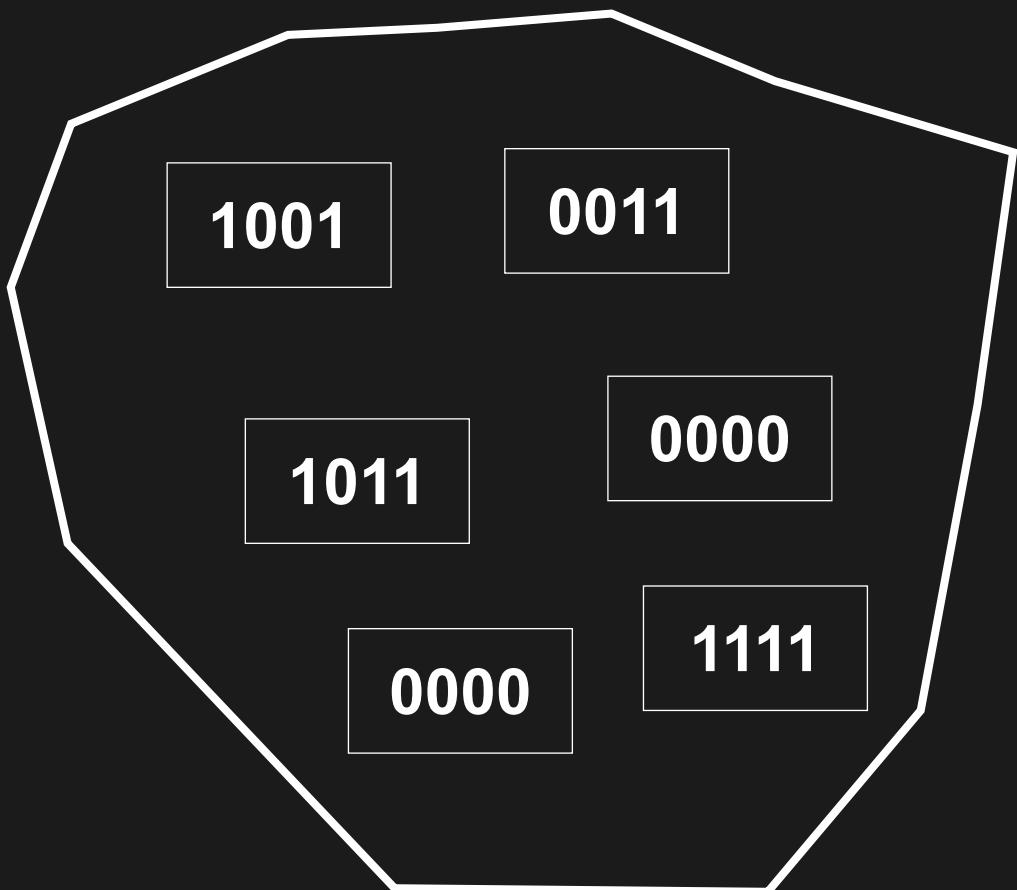
- Several sampling units surveyed

# 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?

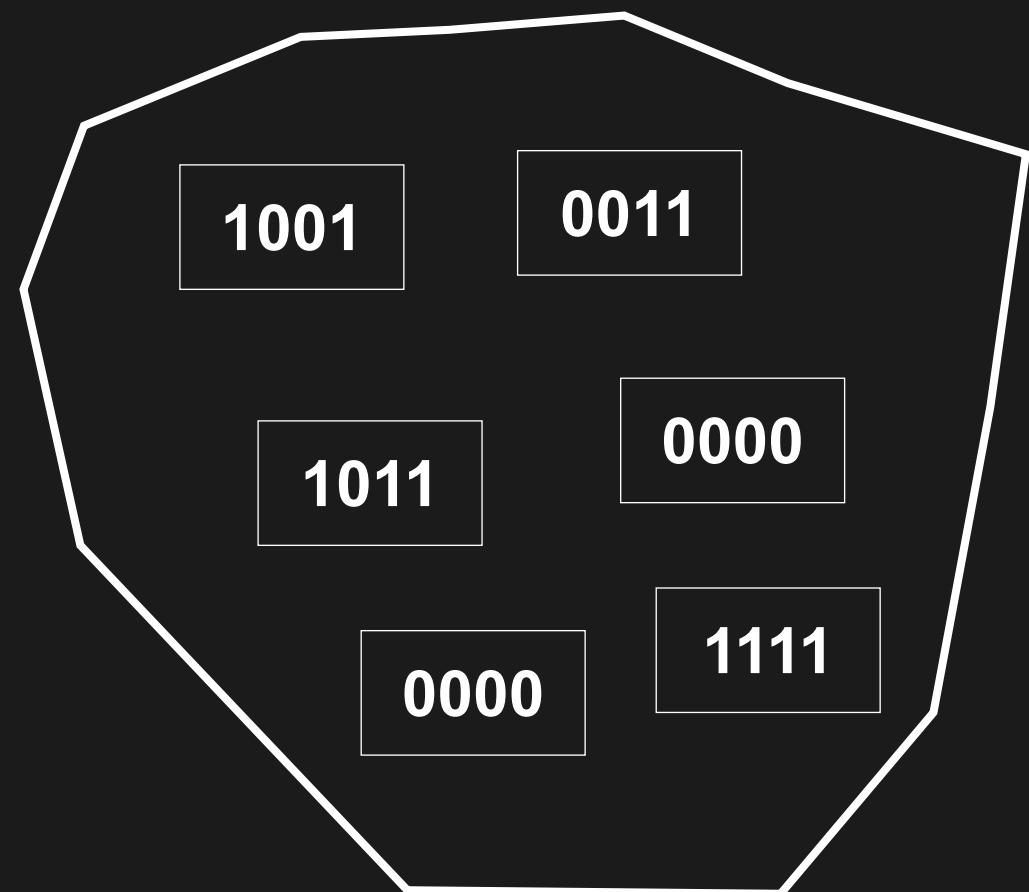


reality

# True or false absence?



reality



observation

# True or false absence?



reality



observation

# True or false absence?



reality



observation

# 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 as a HMM

## 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 as a HMM

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 as a HMM

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

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

hidden

O = occupied; U = unoccupied

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

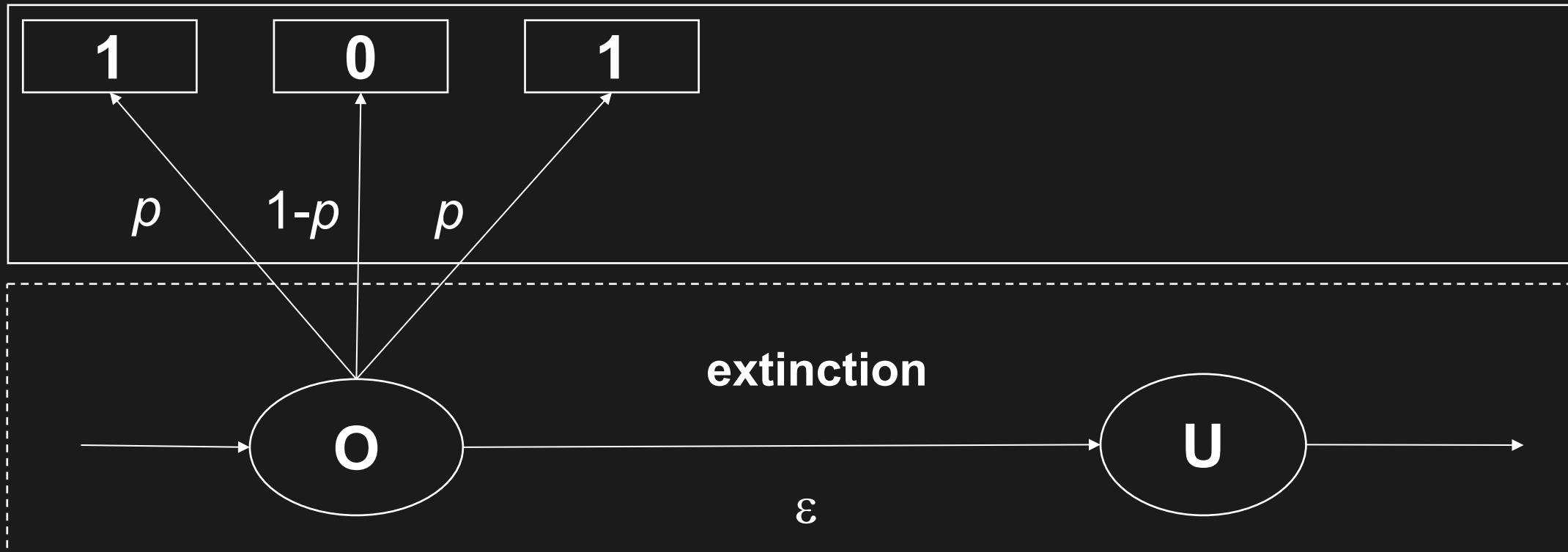
# Dynamic (multi-season) occupancy models



O = occupied; U = unoccupied

# Dynamic (multi-season) occupancy models

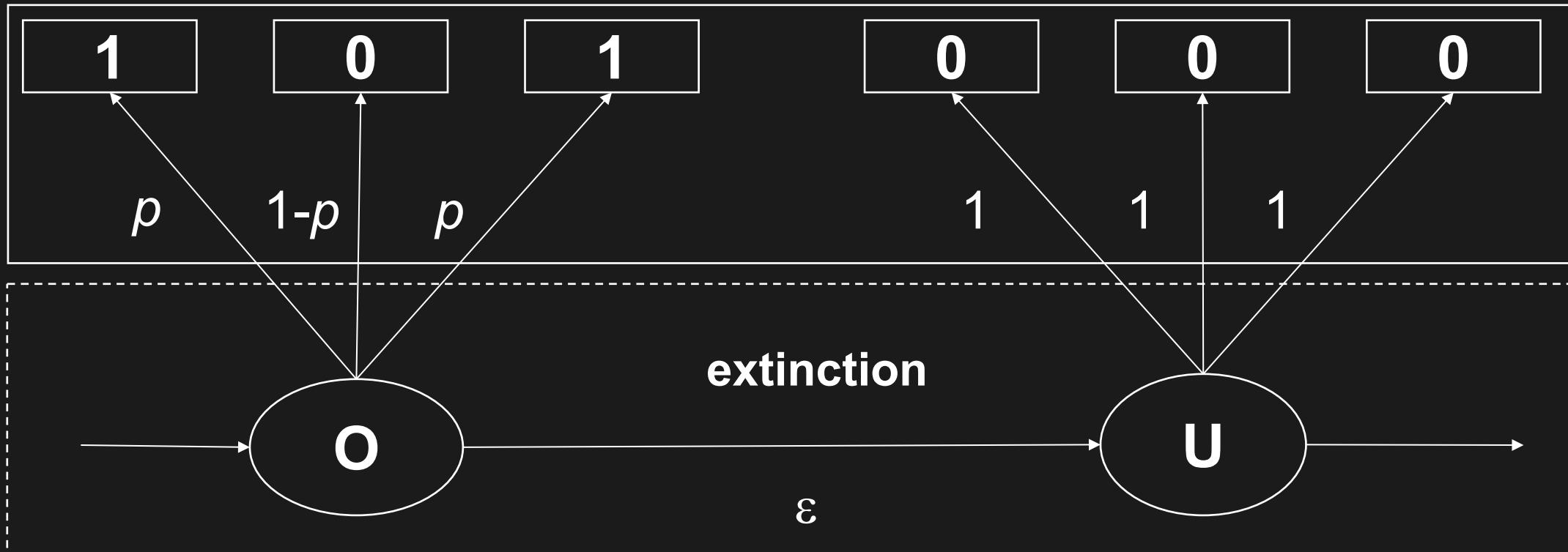
1 = species detected; 0 = species undetected



O = occupied; U = unoccupied

# Dynamic (multi-season) occupancy models

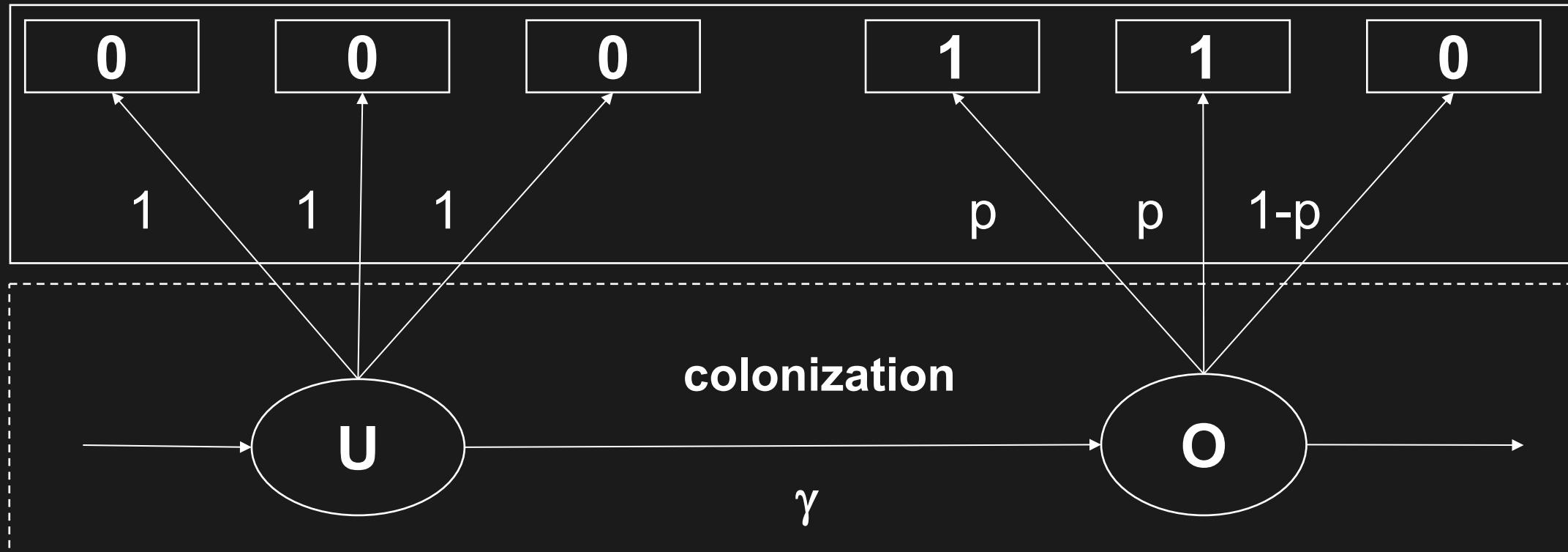
1 = species detected; 0 = species undetected



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**

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

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 as a HMM

Initial states

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

State process

$$\begin{matrix} U & O \\ U & \left( \begin{matrix} 1 - \gamma & \gamma \\ \epsilon & 1 - \epsilon \end{matrix} \right) \\ O & \end{matrix}$$

Markov model

Observation process

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

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
$\begin{matrix} U & O \\ (1 - \psi_1) & \psi_1 \end{matrix}$	$\begin{matrix} U & O \\ U & \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \\ O & \end{pmatrix}$	$\begin{matrix} 0 & 1 \\ U & \begin{pmatrix} 1 & 0 \\ 1 - p & p \end{pmatrix} \\ O & \end{pmatrix}$

# ECOGRAPHY

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AND TIME IN ECOLOGY

Research

 Free Access

## 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



# Determinants and patterns of habitat use by the brown bear *Ursus arctos* in the French Pyrenees revealed by occupancy modelling

Published online by Cambridge University Press: 10 July 2017

Blaise Piédallu, Pierre-Yves Quenette, Nicolas Bombillon, Adrienne Gastineau, Christian Miquel and Olivier Gimenez

Show author details ▾



# Lecture 2

# Heterogeneity

Occupancy crash course (OCC)

# Key occupancy model assumptions

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- Independent detections
- No unmodelled heterogeneity
- No false positives

# Key occupancy model assumptions

---

- Independent detections
- **No unmodelled heterogeneity**
- No false positives

# How to deal with heterogeneity?

- Lynx in the Jura mountains
- Signs of presence between 2002 and 2006
- 197 sites, 5 1-y periods
- Static model



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# Detection heterogeneity

Random effect

$$\text{logit}(p_i) = \mu + \eta_i$$

$$\eta_i \sim N(0, \sigma^2)$$

# Detection heterogeneity

## Random effect

$$\text{logit}(p_i) = \mu + \eta_i$$

$$\eta_i \sim N(0, \sigma^2)$$

## Finite mixture

$$U1 \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$$
$$U2 \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$$
$$O1 \begin{pmatrix} 1 - p^1 & p^1 \\ 1 - p^2 & p^2 \end{pmatrix}$$

# Model selection

	Model	AIC
$M_0$	$[\psi(\text{forest}), p]$	1000.1
$M_{ran}$	$[\psi(\text{forest}), p(\text{random})]$	978.6
$M_{mix}$	$[\psi(\text{forest}), p(\text{mixture})]$	980.2

# Results

## Random effect

$\hat{\mu} = .10$  (SE=0.20)  
 $\hat{\sigma} = 1.25$  (SE=0.22)

## Finite mixture

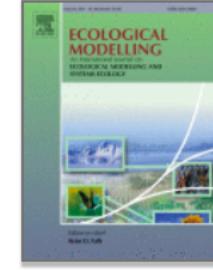
$\hat{p}^1 = .25$  (SE=0.05)  
 $\hat{p}^2 = .74$  (SE=0.08)  
 $\hat{\pi} = 0.54$  (SE=0.1)

- Occupancy is higher in heterogeneity models
- Relationship between occupancy and forest cover is stronger



Ecological Modelling

Volume 387, 10 November 2018, Pages 61-69



# Accounting for misidentification and heterogeneity in occupancy studies using hidden Markov models

Julie Louvrier <sup>a, b</sup>  , Thierry Chambert <sup>a</sup>, Eric Marboutin <sup>c</sup>, Olivier Gimenez <sup>a</sup>

# Lecture 3

Multistate occupancy models incorporating  
uncertainty

Occupancy crash course (OCC)

# Multistate occupancy model



*Conservation Biology*



## Spatial Patterns of Breeding Success of Grizzly Bears Derived from Hierarchical Multistate Models

JASON T. FISHER,\* MATTHEW WHEATLEY,† AND DARRYL MACKENZIE‡

2014

- Spatial patterns of grizzly bears *breeding success* (Rocky mountains)
- Breeding success = bear with at least one cub
- Relationship between breeding success and type of land cover

# Define the states and observations

---

## Breeding states

- U = not occupied
- ONB = non-breeders only
- OB = at least some breeders

## • Observations

- Species undetected = 0
- Species detected without young = 1
- Species detected with young = 2

# HMM formulation of multistate occupancy model

## Initial states

$$\begin{matrix} U & ONB & OB \\ (1 - \psi_1 - \psi_2) & \psi_1 & \psi_2 \end{matrix}$$

## State process

$$\begin{matrix} U & ONB & OB \\ U & \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \\ ONB & & \\ OB & & \end{matrix}$$

$\psi^1$  (resp.  $\psi^2$ ) probability the site is occupied by non-breeders (resp. by breeders)

# HMM formulation of multistate occupancy model

## Observation process

$$\begin{matrix} & \begin{matrix} 0 & 1 & 2 \end{matrix} \\ \begin{matrix} U \\ ONB \\ OB \end{matrix} & \left( \begin{matrix} 1 & 0 & 0 \\ 1 - p^1 & p^1 & 0 \\ 1 - p^2 & p^2(1 - \delta) & p^2\delta \end{matrix} \right) \end{matrix}$$

$p^1$  (resp.  $p^2$ ) detection probability of non-breeders (resp. of breeders)

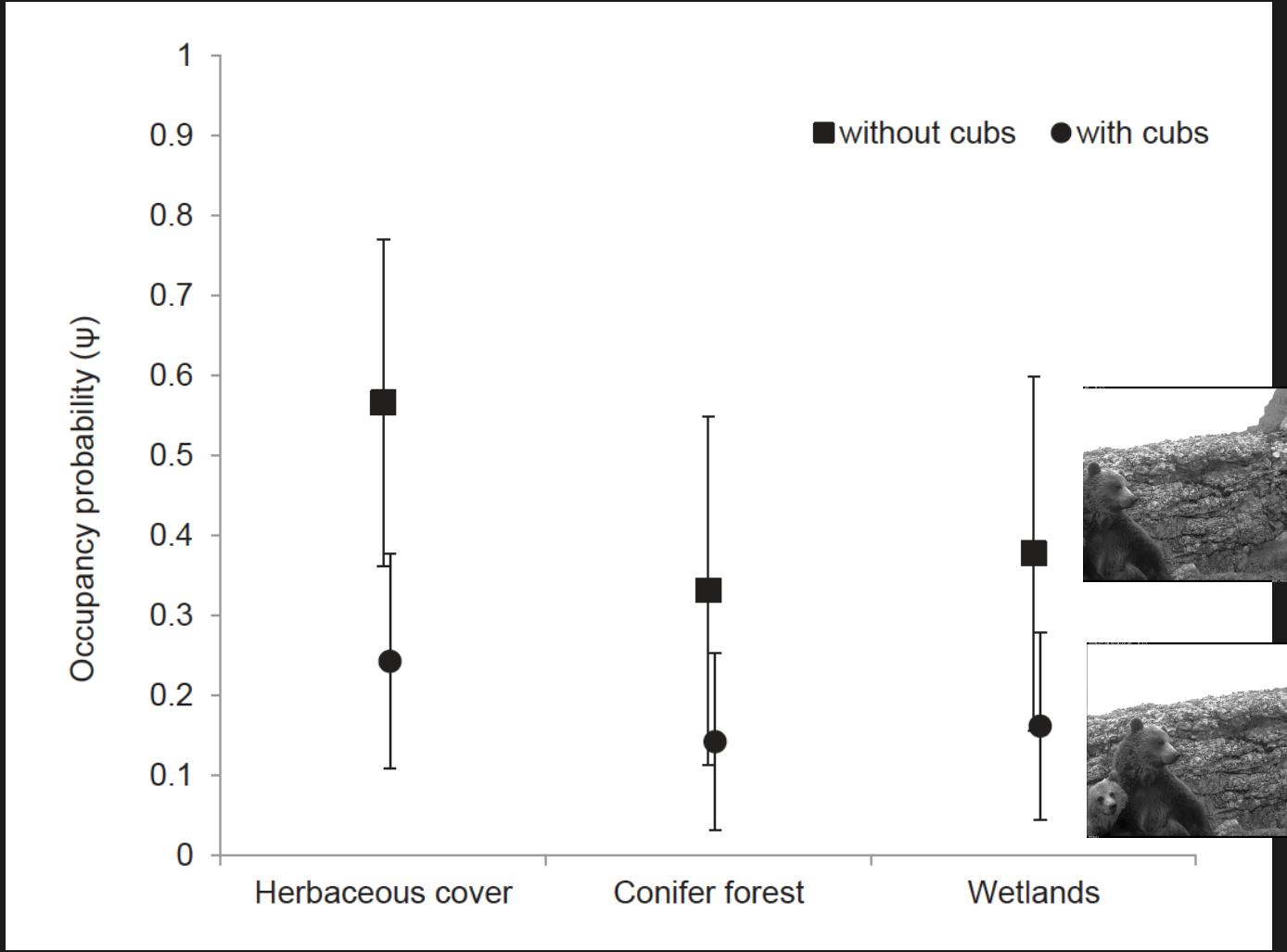
# HMM formulation of multistate occupancy model

## Observation process

$$\begin{matrix} & \begin{matrix} 0 & 1 & 2 \end{matrix} \\ \begin{matrix} U \\ ONB \\ OB \end{matrix} & \left( \begin{matrix} 1 & 0 & 0 \\ 1 - p^1 & p^1 & 0 \\ 1 - p^2 & p^2(1 - \delta) & p^2\delta \end{matrix} \right) \end{matrix}$$

State uncertainty; reproduction may occur on a site, but the young may not be detected.  $\delta$  probability of detecting evidence of reproduction, given the site is occupied with young

# Results



# Alternative parameterization

---

We had:

$\psi_1$  = prob. a site is occupied by species **non-breeding**

$\psi_2$  = prob. a site is occupied by species **breeding**

Now let's define:

$\psi = \psi_1 + \psi_2$  = prob. of occupancy

$R = \psi_2 / \psi$  = prob. a being in state 2, given site occupied  
= conditional prob. of successful reproduction

# Hidden Markov model – part 1 modified

## Initial states

$$\begin{matrix} \text{U} & \text{ONB} & \text{OB} \\ \left[ \begin{array}{ccc} 1 - \psi & \psi(1 - R) & \psi R \end{array} \right] \end{matrix}$$

# Lecture 4

Occupancy models with species misidentification

Occupancy crash course (OCC)

# 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

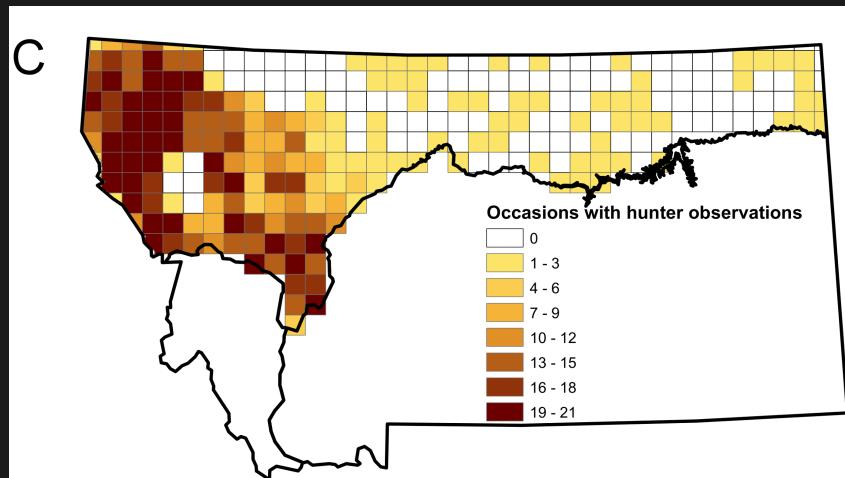
David A. W. Miller<sup>1,2\*</sup>, James D. Nichols<sup>1</sup>, Justin A. Gude<sup>3</sup>, Lindsey N. Rich<sup>4</sup>, Kevin M. Podruzny<sup>3</sup>, James E. Hines<sup>1</sup>, Michael S. Mitchell<sup>4</sup>

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

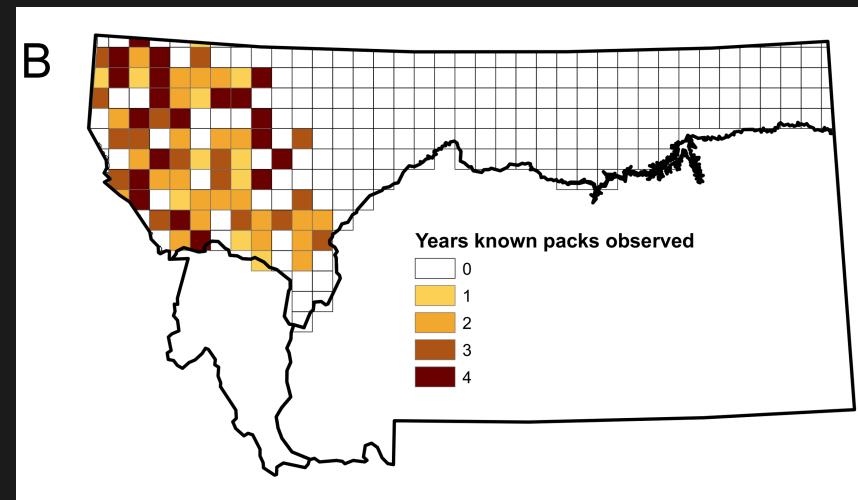


# Data

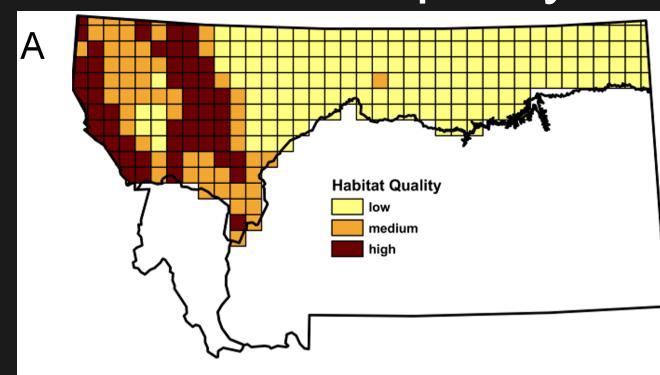
Observations by hunters (phone interviews);  
*uncertainty* in species identification



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

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

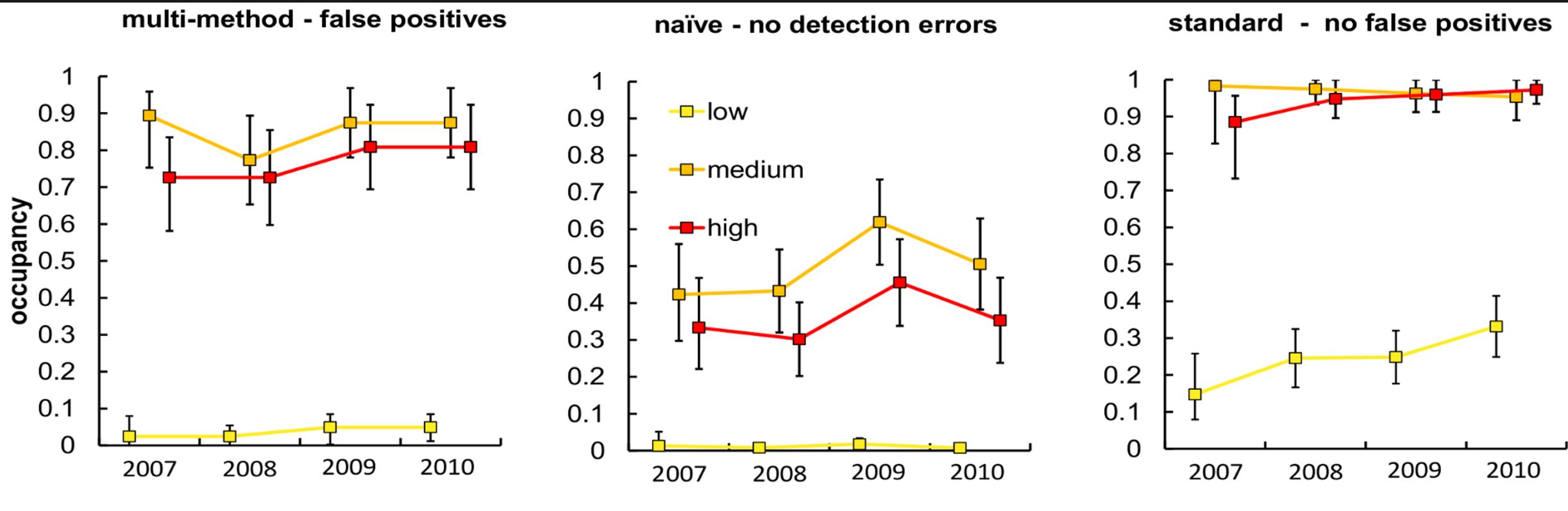
$p_{11}$  = probability of detection

$b$  = 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



# Conservation Biology



Conservation Methods

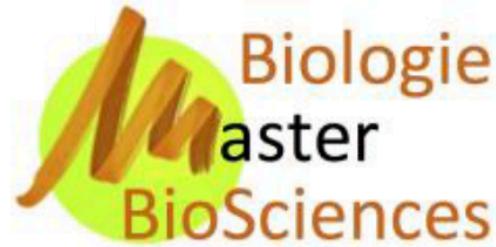
## Use of ambiguous detections to improve estimates from species distribution models

Julie Louvrier✉, Anja Molinari-Jobin, Marc Kéry, Thierry Chambert, David Miller, Fridolin Zimmermann, Eric Marboutin, Paolo Molinari, Oliver Müller, Rok Černe, Olivier Gimenez

First published: 16 July 2018 | <https://doi.org/10.1111/cobi.13191> | Citations: 4

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LAURET Valentin

Dealing with species misidentification to make the best of citizen  
science data: a case study with wolf distribution in France

M2 Internship report

Internship dates : 04/01/2017 – 24/05/2017

Laboratory : CEFE, Montpellier

Supervisor : Olivier Gimenez & Julie Louvier

*Nb of words : 4139*

# Lecture 5

Estimating co-occurrence of interacting species

Occupancy crash course (OCC)

# Rationale

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- 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

# Hidden Markov model – part 1

## Initial states

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

# Hidden Markov model – part 2

## State process

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

# Hidden Markov model – part 3

## Observation process

$$\begin{matrix} & \begin{matrix} 0 & 1 & 2 & 3 \end{matrix} \\ \begin{matrix} U \\ A \\ B \\ AB \end{matrix} & \left[ \begin{matrix} 1 & 0 & 0 & 0 \\ 1 - p^A & p^A & 0 & 0 \\ 1 - p^B & 0 & p^B & 0 \\ 1 - \Sigma & r^{Ab} & r^{aB} & r^{AB} \end{matrix} \right] \end{matrix}$$

# 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

# Hidden Markov model – part 1 modified

Initial states, in 2 steps

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

# Testing interactions

- A and B independent?

Compare:

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

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



Université de Montpellier et Montpellier SupAgro  
Master Mention "Biodiversité, Écologie, Évolution, B2E"  
Parcours «ÉcoSystèmeS»



Projet de recherche :

**Quantifier les interactions prédateur-proies grâce au  
piégeage photographique et à la modélisation  
d'occupation multi-espèce**

Le cas du système lynx-chevreuil-chamois dans le Jura français



Par  
KERVELLEC Maëlis  
Stage de M1

Réalisé sous la direction de  
GIMENEZ Olivier, Directeur de Recherche  
Centre d'Écologie Fonctionnelle et Évolutive, UMR 5175, Équipe HAIR  
Sous tutelles du CNRS, l'Université de Montpellier, l'Université Paul-Valéry  
Montpellier, l'IRD, l'EPHE

DUCHAMP Christophe, Chargé de recherche  
Office Français de la Biodiversité, Unité PAD, Équipe Loup-Lynx  
Sous tutelles du ministère de la Transition écologique et solidaire et du ministère de  
l'Agriculture et de l'Alimentation.

# ECOGRAPHY

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## Inferring wildlife poaching in southeast Asia with multispecies dynamic occupancy models

Lucile Marescot✉, Arnaud Lyet, Rohit Singh, Neil Carter, Olivier Gimenez

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# A dynamic and hierarchical spatial occupancy model for interacting species

Eivind Flittie Kleiven, Frederic Barraquand, Olivier Gimenez, John-André Henden, Rolf Anker Ims,  
Eeva M. Soininen, Nigel Gilles Yoccoz

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This article is a preprint and has not been certified by peer review [what does this mean?].

## Abstract

Full Text

Info/History

Metrics

 Preview PDF

## 1 Abstract

Occupancy models are currently being developed in two major directions: to account for spatial structure and species interactions. As interacting species (e.g., predators and prey) often operate at different spatial scales, including nested spatial structure might be especially relevant in models for interacting species. Here we bridge these two model frameworks by developing a spatially hierarchical two-species occupancy model. The model is dynamic, i.e. it estimates initial occupancy, colonization and extinction probabilities - including probabilities conditional to the other species' presence. With a simulation study, we demonstrate that the model is able to estimate parameters without bias under low, medium and high average occupancy probabilities, as well as low, medium and high detection probabilities. We further show the model's ability to deal with sparse field data by applying it to a spatially hierarchical camera trapping dataset on a mustelid-rodent predator-prey system. The field study illustrates that the model allows estimation of species interaction effects on colonization and extinction probabilities at two spatial scales. This creates opportunities to explicitly account for the spatial structure found in many spatially nested study designs, and to study interacting species that have contrasted movement ranges with camera traps.

# Lecture 6

## Conclusions

Occupancy crash course (OCC)

# Conclusions

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## 1. (Almost?) all occupancy models in a unified HMM framework

- Single-season, dynamic models
- Mixture/random effects and multistate models to account for heterogeneity
- False-positives
- Species interactions

# Conclusions

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## 2. HMM: link occupancy and capture-recapture communities

- Goodness-of-fit
- Accounting for lack of dependence

# Conclusions

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## 3. There is a learning curve to understand HMM, is it worth it?

- HMM is a general framework
- All models can be obtained as particular cases (?)

# What 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, cluster sampling, ...

*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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