

# Survey design in occupancy studies

---

Gesa von Hirschheydt

25 June 2024

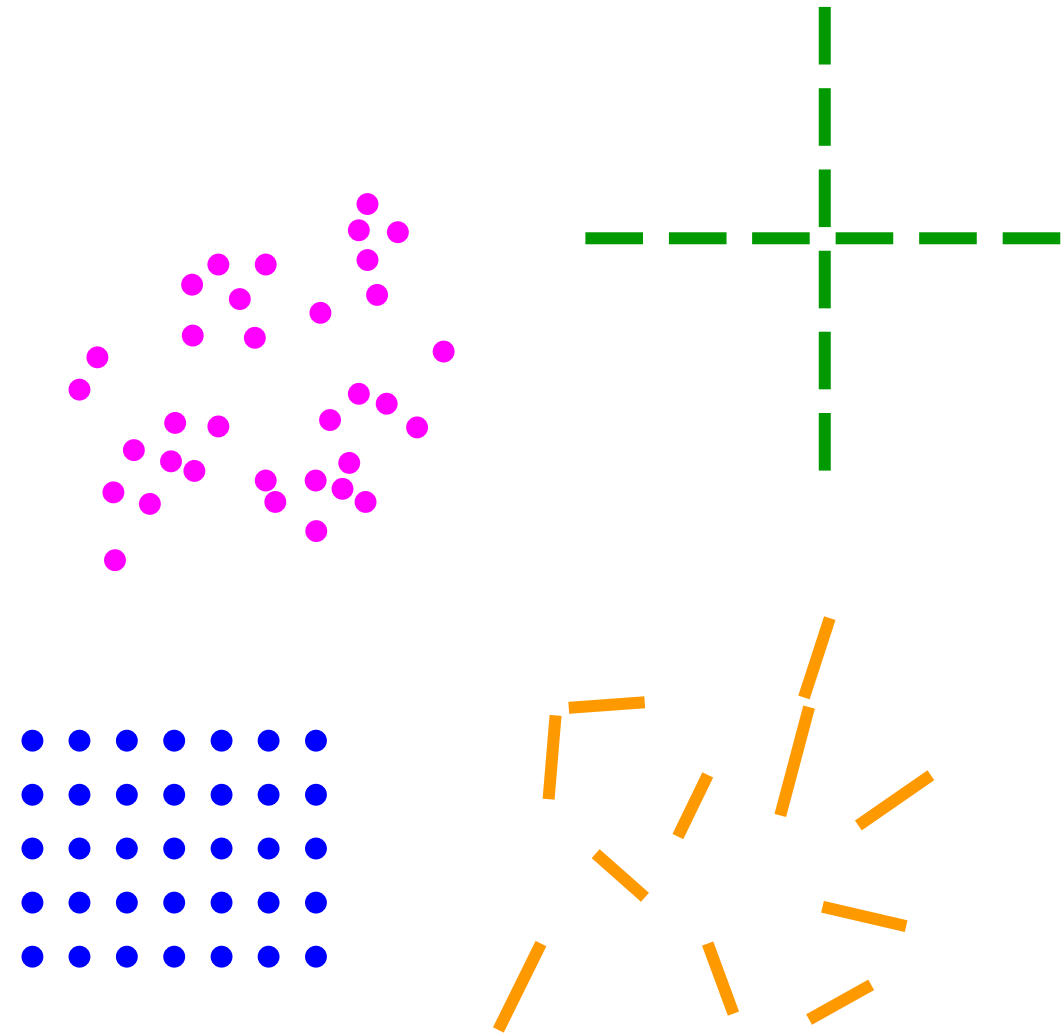




# Standard sampling design

- $J$  sites with  $K$  visits each

	True state	Visit 1	Visit 2	Visit 3	Visit 4	Visit 5
Site 1	1	1	0	0	1	0
Site 2	0	0	0	0	0	0
Site 3	1	0	0	1	1	0
Site 4	1	0	0	0	0	0
Site 5	1	0	1	0	0	1
Site 6	0	0	0	0	0	0
Site 7	0	0	0	0	0	0
Site 8	1	0	0	0	0	1



# Standard sampling design

- $J$  sites with  $K$  visits each → how to define  $J$  and  $K$ ?

## ***Do you want to...***

*... estimate occupancy with a certain degree of precision?*

*... compare occupancy between two habitats or points in time?*

*... evaluate the detection probability of a new sampling method?*

*... compare co-occurrence patterns of a predator-prey pair?*

*... estimate local population dynamics?*



# Standard sampling design

- $J$  sites with  $K$  visits each → how to define  $J$  and  $K$ ?

*Goal: estimate occupancy with a certain degree of precision*

$$\text{var}(\hat{\psi}) = \frac{\psi K}{TS} \left[ (1 - \psi) + \frac{(1 - p^*)}{p^* - Kp(1 - p)^{K-1}} \right]$$

$\psi$   $psi$  = occupancy probability

$K$  number of repeated visits

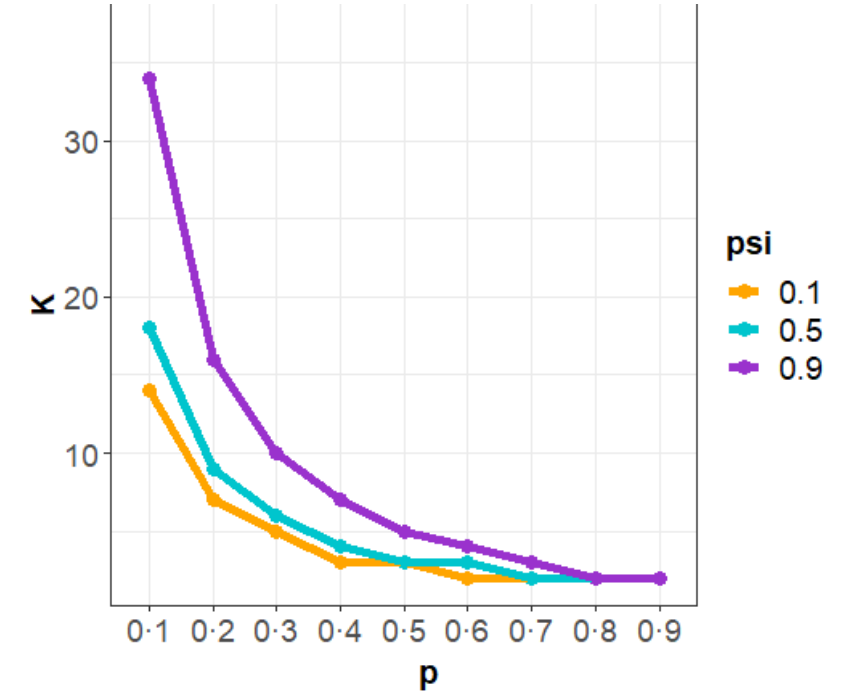
$TS$  total number of conducted surveys ( $J \cdot K$ )

$p$  detection probability

$p^*$  cumulative detection probability =  $1 - (1 - p)^K$

→ define  $TS$ ,  $psi$ ,  $p$

→ optimize for  $K$

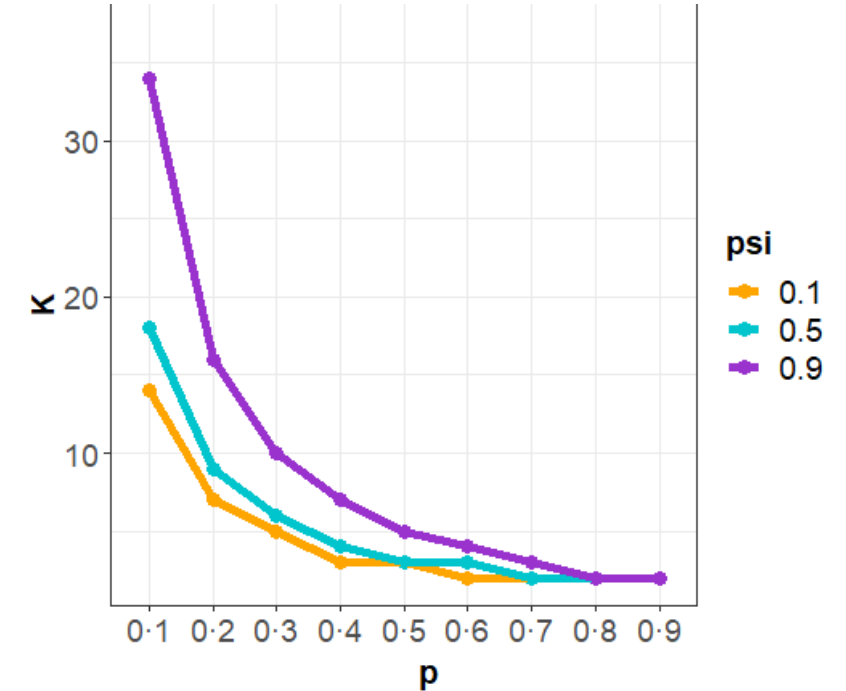


# Standard sampling design

- $J$  sites with  $K$  visits each  $\rightarrow$  how to define  $J$  and  $K$ ?

## Conclusions

- low detectability  $\rightarrow$  fewer sites with more visits
- low occupancy  $\rightarrow$  more sites with fewer visits

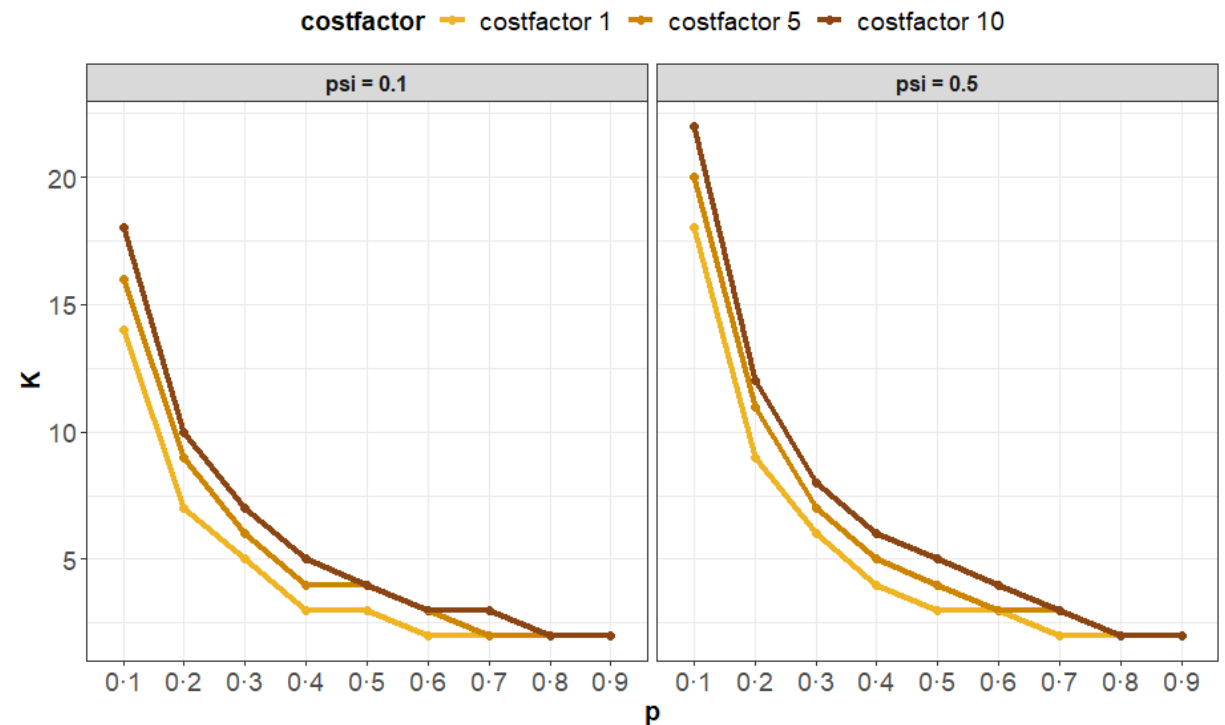


# Standard sampling design

- $J$  sites with  $K$  visits each → how to define  $J$  and  $K$ ?

## Conclusions

- low detectability → fewer sites with more visits
- low occupancy → more sites with fewer visits
- when new sites are more costly



# Standard sampling design

- $J$  sites with  $K$  visits each → how to define  $J$  and  $K$ ?

## Conclusions

- low detectability → fewer sites with more visits
- low occupancy → more sites with fewer visits
- when new sites are more costly → fewer sites with more visits

# Standard sampling design

- $J$  sites with  $K$  visits each → how to define  $J$  and  $K$ ?

## Conclusions

- low detectability → fewer sites with more visits
- low occupancy → more sites with fewer visits
- when new sites are more costly → fewer sites with more visits
- if detectability is of key interest → fewer sites with more visits
- for most situations,  $K$  should ideally be  $\geq 3$
- if a design has to meet the objectives of several species, it is generally the design of the rarer & more difficult-to-detect species that works better for all



# Different sampling designs

## Standard design

- visit  $J$  sites  $K$  times each

## Removal design

- visit  $J$  sites until first detection or up to  $K$  times

## Conditional design

- visit  $J$  sites once, then resurvey sites with a detection an additional  $K-1$  times

## “Mixed design”

- visit  $J_S$  sites once,  $J_R$  sites  $K$  times

Any mixture of the above

	Standard					Removal					Conditional				
True state	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
1	1	0	1	1	0	1					1	0	1	1	0
1	0	0	0	0	0	0	0	0	0	0	0				
1	0	0	1	1	0	0	0	1			0				
1	0	0	0	0	1	0	0	0	0	1	0				
0	0	0	0	0	0	0	0	0	0	0	0				

Specht et al. (2017) *Methods in Ecology and Evolution*

# Removal sampling design

- visit  $J$  sites until first detection or up to  $K$  times

Removal				
1	2	3	4	5
1				
0	0	0	0	0
0	0	1		
0	0	0	0	1
0	0	0	0	0

# Removal sampling design

- visit  $J$  sites until first detection or up to  $K$  times

*Ratio of standard errors for standard vs. removal designs.*

*Colours indicate whether removal design (orange) or standard design (blue) yield higher precision.*

$p$	$\psi$								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	0.9	0.94	0.98	1.04	1.1	1.18	1.3	1.46	1.74
0.2	0.91	0.94	0.99	1.04	1.1	1.18	1.28	1.44	1.71
0.3	0.92	0.95	0.99	1.04	1.1	1.17	1.27	1.42	1.68
0.4	0.93	0.96	0.99	1.03	1.09	1.17	1.26	1.4	1.64
0.5	0.93	0.96	1	1.04	1.08	1.16	1.24	1.37	1.6
0.6	0.94	0.97	1.01	1.06	1.09	1.15	1.22	1.35	1.55
0.7	0.95	0.96	0.97	1.01	1.07	1.13	1.22	1.31	1.48
0.8	1	1.02	1.04	1.07	1.09	1.11	1.15	1.25	1.45
0.9	1.02	1.05	1.07	1.1	1.13	1.17	1.2	1.24	1.31

## Conclusion

Removal design is more efficient than standard design for any species with  $psi \geq 0.4$ .

# Conditional sampling design

- visit  $J$  sites once, then resurvey sites with a detection an additional  $K-1$  times

Conditional				
1	2	3	4	5
1	0	1	1	0
0				
0				
0				
0				

# Conditional sampling design

**RMSE( $\hat{\psi}$ )**

$p$	$\psi$								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.000	.002	.002	.004	.009	.012	.024	.025	.029
0.2	.013	.008	.005	.011	.017	.006	.003	.013	.021
0.3	.024	.007	.003	.016	.017	.004	.004	.013	.010
0.4	.036	.012	.004	.015	.004	.008	.013	.021	.019
0.5	.037	.015	.000	.009	.004	.014	.015	.024	.029
0.6	.045	.023	.010	.005	.015	.020	.023	.032	.033
0.7	.045	.024	.011	.005	.015	.021	.029	.040	.039
0.8	.045	.032	.017	.000	.015	.027	.037	.040	.046
0.9	.045	.035	.019	.006	.011	.023	.029	.035	.046

**SE( $\hat{\psi}$ )**

$p$	$\psi$								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.012	.005	.004	.008	.022	.038	.055	.070	.078
0.2	.008	.003	.002	.006	.015	.026	.037	.047	.052
0.3	.006	.002	.002	.005	.012	.020	.028	.036	.040
0.4	.006	.001	.001	.003	.010	.016	.023	.029	.033
0.5	.005	.001	.000	.003	.007	.014	.019	.024	.027
0.6	.004	.000	.001	.005	.007	.011	.015	.020	.022
0.7	.003	.000	.002	.001	.005	.009	.013	.016	.018
0.8	.004	.001	.003	.004	.006	.007	.008	.012	.015
0.9	.006	.005	.001	.006	.008	.009	.010	.010	.010

**RMSE( $\hat{p}$ )**

	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.067	.050	.026	.024	.020	.007	.008	.008	.008
0.2	.056	.029	.027	.013	.007	.008	.000	.000	.010
0.3	.039	.028	.027	.013	.007	.008	.000	.000	.000
0.4	.047	.032	.023	.013	.014	.016	.008	.000	.000
0.5	.050	.035	.024	.013	.007	.008	.000	.000	.000
0.6	.059	.041	.019	.014	.008	.008	.000	.000	.000
0.7	.072	.043	.014	.008	.000	.000	.000	.000	.000
0.8	.090	.037	.023	.008	.000	.000	.000	.000	.000
0.9	.118	.050	.019	.013	.013	.000	.000	.000	.000

**SE( $\hat{p}$ )**

	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.061	.031	.019	.010	.005	.001	.003	.006	.003
0.2	.080	.043	.022	.014	.007	.000	.003	.009	.004
0.3	.085	.043	.026	.020	.005	.002	.003	.007	.003
0.4	.109	.045	.027	.013	.008	.001	.003	.008	.003
0.5	.089	.040	.028	.021	.006	.003	.007	.009	.001
0.6	.102	.066	.038	.029	.003	.000	.002	.004	.003
0.7	.080	.038	.027	.020	.002	.003	.010	.006	.000
0.8	.043	.002	.001	.003	.005	.006	.002	.001	.003
0.9	.000	.002	.004	.005	.006	.007	.007	.004	.001

**A-optimality (RMSE)**

	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.067	.048	.024	.020	.011	.004	.004	.015	.016
0.2	.069	.037	.022	.002	.010	.010	.012	.027	.037
0.3	.063	.035	.024	.024	.003	.016	.019	.036	.009
0.4	.083	.044	.019	.019	.002	.004	.026	.013	.010
0.5	.087	.050	.024	.000	.000	.013	.028	.001	.010
0.6	.105	.063	.029	.014	.014	.000	.017	.016	.014
0.7	.117	.067	.025	.018	.018	.005	.007	.022	.029
0.8	.134	.068	.050	.024	.024	.005	.018	.030	.033
0.9	.163	.090	.048	.034	.028	.028	.006	.022	.046

**A-optimality (SE)**

	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.073	.026	.011	.030	.007	.016	.038	.058	.072
0.2	.088	.040	.003	.025	.023	.003	.015	.032	.044
0.3	.091	.041	.012	.009	.031	.010	.005	.021	.032
0.4	.115	.044	.016	.010	.027	.018	.000	.013	.024
0.5	.094	.039	.020	.003	.022	.007	.004	.012	.021
0.6	.105	.066	.033	.018	.018	.013	.003	.012	.017
0.7	.083	.038	.022	.009	.012	.003	.005	.007	.015
0.8	.048	.004	.002	.009	.015	.015	.002	.009	.018
0.9	.007	.005	.001	.003	.006	.002	.002	.004	.009

Standard Removal Conditional

Standard Removal Conditional



# Conditional sampling design

$p$	$\psi$								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.000	.002	.002	.004	.009	.012	.024	.025	.029
0.2	.013	.008	.005	.011	.017	.006	.003	.013	.021
0.3	.024	.007	.003	.016	.017	.004	.004	.013	.010
0.4	.036	.012	.004	.015	.004	.008	.013	.021	.019
0.5	.037	.015	.000	.009	.004	.014	.015	.024	.029
0.6	.045	.023	.010	.005	.015	.020	.023	.032	.033
0.7	.045	.024	.011	.005	.015	.021	.029	.040	.039
0.8	.045	.032	.017	.000	.015	.027	.037	.040	.046
0.9	.045	.035	.019	.006	.011	.023	.029	.035	.046

0.1	.067	.050	.026	.024	.020	.007	.008	.008	.008
0.2	.056	.029	.027	.013	.007	.008	.000	.000	.010
0.3	.039	.028	.027	.013	.007	.008	.000	.000	.000
0.4	.047	.032	.023	.013	.014	.016	.008	.000	.000
0.5	.050	.035	.024	.013	.007	.008	.000	.000	.000
0.6	.059	.041	.019	.014	.008	.008	.000	.000	.000
0.7	.072	.043	.014	.008	.000	.000	.000	.000	.000
0.8	.090	.037	.023	.008	.000	.000	.000	.000	.000
0.9	.118	.050	.019	.013	.013	.000	.000	.000	.000

0.1	.067	.048	.024	.020	.011	.004	.004	.015	.016
0.2	.069	.037	.022	.002	.010	.010	.012	.027	.037
0.3	.063	.035	.024	.024	.003	.016	.019	.036	.009
0.4	.083	.044	.019	.019	.002	.004	.026	.013	.010
0.5	.087	.050	.024	.000	.000	.013	.028	.001	.010
0.6	.105	.063	.029	.014	.014	.000	.017	.016	.014
0.7	.117	.067	.025	.018	.018	.005	.007	.022	.029
0.8	.134	.068	.050	.024	.024	.005	.018	.030	.033
0.9	.163	.090	.048	.034	.028	.028	.006	.022	.046

Standard Removal Conditional

$p$	$\psi$								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	.012	.005	.004	.008	.022	.038	.055	.070	.078
0.2	.008	.003	.002	.006	.015	.026	.037	.047	.052
0.3	.006	.002	.002	.005	.012	.020	.028	.036	.040
0.4	.006	.001	.001	.003	.010	.016	.023	.029	.033
0.5	.005	.001	.000	.003	.007	.014	.019	.024	.027
0.6	.004	.000	.001	.005	.007	.011	.015	.020	.022
0.7	.003	.000	.002	.001	.005	.009	.013	.016	.018
0.8	.004	.001	.003	.004	.006	.007	.008	.012	.015
0.9	.006	.005	.001	.006	.008	.009	.010	.010	.010

0.1	.061	.031	.019	.010	.005	.001	.003	.006	.003
0.2	.080	.043	.022	.014	.007	.000	.003	.009	.004
0.3	.085	.043	.026	.020	.005	.002	.003	.007	.003
0.4	.109	.045	.027	.013	.008	.001	.003	.008	.003
0.5	.089	.040	.028	.021	.006	.003	.007	.009	.001
0.6	.102	.066	.038	.029	.003	.000	.002	.004	.003
0.7	.080	.038	.027	.020	.002	.003	.010	.006	.000
0.8	.043	.002	.001	.003	.005	.006	.002	.001	.003
0.9	.000	.002	.004	.005	.006	.007	.007	.004	.001

0.1	.073	.026	.011	.030	.007	.016	.038	.058	.072
0.2	.088	.040	.003	.025	.023	.003	.015	.032	.044
0.3	.091	.041	.012	.009	.031	.010	.005	.021	.032
0.4	.115	.044	.016	.010	.027	.018	.000	.013	.024
0.5	.094	.039	.020	.003	.022	.007	.004	.012	.021
0.6	.105	.066	.033	.018	.018	.013	.003	.012	.017
0.7	.083	.038	.022	.009	.012	.003	.005	.007	.015
0.8	.048	.004	.002	.009	.015	.015	.002	.009	.018
0.9	.007	.005	.001	.003	.006	.002	.002	.004	.009

Standard Removal Conditional

$p$	$\psi$								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	C	S	S	R	R	R	R	R	R
0.2	C	S	S	R	R	R	R	R	R
0.3	C	S	S	R	R	R	R	R	R
0.4	C	S	R/S	R	R	R	R	R	R
0.5	C	S	R/S	R	R	R	R	R	R
0.6	C	C/S	R/S	R	R	R	R	R	R
0.7	C	C/S	S	R/S	R	R	R	R	R
0.8	C	C	R	R	R	R	R	R	R
0.9	C	C	C	R	R	R	R	R	R

Specht et al. (2017) *Methods in Ecology and Evolution*

Reich (2020) *Biometrics*



# Conditional sampling design

## Conclusions

- Conditional design is most efficient for rare species
- Standard design is most efficient for intermediate-occupancy species
- Standard design was generally the next-best performing model
- Removal design is most efficient when species is common

	$\psi$								
$p$	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	C	S	S	R	R	R	R	R	R
0.2	C	S	S	R	R	R	R	R	R
0.3	C	S	S	R	R	R	R	R	R
0.4	C	S	R/S	R	R	R	R	R	R
0.5	C	S	R/S	R	R	R	R	R	R
0.6	C	C/S	R/S	R	R	R	R	R	R
0.7	C	C/S	S	R/S	R	R	R	R	R
0.8	C	C	R	R	R	R	R	R	R
0.9	C	C	C	R	R	R	R	R	R

*Note: This design assumes that the first visit does not have a systematically different detection probability than subsequent visits.*

# “Mixed sampling design” “Double sampling design” / “Fractional replication”

- visit  $J_S$  sites once,  $J_R$  sites up to  $K$  times



True state	Mixed				
	1	2	3	4	5
1	1	0			
1	0				
1	0	0	1	1	0
1	0	0	0		
0	0				
1	1				
0	0				
0	0	0			
1	0				

# “Mixed sampling design” “Double sampling design” / “Fractional replication”

- visit  $J_S$  sites once,  $J_R$  sites up to  $K$  times

*Proportion of survey effort that should be conducted at single-visit sites.*

$p$	$\psi$								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	
0.1	0	0	0	0	0	0	0	0	0
0.2	0	0	0	0	0	0	0	0	0
0.3	0	0	0	0	0	0	0	0	0
0.4	0	3	0	0	0	0	0	0	0
0.5	6	1	0	0	0	0	0	0	0
0.6	0	0	0	12	4	0	0	0	0
0.7	9	5	0	0	0	0	0	0	0
0.8	33	30	26	21	14	5	0	0	0
0.9	56	54	51	48	44	39	31	17	0

## Conclusions

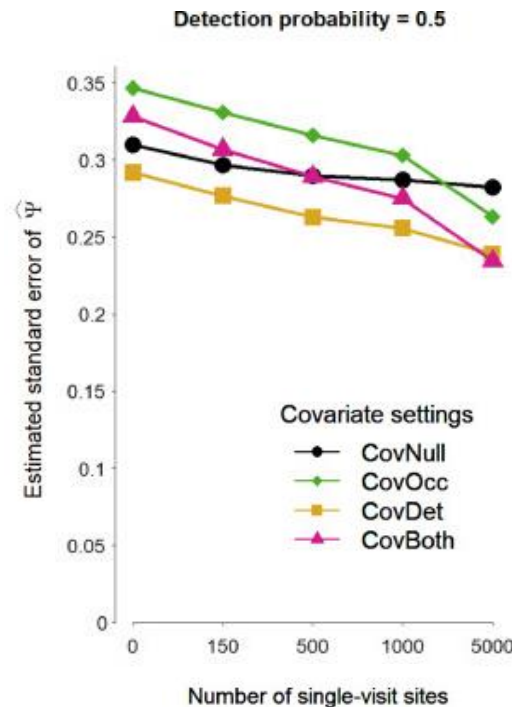
It is only beneficial to plan for single visits when the species is very easy to detect.

In all other cases, repeated visits at all sites yield better results than mixed designs.

# “Mixed sampling design” “Double sampling design” / “Fractional replication”

- visit  $J_S$  sites once,  $J_R$  sites up to  $K$  times

*Do single visits contribute any information at all?*



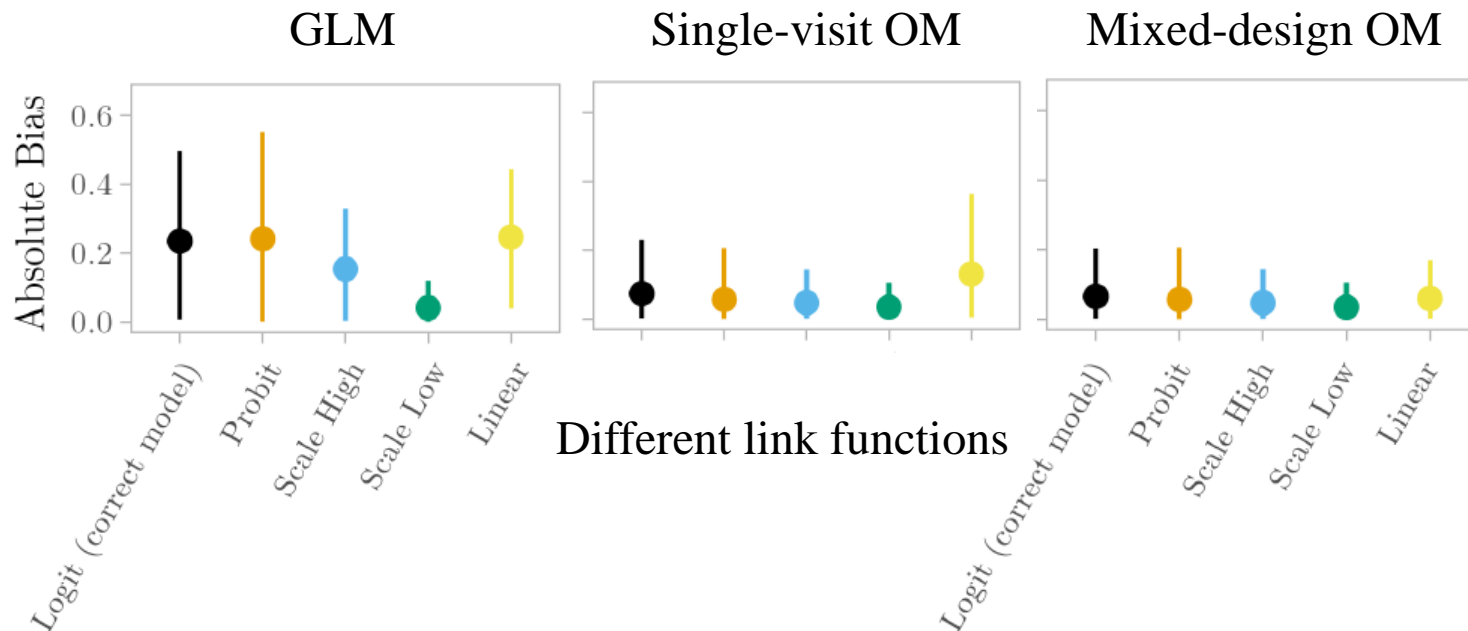
## Conclusion

**If combined with repeated-visit data, single-visit data contribute some information** to the estimation of occupancy (and partly also of detection), especially when occupancy and detection are each explained by a **continuous covariate**.

# “Mixed sampling design” “Double sampling design” / “Fractional replication”

- visit  $J_S$  sites once,  $J_R$  sites up to  $K$  times

*Do so few repeated visits make any difference in parameter estimation?*



## Conclusion

An **occupancy model fitted to mixed data** with only a few repeated visits still **performs better than a single-visit occupancy model or a GLM** that ignores imperfect detection.

# Occupancy dynamics

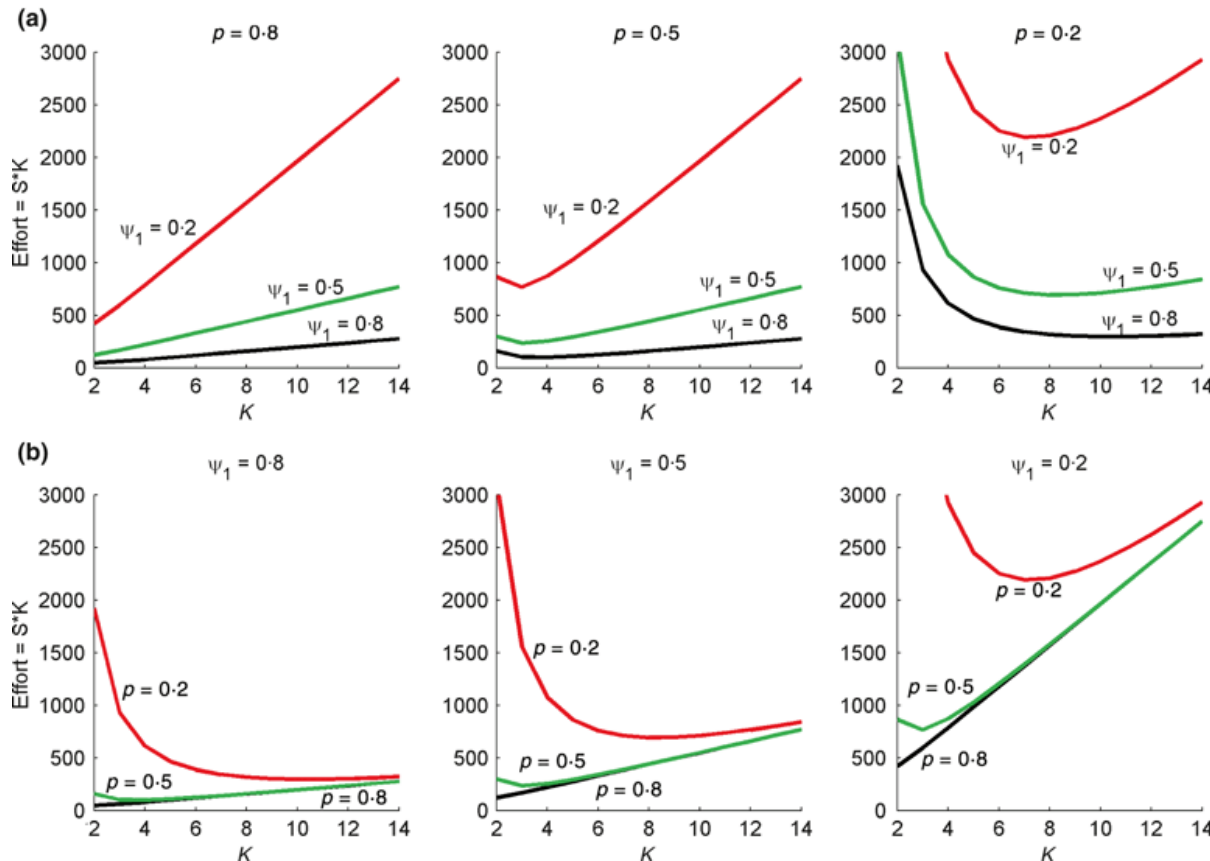
Goal: estimate change in occupancy over time with some degree of certainty



# Occupancy dynamics

Goal: estimate change in occupancy over time with some degree of certainty

→ find minimum survey effort to achieve a power of 0.8 when true decline is 0.5, for varying  $K$  and different levels of starting occupancy and detectability



## Conclusions

- with low  $p$  and low  $\psi_1$  and few repeated visits, it requires huge effort to detect a change with certainty
- when  $p$  is low, increasing  $K$  towards the optimal value yield a great improvement in power
- when  $p$  is high, increasing  $K$  above 2 does not increase power

# Additional heterogeneity or error

## detection heterogeneity

- variation in abundance
- unmodelled environmental covariate
- observer differences

Royle (2006) *Biometrics*

## false-positive sampling error

- standardization of sampling methods
- two types of observation  
certainties/methods

Royle & Link (2006) *Ecology*

Miller et al. (2011) *Ecology*

Ruiz-Gutiérrez et al. (2016) *Methods in Ecology and Evolution*

## availability for detection

- habitat use
- undetectable life stages

Kéry & Schmidt (2008) *Community Ecology*

Efford & Dawson (2012) *Ecosphere*

DiRenzo et al. (2022) *Methods in Ecology and Evolution*

## spatial pattern

- unmodelled covariates
- spatial autocorrelation

Guélat & Kéry (2018) *Methods in Ecology and Evolution*

Doser et al. (2022) *Methods in Ecology and Evolution*

# What is your goal?



- Estimate occupancy with the greatest possible precision?
- Evaluate detection probability of a new sampling method?
- Detect a supposed decline with some degree of certainty?
- Predict colonization and future distribution?
- Investigate co-occurrence patterns?
- Analyse local population dynamics?
- Minimize type I or type II error?

# What is your system?



- single/multiple species
- sessile/mobile species
- scale (interpretation of occupancy and detection)
- seasonality
- period of closure
- destructive sampling
- probability of false-positive detections
- degree of spatial correlation
- cost of establishing new sites
- logistic constraints

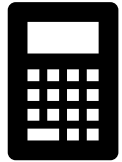
## **Static systems**

- expected occupancy probability
- expected detection probability
- expected detection heterogeneity
- expected false-positive error
- dependence between sites (transect sampling)

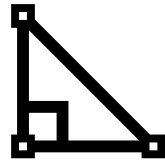
## **Dynamic systems**

- expected rate of change (long-term trend)
- expected fluctuation/temporal variation
- expected local colonization/extinction rates

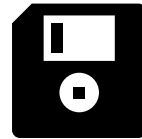
# How to find the suitable design?



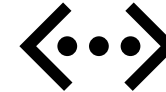
## Math



Numerical optimization or asymptotic approximation of the function that describes the variable of interest (precision, statistical power, etc.)



## Simulation



1. simulate true occupancy and detection/nondetection data under possible scenarios
  2. analyze data with the intended model
  3. compare variable of interest (precision/bias of the estimator, probability of type I error, probability of type II error (1-statistical power))
- easier for non-mathematicians
  - forces to understand the data-generating and data-analyzing process
  - especially useful for small sample sizes

# Simulation example

Simulate data to see how precision of the occupancy estimate depends on

- occupancy and detection probability of the species of interest
- the distribution of survey effort in a standard sampling design

What would the optimal number of repeated visits be for different species?

```
05-occupancy-model-survey-design-simulation.R
```





# Cited literature 1

- Bailey, L.L., Hines, J.E., Nichols, J.D. & MacKenzie, D.I. (2007). Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. *Ecological Applications*, 17 (1), 281–290. [https://doi.org/10.1890/1051-0761\(2007\)017\[0281:SDTIOS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2007)017[0281:SDTIOS]2.0.CO;2)
- DiRenzo, G.V., Miller, D.A.W. & Grant, E.H.C. (2022). Ignoring species availability biases occupancy estimates in single-scale occupancy models. *Methods in Ecology and Evolution*, n/a (n/a). <https://doi.org/10.1111/2041-210X.13881>
- Doser, J.W., Finley, A.O., Kéry, M. & Zipkin, E.F. (2022). spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, n/a (n/a). <https://doi.org/10.1111/2041-210X.13897>
- Doser, J.W. & Stoudt, S. (2024). “Fractional replication” in single-visit multi-season occupancy models: Impacts of spatiotemporal autocorrelation on identifiability. *Methods in Ecology and Evolution*, 15 (2), 358–372. <https://doi.org/10.1111/2041-210X.14275>
- Efford, M.G. & Dawson, D.K. (2012). Occupancy in continuous habitat. *Ecosphere*, 3 (4), art32. <https://doi.org/10.1890/ES11-00308.1>
- Field, S.A., Tyre, A.J. & Possingham, H.P. (2005). Optimizing allocation of monitoring effort under economic and observational constraints. *The Journal of Wildlife Management*, 69 (2), 473–482. [https://doi.org/10.2193/0022-541X\(2005\)069\[0473:OAOMEU\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)069[0473:OAOMEU]2.0.CO;2)
- Guélat, J. & Kéry, M. (2018). Effects of spatial autocorrelation and imperfect detection on species distribution models. *Methods in Ecology and Evolution*, 9 (6), 1614–1625. <https://doi.org/10.1111/2041-210X.12983>
- Guillera-Arroita, G. & Lahoz-Monfort, J.J. (2012). Designing studies to detect differences in species occupancy: power analysis under imperfect detection. *Methods in Ecology and Evolution*, 3 (5), 860–869. <https://doi.org/10.1111/j.2041-210X.2012.00225.x>
- Guillera-Arroita, G., Ridout, M.S. & Morgan, B.J.T. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, 1 (2), 131–139. <https://doi.org/10.1111/j.2041-210X.2010.00017.x>
- von Hirschheydt, G., Stofer, S. & Kéry, M. (2023). “Mixed” occupancy designs: When do additional single-visit data improve the inferences from standard multi-visit models? *Basic and Applied Ecology*, 67, 61–69. <https://doi.org/10.1016/j.baae.2023.01.003>
- Kéry, M. & Schmidt, B. (2008). Imperfect detection and its consequences for monitoring for conservation. *Community Ecology*, 9 (2), 207–216. <https://doi.org/10.1556/ComEc.9.2008.2.10>
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83 (8), 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- MacKenzie, D.I. & Royle, J.A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, 42 (6), 1105–1114. <https://doi.org/10.1111/j.1365-2664.2005.01098.x>

# Cited literature 2

- Miller, D.A.W., Nichols, J.D., McClintock, B.T., Grant, E.H.C., Bailey, L.L. & Weir, L.A. (2011). Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. *Ecology*, 92 (7), 1422–1428. <https://doi.org/10.1890/10-1396.1>
- Reich, H.T. (2020). Optimal sampling design and the accuracy of occupancy models. *Biometrics*, 76 (3), 1017–1027. <https://doi.org/10.1111/biom.13203>
- Royle, J.A. (2006). Site occupancy models with heterogeneous detection probabilities. *Biometrics*, 62 (1), 97–102. <https://doi.org/10.1111/j.1541-0420.2005.00439.x>
- Royle, J.A. & Link, W.A. (2006). Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*, 87 (4), 835–841. [https://doi.org/10.1890/0012-9658\(2006\)87\[835:GSOMAF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[835:GSOMAF]2.0.CO;2)
- Ruiz-Gutiérrez, V., Hooten, M.B. & Campbell Grant, E.H. (2016). Uncertainty in biological monitoring: a framework for data collection and analysis to account for multiple sources of sampling bias. *Methods in Ecology and Evolution*, 7 (8), 900–909. <https://doi.org/10.1111/2041-210X.12542>
- Specht, H.M., Reich, H.T., Iannarilli, F., Edwards, M.R., Stapleton, S.P., Weegman, M.D., Johnson, M.K., Yohannes, B.J. & Arnold, T.W. (2017). Occupancy surveys with conditional replicates: An alternative sampling design for rare species. *Methods in Ecology and Evolution*, 8 (12), 1725–1734. <https://doi.org/10.1111/2041-210X.12842>
- Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K. & Possingham, H.P. (2003). Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications*, 13 (6), 1790–1801. <https://doi.org/10.1890/02-5078>
- Yoccoz, N.G., Nichols, J.D. & Boulinier, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16 (8), 446–453. [https://doi.org/10.1016/S0169-5347\(01\)02205-4](https://doi.org/10.1016/S0169-5347(01)02205-4)

# Additional literature 1

## **THE occupancy book**

MacKenzie, D.I., Nichols, J.D., Royle, A.J., Pollock, K.H., Bailey, L.L. & Hines, J. (2018). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. 2. ed. Elsevier/AP.

## **Transect sampling**

Hines, J.E., Nichols, J.D., Royle, J.A., MacKenzie, D.I., Gopalaswamy, A.M., Kumar, N.S. & Karanth, K.U. (2010). Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications*, 20 (5), 1456–1466. <https://doi.org/10.1890/09-0321.1>

Guillera-Arroita, G., Morgan, B.J.T., Ridout, M.S. & Linkie, M. (2011). Species occupancy modeling for detection data collected along a transect. *Journal of Agricultural, Biological, and Environmental Statistics*, 16 (3), 301–317. <https://doi.org/10.1007/s13253-010-0053-3>

Guillera-Arroita, G., Ridout, M.S., Morgan, B.J.T. & Linkie, M. (2012). Models for species-detection data collected along transects in the presence of abundance-induced heterogeneity and clustering in the detection process: abundance and clustered detections. *Methods in Ecology and Evolution*, 3 (2), 358–367. <https://doi.org/10.1111/j.2041-210X.2011.00159.x>

## **Camera trap data**

Nichols, J.D., Bailey, L.L., O’Connell Jr., A.F., Talancy, N.W., Campbell Grant, E.H., Gilbert, A.T., Annand, E.M., Husband, T.P. & Hines, J.E. (2008). Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, 45 (5), 1321–1329. <https://doi.org/10.1111/j.1365-2664.2008.01509.x>

Goldstein, B.R., Jensen, A.J., Kays, R., Cove, M.V., McShea, W.J., Rooney, B., Kierepka, E.M. & Pacifici, K. (2024). Guidelines for estimating occupancy from autocorrelated camera trap detections. *Methods in Ecology and Evolution*, n/a (n/a). <https://doi.org/10.1111/2041-210X.14359>

## **Co-occurrence patterns of multiple species**

MacKenzie, D.I., Bailey, L.L. & Nichols, J.D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, 73 (3), 546–555. <https://doi.org/10.1111/j.0021-8790.2004.00828.x>

Richmond, O.M.W., Hines, J.E. & Beissinger, S.R. (2010). Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, 20 (7), 2036–2046. <https://doi.org/10.1890/09-0470.1>

# Additional literature 2

## **Accounting for false-positive detections**

Clement, M.J. (2016). Designing occupancy studies when false-positive detections occur. *Methods in Ecology and Evolution*, 7 (12), 1538–1547. <https://doi.org/10.1111/2041-210X.12617>

Louvrier, J., Chambert, T., Marboutin, E. & Gimenez, O. (2018). Accounting for misidentification and heterogeneity in occupancy studies using hidden Markov models. *Ecological Modelling*, 387, 61–69. <https://doi.org/10.1016/j.ecolmodel.2018.09.002>

Spiers, A.I., Royle, J.A., Torrens, C.L. & Joseph, M.B. (2022). Estimating species misclassification with occupancy dynamics and encounter rates: A semi-supervised, individual-level approach. *Methods in Ecology and Evolution*, 13 (7), 1528–1539. <https://doi.org/10.1111/2041-210X.13858>

## **Interpretation of occupancy and detection at different scales**

Nichols, J.D., Bailey, L.L., O’Connell Jr., A.F., Talancy, N.W., Campbell Grant, E.H., Gilbert, A.T., Annand, E.M., Husband, T.P. & Hines, J.E. (2008). Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, 45 (5), 1321–1329. <https://doi.org/10.1111/j.1365-2664.2008.01509.x>

Guillera-Aroita, G., Lahoz-Monfort, J.J., van Rooyen, A.R., Weeks, A.R. & Tingley, R. (2017). Dealing with false-positive and false-negative errors about species occurrence at multiple levels. *Methods in Ecology and Evolution*, 8 (9), 1081–1091. <https://doi.org/10.1111/2041-210X.12743>

## **Two-phase sampling design**

Pacifici, K., Dorazio, R.M. & Conroy, M.J. (2012). A two-phase sampling design for increasing detections of rare species in occupancy surveys. *Methods in Ecology and Evolution*, 3 (4), 721–730. <https://doi.org/10.1111/j.2041-210X.2012.00201.x>