Wildtierkundekurs II

Theory 2: Abundance

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Ecologists ask: why, where, how many?

Ecology is the science of the relationships between organisms and their environments.

The central question in ecology is:
Which factors determine the presence, distribution and abundance of organisms?
population ecology studies changes of number of individuals in space and time

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The pleasure of counting

Knowing how many animals there are may be one of the most fundamental questions in population ecology.

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The pleasure of counting

Animal abundance and its change over time is the key information to determine management actions:

How can a negative population trend be reversed?

How many animals can be harvested?

How can pest species be reduced?

etc.

Yet animals are notoriously difficult to count!

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What determines population change?

Important population characteristics are:

Birth
Death
} Life history

Immigration
Emigration
} Movement

BIDE equation of population vital rates:

$$\mathbf{N_{t+1} = N_t + Births + Immigration - Deaths - Emigration}$$

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Population characteristics

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Rate of increase or population growth

depends on birth and death rates, immigration and emigration

$$\mathbf{N_{t+1} = N_t + Births + Immigration - Deaths - Emigration}$$

or $N_{t+1} = N_t \times \lambda$

Population growth rate

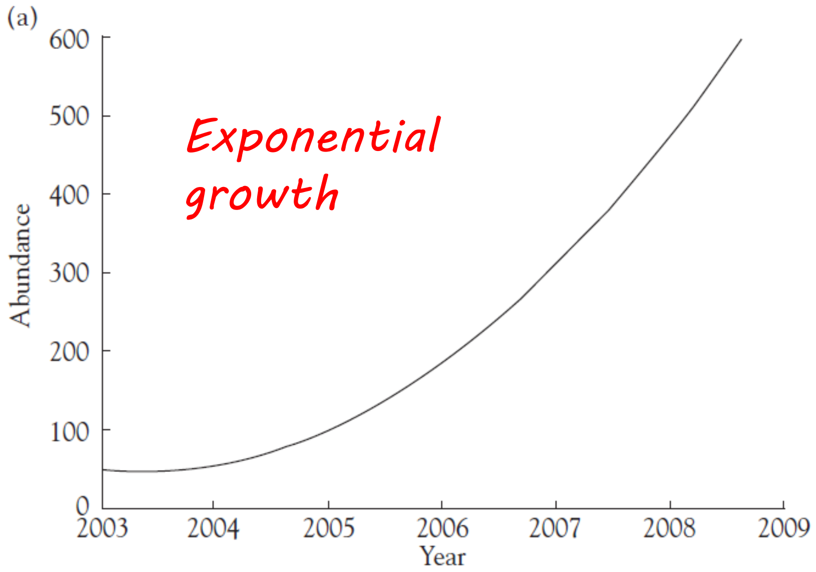
Population characteristics

λ is the geometric growth rate → discrete growth
abundance next year as a multiple of abundance this year

$$N_3 = N_0 \times \lambda \times \lambda \times \lambda = N_0\lambda^3 \quad \textit{general} \quad N_t = N_0\lambda^t$$

r is the exponential growth rate → continuous growth
time intervals for calculating abundance are infinitesimal

$dN/dt = rN$ *derivative*

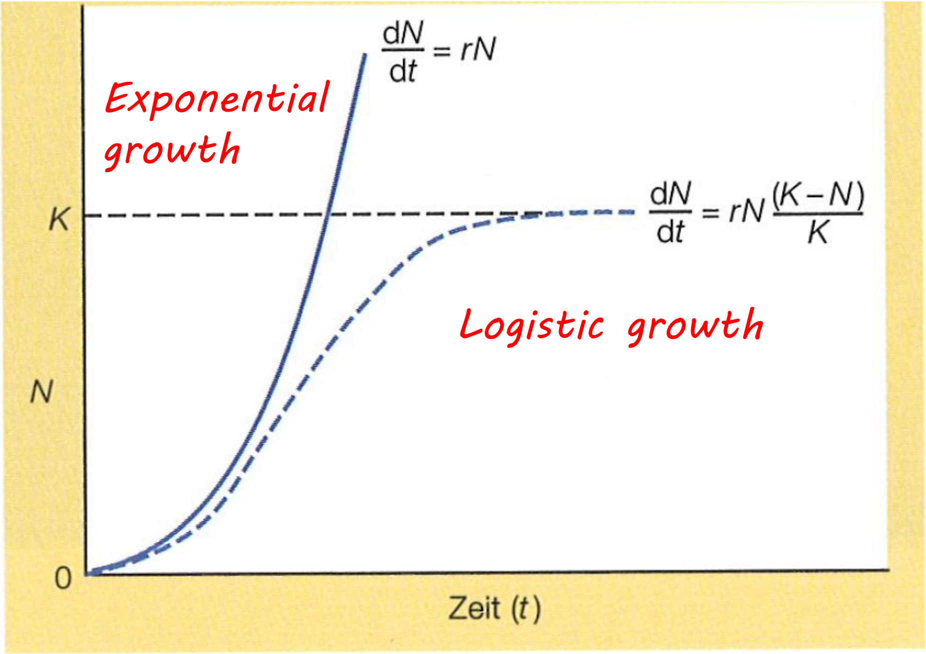


Population characteristics

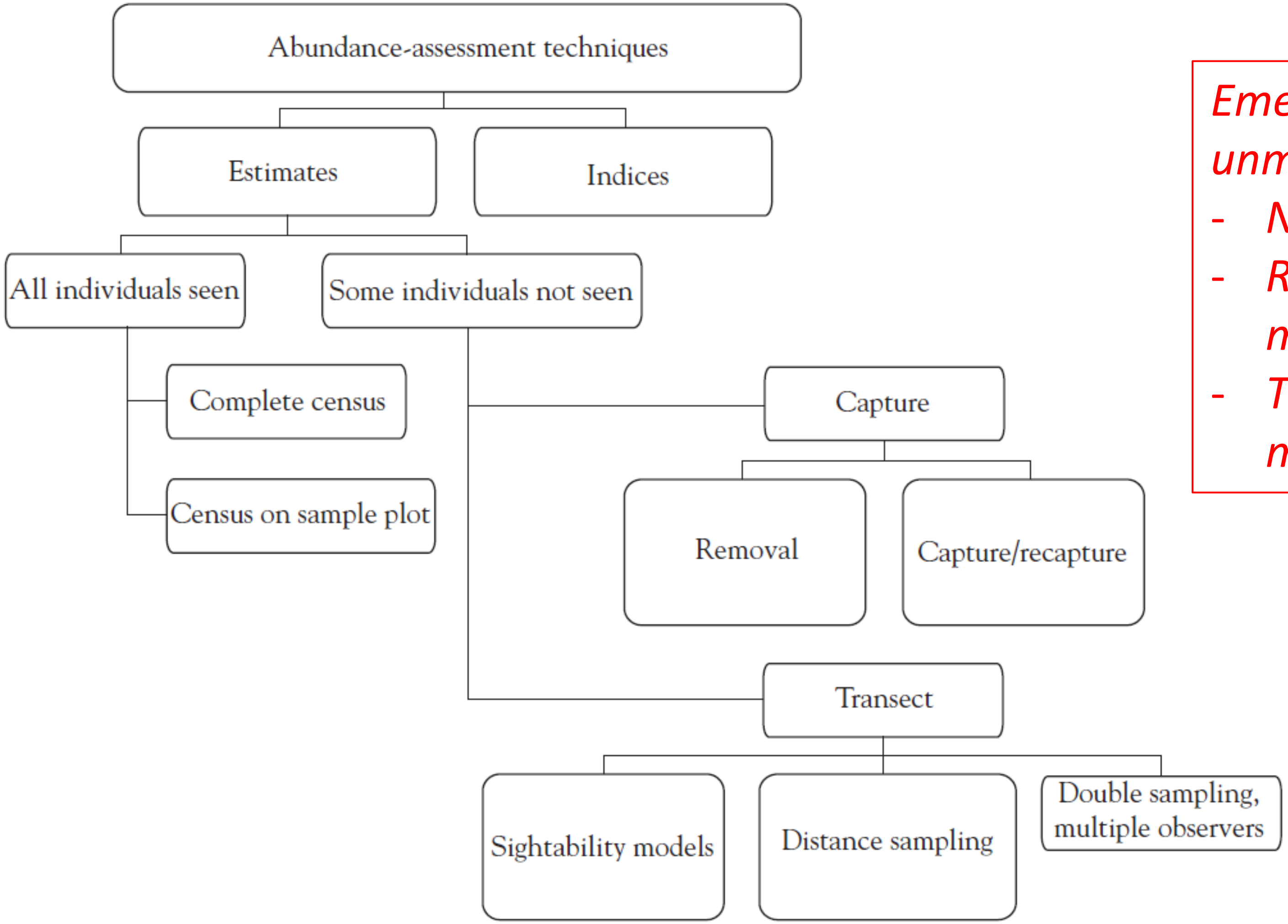
r and λ relate to each other

$r = \ln \lambda$ ➡ $N_t = N_0 \lambda^t$ → $N_t = N_0 e^{rt}$

Many models of population growth exist!
→ Relevant for conservation and management of populations

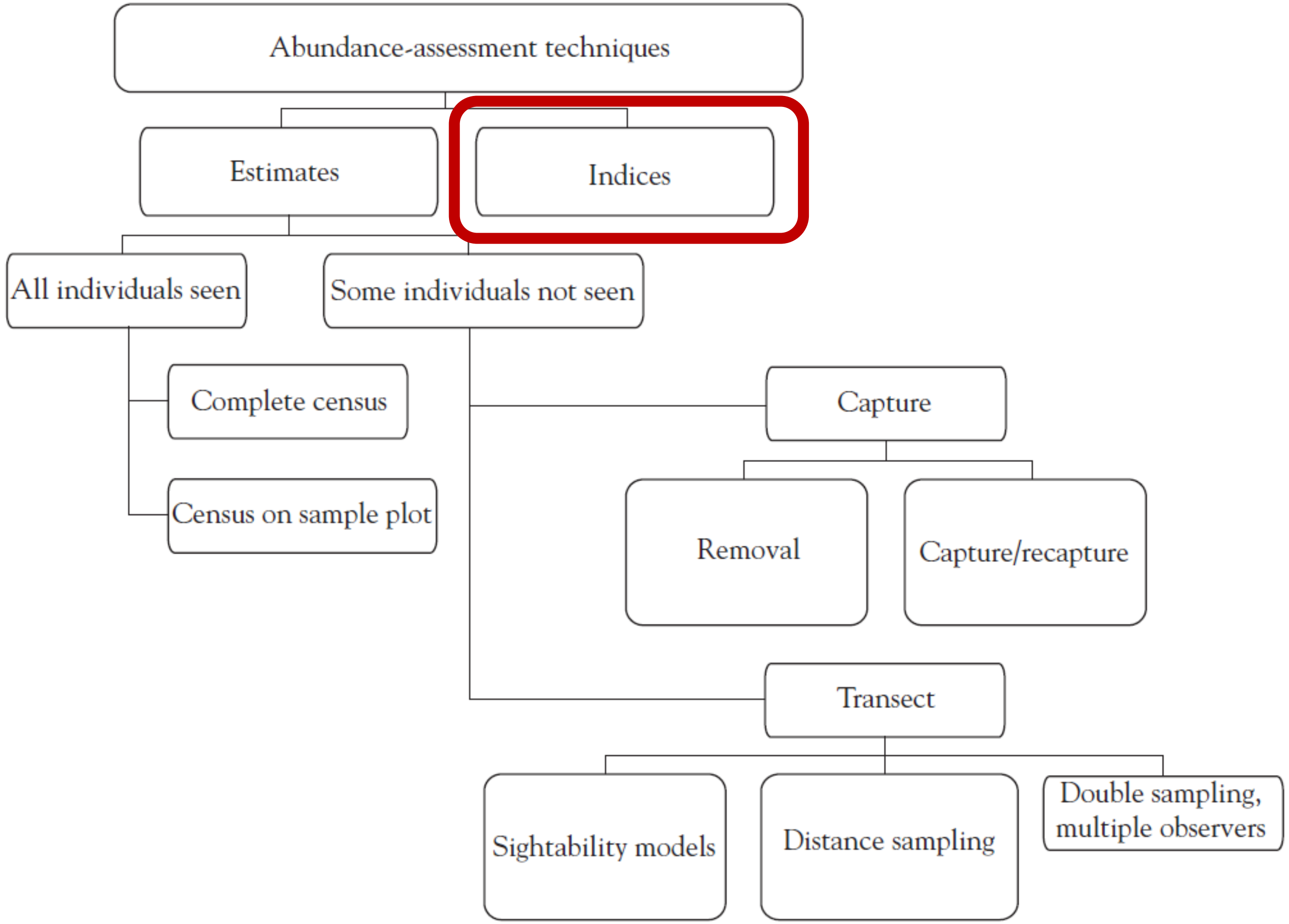


Many ways to assess animal abundance



Emerging methods for unmarked populations
- *N-mixture models*
- *Random encounter models*
- *Time-to-event models*

Many ways to assess animal abundance



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Abundance assessment: Index

Index:

A count of animals or signs thereof that hopefully* contain information on true abundance.

*Assumption: index is directly related to true abundance, hopefully linearly.

- Count of animals, e.g. mammal captures
- Count of animal signs, e.g. pellet counts, bird-call counts, track counts
- Catch per unit effort, e.g. hunting bags including information on effort

Abundance assessment: Index

Advantage of indices: Usually cheap and easy to assess

Problem with indices: the underlying assumption is rarely met in reality. The relationship with true abundance often varies over space and time and may not even be linear.

e.g. hunting bag may be more dependent on hunting quotas, weather conditions, changes in public perception of hunting, habitat conversion, etc.

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Abundance assessment: Index

- usefulness of an index should be validated using a robust estimater of true abundance (e.g. distance sampling, CMR)

- Precision of index should always be assessed (replicated counts are aimed at averaging out sampling variance → assess repeatability of index)

- Define goal to be achieved with a given index → trend in population change (e.g. 5% change in populatin growth over 10 years)

→ Choose effort to achieve required precision to meet goal!

→ Combine index with indicators of ecological change

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Monitoring population trend of chamois in France

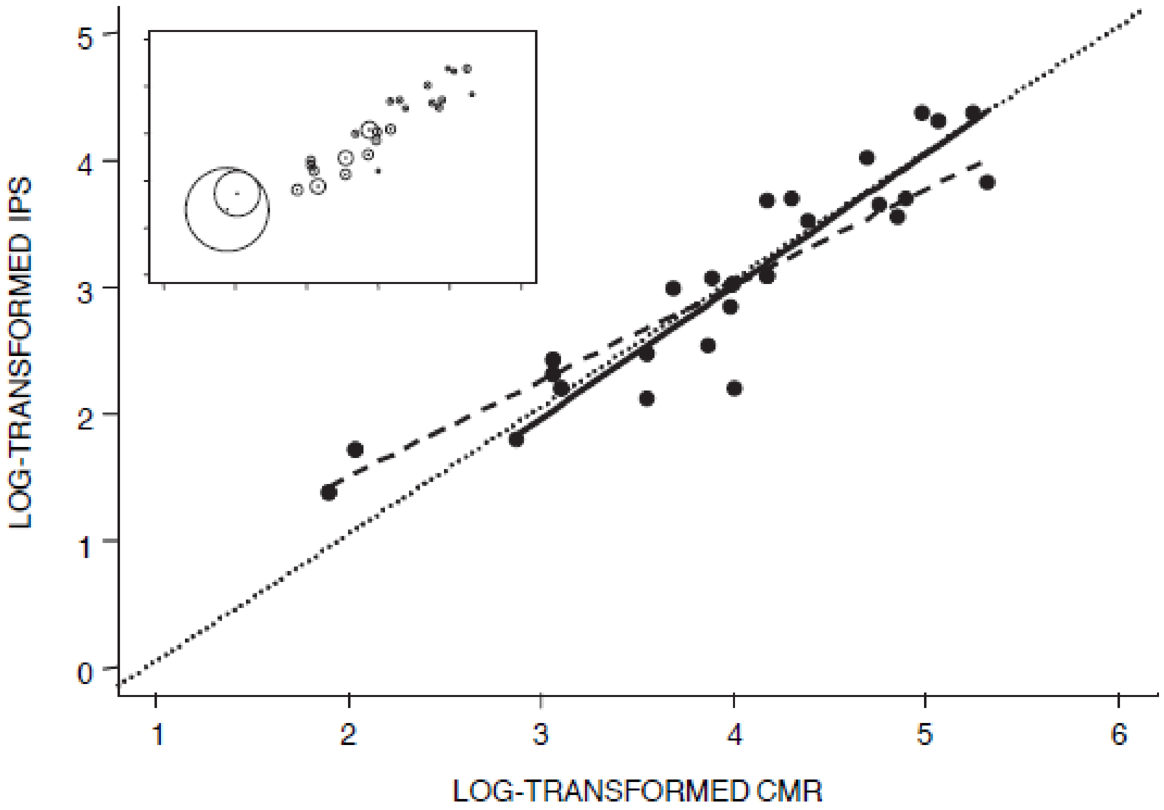
- Compared kilometer index of counted chamois to statistical estimator of abundance (CMR) in two pouplations

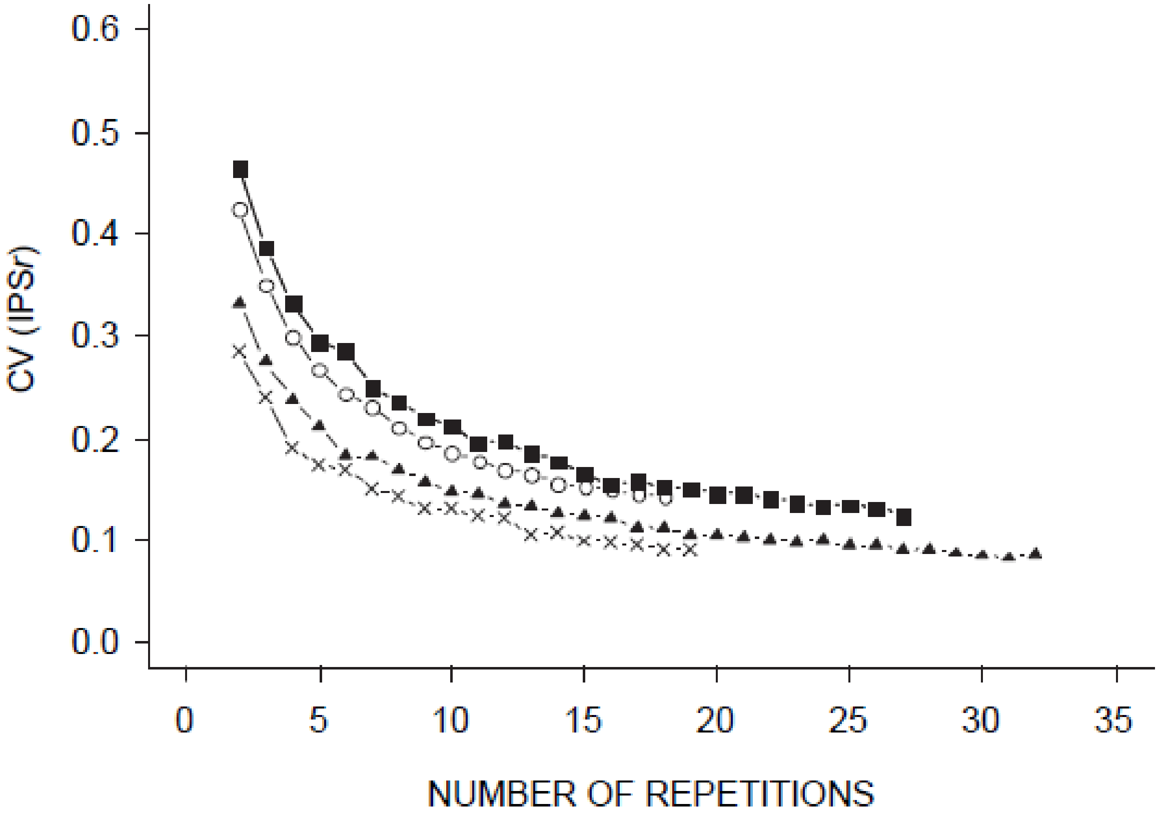
- Estimated precision of index performing replicated counts

- estimated required nr of years to detect change in population trend
  → using subsampling techniques

Loison et al. 2006, Wildlife Biology

Monitoring population trend of chamois in France





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Monitoring population trend of chamois in France

- Replicated counts correlated well with CMR estimators of true abundance

- Precision of index increased and reached an asymptote with increasing nr of replicates
  → up to 12 replicates were necessary to reach reliable estimate of population index

- Minimum nr of years necessary to detect true change in population growth differed between 5-7 years

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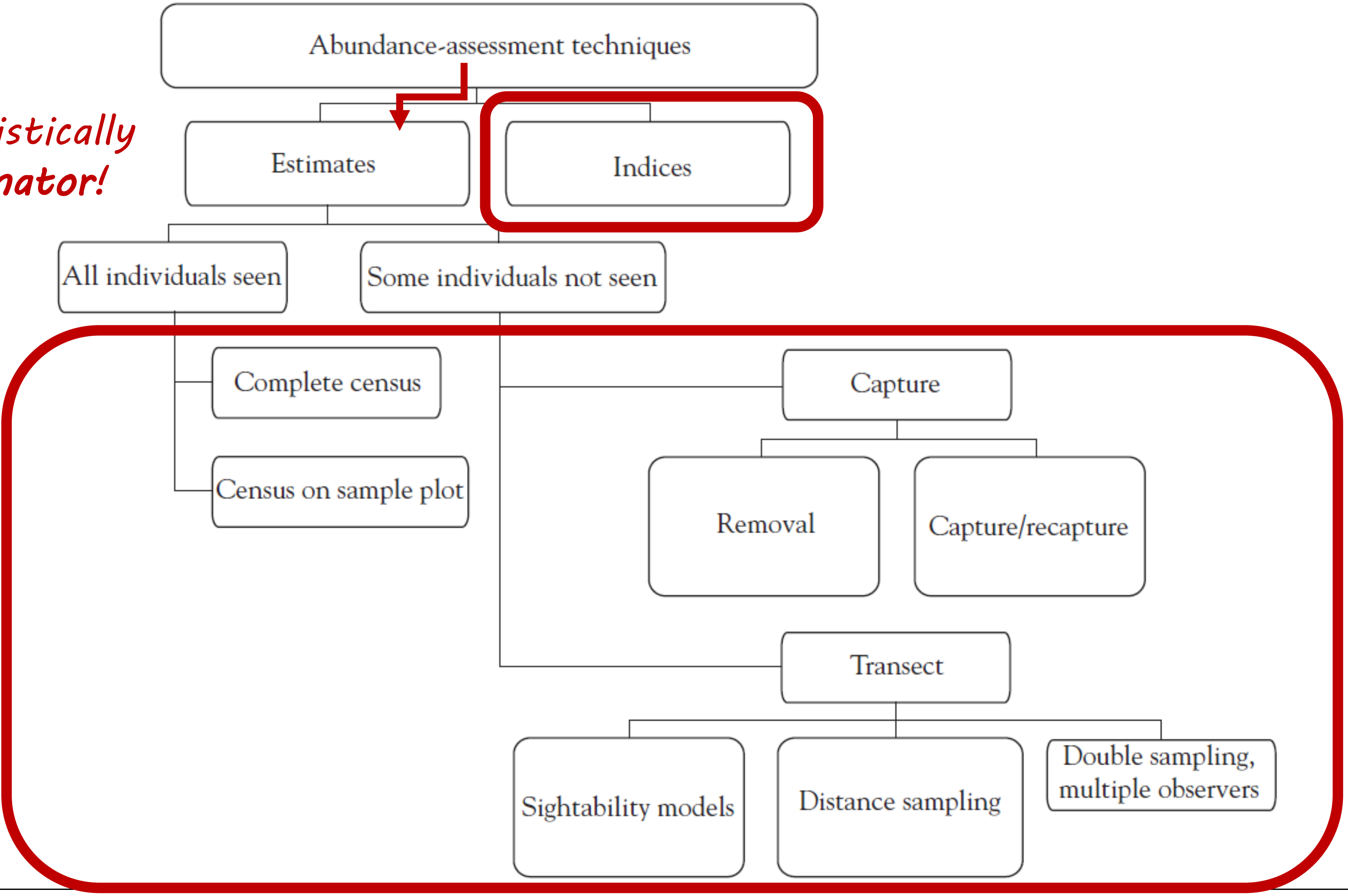
Many ways to assess animal abundance

Use a statistically based **estimator!**



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Estimates of animal abundance

All estimates of animal abundance (N) come down to one simple equation:

$$N = \frac{C}{p}$$

C = Count of animals

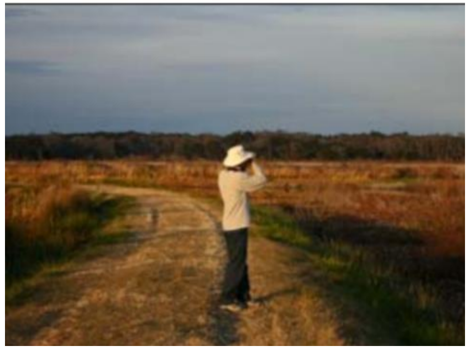
Difference between estimates and indices!

p = estimated probability of detection

Estimates of animal abundance

Probability of detection (p) depends on:

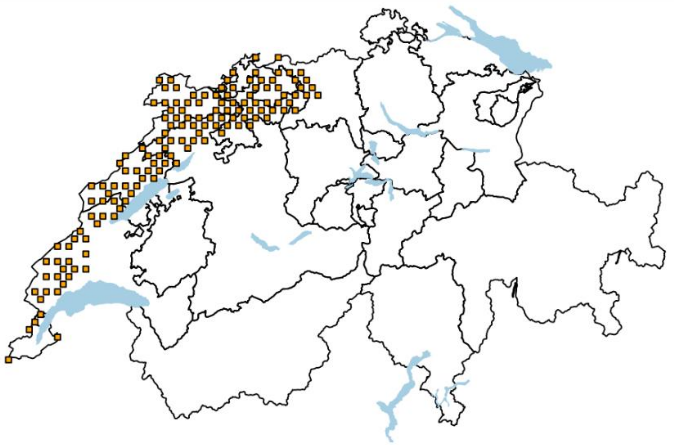
- Detectability of animals within sampled area (β)



Sometimes individuals are not visible to the observer (hidden behind bush or camouflaged)

- Fraction of total area sampled (α)

Entire study area is often to large to be entirely covered by sampling



$$N = C / p$$

$$N = C / \alpha\beta$$

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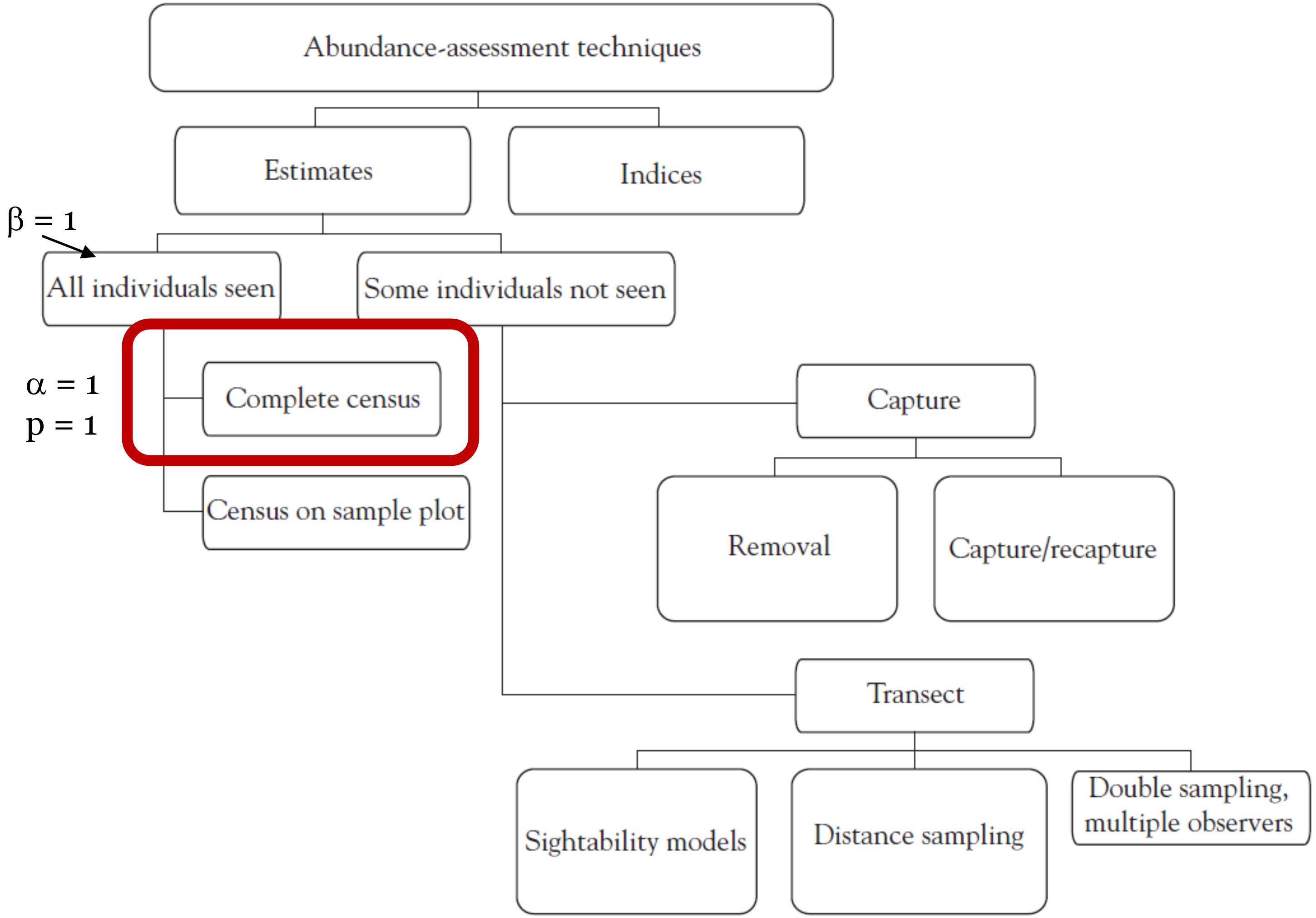
Many ways to estimate animal abundance

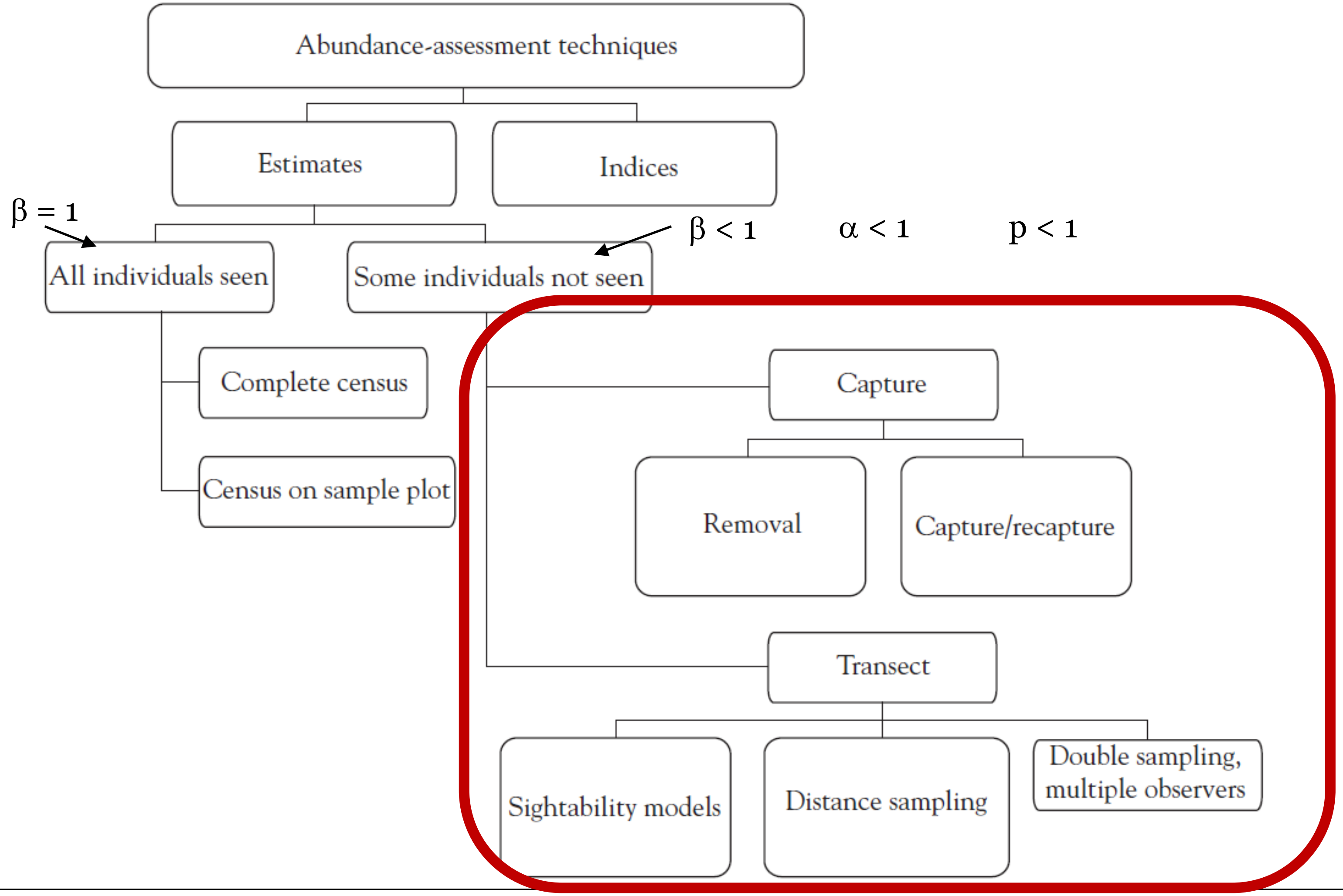


Abundance estimate: Complete census

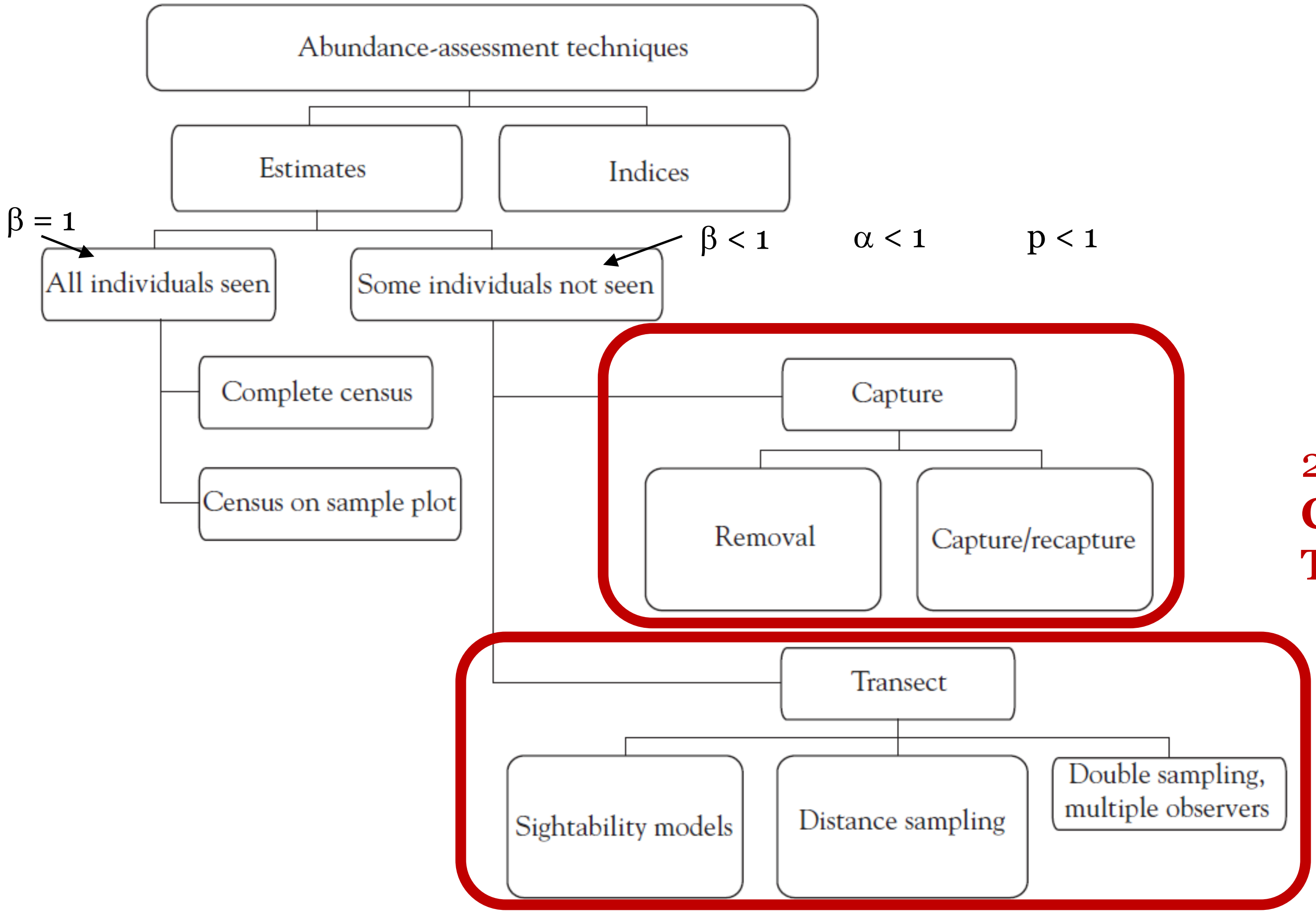
Complete census: count of all individuals of the entire population in the entire area → count equals the abundance estimate (i.e. p = 1)

- sessile organisms (e.g. plants)
- large animals within confined area
  (e.g. tortoises on an island, fishes in a pond)
- Animals in open habitats (e.g. ibex)

Many ways to estimate animal abundance

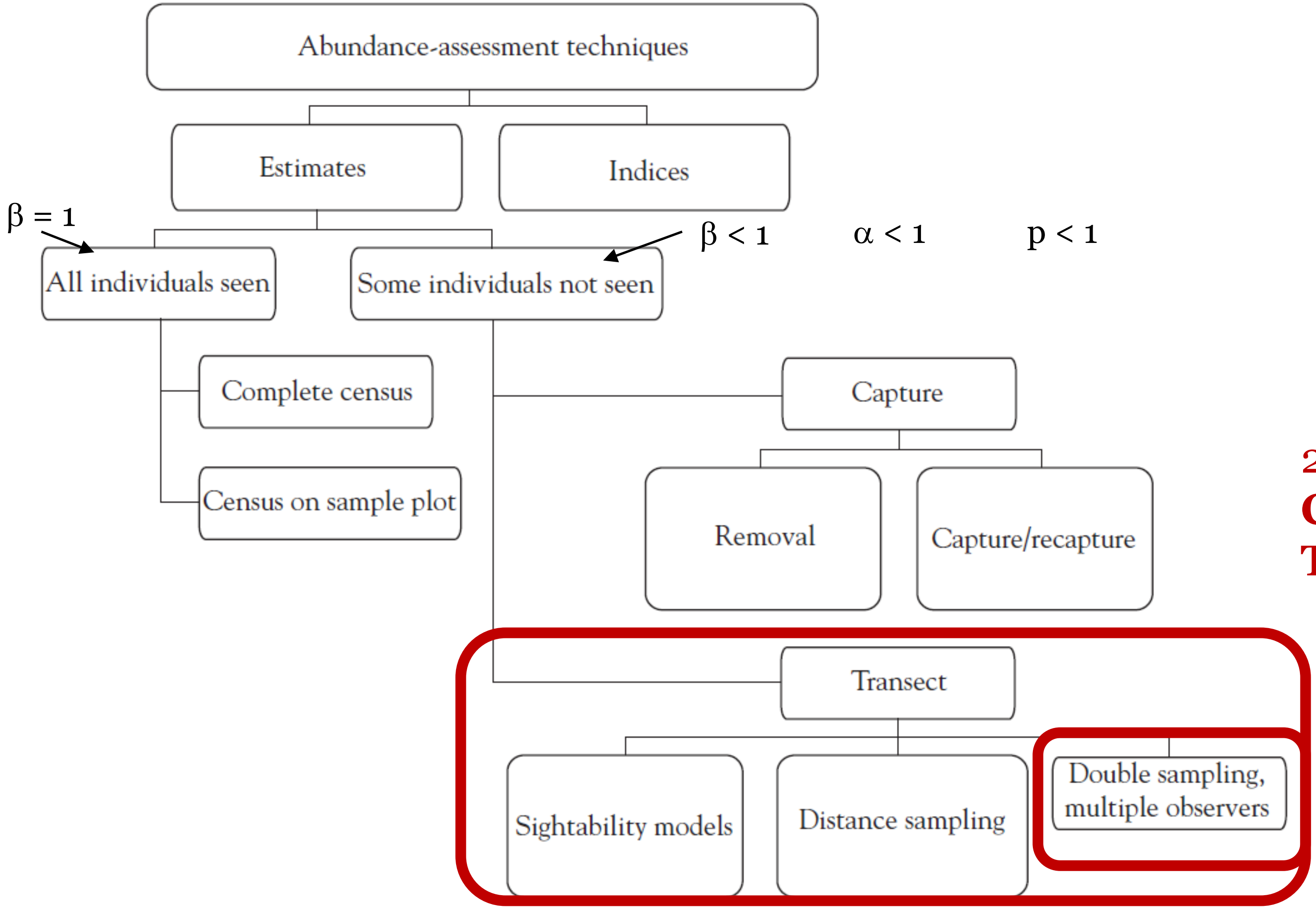


Many ways to estimate animal abundance



2 main approaches:
Capture methods
Transect methods

Many ways to estimate animal abundance

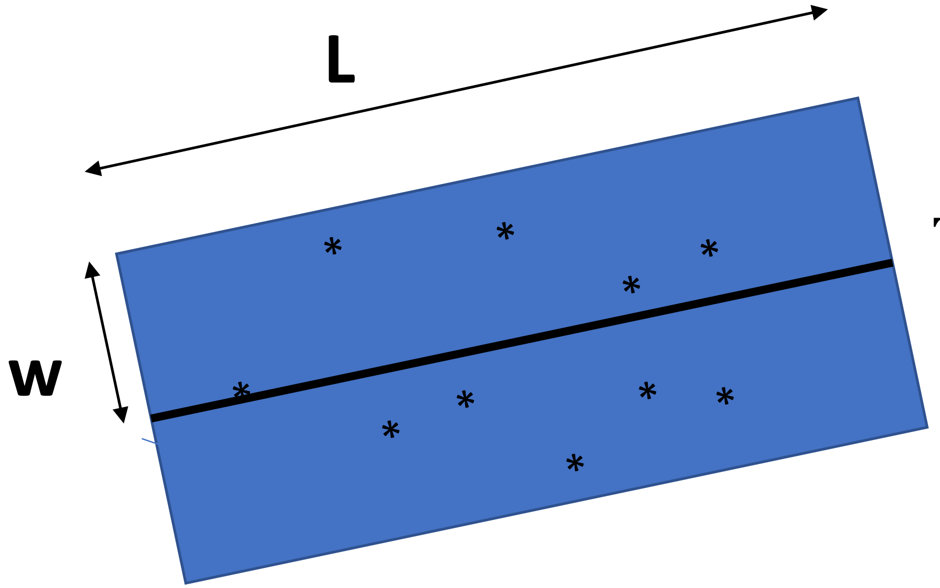


2 main approaches:
Capture methods
Transect methods

Transect definition

A transect is a line through the study area.

One or more transects of length L and wide w is set out through the study area to be sampled.



Area of one transect = L2w

Transect line of length L

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Transects: Double sampling

Combination of incomplete counts over wide area (e.g. aerial count) with complete census (on the ground) on subset of transects

Estimate p from ratio of means (n) of complete and incomplete counts of subset

Count of European hare in Selzach SO

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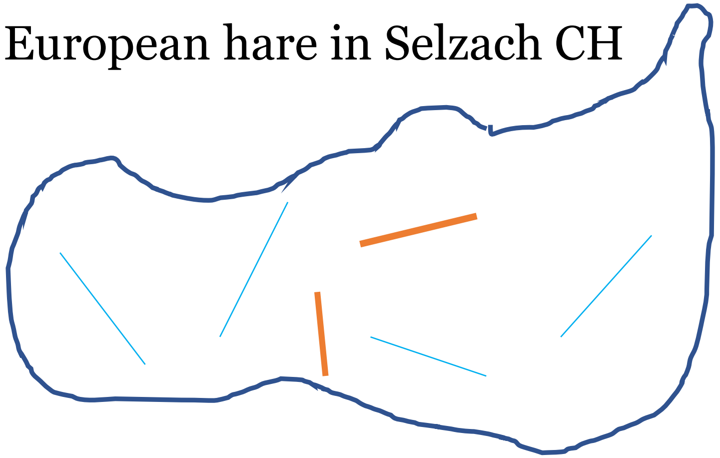
Transects: Double sampling

Combination of incomplete walking counts during the day with complete census counts at night on subset of transects

Estimate p from ratio of means (n) of complete and incomplete counts of subset

$$N = \frac{C}{p} = C \times \frac{n_{complete}}{n_{incomplete}}$$

Count of European hare in Selzach CH



Sum incomplete counts of all transects:
(4 + 5 + 7 + 5 + 9 + 12) = 42

Mean incomplete counts:
(5+9)/2 = 7

Mean complete counts:
(31 + 23)/2 = 27

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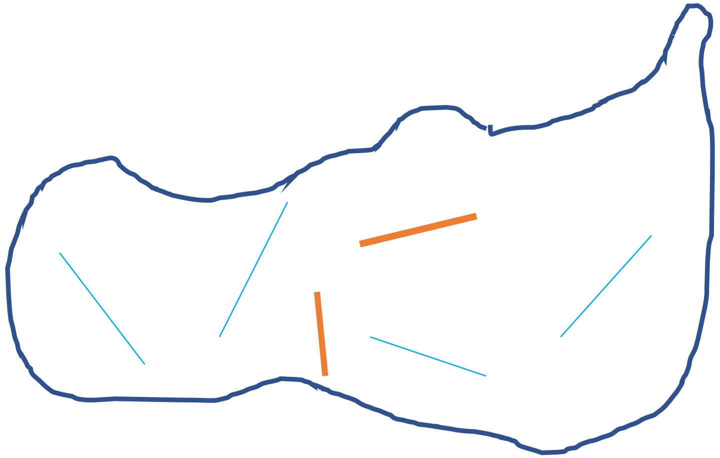
Transects: Double sampling

Combination of incomplete walking counts during the day with complete census counts at night on subset of transects

$$p = \alpha\beta = \frac{n_{incomplete}}{n_{complete}} \times area\ sampled$$

Effective area = 72 ha

mean area of transect = 1km x 2 x 20m = 4 ha



Detectability β = 7/27 = 0.26

Area sampled α = 4/72 = 0.333

Detection probability p = 0.26*0.333 = 0.087

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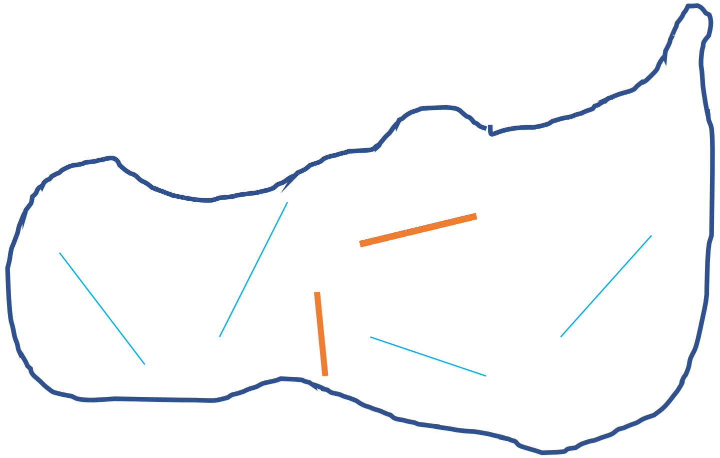
Transects: Double sampling

Combination of incomplete walking counts during the day with complete census counts at night on subset of transects



Abundance on total area = 42/0.087 = **486 hares**

Density = D = N/A = 486/72 = 6.75 ind/ha

Variance estimation for double sampling can be obtained from regression approach

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Side note on detection probability

- Many statistical estimators of abundance only estimate population **available** to be counted
  - deer hiding in patches of forest
  - marine mammals or animals that spend extended periods underground (e.g. Dugons, salamander)

Keep in mind conditional nature of detection probabaility: $p = \mathrm{p}_{\mathrm{area}}\,\mathrm{p}_{\mathrm{avail}}\,\mathrm{p}_{\mathrm{detect|avail}}$



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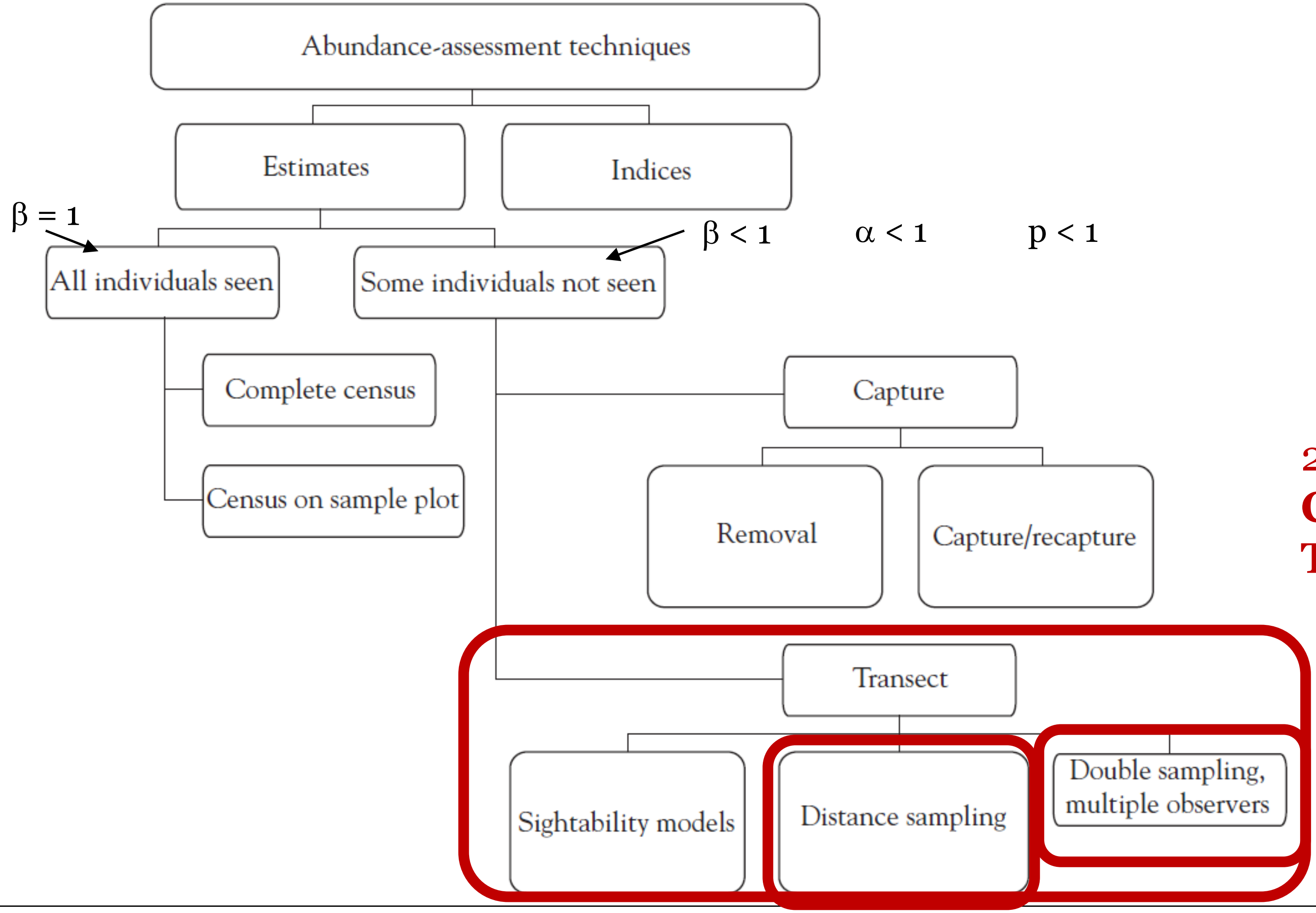
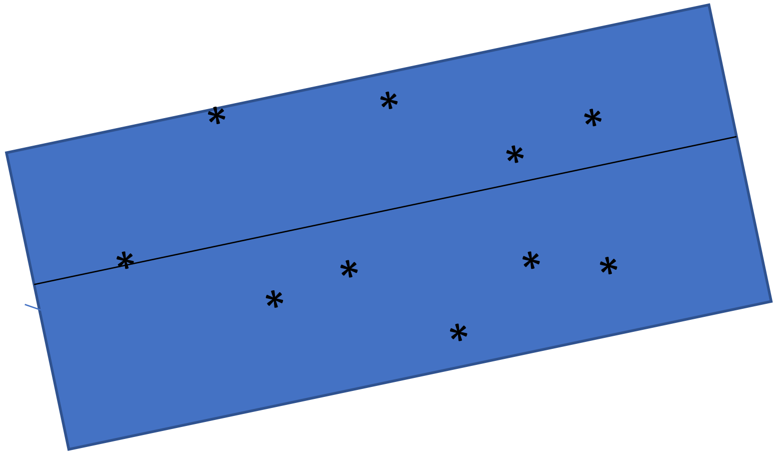
Many ways to estimate animal abundance

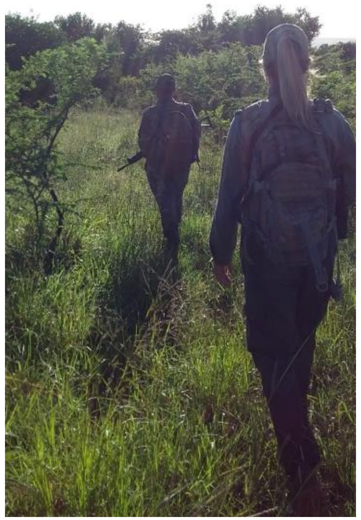


2 main approaches:
Capture methods
Transect methods

Distance sampling: general study design

- Transects of length L are set out through the study area to be sampled
- Placement of transects should be random with respect to distribution of animals - e.g. roads are often not random





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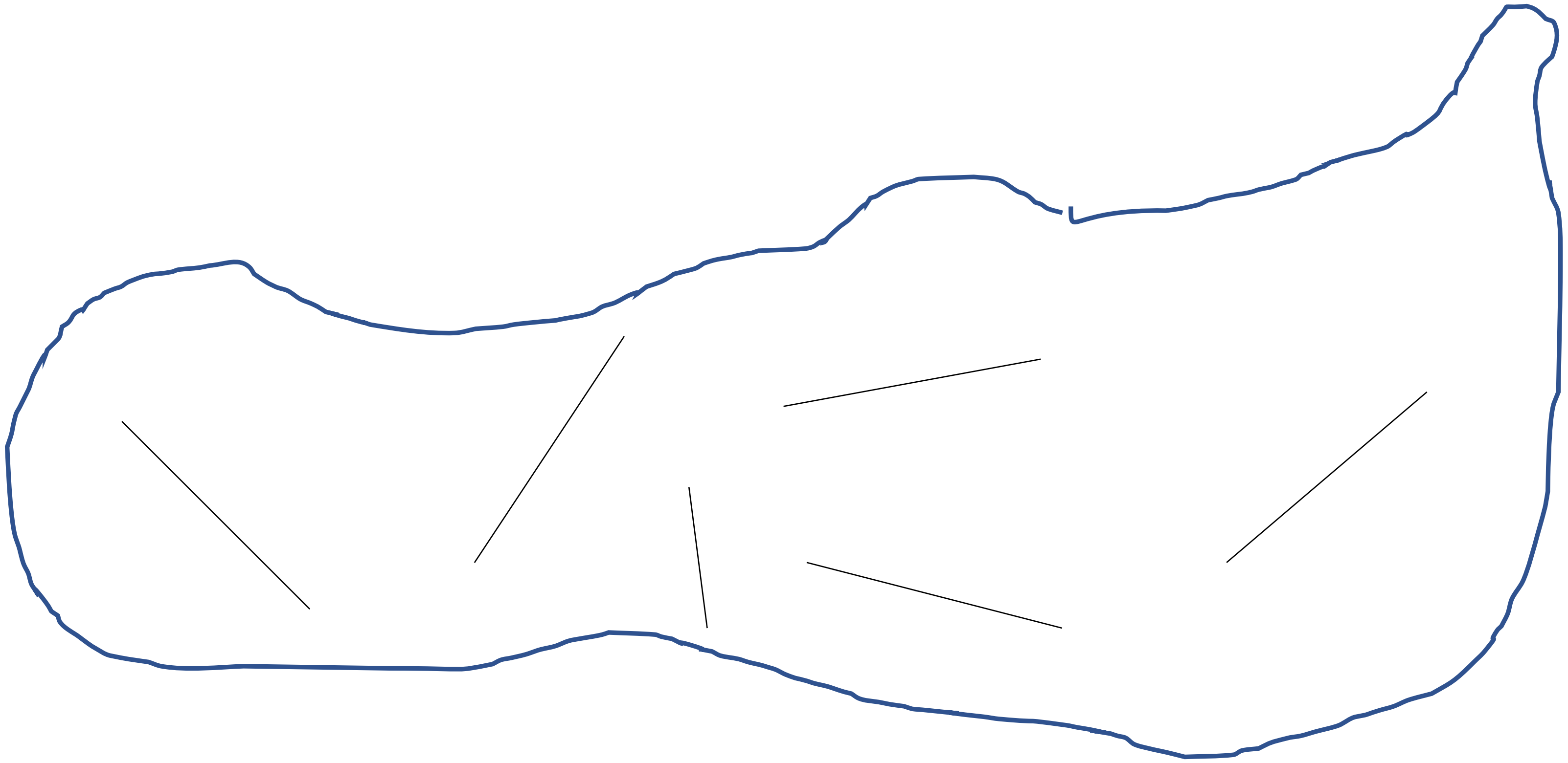
Transect layout: random placement



Equal chance of occurrence for objects at all distances

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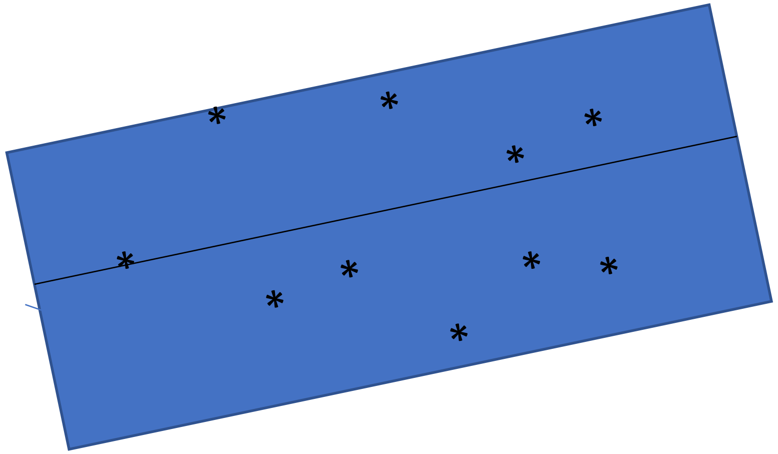
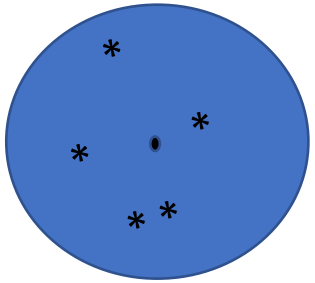
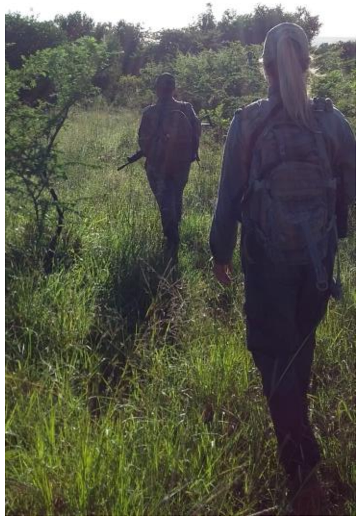
Distance sampling: general study design

- Transects of length L are set out through the study area to be sampled
- Placement of transects should be random with respect to habitat (e.g. vegetation, altitude, etc.) - e.g. roads are often not random
- Transects must not be strigth lines (may be points – point transect and more)







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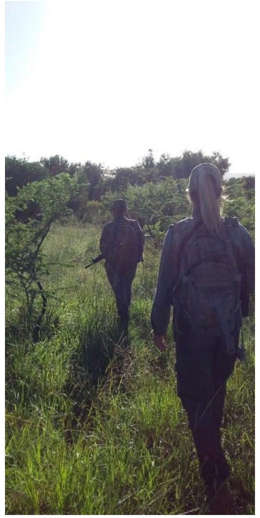
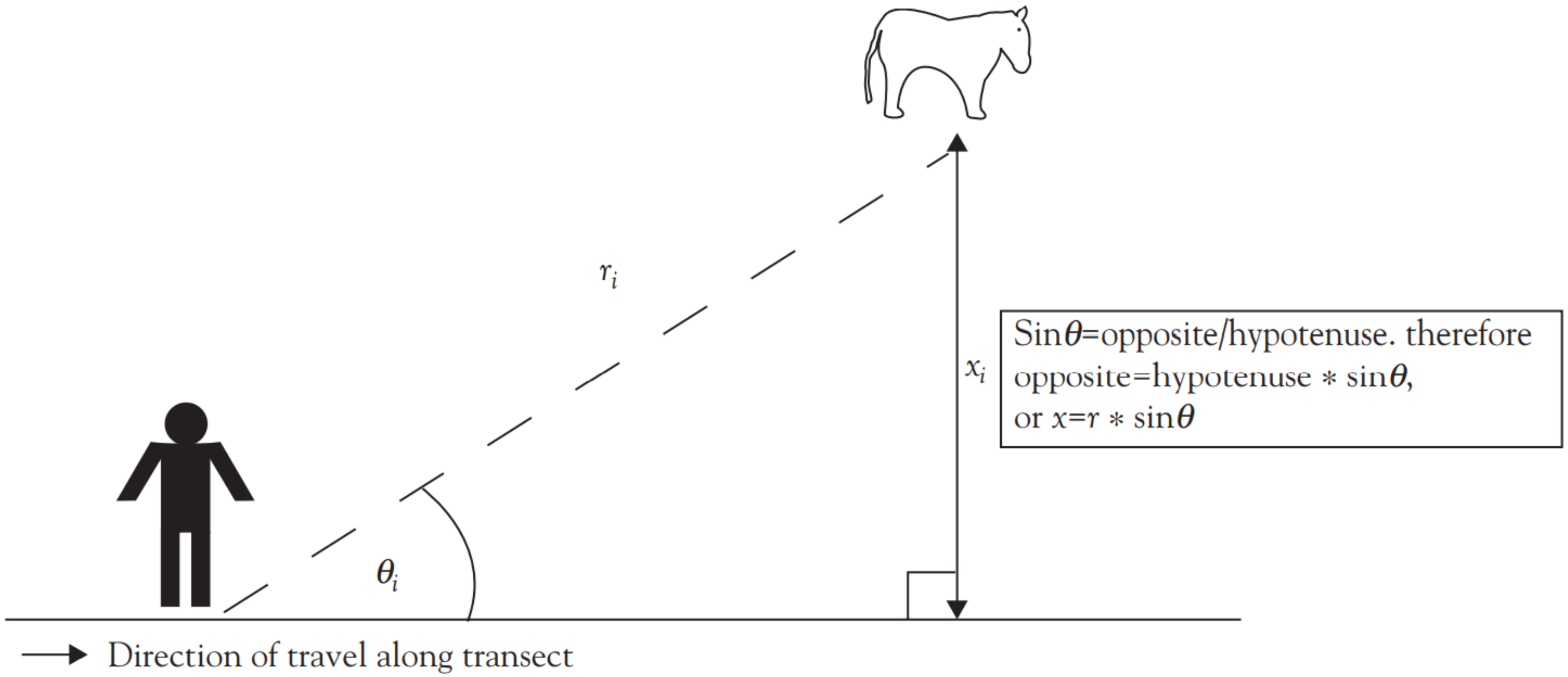
Distance sampling: Approach

- Detectability of objects decreases with distance to the observer
- Record objects along a transect together with perpendicular distance of object to transect line

Objects may be animals, plants, nests…
Objects may occur in clusters



Sighting distance and angle

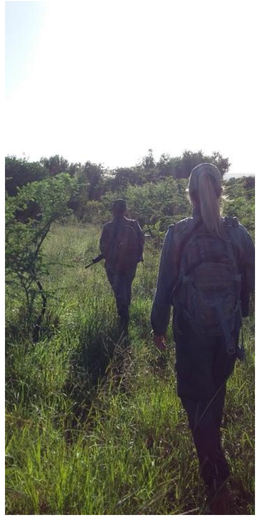


Mills 2006

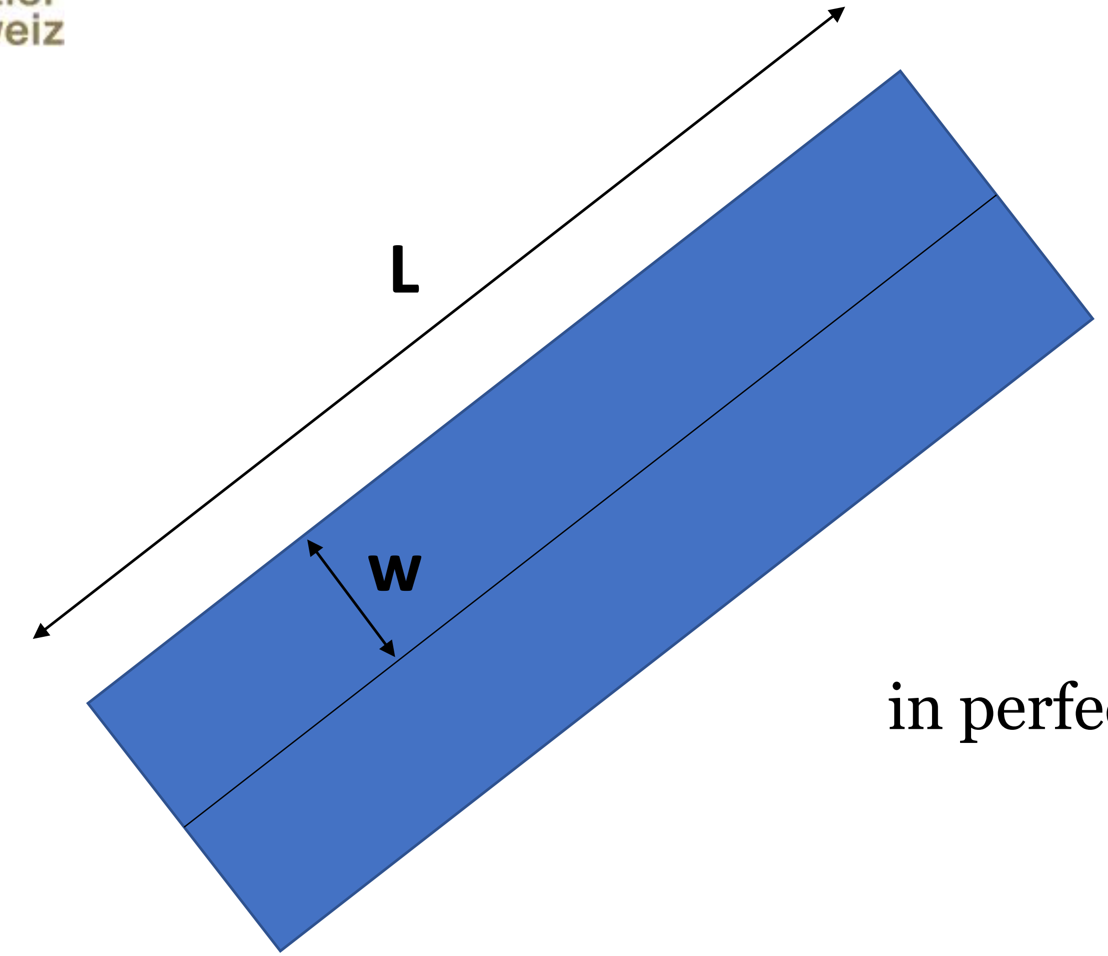
Record the sighting distance (r_i) and sighting angle (θ_i) and calculate: $x_i = r_i \sin(\theta_i)$

Distance sampling: Approach

- Detectability of objects decreases with distance to the observer
- Record objects along a transect together with perpendicular distance of object to transect line
- Model detectability as a function of distance



Perfect detection rectangle



Transect area
A = L2w

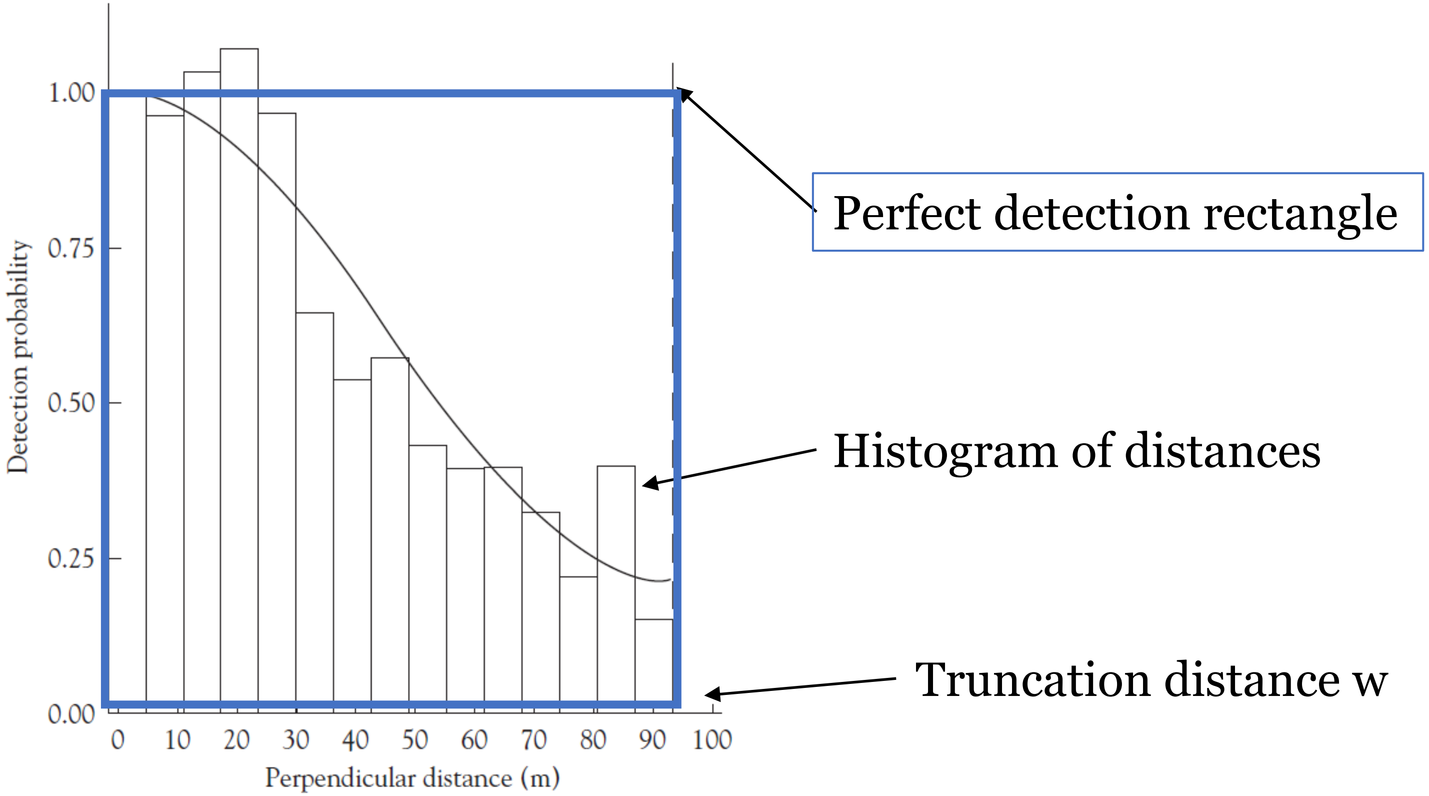
Abundance:
N = n/P
n = counts, (sum of all objects)
P = detection probability

in perfect detection rectangle: P = 1 and
Abundance = N = n
Density = D = n/L2w

Detection function g(x)

Probability of observing an object at a distance x from the transect

Finding a function that models detection probability as a function of distance is a major challenge in distance sampling



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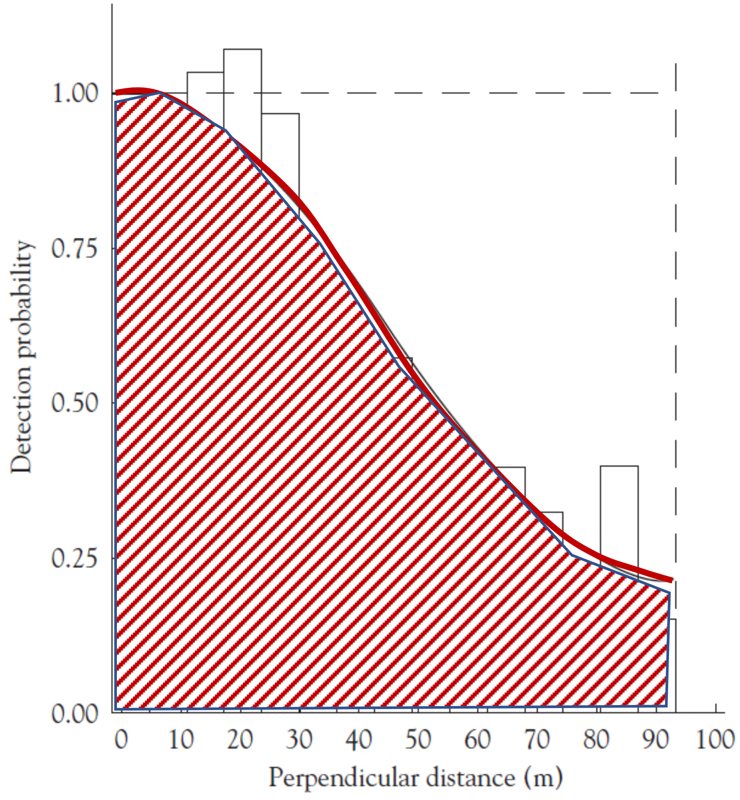
Detection function g(x)

- Fit a **statistical curve** to the data
- Several mathematical functions are fitted and compared – the one that fits the data best is used to estimate g(x)
- Overall detection probability is the proportion of the perfect detectability rectangle under the curve
- Detection probability p_w corresponds to average p across all distances from 0 to maximum distance w:

$$\hat{p}_w = \frac{\left[\int_0^w g(x)\mathrm{d}x\right]}{w}$$



Adding additional variables

Detection probability may be modelled as a function of external variables (e.g. group size, weather, obervers, etc.) → g(x,z); z vector of variables

→ Each observed object is then «inflated» by observation specific detection probability, $p(z_i)$, depending on external variables at each observation

→ Abundance is estimated by summing over all inflated observations

$$N_T = \sum_{i=1}^{n} \frac{s_i}{p(z_i)}$$

N_T = is the abundance over all transects
s_i = are sizes of observed groups (may be always 1)
$P(z_i)$ = is observation specific detection probability as a function of covariates

Miller, BioRxiv, 2021

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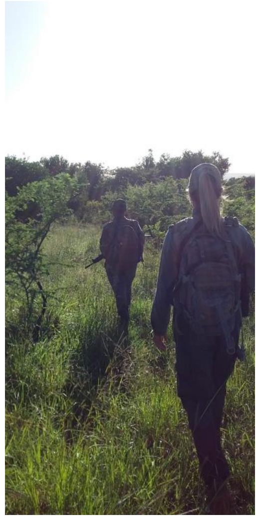
Distance sampling: Approach

- Detectability of objects decreases with distance to the observer
- Record objects along a transect together with perpendicular distance of object to transect line
- Model detectability as a function of distance
- Determine sampling area
- Estimate abundance based on detectability and area sampled



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Abundance and density

Once we know detection probability (p_w) we can correct observed counts (n) to get abundance within transect area (N_T)

$$\text{Abundance } N_T = \frac{n}{p_w}$$

Accounting for total transect area surveyed we can estimate density

$$\text{Density } D = \frac{N}{L2w}$$

Density can be used to extrapolate abundance in total study area

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Distance sampling: Assumptions

1. Individuals (objects, animals) directly on the line will never be missed → p on the line is 100% (can be relaxed).
2. Individuals are located at their initial locations. They do not move before they are sighted → animals are never counted more than once
3. Distances and/or angles are measured and recorded accurately (e.g. using laser range-finders)
4. Sighting of objects are independent events → detection of one object does not influence detection of others (models can accommodate group dwelling species – see next)
5. Random sampling → transects are randomly positioned with respect to the distribution of animals.

Reliability of estimates depends on extent to which assumptions are met!

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Sampling effort

Need sufficient observations (detections) for parameter estimation
– More observations is better!
– Rule of thumb: > 40 detections (at least)

Sampling effort = line length (usually)
– Increasing line length
– Multiple (replicate) lines ← *Usually better!*

How many transects? ← *Do a pilot study to get a good guess of minimum needed!*
– The more transects the better!
– In practice, however, one uses the maximum number (or length) of transects logistically feasible.

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New emerging methods for unmarked populations

Family of N-mixture models (single-, multiple visits)

many different types for sinlge species, multiple species, counts vs presence, temporary emmigration etc.

Random encounter methods (camera traps, acoustic sensors, etc.)

→ Exciting and fast developing fields but still very new and some controversial discussions under way

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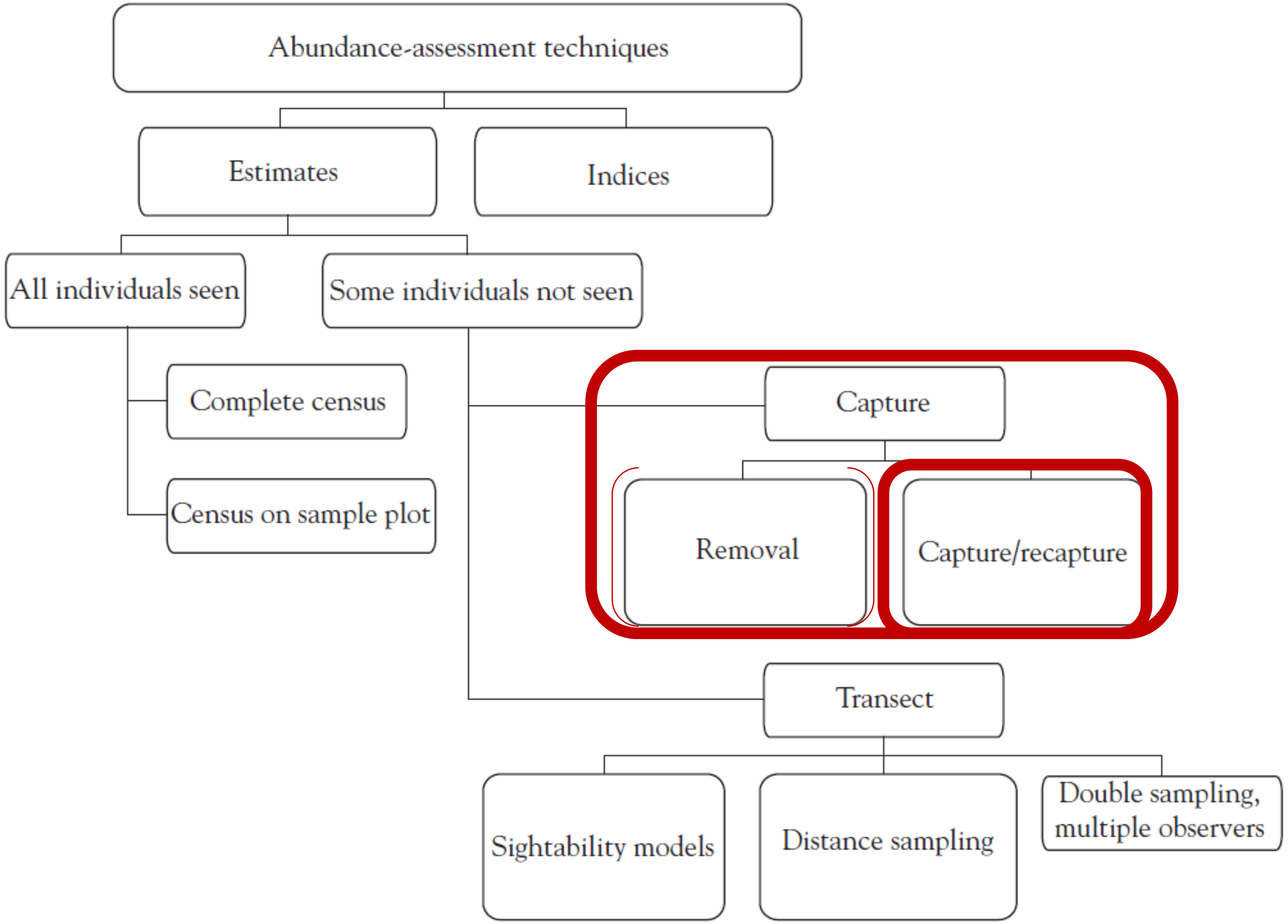
Capture related methods



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Capture – Mark – Recapture methods (CMR)

- One of the most commonly used methods for estimating population parameters (e.g. abundance, survival, recruitment, movement)!
- A sample of the study population is captured, marked, and returned to the population
- The process of CMR is repeated on two or more occasions

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Capture related methods: basic principle

Given that you can recognize some individuals of a population (e.g. tagged or naturally recognizable):

- What is the chance that a recognizable individual gets (re)sighted?
- Depends among other things on how many animals you recognize AND how many there are in total

→ if we know the number of recognizable individuals, the resightings hold information on how many there are, how they survive and reproduce.

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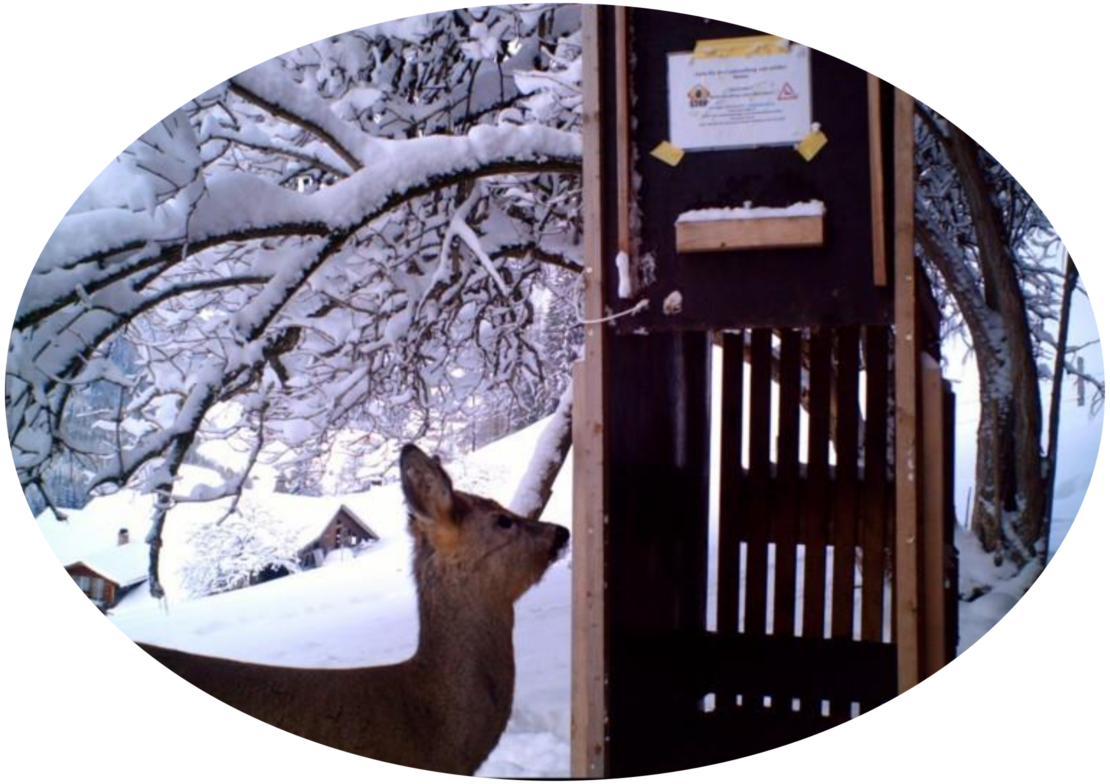
To consider before you start a CMR-based study

- Study design and sampling protocol: How do you design and execute your mark-recapture study?

- Marking methods: How do you mark animals?

- Capture / recapture methods: How do you capture or recapture animals?

- Appropriate Model: Which mark-recapture model to use?



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Choosing an appropriate CMR model

Model choice generally depends on:

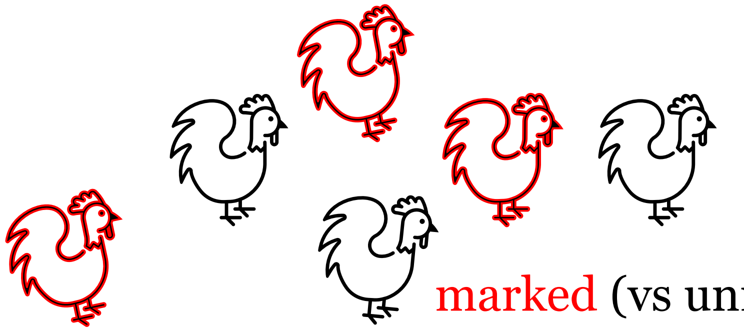
– Study objectives (Abundance only, survival, movement, recruitment?)

– Study organisms

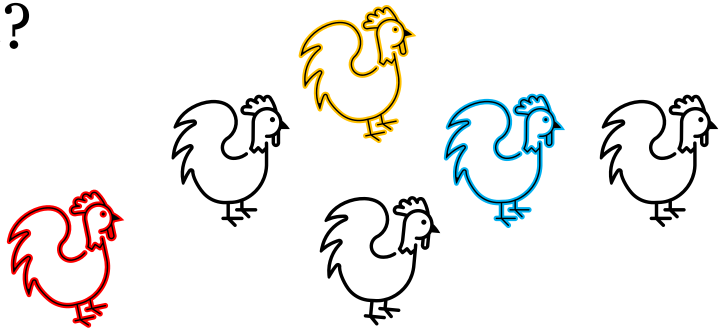
– Closed or open population?

– Time frame: 2 or many (>2) sampling occasions?

– Marked animals individually identifiable?



marked (vs unmarked)



individually marked and identifiable

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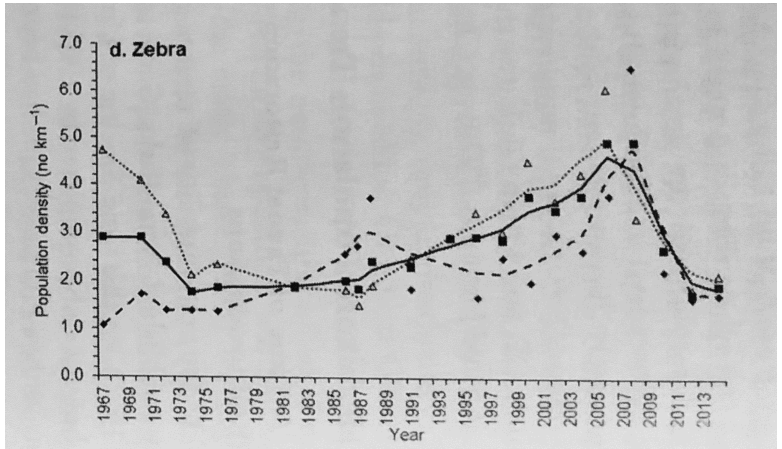
OZI
ERVE
EZEMVELO
KZN WILDLIFE
Mtwazi
Lodge
Hilltop
Camp
HLUHLUWE RIVER
Muntulu
Lodge
Munyawaneni
Lodge
THLYENI
HIDE
HLUHLUWE
R618
BLACK iMFOLOZI
RIVER
iMFOLOZI
BHEJANE
HIDE
SONTULI
LOOP
Sontuli Camp
Gqoyeni Lodge
Hlathikhulu
Lodge
Nselweni
Camp
Nyalazi
Gate
Mpila
Camp
Masinda
Lodge
ngeni
ate
MPHAFA
HIDE
WHITE iMFOLOZI
RIVER
WILDERNESS AREA
- Gate
- Lodge or Camp
- Hide

Capture-Mark-Recapture study

Study goals:

- Drivers of population dynamics?
- Drivers of movement and animal distribution?
- Link between genetic constitution and population dynamics?



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Harem G45 (Mfolozi) — 9 individuals — last seen: 2020-09-23

M388, Stallion, first seen as M A in Sep 2018

M121, first seen as F A in Mai 2018

M122, first seen as F A in Mai 2018

M123, first seen as Unknown Y in Mai 2018, Mother: M122, motherhood to be checked

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Two classes of CMR models

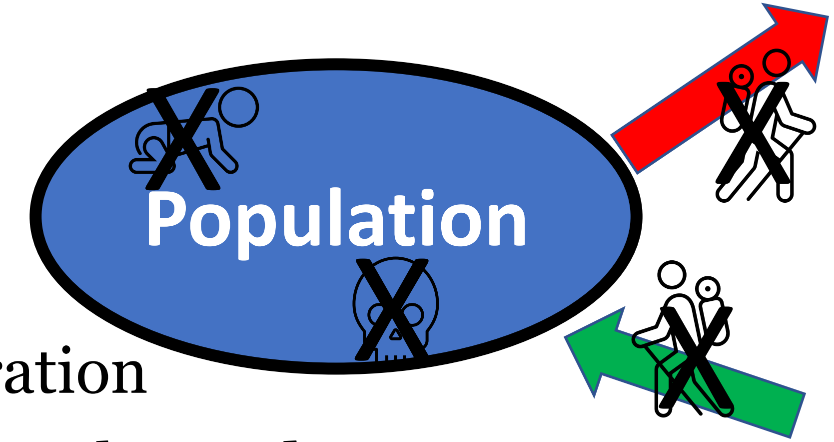
1. **Closed** Population Models:

Assumption of "closed study population"

i.e. no birth, death, immigration, or emigration

population size remains constant during the study

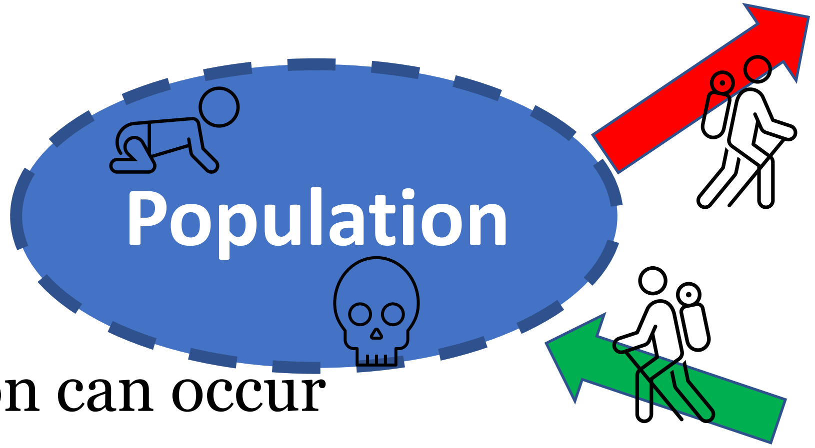
→ usually short periods between capture sessions



For some closed CMR models, you only need to know whether an animal is marked or unmarked.

However, for more rigorous analyses, capture history of each animal (individually recognized!) is needed.

Two classes of CMR models



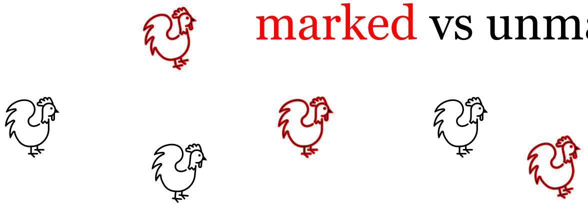
2. **Open** Population Models:

Assumption of "closed population" is relaxed

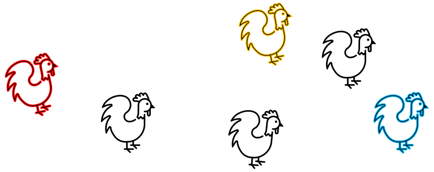
i.e. birth, death, immigration, or emigration can occur

population size can change during the study

You must know the capture history of each animal, i.e. you need to recognize each animal individually, not just whether it is marked or unmarked.



marked vs unmarked

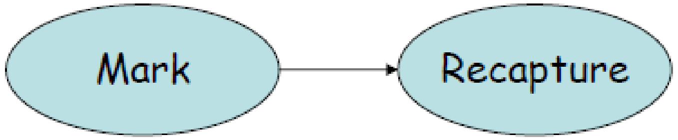


individually marked and identifiable

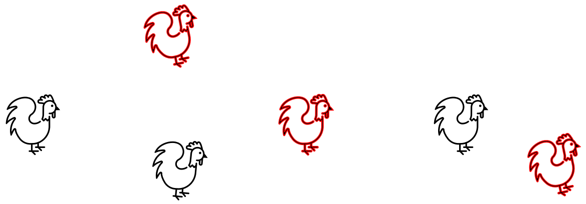
Closed pop. CMR: Lincoln-Peterson (LP) method

LP is the simplest of all closed-population mark-recapture models.

It only requires a single episode of marking, and a single episode of recapturing individuals.



You only need to know whether an animal is marked or unmarked.



Closed pop. CMR: Lincoln-Peterson (LP) method

A random sample of the population is captured, marked, and released back to the population.

After a complete intermixing, a second random sample is taken.

Remember:

$$\text{Abundance estimate (N)} = \frac{\textit{Count of animals}}{\textit{Estimated probability of detection}} = \frac{C}{p}$$

→ For the LP estimator: in the first sampling period, animals are counted and in the second, detection probability is estimated.

Closed pop. CMR: Lincoln-Peterson (LP) method

In the first sampling period animals are counted in the second period probability of detection is estimated.

$$\hat{N} = \frac{n_1}{\hat{p}} = \frac{n_1}{\left(\frac{m_2}{n_2}\right)}$$

proportion of animals marked compared to unmarked animals

$$\hat{N} = \frac{n_1 n_2}{m_2}$$

N: Abundance

n_1: animals captured and marked in first sampling period

n_2: animals captured in second sampling period

m_2: marked animals recaptured in second sampling period

Closed pop. CMR: Lincoln-Peterson (LP) method

LP estimate is biased: it tends to underestimate the population size.

Thus, LP estimator is adjusted:

$$\hat{N} = \left[\frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} \right] - 1.$$

This is more relevant for small sample sizes

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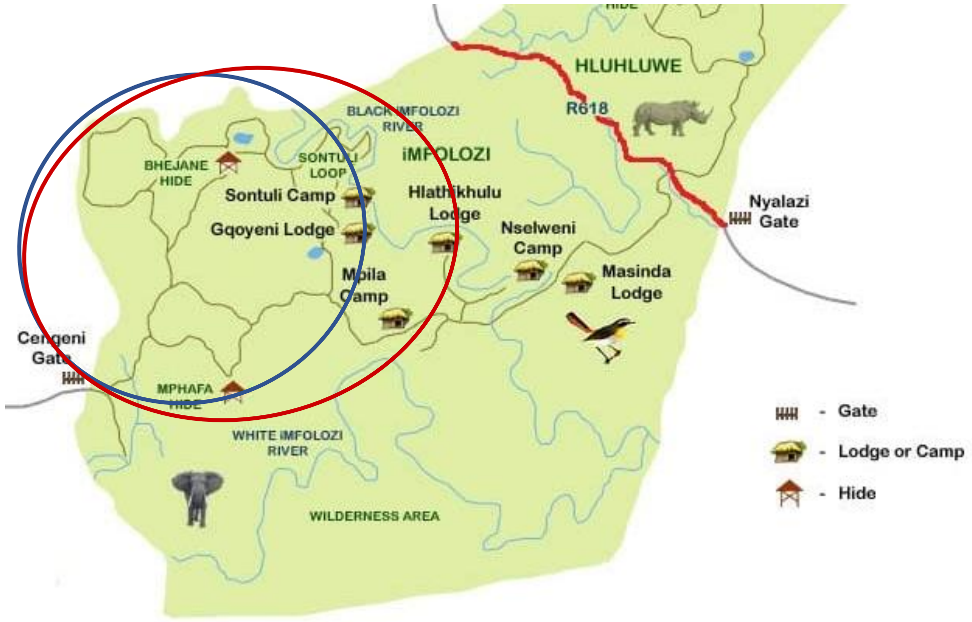
Example of unbiased LP method

Goal: Estimating abundance of zebras in Mfolozi NP, SA based on 3 x 5-day sampling periods.

→ 1.3.23 – 5.3.23

→ 13.13.23 – 17.3.23

→ 4.4.23 - 8.3.23



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Example of unbiased LP method

1st survey

First sampling: 106 zebras captured and marked (= n_1)
Second sampling: 152 zebras (= n_2)
of which 63(= m_2) were resightings
→ naive P(detection) = 63/152 = 0.41

Estimated population size:
N = [(106+1) * (152+1)/(63+1)] - 1
= 255 zebras

Example continued – Second survey

Second sampling: 152 zebras captured and marked (= n_1)

third sampling: 120 zebras (= n_2)

of which 43(= m_2) were resightings

→ Naive P(detection) =43/120 = 0.36

Estimated population size:

N_2 = [(152+1) * (120+1)/(43+1)] - 1 = 420 zebras

Assumptions of LP estimator

- Closed population → No birth, death, immigration or emigration during the interval between the first marking period and the subsequent recapture period
- Equal catchability → All animals are equally likely to be caught within each capture period
- No effect of marking → Marking individuals does not affect their catchability
- Animals do not lose marks
- All marks are seen and recorded

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Violations of assumptions

Three ways equal catchability assumption can be violated:

Time: Capture probability may differ due to seasons, weather, moon phase etc.

Individual heterogeneity: different animals differ in capture probability → e.g. sex, age, dominance status, placement of trap, etc.

Behavioral response to trapping: trap happy or trap shy animals. Some will not be captured any more, others learn that trapping does no harm and may even give them shelter and food

Example continued – compare two LP estimators

1st servey: $95\%CI = 255 \mp 30.07$ → between 225 and 285 zebras

2nd servey: $95\%CI = 420 \mp 82.77$ → between 337 and 503 zebras

→ Large difference – why?

- p_t was accounted for & similar → 0.36 vs 0.41
- non-standardized sampling
- p_h may have been different – e.g. groups differ in detection
- non-independence between p of same group members

Example continued – account for grouping

Alternative approach – estimate group abundance and augment by group size – group as the sampling unit

1st servey: between 28 and 44 groups (ϕ_1 = 36)

2nd servey: between 35 and 71 groups (ϕ_1 = 53)

Augment by mean group size of 4.9 zebras →

176 (137/216) vs 259 (172/348) zebras

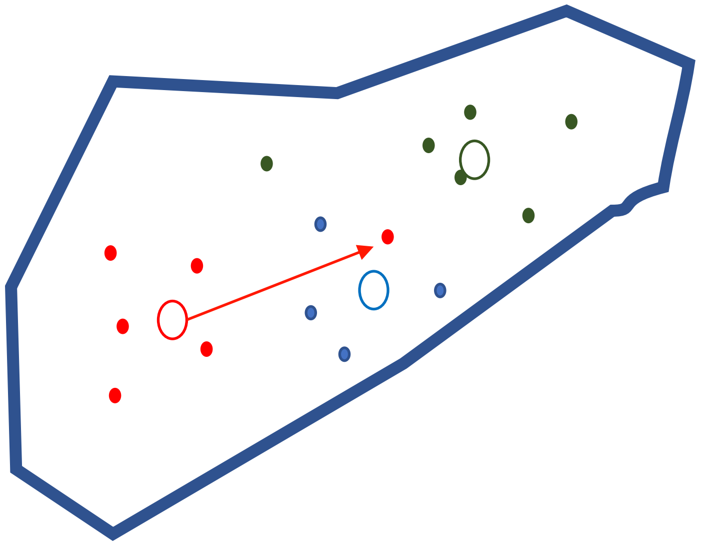
→ More formal: ML framework estimating group & individual abaundance simultaneously

Spatial capture-recapture models

Estimates activity centers for individuals or groups from capture data

Models capture probability as function of distance to activity centers

Deal with heterogeneity in capture probability due to spatial distribution of individuals/groups relative to capture area



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Violations of assumptions: solutions

- Using different methods for mark and recapture (mark-resight) can improve issues of capture response or heterogeneity in catchability.

- Closed population models with **more than one** capture period allow relaxing and testing for equal catchability assumption of LP estimator.

- Build different models and test which model fits best to the data using a probabilistic framework – maximum likelihood estimation

→ *individual capture histories are required!*

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Wildtier Schweiz

Extending LP estimator (more than one capture)

Closed population models with **more than one** capture period allow relaxing and testing for equal catchability assumption of LP estimator

Candidate models:

M_o: equal catchability – Null model!

M_t: Time variation – p_t for each capture period

→ Simple extension of LP where for each capture period a different capture probability is estimated

For M_0 and M_t individual capture histories are theoretically not required
But testing equal catchability or time variation against other models using maximum likelihood estimation requires individual capture histories

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Extending LP estimator (more than one capture)

Closed population models with **more than one** capture period allow relaxing and testing for equal catchability assumption of LP estimator

Candidate models:

M_h: Individual heterogeneity (animals differ)

M_b: Behavioral response (trap happy, trap shy, etc.)

Combinations of models are possible, i.e. $M_{tb,}$ M_{hb}, M_{ht}, M_{thb}

For each model parameters N (population size) and p (capture probability) are estimated and the model that best fits the data is chosen

Modelling capture probability using capture histories

Individual capture histories for three sampling (capture - recapture) periods:

1: Animal was captured **with probability p**
0: Animal was not captured **with probability (1-p)**

[1,1,1] – capture every time

[1,0,0] – capture first time only

[1,0,1] – capture first and last time

etc…

→ for three periods there are $2^3 = 8$ possibilities

Modelling capture probability using capture histories

Each capture history has a probability of occurence under a given model

For model M_0

[1,1,1] → p^3

[1,0,0] → $p \times (1-p)^2$

[1,0,1] → $p \times (1-p) \times p$

Modelling capture probability using capture histories

Each capture history has a probability of occurence under a given model

For model M_t

$[1,1,1] \rightarrow p_1 \times p_2 \times p_3$

$[1,0,0] \rightarrow p_1 \times (1-p_2) \times (1-p_3)$

$[1,0,1] \rightarrow p_1 \times (1-p_2) \times p_3$

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Modelling capture probability using capture histories

Information on capture history for each animal can be used to test different models (e.g. M_h, M_b, M_{hb}, etc.)

Question: What is the likelihood (L) to observe parameters p (capture history) and N (abundance) given the data ($\{x_w\}$; capture histories)

→ $\boldsymbol{L(N, p | \{x_w\})}$

Maximisation approaches used to solve for p's and N

(→ maximisation for animals never seen and derive N)

Transects revisited : multiple observer method

Estimate β and N from from animals missed or observed by two or more observers

Two types of methods:

- Independent method: observers count same animals simultaneously

- Dependent method: observer 2 only counts animals missed by observer 1 – observer 1 & 2 switch roles

We won't discuss this approach today

Transects revisited : multiple observer method

Independent method:

animals detected by one or both observers can be identified

Detection probability and abundance are estimated using **capture-mark-recapture estimators**

Estimating number of blue sheep in Annapurna

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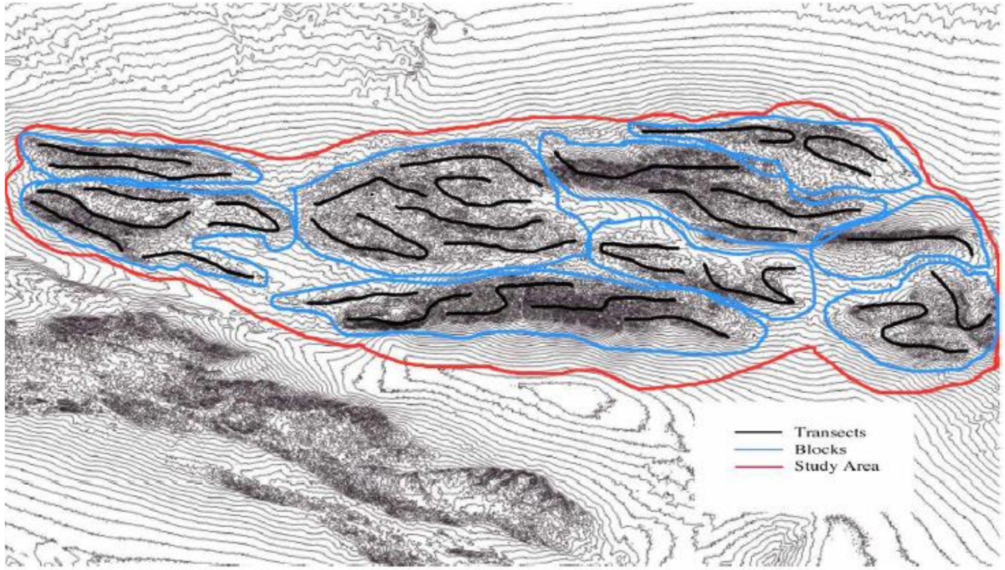
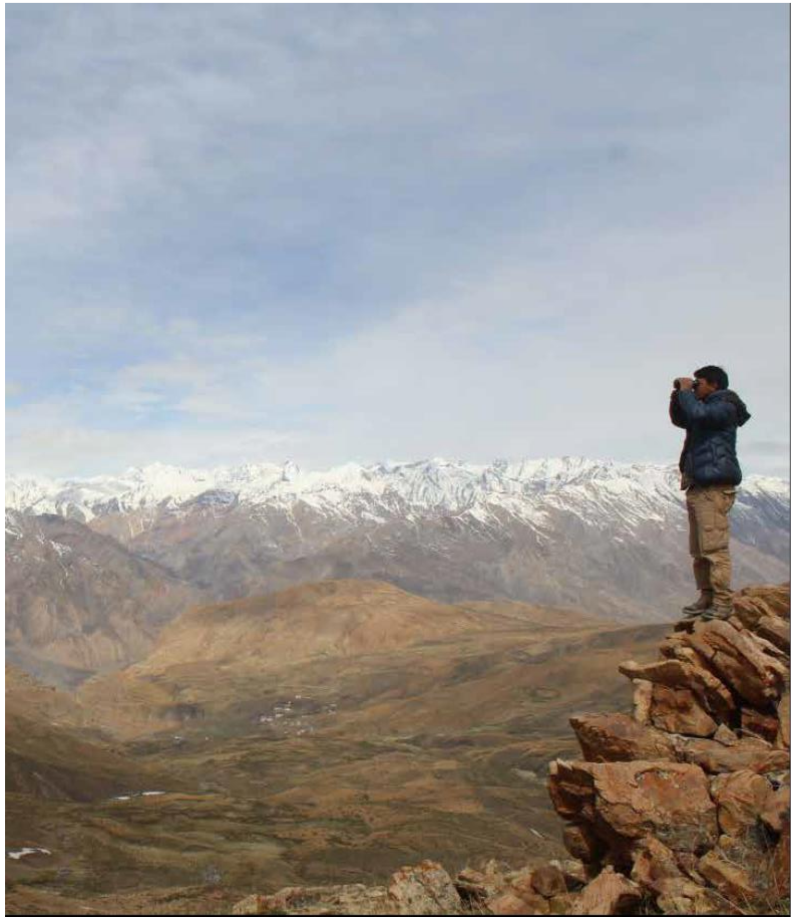
Estimating number of blue sheep in Annapurna





Double observer survey manual 2020

Estimating number of blue sheep in Annapurna

Independent double observer method:

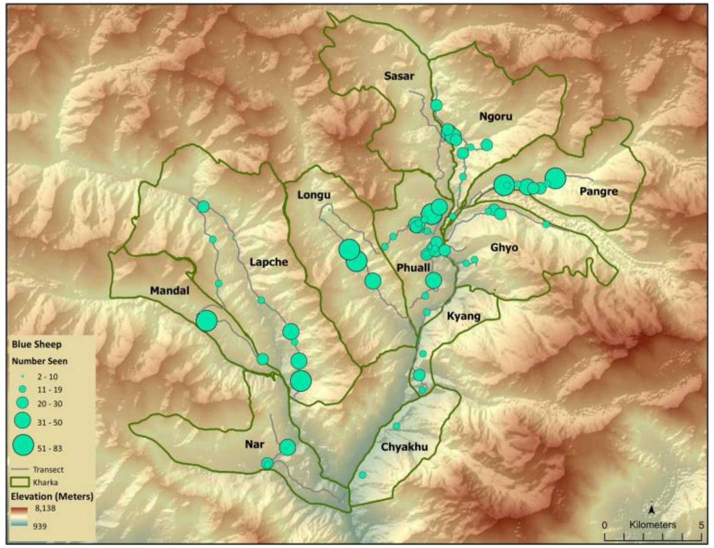
G → total number of groups

B → groups seen by both observers

S1 → groups seen only by first obsevrer

S2 → groups seen only by second observer

μ → mean group size



$$\frac{B}{G} = \frac{(B+S_1)}{G} \cdot \frac{(B+S_2)}{G} \quad \Rightarrow \quad \hat{G} = \frac{(B+S_1+1)\,(B+S_2+1)}{(B+1)} - 1 \quad \Rightarrow \quad \hat{N} = \hat{G}\hat{\mu}$$

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Double observer method

Assumptions:

- All animals have same p (may be relaxed with >2 observers)
- No observer bias

Animals counted by one or both observers must be identifiable (e.g. GPS location of each animal observed, tagged)

To estimate density, one must be able to estimate effective area of the site sampled.