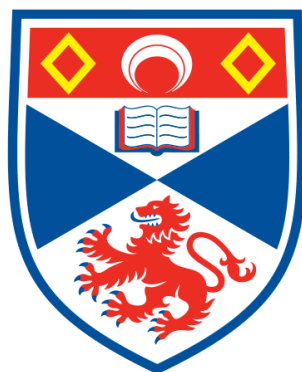


Comparisons between double-observer mark-recapture methods and 2-dimensional linear transect methods for estimating animal demographics

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A dissertation submitted for the degree of MSc
at the University of St Andrews



2025

Original code underpinning this dissertation can be found here:

https://github.com/ncalbyr/Diss_2025

Code and data which underpin the 2-dimensional method and are the product of previous writers can be found here: <https://github.com/david-borchers/LT2Dcal>

Declarations

1. Candidate's declarations:

I, NOAH CALVIN BYRNE, hereby certify that this thesis, which is approximately _____ words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a taught postgraduate student at the University of St Andrews as a candidate for the degree of MSc (taught) in August, 2024.

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2. Supervisors' declaration:

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Introduction

Effective study of animals often requires knowledge of animal abundance. Understanding abundance is connected to many other ecological characteristics such as the density of animals, habitat use, and spatial distributions. Many methods exist to accurately estimate animal abundance, all with different frameworks and assumptions. One broad category of methodology is mark-recapture. These methods rely on multiple observations and individual identification on animals to estimate abundance.

One specialized application of mark-recapture is the double-observer method, requiring two observers to walk a transect and record information on the target species of animal. These two observers however walk the same transect at different times. This introduces the possibility for animals to move between the two observation occasions. Because there are two occasions, the two observers must also use their respective data sheets to determine if they observed the same animals. This introduces a second element of imperfect identification.

A possibly better alternative to this double-observer approach is the 2-dimensional linear transect method proposed by Borchers & Cox (2017). This method only requires one observer to make a pass of the transect. This is because the 2-D method incorporates forward distance to the animal as well as perpendicular distance.

With the use of primate data, I have been able to simulate both forms of survey: double-observer and 2-dimensional linear transect. Through simulation I have also produced estimates of density and abundance from each of these models, which has been compared to the known or *true* density/abundance of this surveyed system. With bias I have been able to determine the effectiveness of each method at estimating the number of animals in this system, and point to possible reasons for why they may not estimate effectively.

Methods

a. Mark-Recapture

Mark-recapture is one of many methods to estimate animal abundance in the field of ecology. It requires more than one sampling occasion to work. Each occasion can be described as a “sampling event”. On the first sampling event, animals are captured (either invasively or non-invasively) and marked in some way. If the species being studied have unique individual markings already on them, such as may be the case for patterned species like cheetahs, then the process of capture and marking is simple. Record an observation of this animal and assign identification to them based on their unique markings. If, however, the individuals of a species are not easily discernable from each other then these animals must be physically restrained and marked with one of many options. Possible marking items include leg bands (often for birds), filing hard structures (used on turtle shells), injecting fluorescent ink under the skin (used with fishes), or simply painting the animal in some way; these are just a few possibilities.

Now with the animals marked on occasion 1, and some system in place to recognize individuals based on these markings later, the animals are released and occasion 1 ends. Then on the second and all subsequent occasions, animals are again captured. Unmarked captures will be marked and assigned an ID linking them to that trapping occasion; this is only if there are more capture occasions to follow. All marked animals that are recaptured are recorded for that occasion as well.

i. Lincoln-Petersen Method

To actually generate an estimate from mark-recapture data requires computation. A common method is to use the Lincoln-Petersen Estimator to calculate estimated abundance. The origin of this work goes back to a paper written by C.G.J. Petersen in 1896, studying fish migration. However, it wasn't until 1930 that Frederick C. Lincoln would publish a paper on waterfowl abundance and add to Petersen's work. These two combined efforts would later lead to what is now known as the Lincoln-Petersen method. The estimator that comes from this methodology only requires *one* marking occasion and *one* capture occasion. The marking occasion (*first* occasion) is when all captured animals are marked. The capture occasion (*second* occasion) is when all *re*-captured animals are recorded.

Lincoln-Petersen Estimator:

$$\hat{N} = \frac{M * n}{x}$$

- \hat{N} = estimated abundance
- M = number of animals marked (during the marking occasion)
- n = total number of observations
- x = number of marked animals captured (during the capture occasion)

(Strandgaard 1967)

A benefit of this estimator is its simplicity in only requiring one of each occasion. No further animals need to be marked after the marking occasion. A key flaw of this estimator is that it is positively biased, meaning it often overestimates animal abundance. This is particularly the case with small populations.

ii. Chapman Estimator

This is a modification of the previous Lincoln-Petersen Estimator.

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

- n_1 = number of animals marked on occasion 1
- n_2 = number of animals marked on occasion 2
- m_2 = number of animals marked on *both* occasions

(Chapman 1951; Borchers et al. 2002)

The Chapman Estimator should always be unbiased when $n_1 + n_2 \geq \hat{N}$ and approximately unbiased when $n_1 + n_2 < \hat{N}$. This highlights an assumption in the Chapman Estimator, which is that all detections are homogeneous (all animals are equally likely to be captured). When the Chapman Estimator is used with data showing homogeneous detectability, the estimate is approximately unbiased. If however the estimator is used with data expressing heterogeneous detectability, the estimates produced will be significantly negatively biased. (Borchers et al. 2002)

iii. Transects

The two main kinds of transects are point and linear. In point transects, observers stand at a set of coordinates and survey the area around them in a circle. A collection of point transects on a map appears as a collection of circles (representing surveyed area) each with a point centered at the middle (the location from which the observer surveyed). In linear transects an observer walks along a straight-line path of some predetermined distance and records animals in front of them. Animals behind the observer in this case are assumed either already surveyed or not present. A map of linear transect plots will look like a series of rectangular strips (representing surveyed area) each with a line centered down the middle of it (representing the path the observer took). The outer boundaries of these circular or rectangular plots are determined by the range animals can be detected at. This would be referred to as radial or perpendicular distance truncation. This defines a detectability window around the observer. The methods below both use linear transects.

The observer(s) in the case of line transects are assumed to be travelling at a constant speed. Their window of detectability travels at the same speed, and thus moves with the observer.

iv. Double Observer Method

A field survey design that implements mark-recapture is the double-observer method. In this survey, two technicians will walk along a predetermined line transect and record observations of animals as they go. The distinction is that the two technicians travel the transect at different times and record what they saw. This introduces new variability to account for, namely how do the two technicians know if they saw the same animal. And, can animal movement between detections bias the estimate of abundance this method produces.

b. 2-Dimensional Linear Transect

The 2-dimensional linear transect (LT2D) is a more comprehensive alternative to conventional distance sampling (CDS). LT2D methods in particular are meant to be free of the assumption in CDS that there is a known uniform distribution of animals. This assumption fails in any scenario where transects cannot be placed randomly, such as is the case when observers must stay on pre-determined trails in their survey area. This was the case with the primate data, in which observers were restricted to jungle paths. (Borchers & Cox 2017)

In LT2D methods both perpendicular distance and forward distance from the observer to the animal is recorded. The distance at which an animal can be detected however is not unlimited. This

practical limit is referred to as the truncation distance, and it is the threshold beyond which animals cannot be detected. Or, conversely it is the distance at which animals can *begin* to be detected. It can also be referred to as the *time until detection*. It is a characteristic which allows the model to no longer require the first assumption of CDS: having a known uniform distribution of animals. A CDS method with time until detection incorporated also behaves as a removal model, where “removal” is interpreted in this study as “detection”. These removal models not only are free of the first assumption about uniform distribution, but they also are free (to some degree) of the second assumption that detectability of animals on the line is 1. This is because when forward distance is truncated, animals may be on the line but still far away and beyond the detectable window.

i. Detection Probability (Hazard Functions)

While animals can *begin* to be detected at certain distances, the probability of detection varies by distance. Specifically, as distance from the observer increases, detection probability decreases accordingly. Detection probability can be manually built into the 2D model by using hazard functions. These functions determine *how* detection probability changes *over time*. It is not a simply linear change but rather a curved line relationship with parameters to adjust its shape. A hazard-function is a more specific type of half-normal function which describes survival time, or time until death. For the purposes of this study, “death” can be interpreted as detection. A typical hazard-rate curve will increase in magnitude as it moves away from $x = 0$, showing how over time individuals are more likely to “die”, or be detected. In this study, detection needed to be highest *on* the transect line (where $x = 0$) so an inverse power hazard detection function was used. Using a hazard function as a detection probability allows the user to specify the distances at which detection probability can be 1, always detected. Now since removal models don’t *require* detectability to be 1 at distance 0, the hazard function can specify otherwise but full detectability on the line is still *allowable*. Hazard functions curves have adjustable shoulders and steepness. The shoulder can represent for how long (at which distances closest to the line) animals remain completely detected. After a certain distance the shoulder drops off and the line steepens, representing *how* detectability declines with distance.

ii. Detectable Distances

Because the observer in LT2D methods is moving at a consistent speed, it is found to be more useful to use forward detection distance instead of time until detection (Borchers & Cox 2017). This detection box is formed by the two truncation distances. Maximum detectable distance in the perpendicular direction is 0.03 km, and maximum detectable distance in the forward direction is also 0.03 km. Effectively, any animal within this 0.03 km by 0.03 km box around the observer is *available* to be detected, however detectability still declines by distance.

Real Data

c. Primate.dat

Collected from a line transect survey in which animals are known to avoid the transect, this primate data contains the perpendicular and forward distances to primate detections from one occasion.

This data, as is, can be inputted into the LT2D framework to produce density estimates. For the double-observer estimation this data needs to undergo movement to a second occasion. Knowing the avoidant behavior towards the transect also allows us to assume the initial distribution of these animals before detection; complimentary half-normal.

The survey used to collect the primate data is also an example of non-random line placement. Due to the forested nature of the area, observers had to place line transects along existing paths in the jungle. Again, a reason why CDS is not a suitable method of estimating abundance for this data and survey design.

Noting that there is no information provided in the primate data about dimensions of the survey, arbitrary values have been set for area and transect length. In this case 100 km

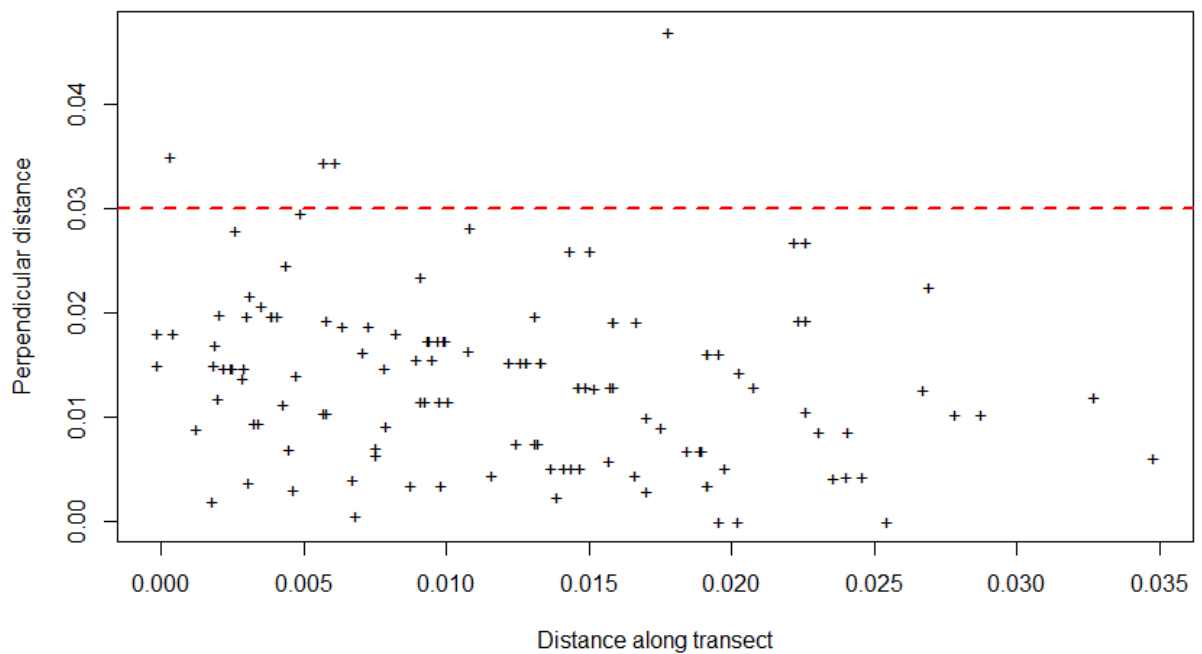


Figure 1: Initial locations of original primate data

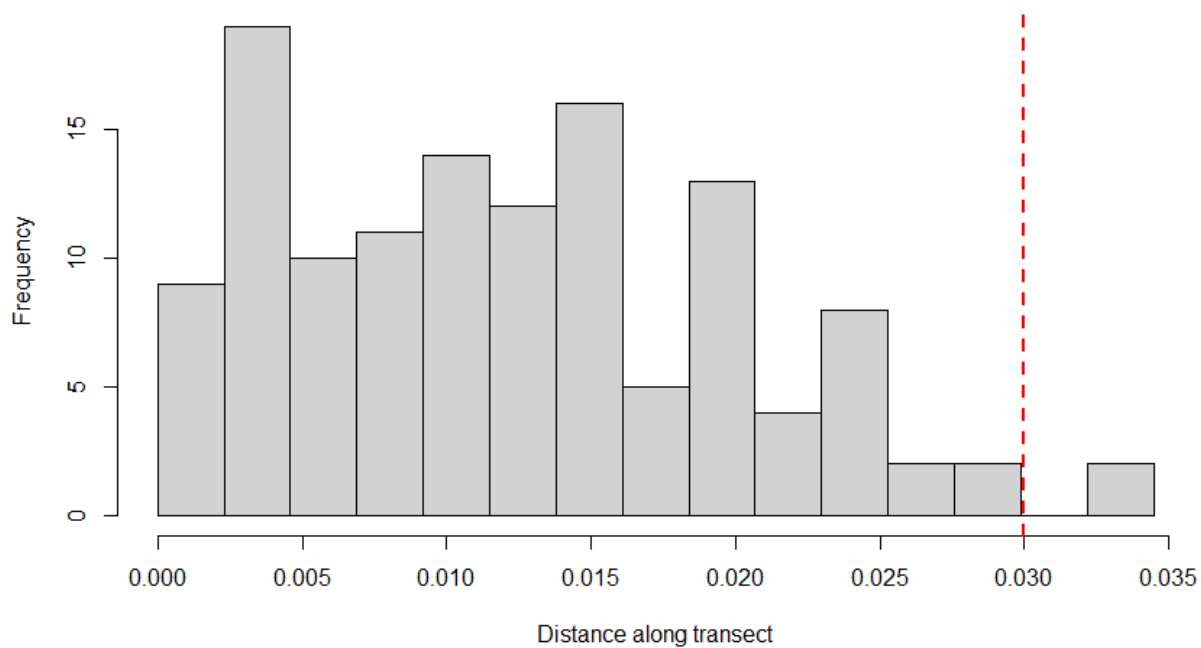


Figure 2: Frequencies of animal occurrences at forward distances

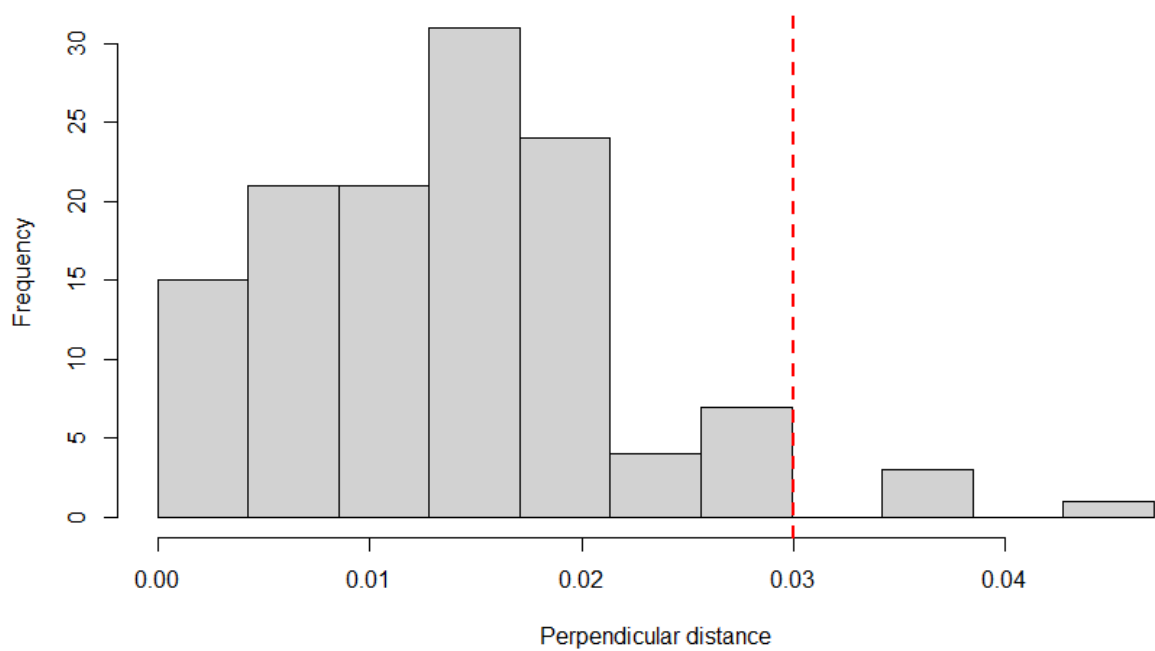


Figure 3: Frequencies of animal occurrences at perpendicular distances

d. Real Data Results

With this collected primate data, the LT2D method estimated a density of approximately 34 animals per 6 km² and a total of 3,445 animals in the whole region. Using the Chapman estimator, the double-observer method produced a density estimate of approximately 21 (with a confidence interval of 19.53 to 21.68). This corresponds to a total abundance estimate of 2,100 animals in the region.

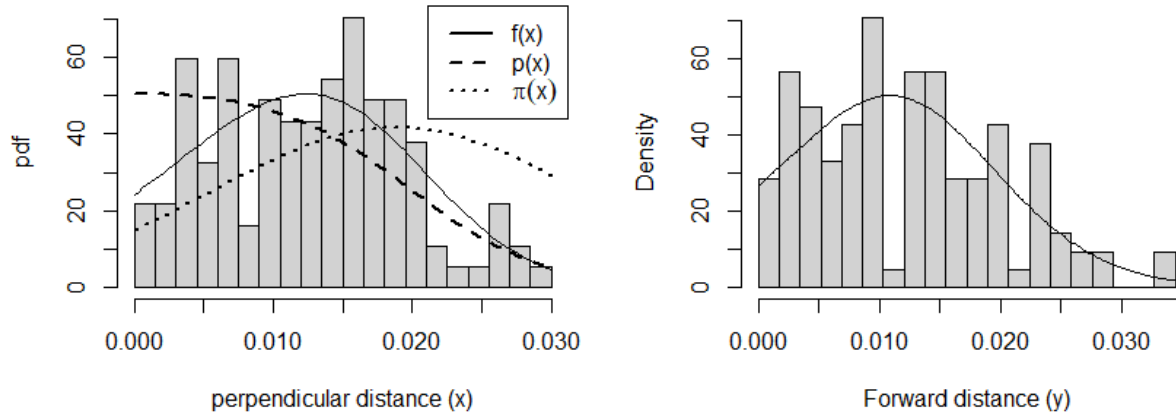


Figure 4: Probability distributions for detection function ($p(x)$) and initial distribution($\pi(x)$), and forward distance distribution of the original primate data.

Simulation

Taking the framework of the original data and reiterating it through simulation is an excellent way to further test the limits and functionality of these methods. It is also necessary as the double-observer method *cannot* be tested with the original primate data. Of course this is because the original data only contains perpendicular and forward distances to the animal from the observer. That is enough information to estimate abundance with the LT2D method, but since mark-recapture requires multiple sampling occasions, movement between those occasions, and matching animals amongst occasions, there is simply not enough information in the existing primate data to support this.

The steps to this simulation first begin with new data. Taking a sample of new perpendicular distances from the original distribution of primate perpendicular distances is the first step. This perpendicular (x) data is applied to a detection function deciding which are seen based on truncation and a hazard detection function. All detected x -values are given forward distances, and now an occasion 1 exists. The data must undergo movement (three possible types to explore later) and arrive at a second location representing occasion 2. Detection is once again carried out and the resulting data is a record of animal locations at two different times, and whether or not they were detected there. Using the distances between all pairings of animals from opposite occasions, mismatching is decided. The mismatching process is meant to introduce practical error to this model, as observers do not truly know if they saw the same animal as each other.

e. Occasion 1: Data Generation and Detection

To simulate new data that behaves like the existing primate data, use the log-phi parameters of the perpendicular distribution of “primate.dat”. These values describe the initial distribution of animals ($\pi(x)$). These parameters are obtained from the process of fitting “primate.dat” to the LT2D model. In the output of the fitted object there is log-phi 1 and log-phi 2. Generate a distribution of values that use these two parameters, and do so within dimensions of space similar to, or slightly larger than, the detection window.

From this distribution, 210 perpendicular distances were sampled. These distances were put through a hazard rate detection function. Just like the log-phi values, the parameters for the hazard function are generated by the fitted object for the original primate data. These two parameters are beta 1 and beta 1. They describe how long animals are perfectly detected for, and how quickly detection declines with distance beyond that point. Every detected point is given a forward distance. The final output of this step is a record of x (perpendicular) and y (forward) distances for each animal out of the 210 that was detected. Therefore the number of rows in this record will be less than 210.

f. Occasion 2: Movement and Detection

To produce a second occasion, the x and y data from Occasion 1 must be moved in some way. There are three different forms of movement to test here: avoidant, random, and no movement. Avoidant movement is in relation to the transect, so it moves animals away from the transect line. To replicate avoidant movement, animals can only travel in a direction *away* from the transect line and for a certain distance. Animals are most likely to travel in a perfectly perpendicular direction away from the line, and as the angle of movement decreases from 90 degrees the probability of an animal movement at that angle also declines. The magnitude of distance travelled is determined by how far a distance is from its origin. This means that while animals move away, the probability of them moving farther and farther away declines with increasing distance. So most animals won't travel an unreasonable distance away and leave the survey altogether.

Random movement is easier to generate as the animals are equally likely to travel in any direction, only the magnitude of distance travelled needs to be limited. This is done the same as with avoidant movement. Of course “no movement” doesn't require any of these previously mentioned steps, but this option is left in as a point of reference to compare estimates of these models later on. In the case of “no movement” there is effectively perfect matching, because the minimum threshold for matching with any degree of error is more than 0.

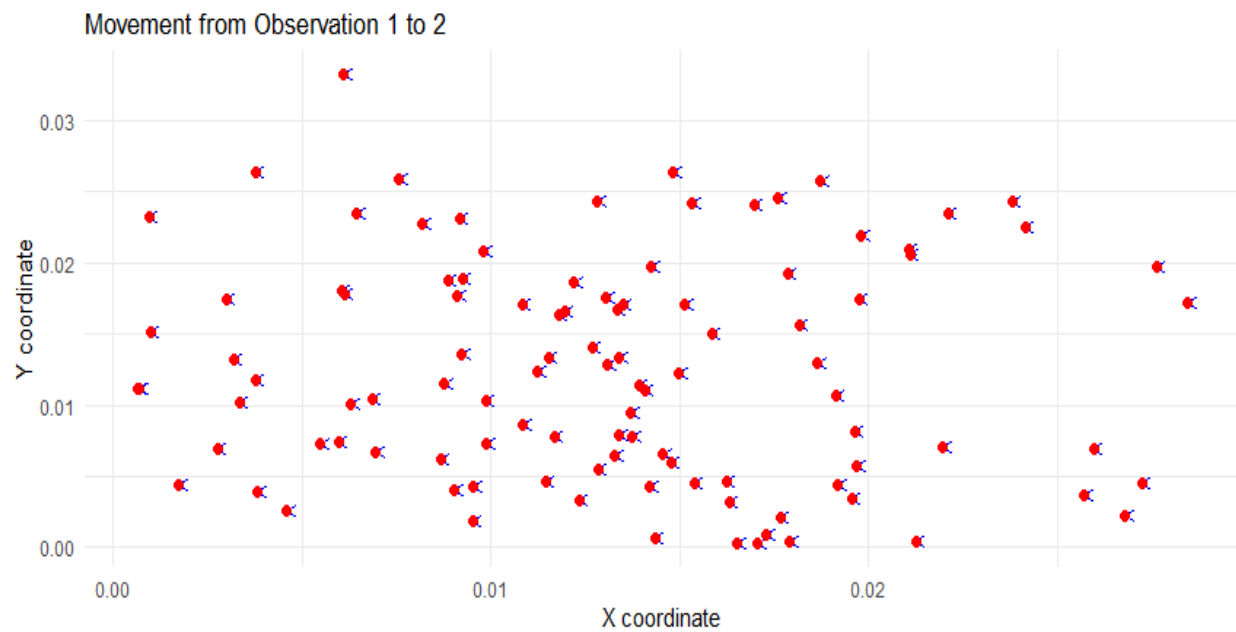


Figure 5: No movement between observation occasions.

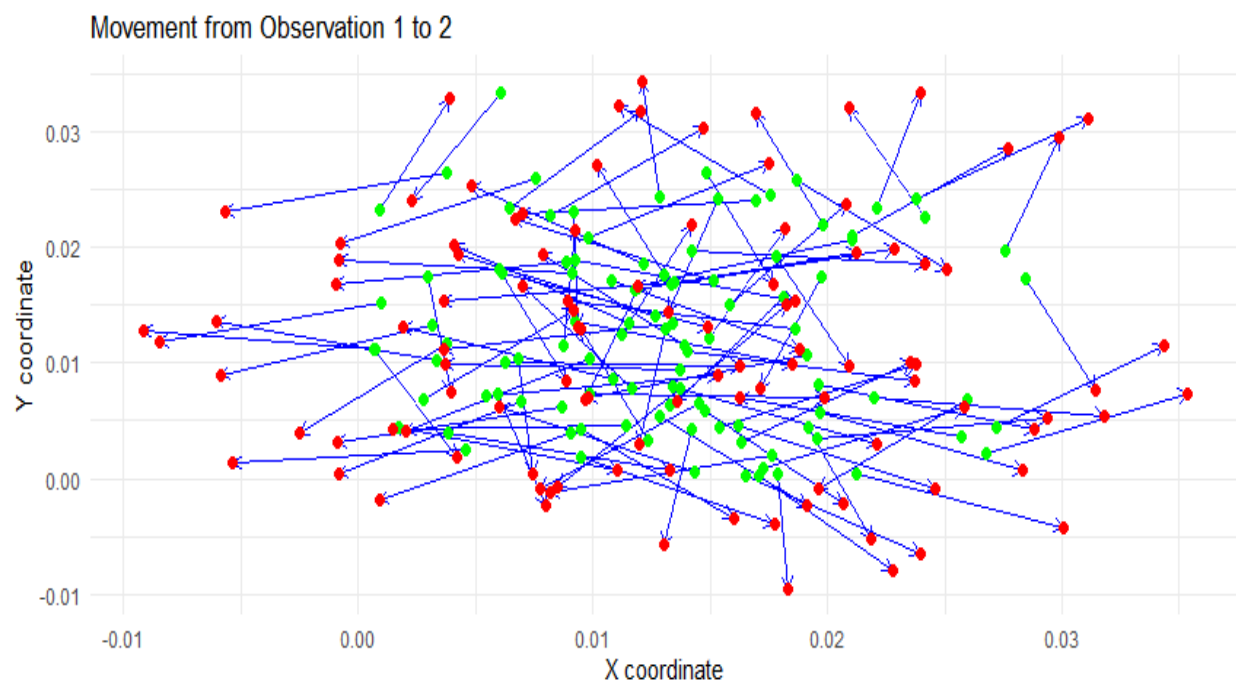


Figure 6: Random movement between observation occasions

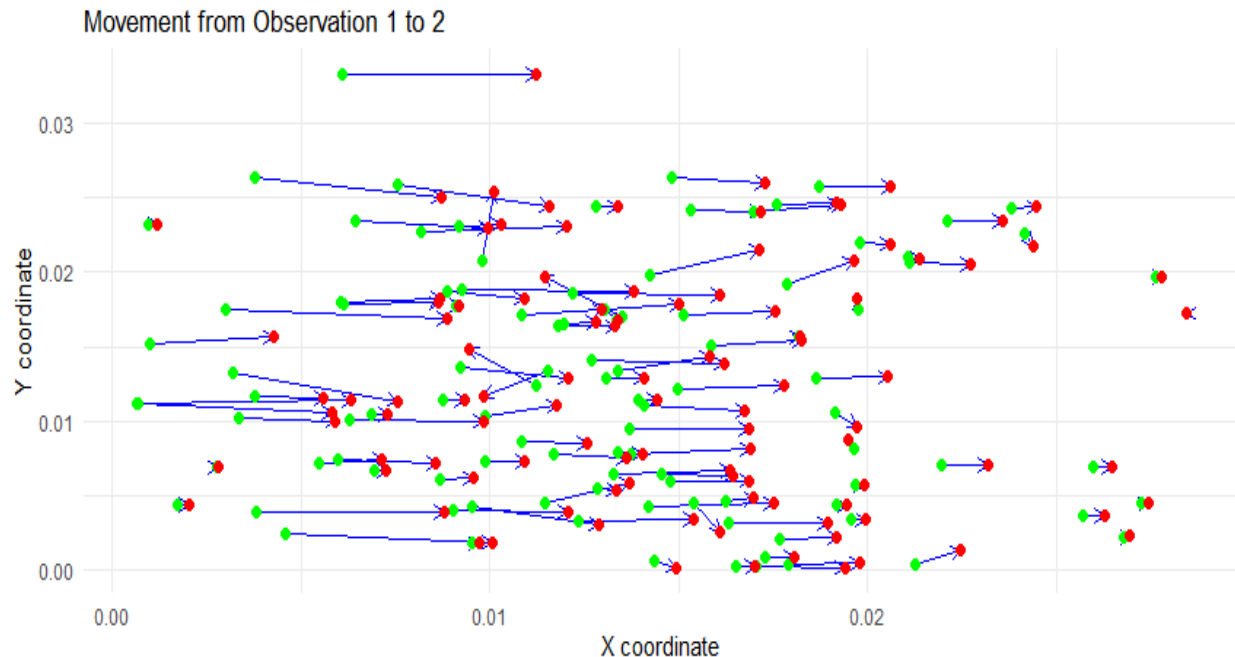


Figure 7: Avoidant movement between observation occasions

g. Detection/Non-detection

The process of determining if an animal is detected requires a function to describe the relationship between detectability and distance from the observer. Using the assumption that detectability of animals decreases across distances, we can easily find a half-normal distribution to be a suitable candidate for the detection function. Arbitrary values were chosen for the beta parameters of this function when fitting the original primate data. When simulating from the primate data, the new beta parameters produced in the fitting of the original data were used.

h. Imperfect matching

Imperfect matching describes the effort of determining which animals between occasion 1 and occasion 2 are the same animal. Remember that the two observers of this mark-recapture double-observer method travel the transect at different times, and do so alone. They do not know for certain if an animal one observer records in a location is the same as an animal the other observer records in a similar location. But the similarity of locations is a key point in deciding this matching. This process had to be introduced because animals have the opportunity to move between occasions. The logic is that two locations of animals from opposite occasions, that are more near to each other than any other animal locations in the dataset, are most likely to be the same animal recorded on different occasions. This matching is critical to the recapture process as well. If the two records are the same animal, then it is a recapture. If the records are different, then there are two records to keep instead of one. This fundamentally affects the structure of the data.

Now the distance thresholds that decide a match must be decided. Arbitrary values can be set for the upper and lower bounds. For example, any two locations more than 10 meters apart are a different

animal and any two locations less than 5 meters apart are the same animal. But, if the distance between points is somewhere between 5 and 10 meters, matching relies on probability to determine detection. Using a hazard rate probability function generate a binary outcome for each pair of points between Occasions 1 and 2:

$$h(y, x) = \theta_1 * \left(\frac{1}{\sqrt{1+x^2+y^2}^{\theta_2+1}} \right)$$

Analyze the difference between all possible pairing of locations between Occasion 1 and Occasion 2. When two locations are closer to each other than any other pairing, this is a match. Even though there may be multiple location pairings between 5 and 10 meters from each other, the closest pairing takes priority and is selected.

i. Bias

The discrepancy between an estimate and the true value is bias. In the case of estimating animal density it relates to whether density is under or over-estimated. Use the following method to calculate bias:

$$\left(\frac{\text{Estimated Value} - \text{True Value}}{\text{True Value}} \right) * 100$$

The “values” referenced above would be the mean averages of density (or whatever other estimate is being tested). This formula represents the difference between our model’s estimates and the truth, as a percentage of the true value (hence the division by true value and multiplication by 100).

Discussion and Conclusions

Estimates of density and abundance from the mark-recapture method are consistently negatively biased. This being most likely due to the violation of key mark-recapture assumptions. Namely, there is not a uniform initial distribution of primates in this survey. It is known from the start that these primates avoid the transect line and thus the initial distribution is more similar to an inverse half-normal curve. The possibility of animal movement between observation occasions is the second violation. This conflicts with the closed population assumption, that animals neither immigrate or emigrate during the survey.

	Method	Percent_Bias
1	LT2D	-11.62954
2	Double-Observer / No mismatch / No movement	-49.83333
3	Double-Observer / No mismatch / Avoidant movement	-49.39524
4	Double-Observer / No mismatch / Random movement	-50.63810
5	Double-Observer / Yes mismatch / No movement	-50.12857
6	Double-Observer / Yes mismatch / Avoidant movement	-50.70952
7	Double-Observer / Yes mismatch / Random movement	-49.87143

Figure 8: Percent bias of density estimates in each method. Further combinations of mismatch and movement options presented for the double-observer method as well.

While this negative bias can be expected for the double-observer method, the same is not true for the LT2D method. Because there is no movement to monitor or mismatching to perform with LT2D, the method is expected to be unbiased. In these results however there is still a slight (11%) negative bias in density estimates from this model. Changing the mismatching boundaries to be more narrow and adjusting to larger truncation distances are options worth considering to try and reduce bias.

Clearly under these current simulations the LT2D method outperforms all of the presented double-observer methods. The challenge for double-observers is that assumptions are violated. When those kinds of conflicts are present it may be difficult to make a valid comparison. But perhaps it is valid if the assumptions are almost never met. If two observers travel the same transect even 10 minutes apart from each other, surely there is adequate time for animals to react and move before the second observer arrives. And if transect lines cannot be placed randomly about the area and there are clear preferences for where to place them, both line placement and animal distribution may respond to this. If there is a valley where animals prefer to collect, and it is also the easier path to walk a transect, then not only will line placement be non-random but animals will in that case exhibit line *attraction*. In this study the primates exhibited line avoidance, perhaps for the fact that the line transects were placed in the jungle. Where the lines are, so are trails which represent the absence of vegetation or trees that primates may prefer to live in. Or simply the primates may avoid highly trafficked roads.

Some abundance estimates may be unreliable because they lack variety in lower or upper limits, meaning the lower and upper limits are equal to the mean. This happens in scenarios where the number of captures on Occasion 2 is equal to the number of animals captured on both occasions (B).

Code Guide

j. Summary

- **move.data(df, move, keep_angle):** Takes data frame with paired columns x and y, and generates one of three movement types (avoidant, random, none) to move the data to a new location with column x2 and column y2
- **move.detect(move, sigma):** Incorporates “move.data()” and uses hazard rate function to determine detection of each location.
- **mismatch(df):** Uses minimum and maximum distance thresholds with hazard rate function to determine if two locations are close enough to be recorded as the same animal.
- **LT2D.fit(DataFrameInput, hr, b, ystart, pi.x, logphi, w, hessian, control)**
- **chapman.mr(df, mismatch):** Function describing the Chapman estimator for animal abundance.
- **simulate_chapman(Fit.n.ip0, n_animals, area, beta, lphi, mismatch):** Generates x and y data based on a distribution from the original primate data, moves it to a second occasion with “move.data()” and then carries out detection on the second occasion.

k. Simulation

1. Double-Observer Mark-Recapture

- 1.1. The following steps are all included in the function “**simulate_chapman()**”
- 1.2. Number of simulations set to 100
- 1.3. Parameters from the fitted LT2D object of the original primate data are used to describe a distribution from which 210 *new* perpendicular distances can be sampled.
- 1.4. “detect2DLT()” uses hazard rate detection on perpendicular distances and assigns a forward distance to each detected x.
- 1.5. “move.data()” to move updated x & y data to an occasion 2 with x2 & y2 data
- 1.6. Use beta parameters from original LT2D fitted object to describe the hazard rate and detect occasion 2 animals
- 1.7. Use “chapman.mr()” to both implement “mismatch()”, if chosen, and estimate animal abundance with the Chapman method.
- 1.8. The “simulate_chapman()” function is used six times; once for each combination of mismatch (TRUE/FALSE) and movement(avoid, random, none).

2. 2-Dimensional Linear Transect

- 2.1. There is no catch-all function here like there is for the method above, so the relevant, modular functions have been placed in a for-loop and used that way.
- 2.2. Because the 2DLT method only requires one occasion, no movement or detection for occasion 2 is necessary (there is no Occasion 2 here).
- 2.3. Generate 210 new perpendicular samples from the original fitted distribution.
- 2.4. Use “detect2DLT()” to give forward distance to all detections at given perpendicular distances.
- 2.5. Build a data frame to input into “LT2D.fit()”.
- 2.6. Fit new, detected data to “LT2D.fit()” and use parameters from the original fitted object again. These parameters describe the hazard rate detection probability (beta) and complementary half-normal initial animal distribution (log phi).

Declaration of Shared Work

This dissertation is a continuation of past work on testing various sampling methods against the proposed 2-dimensional method. Most, if not all, of that past work can be found in the GitHub repository “**david-borchers/LT2Dcal**”, which is the foundation of this dissertation. The LT2Dcal repository is responsible for building the LT2D package, which is referenced throughout the code of this dissertation, and contains many functions essential to this report. The code used to fit the original primate data was provided by David Borchers, meant to replicate the conditions of the primate fit in the paper Borchers & Cox 2017. The “**report.simulation.R**” file in “**david-borchers/LT2Dcal/inst**” provided the structure of the movement, mismatching, and Chapman mark-recapture functions built in this report. Of course, dimensions of those functions were adjusted to fit the primate data, but the structure was able to remain largely the same.


```

# Generate forward distances (y) ONLY for detected individuals
detected_xy[[i]] <- detect2DLT(x = x_set[[i]], hr = "ip0", b =
c(beta1,beta2),
                                ystart = 0.05, ny = 1000,
                                getIDs = TRUE)

# Build data frame for the fitting function
n <- nrow(detected_xy[[i]])
new.df <- data.frame(stratum = rep(1, n),
                     transect = rep(1, n),
                     object = 1:n,
                     size = rep(1, n),
                     area = rep(100, n),
                     L = rep(100, n),
                     x = detected_xy[[i]]$x,
                     y = detected_xy[[i]]$y)

# Fit model
Fit.new <- LT2D.fit(new.df,
                    b = c(beta1, beta2),
                    hr = "ip0",
                    ystart = 0.05,
                    pi.x = "pi.norm",
                    logphi = c(lphi1, lphi2),
                    w = 0.04,
                    hessian = TRUE,
                    control = list(trace = 5, maxit = 1000))

# Store Density estimate
lt2d_density[i] <- Fit.new$ests$D[1]
}

```

Every object in this loop was already created before using ChatGPT. The generative AI here was used to appropriately **place index (i)** symbols and **store density** at the very end. The same is the case for the “simulate_chapman()” function which was used. The generative AI tool was also used to answer troubleshooting questions throughout the process of writing the loops and functions. This was for fixing output issues coming from the loop/function, such as NA’s leading to warning or error messages.

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