Design and inference for line transect surveys in occupancy studies

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Summary: Line transect surveys, fixed paths along which observers record detections of animals or signs of their

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presence, are a core tool in ecological monitoring. In occupancy studies, line transect surveys are used to determine species' presence/absence whilst accounting for imperfect detection and varying availability for detection along the transect. However, which research questions can be answered using such surveys depends on how detections are recorded, ranging from binary presence/absence in transect segments to continuous-time detections. These differing data collection protocols give rise to structurally distinct statistical models, with varying identifiability properties and inferential performance. In this paper, we present the first comprehensive comparison of commonly used line transect occupancy models within a unified framework, structured around data collection design, model formulation, parameter identifiability, and practical performance. Using algebraic analysis and data cloning, we show that widely used models are often either non-identifiable or not practically identifiable. We develop a novel, data-based diagnostic to detect this issue in applied settings. An extensive simulation study illustrates the practical implications of data-collection approaches, model choice, and corresponding inference. We make recommendations regarding choice of detection protocol and line transect survey design and demonstrate the real-world consequences of these findings using a case study on leopards in the Zambesi-Transfrontier Conservation Area in Central Africa. Our results offer methodological innovation and actionable guidance for ecologists and statisticians.

KEY WORDS: Bayesian; Data cloning; Identifiability; Line transect studies; Occupancy models.

1. Introduction

It is important to monitor wildlife populations, particularly as biodiversity is under increasing pressure generic refs to motivate wildlife monitoring. One popular monitoring scheme is occupancy studies which determine species presence/absence across a range of sites in the study area, whilst accounting for imperfect detection (MacKenzie et al., 2002). Occupancy models can be used to monitor changes in species abundance and distribution, and species response to habitat changes generic refs. Line transect surveys are widely used to collect spatially structured data for ecological studies, including occupancy studies. They are employed in varied environments, such as terrestrial and aquatic systems, and increasingly incorporate improved survey technologies such as GPS locations generic line transect papers?.

1.1 *Line transect surveys*

During a line transect survey, the study region is divided into distinct sites, with a set of fixed paths (transects) located within each site. We say a site is occupied if the species was present at the site during the sampling period. Typically, each line transect is divided into sub-units of equal length, called segments.

During line transect surveys, observers travel along the transects and record encounters with animals (direct) or signs of their presence (indirect) such as nests, dung, or vocalizations Refs for types of signs. We refer to these encounters as detections. The detection process is fundamentally shaped by the spatial relationship between the species' home range and the transect line, as illustrated in Figure 1 a)i, where a set of transects may lie within, without, or intersect the species' home range. We say a segment is occupied if it intersects the species' home range; given a segment is occupied, detections of the species or signs of their presence can be made by an observer. No detections can be made on segments that do not intersect the home range of the species (termed unoccupied segments). In this way, whilst a site may be occupied, it may not be possible to make a detection on all transect segments. Furthermore, the probability of making a detection on an occupied segment is typically less than 1, and so observation error must be accounted for.

1.2 *Modelling framework*

Line transect surveys are often used in occupancy studies (Refs line transect in occ studies). Occupancy models for such data are used to infer species presence or absence across a survey area (site occupancy), whilst accounting for imperfect detection (conditional on the occupancy of the site) (MacKenzie et al., 2002; Tyre et al., 2003). For line transect data, occupancy models comprise three stages: site level occupancy, segment occupancy conditional on site occupancy, and finally detections conditional on segment occupancy using a multi-scale occupancy model (Nichols et al., 2008; Mordecai et al., 2011; Pavlacky et al., 2012).

As observers travel along the transects, detections are recorded on each transect segment. Several different detection protocols are used in practice - differing by their observation method and amount of replication. Common observation methods include binary detection/non-detection (DND), which are popular as they are easy to implement. Increasingly, distance to first detection (DTD) observations are being taken (Garrard et al., 2008; Bornand et al., 2014; Henry et al., 2020), as well as inter-detection distances (IDD) (Guillera-Arroita et al., 2011) due to improvements in survey technology (for example camera time-stamps or GPS locations). Another observation method comprises counts (C) of detections within some interval (Emmet et al., 2021), which are relatively simple to implement in field surveys. Finally, independent replicate observations per transect segment can be taken by multiple devices or observers (Nichols et al., 2008; Whittington et al., 2015).

The latent segment occupancy process is expected to be highly correlated - since adjacent transect segments are likely to share the same occupancy status. This means that the occupancy status of a segment is unlikely to be independent of the status of neighbouring segments. Failure to account for this spatial dependence can lead to biased estimates of occupancy and detection probabilities (Hines et al., 2010). Models for spatial autocorrelation in segment occupancy include discrete Markov Processes (MP) (Hines et al., 2010; Whittington et al., 2015), intrinsic conditional auto-regressive processes (ICAR) (Crosby and Porter, 2018; Aing et al., 2011) and continuous-time Markov chain processes (CTMC) (Guillera-Arroita et al., 2011). An overview of the modelling framework can be seen in Figure 1 a).

1.3 *Ecological Background*

Line transect practitioners have a range of detection protocols to choose from when establishing a survey design. The most appropriate choice of protocol depends on the ecological question of interest, the target species (such as species rarity or elusivity), as well as cost and feasibility. Pautrel et al. (2024) compare detection/non-detection, counts, and inter-detection distance protocols in their ability to infer occupancy probabilities (in a modelling framework without a sub-unit occupancy layer). In addition to occupancy, increasing interest lies in understanding the ecological behaviour of species, their relationship with the environment and habitat preferences (Efford and Dawson, 2012; Wright and Hooten, 2025), or in maximising species detections in future surveys by optimising study design (refs for survey optimisation). In these cases, segment occupancy is a core parameter of interest. Being able to infer which segments are occupied/unoccupied enables much finer-scale maps of the home ranges of the species within occupied sites to be built. These can then be modelled against environmental covariates to determine the hierarchical habitat selection process of the species (refs to support this bit).

However, in the case of inferring segment occupancy, little has been done to compare all the methods discussed previously whilst accounting for the spatial autocorrelation across adjacent transect segments. Many models have been developed in isolation or are motivated by particular case studies. However, as we illustrate in this paper, these models share a common structure, and formalising links between them facilitates direct comparisons of common modelling parameters and corresponding inference. Understanding the inferential ability of each model under a variety of survey designs and target species behaviours supports informed choice of detection protocol and study design.

In this paper we present a unifying framework for the detection protocols discussed in the previous sections and presented in Figure 1. Models are classified according to their latent segment occupancy process 'L', their detection protocol 'O', and the number of independent replicate observations per segment 'J', so that the models are identified by label L/O/J. A general schematic for this is shown in Figure 1 b).

1.4 *Identifiability*

The identifiability of parameters in multi-scale occupancy studies (and ecological models more generally) is important to consider. If a parameter cannot be uniquely identified from the data then it cannot be estimated reliably. Non-identifiability can result in biased parameter estimates, large variability, and, in a Bayesian context, poor mixing (Stoudt et al., 2023; Cole, 2020). Identifiability issues can be caused by the inherent model structure or by a particular data set (Gimenez et al., 2004; Cole, 2020). The former is known as structural non-identifiability, the latter either is termed as practical non-identifiability (Raue et al., 2009), weak identifiability (Gimenez et al., 2009) or the model is termed non-estimable (Ponciano et al., 2012). Various methods exist for examining identifiability. Structural identifiability can be examined using symbolic differentiation (Cole et al., 2010). Whether a model is non-estimable can be investigated using data cloning (Lele et al., 2010; Ponciano et al., 2012; Mosher et al., 2018). Within a Bayesian setting, identifiability can also be investigated by measuring the overlap between prior and posterior distributions (Gimenez et al., 2009; Abadi et al., 2010), with weakly identifiable parameters having overlap greater than some threshold (usually 35%). However, no single clear threshold value indicates identifiability issues in general settings (refs for this section). In this paper we highlight the usefulness of data cloning, particularly as it can be used to identify issues in data sets for which the true parameter values are unknown. Alternative methods are described in Cole (2020).

Within line transect surveys in occupancy studies, and multi-scale occupancy studies generally, the identifiability of model parameters for the detection and segment occupancy parameters is often a concern. For example, Kendall et al. (2013) require suitable constraints in their model (with temporally correlated sub-units) to avoid confounding detection and sub-unit occupancy probabilities, and Nichols et al. (2008) require replicated sub-unit observations to guarantee identifiability in their model (with independent sub-units). A popular method is the single replicate detection/non-detection protocol with Markovian segment occupancy model (MP/DND/1) (Hines et al., 2010). However, Hines et al. (2010) note convergence issues with the model, particularly in the absence of correlation in segment occupancy where it also struggled to estimate detection and segment occupancy parameters. For multi-scale occupancy models, the independence or autocorrelation between the sub-units, and how these are modelled, is a significant factor influencing the identifiability of the model.

1.5 *Paper Structure*

The paper is structured as follows. In Section 2 we describe the detection protocols introduced in this section under a unifying framework. In Section 3 we conduct an extensive simulation study, comparing models in the framework under different scenarios, with a particular focus on the amount of spatial correlation in the underlying latent segment occupancy process. Section 4 investigates identifiability issues of the models. Section 4 discusses study design recommendations and introduces a novel, data-based diagnostic for detecting identifiability issues, both backed by simulation studies. The ability of the data-based diagnostic, a computationally cheap and simple calculation from observed data, to detect these issues is supported by extensive data cloning simulations, which are computationally very expensive and require expertise to fit. Section 5 illustrates the findings on leopard data in the Zambezi Trans-frontier conservation area. The case study highlights the importance of study design choices and of selecting the correct detection protocol when inferring the occupancy status of line transect segments throughout the surveyed region.

2. The Models

In this section we develop the framework under which we introduce the models described in the previous section. Consider S sites, where each site $i = 1, \cdots, S$ has probability ψ of being occupied, independently of other sites. We denote the latent occupancy status of site i by w_i, such that $w_i \sim \text{Bern}(\psi)$, where we assume that the occupancy status of each site remains unchanged during the sampling period (MacKenzie et al., 2002).

Site i contains M_i transects of length L_{im}, so that the total survey effort across site i is $L_i = \sum_{m=1}^{M_i} L_{im}$, and all sites is $L = \sum_{i=1}^{S} L_i$. A transect of length L_{im} is then divided into segments of some constant length R. Assuming that segment length R perfectly divides the transect lengths L_{im}, this gives $K_{im} = L_{im}/R$ segments for transect m at site i. Conditional on the site being occupied, transect m may intersect wholly, partially, or not at all with the home range of the species of interest. A segment is occupied if it intersects with the species' home range. The latent segment occupancy status is denoted $z_{i,m,k} \in \{0, 1\}$ for segments $k = 1, \cdots, K_{im}$ at site i and transect m.

The above process describes a general multi-scale occupancy model (Kery and Royle, 2015) with the following three processes (site-level occupancy, segment-level occupancy, and detections):

$$\begin{aligned} w_i &\sim \text{Bernoulli}(\psi), \\ z_{i,m,k} | w_i &\sim \text{Bernoulli}(w_i \theta_{i,m,k}), \qquad (1) \\ y_{i,m,k,j} | z_{i,m,k} &\sim f(z_{i,m,k}, \beta), \end{aligned}$$

where $\theta_{i,m,k}$ is the probability that segment k at site i and transect m is occupied (given site occupancy). We denote by $y_{i,m,k,j}$ the j-th replicate observation on that segment, where observations arise from a distribution with density function f and detection parameters β.

It is common to model the segment occupancy process using a first order spatial MP. If a segment is occupied, the next segment is occupied with probability θ_{11}, and if a segment is unoccupied, the next is occupied with probability θ_{01}. The conditional distribution of $z_{i,m,k}$ is then:

$$z_{i,m,k}|z_{i,m,k-1}, w_i \sim \text{Bern}\left(w_i\left\{z_{i,m,k-1}\theta_{11} + (1 - z_{i,m,k-1})\theta_{01}\right\}\right). \tag{2}$$

We let $z_{i,m,1}|w_i \sim \text{Bern}(w_i\eta)$. There are three common possibilities for η, either we estimate η as an additional parameter, set $\eta = \theta_{01}$, or we assume stationarity with $\eta = \theta_{01}/[\theta_{01}+1-\theta_{11}]$. Stationarity may be applicable if the transect begins in the middle of an established trail. Setting $\eta = \theta_{01}$ may be applicable if the survey is started from a point where individuals are unlikely to occupy the preceding space (such as a forest boundary).

The models considered in this paper share the site occupancy and segment occupancy process described above. However, the models differ by the detection protocols, which we describe in Section 2.1. The different models are outlined in Figure 1 a), showing the latent segment occupancy, the observation methods, and replication in the observation process.

2.1 *Detection process and model likelihoods*

The general framework for the likelihood functions for line transect occupancy models is:

$$\mathcal{L} = \prod_{i=1}^{S}\left\{\psi \prod_{m=1}^{M_i} H_{i,m} + (1-\psi)\mathbb{I}(\delta_i = 0)\right\}, \tag{3}$$

where δ_i is the number of detections of the species at site i, and $H_{i,m}$ is the likelihood function for the observations at site i and transect m conditional on the site being occupied. The equation for $H_{i,m}$ is varies both by the latent segment occupancy model and the detection protocol. When modelling the latent segment occupancy process with a MP, $H_{i,m}$ takes the following form:

$$H_{i,m} = [1-\eta, \eta]\Big\{\prod_{k=1}^{K_{im}-1} \mathrm{diag}(P_{i,m,k})\Theta\Big\}P_{i,m,K_{iM_i}}, \tag{4}$$

where the matrix Θ:

$$\Theta = \begin{bmatrix} 1-\theta_{01} & \theta_{01} \\ 1-\theta_{11} & \theta_{11} \end{bmatrix},$$

and the vector $P_{i,m,k} = [P^0_{i,m,k}, P^1_{i,m,k}]$ for $P^0_{i,m,k}$ and $P^1_{i,m,k}$ the likelihoods of the observations on segment k at site i and transect m conditional on $z_{i,m,k} = 0$ and $z_{i,m,k} = 1$ respectively.

In each of the following models, along occupied segments, detections are made according to a homogeneous Poisson process with rate λ. The distance between consecutive detections is then exponentially distributed with rate λ, and the probability of a single observer making at least one detection on an occupied segment of length R is $p = 1 - \exp(-\lambda R)$.

2.1.1 *MP/DND/J.* Models denoted MP/DND/J use a MP to model the latent segment occupancy process, and require J replicate detection/non-detection observations per segment. In other words, at site i, transect m, and segment k, $j = 1, \cdots, J$ independent detection or non-detections observations, $h_{i,m,k,j} \in \{0,1\}$, are made. Let $\delta_{i,m,k} = \sum_{j=1}^{J} h_{i,m,k,j}$ denote the number of detections per segment k. Then:

$$P_{i,m,k} = [\mathbb{1}(\delta_{i,m,k} = 0), \prod_{j=1}^{J} p^{h_{i,m,k,j}}(1-p)^{1-h_{i,m,k,j}}]^T \tag{5}$$

2.1.2 *MP/DTD/J.* Models denoted MP/DTD/J use a MP to model the latent segment occupancy process, and require J replicate distance to first detection observations per segment. In other words, at site i, transect m, and segment k, $j = 1, \cdots, J$ independent observations, $l_{i,m,k,j}$, are made between the start of the segment and the first detection. If no detection is made, then let $l_{i,m,k,j} = R$. Then:

$$P_{i,m,k} = [\mathbb{1}(\delta_{i,m,k} = 0), \prod_{j=1}^{J} \lambda^{\mathbb{1}(l_{i,m,k,j}\neq R)} \exp\big(-\lambda l_{i,m,k,j}\big)]^T \tag{6}$$

2.1.3 *MP/C/J.* Models denoted MP/C/J use a MP to model the latent segment occupancy process, and require J replicate count observations per segment. In other words, at site i, transect m, and segment k, $j = 1, \cdots, J$ independent counts $c_{i,m,k,j}$ are made of the number of detections. Then:

$$P_{i,m,k} = [\mathbb{1}(\delta_{i,m,k} = 0), \prod_{j=1}^{J} \frac{(\lambda R)^{c_{i,m,k,j}} \exp(-\lambda R)}{c_{i,m,k,j}!}]^T \tag{7}$$

2.2 *Assumptions*

The modelling framework above makes the following assumptions, which are common to single season occupancy models:

- The occupancy status of sites and segments are unchanged throughout the survey period (otherwise known as closure). Relaxations to this assumption include multi-season occupancy models (Mackenzie et al., 2003).
- Replicate detections on a segment are independent given segment occupancy, and there are no false positives in the detection process. Occupancy models can be relaxed to allow for false positives (J. Andrew Royle, 2006).

In this paper we also assume that site occupancy probabilities, segment occupancy transition probabilities, and detection probabilities are constant. However, the models readily extend to parameters that vary as a function of site or segment level covariates.

3. Simulations

Throughout the rest of the paper, we will be comparing the following models in particular (where all models share the latent Markovian segment occupancy process):

- MP/DND/1: single replicate detection/non-detection observation per segment (Hines et al., 2010).
- MP/DND/2: two independent replicate detection/non-detection observation per segment.

- MP/DTD/1: single replicate distance to first detection observation per segment.
- MP/DTD/2: two independent replicate distance to first detection observation per segment.
- MP/C/1: single replicate count observation per segment.

In this section, we compare the mean square error (MSE) of posterior distributions of models MP/DND/1, MP/DND/2, MP/DTD/1, MP/DTD/2, and MP/C/1 under a range of different parameter settings. As discussed in Section 1.4, the presence or absence of spatial correlation in the segment occupancy process has an effect on the ability of the MP/DND/1 model to infer detection and segment occupancy parameters. Therefore we look at simulations that vary the amount of spatial correlation between line transect segments, as $\theta_{01} \to \theta_{11}$, under high and low detectability. We denote by θ and $\hat{\theta}_q$ the true value for some parameter and the q-th posterior sample of the parameter. For Q samples, we let the MSE for this parameter be:

$$MSE = \frac{1}{Q}\sum_{q=1}^{Q}(\hat{\theta}_q - \theta)^2. \tag{8}$$

All code is available at [LOC]. All models are implemented in NIMBLE (de Valpine et al., 2017) in R (R Core Team, 2025). Model code for MP/DND/1 uses automated factor slice sampling (Tibbits et al., 2014) on parameters θ_{01}, θ_{11}, and p due to high correlation in posterior samples near model redundancy.

We take $n = 10$ sites, $M = 10$ transects, and $K = 20$ segments of length 500 per site. Across all simulations, we fix $\psi = 0.75$. The data are simulated using the discrete latent MP process with $\theta_{11} = 0.7$ and then vary $\theta_{01} \in \{0.2, 0.3, 0.4, 0.5, 0.6, 0.7\}$. The first segment on each transect is drawn from stationarity. We consider two levels of detectability, one high (with $\lambda = 1/300$, so $p \approx 0.81$), and one low (with $\lambda = 1/1200$, so $p \approx 0.34$). For each set of parameters we simulate $N = 100$ data sets where detections are generated according to an exponential process on occupied segments; then detections are summarised according to the corresponding model. For example, detections on each segment are binarised for

MP/DND/1 or only the distance to first detection is kept for MP/DTD/1. Details about prior distributions and MCMC runs can be found in Section S1.1.

Figure 2 shows the boxplots of log(MSE) for parameters ψ, p, θ_{01} and θ_{11} across $\theta_{01} \in \{0.2, 0.3, 0.4, 0.5, 0.6, 0.7\}$ and models MP/DND/1, MP/DND/2, MP/DTD/1, MP/DTD/2, MP/C/1 when $p \approx 0.81$ and 0.34 respectively. The site occupancy parameter, ψ, is consistently estimated across all scenario and all models. However, the model MP/DND/1 has much higher MSE for parameters p, θ_{01} and θ_{11} compared to the other models. The MSE also increases rapidly as $\theta_{01} \rightarrow \theta_{11}$ under MP/DND/1 for these parameters. Overall, we can see that taking continuous observations leads to lower MSE (for example MP/DTD/1 has lower MSE than MP/DND/1), but taking replicated observations leads to considerably smaller MSE (for example MP/DND/2 and MP/DTD/2 have the lowest MSE values). Figure S1 shows results for $p \approx 0.34$; as expected, the MSE increases for all parameters and models as detectability decreases. Furthermore, as $\theta_{01} \rightarrow \theta_{11}$ the aforementioned behaviours are exaggerated when detectability is low.

Even under ideal conditions, when p is high, as $\theta_{01} \rightarrow \theta_{11}$ the MSE for MP/DND/1 increases drastically across parameters p, θ_{01}, and θ_{11}. This behaviour is markedly different to that of the other models considered. We investigate the causes of this behaviour in the next section.

4. Identifiability

This section explores issues of identifiability in the the MP/DND/1 model, with a focus on the latent segment occupancy process and its implications for inference and survey design. We begin in Section 4.1 by formally checking the identifiability of the MP/DND/1, which shows structural non-identifiability occurs when there is no correlation in the latent segment process. Section 4.2 looks at how correlations in the observed detection process can serve as an indicator for correlation in the latent segment occupancy process. A novel data-based metric (derived from detection/non-detection observations) is then introduced to measure the degree of correlation in the detection process. In Section 4.3 data cloning is used to investigate the identifiability of model parameters over a range of parameter values. Crucially we show that the data-based metric, which is simple and computationally very cheap, serves as an indicator of identifiability issues determined by data cloning, which requires expertise and is computationally very demanding.

We then explore the minimum number of segments required for identifiability using symbolic differentiation (Section 4.4), and extend this analysis through data cloning to reveal weak identifiability at low segment numbers (Section 4.5). Finally, in Section 4.6 we discuss the implications of segment length for survey design.

4.1 *Independence of spatial replicates*

Consider Equation 1; for single replicate detection/detection observations we can write the observation process as $y_{i,m,k}|z_{i,m,k} \sim \text{Bernoulli}(\theta_{i,m,k}p)$ for detection probability p. If $\theta_{i,m,k} = \theta$, so that the segments are independent, then the model above requires that $J > 1$; without replicated observations the model is not identifiable (Nichols et al., 2008). Kery and Royle (2015) call this a restricted three-level occupancy model, wherein the observation process becomes $y_{i,m,k,j}|z_{i,m,k} \sim \text{Bernoulli}(z_{i,m,k} \times \theta \times p)$, and one can only estimate θp jointly.

Placing an additional structure on $\theta_{i,m,k}$, such as a MP, removing the assumption of independence between segments, makes this model estimable when $J = 1$ (Hines et al., 2010; Crosby and Porter, 2018). However, whilst this is theoretically the case, Figure 2 shows that if the MP is such that $\theta_{01} = \theta_{11}$ (and indeed as we approach the equality), then this support collapses and the model returns to the restricted three-level occupancy model where the parameters are not fully estimable.

Fixing any $\tilde{\theta}_{11}$, and then setting $\tilde{\theta}_{01} = \tilde{\theta}_{11}$ and $\tilde{p} = \theta_{11}p/\tilde{\theta}_{11}$ gives the same likelihood function as with $\theta_{11}, \theta_{01} = \theta_{11}, p$.

4.2 *Correlation in detections*

From the previous section, model identifiability issues occur in the MP/DND/1 model when $\theta_{01} = \theta_{11} = \theta$. However, the segment occupancy process is latent and unobserved and so it is difficult to predict whether the model will be identifiable prior to analysis. The detection process, however, is observed. We therefore consider how the correlation in the latent segment occupancy process (or indeed the lack of correlation when $\theta_{01} = \theta_{11}$) affects the correlation in the observed detection process.

If single replicate detection/non-detection observations ($h_{i,m,k} \in \{0, 1\}$) are made on each segment k, transect m, and site i, then $\mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 1)$ denotes the probability a detection will be made on the next segment given a detection was made on the current segment and the site is occupied. Conversely, $\mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 0)$ denotes the probability a detection is made on the next segment given no detection was made on the current segment and the site is occupied. We then have the following result.

Theorem 1: *Let site i be occupied and the latent segment occupancy process be modelled as a MP. Let η be the stationary probability for segment occupancy, and $h_{i,m,k} \in \{0, 1\}$ denote detection or non-detection on segment k of transect m. Then the following holds:*

$$\mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 1, w_i = 1) = \theta_{11}p, \tag{9}$$

$$\mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 0, w_i = 1) = \frac{p\theta_{01}(1 - \theta_{11}p)}{1 - \theta_{11} + \theta_{01}(1 - p)}. \tag{10}$$

Proof. See Section S2.2

It is then easy to show that when $\theta_{01} = \theta_{11}$, that $\mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 1, w_i = 1) = \mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 0, w_i = 1)$. Therefore, when the occupancy status of a segment is independent of the previous segment, the probability of making a detection on a segment is independent of a detection on the previous segment. This means that Equations 9 and 10 are equal when the underlying latent segment occupancy parameters give rise to a data set that is non-identifiable.

We therefore consider whether the equality of Equations 9 and 10 can serve as an indicator for model identifiability problems. Indeed, $\mathbb{P}(h_{i,m,k} = 1 | h_{i,m,k-1} = 1, w_i = 1) = \mathbb{P}(h_{i,m,k} = 1 | h_{i,m,k-1} = 0, w_i = 1)$ when $\theta_{11} = \theta_{01}$, or when $p = 0$ or $\theta_{11} = 1$. Having $p = 0$ is an extreme edge case, and p sufficiently small would result in extremely sparse data that would prevent sensible model fitting. When $\theta_{11} = 1$, another edge case, and assuming transects start from stationarity (so $\eta = 1$), then segments along a transect are always occupied, and the MP is attempting to model a process in which no state switches occur (or for θ_{11} sufficiently close to 1, are exceedingly rare). This will also leads to identifiability problems. Finally, $\theta_{11} = \theta_{01}$ leads to a redundant model under the MP/DND/1 design (shown in the previous section).

Therefore, when there is no correlation in detections at occupied sites, an analysis of the data using MP/DND/1 is likely to lead to model identifiability problems. In the following, we let $\Delta = \mathbb{P}(h_{i,m,k} = 1 | h_{i,m,k-1} = 1, w_i = 1) - \mathbb{P}(h_{i,m,k} = 1 | h_{i,m,k-1} = 0, w_i = 1)$ denote the magnitude of the difference in the conditional probabilities of observing a detection.

4.3 *Metric*

In the previous section, we showed that when $\Delta = 0$, identifiability issues will arise using the MP/DND/1 model. In this section, we investigate how the identifiability of model parameters (across all models considered) changes as $\Delta \to 0$ using data cloning. Fixing $\psi = 0.75$, $n = 10$ sites, $M = 10$ transects per site, and $K = 20$ segments per transect, 5 data sets are generated over each of 12 different parameter setting (see Section S1.2 for full simulations details). Each data set is then cloned $D \in \{1, 2, 5, 10, 15, 20\}$ times (by copying the detection histories successively to get a data set of nD sites). We determine the posterior variances $\sigma^2_D(.)$ for each D and parameter '.', and then compute the scaled variances: $\sigma^2_D(.)/\sigma^2_1(.)$. Fully estimable parameters have variances that scale with $1/D$, with weakly or non-estimable parameters showing different scaling (Lele et al., 2010; Ponciano et al., 2012; Mosher et al., 2018).

We compute the MSE of the scaled variances with respect to the expected scaled variances using the following equation over $D \in \{1, 2, 5, 10, 15, 20\}$:

$$MSE = \sum_{D} \left(\frac{\sigma_D^2(.)}{\sigma_1^2(.)} - \frac{1}{D} \right)^2. \tag{11}$$

Figure 3 shows the log MSE of the scaled variances for each parameter and data set against Δ for each of the models. Ten data sets for MP/DND/1 were removed where $\Delta < 0.1$ as the chains did not converge within reasonable time (due to identifiability problems). As Δ decreases, the MSE for MP/DND/1 increases - which indicates that the parameters become increasingly weakly or non-estimable. Estimability issues are therefore likely even when $\Delta > 0$. The MSE for MP/DTD/1 also increases significantly at small values of Δ across each parameter. Results for other detection protocols are stable across the values of Δ considered, and indicate that variances scale as expected.

4.4 *Study Design*

We investigate the minimum number of segments required per transect in order to fully identify all model parameters in an MP/DND/1 using symbolic differentiation - which considers the rank of the matrix of exhaustive model summaries (Cole, 2020). Table 1 looks at a range of common assumptions for the initial segment occupancy parameter η (where the first column η simply denotes that it is estimated as its own model parameter). We look at $K_{im} = 2, 3$, and 4 segments per transect, and whether site occupancy probabilities are to be estimated (first set of columns) or are assumed to be known and equal to 1 (for example in integrated models where occupancy is known from other data). Entries denote the deficiency in model identifiability, with 0 showing that the model is identifiable, and the value of the deficiency otherwise. Table 1 shows that $K = 4$ segments are generally required for the model to be identifiable under the range of modelling assumptions considered here.

Table 1

MP/DND/1 identifiability under different modelling assumptions. For transects with K segments, initial MP segment occupancy parameter η, and site occupancy probabilities ψ. $\tilde{\theta} = \theta_{01}/[\theta_{01} + 1 - \theta_{11}]$. The table entries show the model deficiency. A deficiency of 0 indicates an identifiable model, a deficiency > 0 indicates a non-identifiable model.

	ψ			$\psi = 1$		
K	η	$\eta = \theta_{01}$	$\eta = \tilde{\theta}$	η	$\eta = \theta_{01}$	$\eta = \tilde{\theta}$
2	2	1	2	1	0	1
3	0	0	1	0	0	0
4	0	0	0	0	0	0

4.5 *Number of segments*

In the previous section we showed that a minimum of $K = 4$ segments per transect are required for identifiability (independently of the value of Δ) under most modelling assumptions. In this section we use data cloning to investigate the estimability of parameters p, θ_{01} and θ_{11} as the number of segments increases. We take $n = 10$ sites, $M = 10$ transects per site, and vary $K \in \{4, 6, 8, 10, 15, 20\}$. We fix $\psi = 0.75$, $\theta_{11} = 0.7$, and $\theta_{01} = 0.1$ and let the first segment on each transect be drawn from stationarity. The detection rate is $\lambda = 1/300$, so that $p \approx 0.81$. We generate $N = 10$ data sets for each K, and for each data set we clone the data $D \in \{1, 2, 5, 10, 15, 20\}$ times. For full simulation details see Section S1.3. The distribution of Δ for each data set across K is shown in Figure S2 and show that the mean Δ across K is roughly constant (though with increasing variability).

Figure 4 shows the box plot of log MSE of scaled variances across the number of segments K for parameters p, θ_{01}, and θ_{11} and each of the models. For MP/DND/1, the box plots indicate the log MSE increases as the number of segments decreases, and that the MSE is often greater than for other models. So whilst $K = 4$ ensures identifiability, model parameters can be weakly estimable and require far more segments to be strongly estimable. Results for models MP/DND/2, MP/DTD/1, MP/DTD/2, and MP/C/1 show that model parameters are largely estimable across K.

4.6 *Choosing segment lengths*

Closely related to the number of segments is the length of the segments in the survey design. The previous sections show that for MP/DND/1 is sensitive to both Δ and K. In this section we show that these are linked through the choice of segment length R. Since the true latent process is likely to be continuous, we find $\mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 1)$ and $\mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 0)$ when the latent process is modelled using a CTMC, and derive the following result:

THEOREM 2: *Let the site be occupied. Let the latent segment occupancy process be modelled using a CTMC. Let η be the stationary probability of occupancy at the start of the transect, and $h_{i,m,k} \in \{0, 1\}$ denote detection or non-detection on segment k of transect m. Let segments have length R. Then the following holds:*

$$\lim_{R\to\infty} \Delta = \lim_{R\to\infty} \left\{ \mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 1) - \mathbb{P}(h_{i,m,k} = 1|h_{i,m,k-1} = 0) \right\} = 0. \tag{12}$$

Proof. See Section S2.4

Equation (12) confirms the known observed behaviour that increasing segment lengths decreases correlations in detections (for example, Thorn et al. (2011) and Hines et al. (2010) recommend aggregating detection histories along segments to reduce spatial dependence).

Figure S3 shows Δ values as segment lengths R increase over a range of simulated species detection rates (ranging from low to high) and the switching rate between occupancy and non-occupancy of the transect (from from low to high). As R increases, we see that the average Δ goes to zero for all simulation scenarios, but that the variability also increases. This is because for fixed transect lengths, the number of segments is becoming increasingly smaller as R gets larger so that fewer observations are taken. Across most simulation scenarios, there is a value of R that maximises Δ (although in some cases, such as with species with low detection rates and high switching Δ remains quite flat over R). However, the maximal Δ varies significantly between the simulation scenarios. For species with low switching rates (possibly indicating larger home ranges on average) and high detection rates, the maximum Δ value is the greatest. As switching rates increase, and detection rates decrease, the maximal Δ decrease.

Choosing R is complex, and requires knowledge of species' behaviour and mobility (Emmet et al., 2021). Theorem 2 and Figure S3 show that the choice of segment length R has substantial impact on the value of Δ. The choice of how data are discretised can be the difference between getting an identifiable or non-identifiable set of data. Furthermore, results show that the underlying characteristics of the species (such as size of home range and detectability) can also impact on Δ, which in turn limits which detection protocols will be identifiable for that species. However, R too small often increases run-time and complexity.

5. Case Study

We consider an application of this work to a case study in the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA) (Lines et al., 2018). This was a large study of several carnivore species from which we focus on the leopard (*Panthera pardus*) data. During May-October 2015, a systematic randomized spoor and sightings survey was conducted on foot over 102 4-km transects (Lines et al., 2018). During each visit, detection-non-detection data were recorded on each transect segment of length 1km. Each transect was visited three times over a 10 day window. The surveyed region was divided into $n = 10$ sites, with between 8 and 19 transects per site. The total number of leopard detections were 279 over the $102 \times 4 \times 3$ replicated segments, made at 61 of the 102 transects.

To calculate Δ, we look at transects from sites in which at least one detection was made over replicates J. When $J = 1$ we have $\Delta = 0.303$, $J = 2$ gives $\Delta = 0.382$, and $J = 3$ gives $\Delta = 0.382$.

We analyse these data using MP/DND/1, MP/DND/2, and MP/DND/3. For $J = 1$ and 2, we simply take the first and first two sets of replicates at each site from the detection histories respectively. One transect did not have three replicates, so for the MP/DND/3 we only take the first two replicates. We assume that the segment occupancy process starts at stationarity. See Section S3 for details on prior distributions and for summaries of the effective sample size and Gelman-Rubin diagnostic for each parameter.

Figure 5(a) shows posterior means (circles) and 95% PCIs (bars) for each model and model parameter. MP/DND/2 and MP/DND/3 show smaller PCIs in model parameters p and θ_{11} than the MP/DND/1. Posterior distributions are comparable for ψ. Data cloning results for each model are shown in Figure 5(b). The scaled variances are shown for $D \in \{1, 2, 3, 4, 5, 10, 15, 20\}$ data copies, and for each model parameter MP/DND/2 and MP/DND/3 show a scaled variance that decreases in line with the expected rate of $1/D$. However, MP/DND/1 shows slower decrease for parameters p and θ_{11}, and faster for θ_{01}. The rate for ψ was comparable across all three models. These results are consistent with those from Section 4, where a combination of Δ being relatively low and a small number of segments K leads to more weakly estimable parameters for MP/DND/1 when compared to other models.

6. Discussion

Occupancy models are a widely used tool in species monitoring programmes. Where multi-scale occupancy model designs are used, and spatial autocorrelation between sub-units needs to be accounted for, modelling segment occupancy using a MP is a popular method. However, using single replicate detection/non-detection observations with this latent process is susceptible to identifiability issues where other data collection methods are not.

This paper provides a framework to analyse these models, comparing various data collection methods. We did extensive simulation studies to show that correlation in detections can be a metric for identifiability, and the number of segments per transect (and their length) is an important but often overlooked consideration when selecting study design.

We make the following recommendations to study design. In terms of detection protocol, a single detection/non-detection observation per segment is the most susceptible to identifiability issues. Considering continuous detection protocols, such as distance to first detection and counts in general have lower MSE and are less susceptible to identifiability issues in most cases. Henry et al. (2020) and Bornand et al. (2014) who compare DTD and DND detection protocols in their occupancy models also show that DTD generally performs better. However, whilst MP/DTD/1 shows reduced MSE and bias compared to MP/DND/1 when p is high, it only shows small improvement when p is low. Similarly, MP/DTD/1 and MP/C/1 exhibit identifiability issues in cases when data is sparse. Increasing replication from $J = 1$ to 2 in the models increases the robustness of the models to spatial independence of the segments and low detectability. Taking more replicate observations per segment can yield better results than continuous observations; for example the MP/DND/2 is more robust than MP/DTD/1 at low detectability. Doser and Stoudt (2023) show in their occupancy model that fractional replication (where only a select number of sites are visited more than once) also yields improved estimates - further work here would likely show this to be the case in these models. An important consideration with replication is that the timescale over which replicate observations are conducted must be small enough to guarantee closure in the occupancy status of the segments.

When selecting segment number and length, 4 segments per transect are required for identifiability when using MP/DND/1. In reality, many more segments are needed for all parameters to be strongly estimable for MP/DND/1, whereas 4 segments is generally sufficient for other detection protocols. Segment length has been shown to affect Δ- and subsequently identifiability for some detection protocols. If the locations of all detections are recorded (for example in a pilot study) then an optimal segment length can be determined by selecting the length that maximises Δ for resulting discretised data sets.

Where the parameter of interest is ultimately ψ, then across the various simulation scenarios considered here, this parameter is reasonably robust. Pautrel et al. (2024) compare the estimability of occupancy probabilities across various data collection methods and under different levels of data sparsity. However - there are many instances where estimates of detection probability and segment occupancy probabilities may be of interest, in which case model choice becomes more important (particularly when trying to design future studies to maximise species' detection). Strengthen need to infer these probabilities - idea of hierarchical habitat selection, finer-scale occupancy maps.

In this work we have not considered the use of covariates in order to help the estimability of model parameters, and in fact Kery and Royle (2015) warn against relying on covariates in order to provide identifiability. Particularly since this is dependent upon finding a covariate with significant effect on the parameter. In this work replicate detections have been in the same observation method, and we make no distinction between detections of different types of sign. However, this need not be the case. For example, a study may separate replicate detections by sign type (eg spoor and scat) and give each type a distinct detection rate. The same can be applied to different observation methods, for example one replicate may employ DTD observations and another DND, which may occur if time and/or resources prohibit taking two independent DTD replicates. However, the independence of replicate observations per segment (either by different detection protocol or sign type) must be guaranteed under the modelling assumptions.

Finally, whilst we look at a MP for the discrete latent segment occupancy process, other latent models have been investigated, and further work could focus on the identifiability of model parameters under different detection protocols across these latent models. We have assumed that transects start at stationarity in simulations and case studies. This is a common assumption, and is appropriate under the case study considered here. However, if transects begin at study area boundaries or on habitat boundaries this may not be an appropriate assumption. When transects have many segments, then the effect of misspecification of the initial condition will be minimised. However, with small numbers of segments then the MP will not sufficiently approach stationarity towards the end of the transect. (Crosby and Porter, 2018) raise that the reversibility of the MP may bias results, and this is true if stationarity is not given.

Closing remarks...

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Supporting Information

Please see Supplementary Material for XXX.

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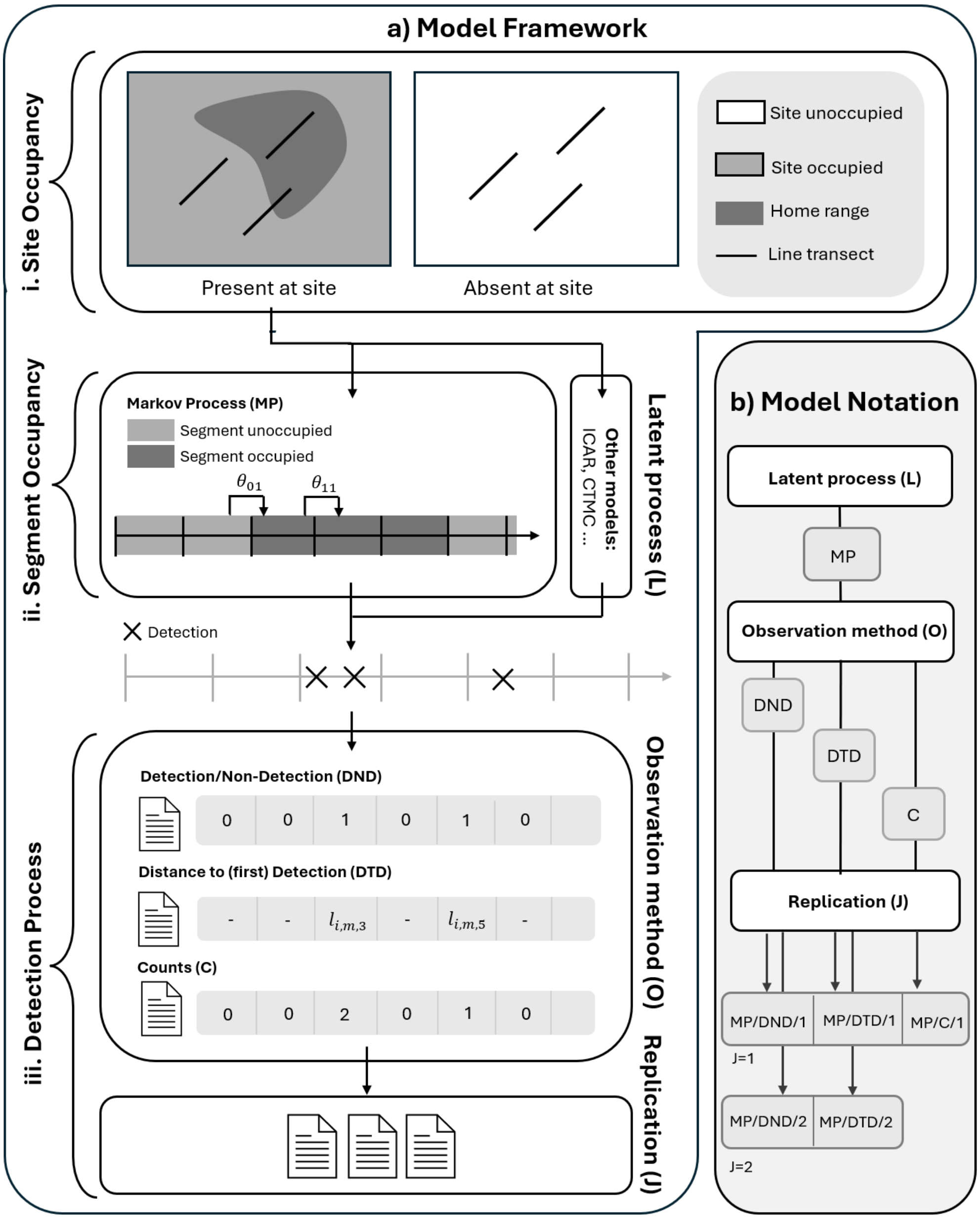
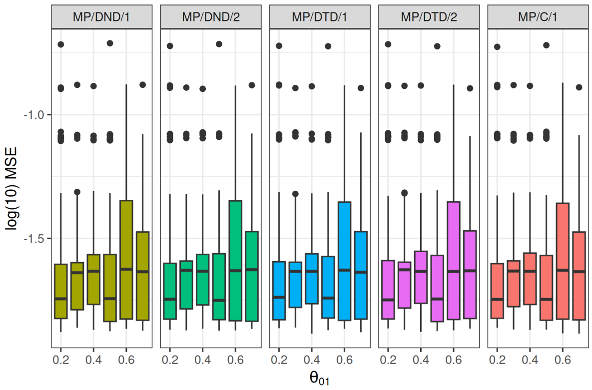
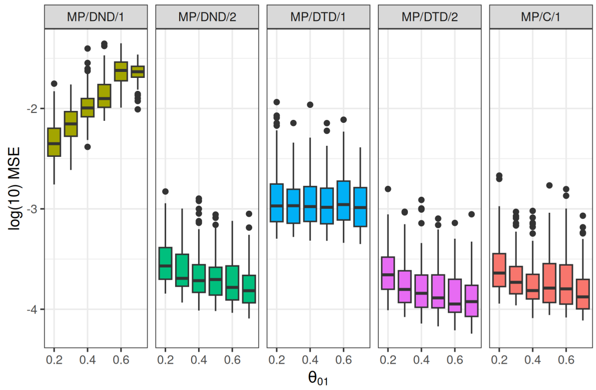


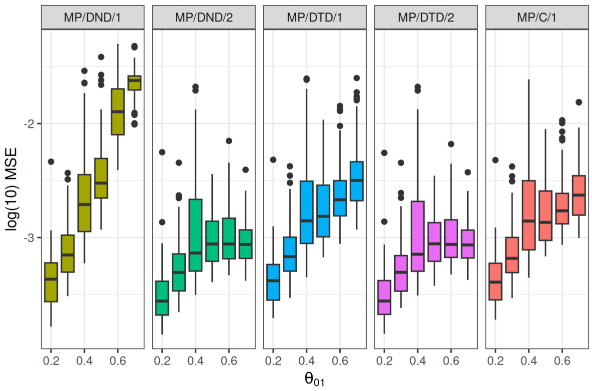
Figure 1. a) Modelling framework including site occupancy, segment occupancy and the detection process. i. A site may be unoccupied or occupied, with transects wholly, partially, or not intersecting the home range of species' at occupied sites. ii. The latent segment occupancy process models the intersection of transects with the home range. iii. The detection process comprises the observation method and replication of observations. b) Models are labelled L/O/J according to their latent segment occupancy process (L), observation method (O), and amount of replication (J)



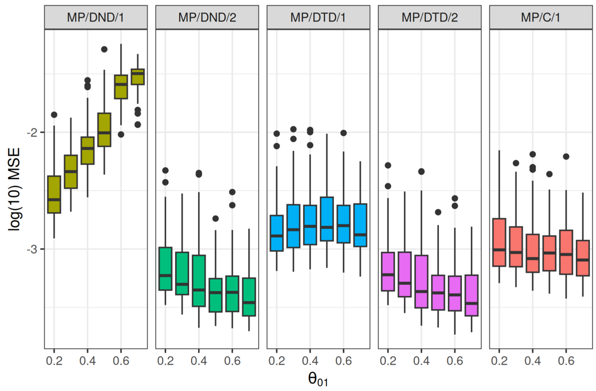
(a) ψ



(b) p

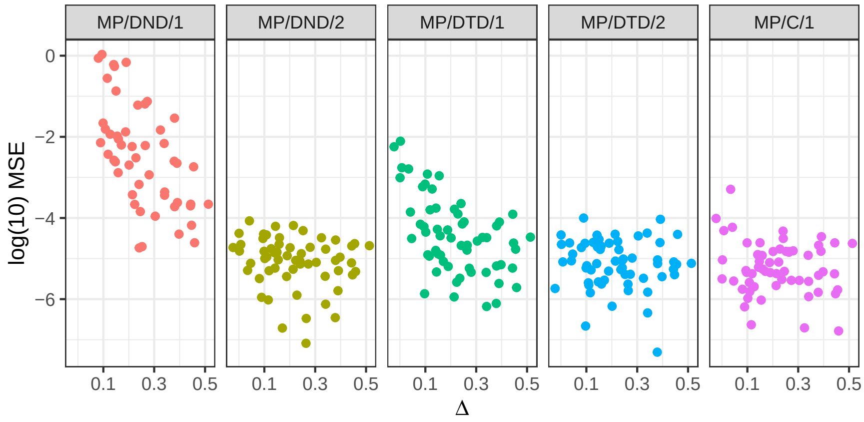


(c) θ_{01}

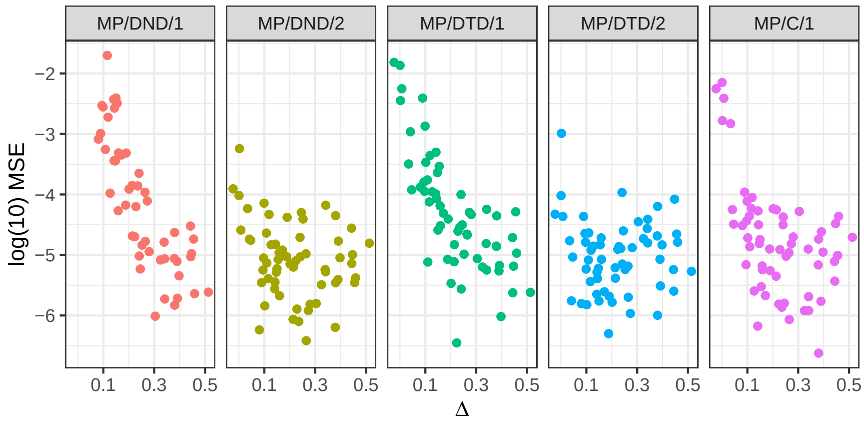


(d) θ_{11}

Figure 2. Boxplot of log(MSE) for parameters ψ, p, θ_{01} and θ_{11} across $\theta_{01} \in \{0.2, 0.3, 0.4, 0.5, 0.6, 0.7\}$ when $p \approx 0.81$ and models MP/DND/1, MP/DND/2, MP/DTD/1, MP/DTD/2, MP/C/1.



(a) p



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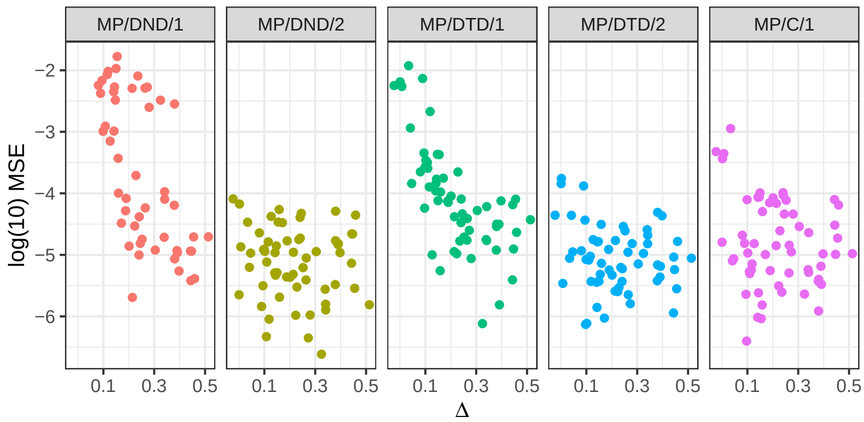
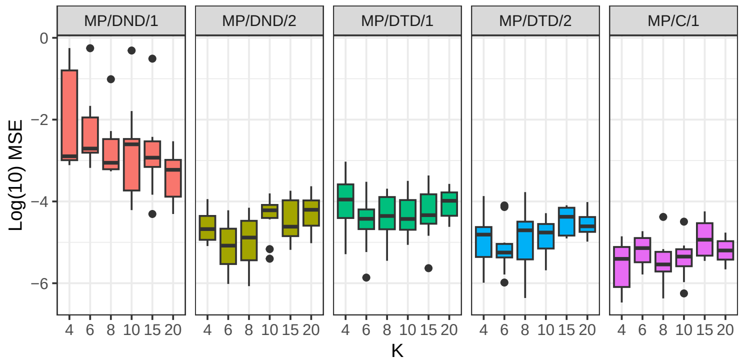
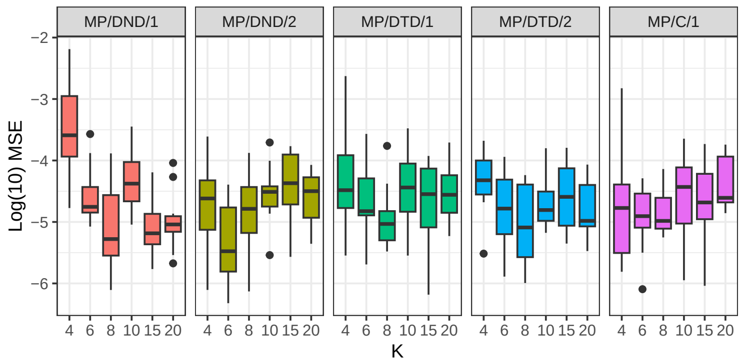


(c) θ_{11}

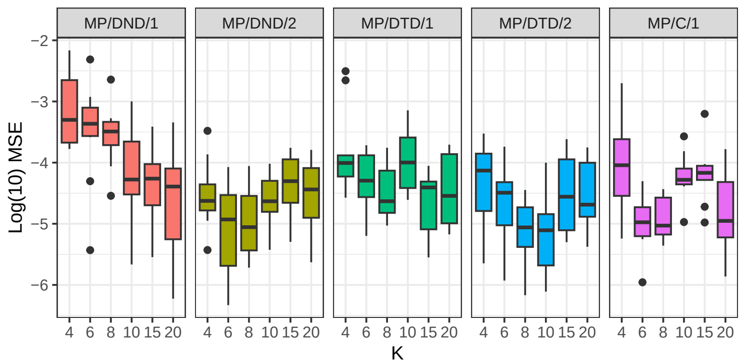
Figure 3. Log(10) MSE for parameters p, θ_{01} and θ_{11} across metric values Δ and models MP/DND/1, MP/DND/2, MP/DTD/1, MP/DTD/2, MP/C/1.



(a) p

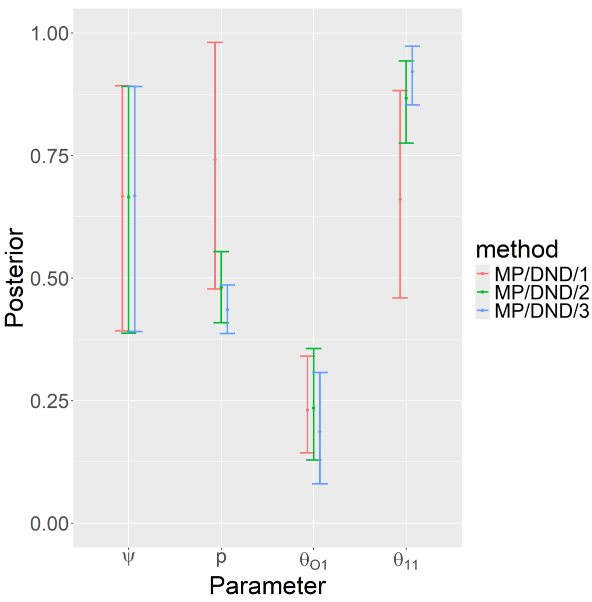


(b) θ_{01}

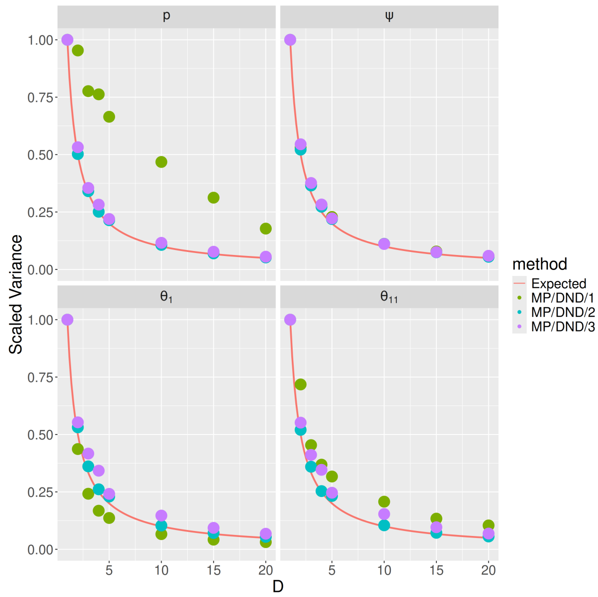


(c) θ_{11}

Figure 4. Log(10) MSE for parameters p, θ_{01} and θ_{11} across number of segments $K \in \{4, 6, 8, 10, 15, 20\}$ and models MP/DND/1, MP/DND/2, MP/DTD/1, MP/DTD/2, MP/C/1.



(a)



(b)

Figure 5. (a) Posterior means (circles) and 95% PCIs (bars) for MP/DND/1, MP/DND/2, and MP/DND/3. (b) Scaled variances (points) for models MP/DND/1, MP/DND/2, and MP/DND/3 for $D \in \{1, 2, 3, 4, 5, 10, 15, 20\}$. The expected scaled variance $1/D$ is the plotted line.