Methods in Ecology and Evolution

Methods in Ecology and Evolution 2014, **5**, 1180–1191 doi: 10.1111/2041-210X.12294

Using mark–recapture distance sampling methods on line transect surveys

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Summary

1. Mark–recapture distance sampling (MRDS) methods are widely used for density and abundance estimation when the conventional DS assumption of certain detection at distance zero fails, as they allow detection at distance zero to be estimated and incorporated into the overall probability of detection to better estimate density and abundance. However, incorporating MR data in DS models raises survey and analysis issues not present in conventional DS. Conversely, incorporating DS assumptions in MR models raises issues not present in conventional MR. As a result, being familiar with either conventional DS methods or conventional MR methods does not on its own put practitioners in good a position to apply MRDS methods appropriately. This study explains the sometimes subtly different varieties of MRDS survey methods and the associated concepts underlying MRDS models. This is done as far as possible without giving mathematical details – in the hope that this will make the key concepts underlying the methods accessible to a wider audience than if we were to present the concepts via equations.

2. We illustrate use of the two main types of MRDS model by using data collected on two different types of survey: a survey of ungulate faecal pellets where two observers searched independently of each other; and a cetacean survey that used a search protocol that could accommodate responsive movement, with only one observer searching independently and the other being aware of all detections.

3. *Synthesis and applications*. Mark–recapture DS is a widely used method for estimating animal density and abundance when detection of animals at distance zero is not certain. Two observer configurations and three statistical models are described, and it is important to choose the most appropriate model for the observer configuration and target species in question. By way of making the methods more accessible to practicing ecologists, we describe the key ideas underlying MRDS methods, the sometimes subtle differences between them, and we illustrate these by applying different kinds of MRDS method to surveys of two different target species using different survey configurations.

Key-words: mark–recapture, distance sampling, line transects, double-observer survey, program DISTANCE

Introduction

Line transect distance sampling (DS) methods are frequently used to estimate density and abundance of wild populations. Two key assumptions of DS are that objects on the transect line (referred to as the trackline) are certain to be detected and objects are detected at their original location (Buckland *et al.* 2001). When these assumptions are violated, conventional DS estimators give biased estimates of density and abundance. Mark–recapture (MR) methods provide a way of estimating abundance without making these assumptions; a MR model can be used to check the assumption that detection on the trackline is certain, and if this assumption does not hold, allow the probability of detection on the trackline to be estimated. MR methods may also be used to deal with responsive movement (see, for example, Buckland & Turnock 1992; Hammond *et al.* 1995; Cañadas, Desportes & Borchers 2004). However, MR methods do make the assumption that, conditional on the covariates in the detection or capture function models, all objects in the population are equally likely to be 'marked' and 'recaptured' and, if this assumption is not valid, the resulting abundance estimate will be negatively biased (Barker 2008). Implementing both MR and DS methods on a survey is logistically more difficult than implementing only DS methods, but it does allow the advantages of each method to be employed. Borchers, Zucchini & Fewster (1998a) and Laake & Borchers (2004) provided a unifying theoretical basis for mark–recapture distance sampling (MRDS) methods, but prior to their implementation in program DISTANCE (Thomas *et al.* 2010), user-friendly software to implement the methods was lacking. Program DISTANCE has for many years been used for analysing conventional DS data, and now, that MRDS methods have been incorporated in it. DISTANCE is a convenient

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software package for analysing MRDS survey data as well. Some extensions to basic DS are described in Marques *et al.* (2007), which deals with modelling the effects of explanatory variables (in addition to distance) on detection probability, and Miller *et al.* (2013), who provide practical advice for modelling spatial distributions using DS methods. This study is to explain key MRDS methods and design concepts and to provide guidance on using them appropriately. Two case studies, with fully worked analyses, serve as a tutorial. We begin by considering conventional DS estimators and simple MR estimators before considering MRDS estimators and analysis issues. An introduction to DS and MR follows below, while more extensive details of DS and MR are provided in Appendix S1 in Supporting Information.

Conventional distance sampling

Wild populations are often cryptic, or the region of interest is too large to undertake a census and so sampling strategies are required (Buckland *et al.* 2001). Distance sampling has been used to survey a wide variety of taxa, from plants to vertebrates (e.g. Focardi, Isotti & Tinelli 2002; Buckland *et al.* 2007), in different habitats, from the tropics to polar regions (e.g. Plumptre 2000; Wegge & Storaas 2009; Heide-Jørgensen *et al.* 2010), using a range of survey platforms, such as boats, planes, helicopters, cars and walking observers (e.g. Marini *et al.* 2009; Schnupp *et al.* 2013). Lines, or points, are laid down at random (or with some random component), and an observer travels along the lines, or stands at points, collecting information about the target species. Here, we concentrate on line transects rather than points, but the methods are applicable to both. Using a conventional line transect DS search protocol, a single observer (where the term observer is used to mean either a single observer or a team of observers performing the same role) searches for the objects of interest from the tracklines. On detecting an object, the observer records the perpendicular distance (y) from the trackline to the object. The probability of detection is then modelled as a function of distance, $g(y)$, under the assumption that all objects on (or very close to) the trackline will be detected [denoted by $g(0) = 1$)]. We refer to this as the DS model. The number of objects detected in the searched region (with area $2\,wL$ where w is the truncation distance of detections and L is the total length of transects covered) is then scaled up in inverse proportion to the probability of detection to obtain an estimate of the number of objects that would have been detected had detection been certain at all distances within w from the trackline. If detection on the trackline is not certain, the resulting abundance estimate will be negatively biased. A key assumption is that objects have not moved in response to the observer before being detected: if objects are detected after moving towards the observer, the probability of detection will be underestimated; likewise, if objects are detected after they have moved away from the observer, the probability of detection will be overestimated. MR methods provide a way of estimating detection probability on the trackline and, with certain observer configurations, can accommodate responsive movement.

Simple mark–recapture

Mark–recapture methods can be used on DS surveys with two independent observers acting as 'capture occasions'. Search protocols for using MR methods on DS surveys are more complicated as there needs to be (at least) two opportunities for detection of the same object; firstly to 'mark' it through initial detection and secondly to 'recapture' it through detection by the other observer. This could mean that there are two human observers or 'observer' could be an acoustic sampler or radio detector of radio-tagged objects. Objects detected by both observers are termed duplicates, and it is important that duplicates can be identified as such. If all animals are equally detectable, the Lincoln–Petersen MR estimator (Petersen 1896; Lincoln 1930) can be used to estimate the probability of detection for observer 1. It is conditional on some objects having been previously marked, and in the DS context, this is done by observer 2 who conceptually (but not physically) 'marks' objects by detecting them. Given that observer 2 detected n_2 objects, the conditional probability of observer 1 detecting an object can be estimated by $\hat{p}_{1|2} = m/n_2$, where m is the number of duplicates; $\hat{p}_{2|1}$ can be estimated similarly. If all objects in the population (i.e. objects marked and unmarked) are equally likely to be detected, then these conditional probabilities of detection apply to the whole population, and not just to the marked objects, and an estimate of the population can be obtained using the Lincoln–Peterson MR estimator or the modified estimator of Chapman (1951). If detections by each observer are independent, these conditional probabilities can also be used to estimate the probability of detection by at least one observer using $\hat{p}_{1\cup 2} = \hat{p}_{1|2} + \hat{p}_{2|1} - \hat{p}_{1|2}\hat{p}_{2|1}$. However, if objects are not equally detectable, then ignoring any differences in detectability can lead to negatively biased abundance estimates using these simple MR estimators (e.g. Walter & Hone 2003). This is because both observers preferentially sample the more detectable animals, so the abundance estimate tends towards the abundance of more detectable animals, rather than of all animals. (In the most extreme case, if both observers detected only the more detectable animals, it would be the abundance of more detectable animals, not all animals, that is estimated.) More sophisticated estimators have been developed that alleviate this problem (e.g. Huggins 1989), by including distance and other explanatory variables in the detection probability model.

More complicated MR models

Detections by observer 1 can be thought of as setting up a trial for the observer 2 and *vice versa*; a success means detection by the other observer, and a failure means the other observer failed to detect the same object. A logistic regression model can be fitted to the success/failure data to provide an estimate of the probability of detection for an observer, given detection by the other observer, based on perpendicular distance (y) and other explanatory variables ($\underline{z}$), $p_{j|3-j}(y, z)$:

$$p_{j|3-j}(y, \underline{z}) = \frac{\exp\left(\beta_0 + \beta_1 y + \sum_{k=1}^{K} \beta_{k+1} z_k\right)}{1 + \exp\left(\beta_0 + \beta_1 y + \sum_{k=1}^{K} \beta_{k+1} z_k\right)}$$

where j (j = 1,2) is observer and the β s are the model coefficients. The above equation can be viewed as a generalization of the Lincoln–Petersen estimator to include explanatory variables y and $\underline{z}$. It is also referred to as the conditional detection function because of its dependent nature; estimation of one observer's detection function is conditional on the other observer having detected the object. If we assume that the above conditional probability on the trackline (at $y = 0$) is the same as the unconditional probability on the trackline, detection probability on the trackline can be estimated by evaluating it at distance zero, rather than assuming detection to be certain at distance zero.

INDEPENDENCE AND UNMODELLED HETEROGENEITY

The detection probabilities of two observers may be correlated even when the observers act independently and objects are always available. Laake *et al.* (2011) provided a detailed explanation of this apparent paradox; we describe it briefly here. If an object is a long way from the trackline, then it is more likely to be detected if, say, it is a large object. Thus, if observer 1 detects an object with a long perpendicular distance, it is likely to be a large object and, because it is a large object, observer 2 is also more likely to detect it. Detections by the two observers are not independent; variation in a covariate that is not in the model and which affects detection probability (object size in our example) has induced dependence. Leaving variables that affect detection probability out of the detection probability model (e.g. Beaufort sea state, vegetation type) results in what is called 'unmodelled heterogeneity' in detection probability. This induces positive bias in detection function estimates and negative bias in object abundance estimates – because (in our example) large objects are preferentially sampled and large objects are both more detectable than randomly selected objects on average and less abundant than all objects. The bias is removed if the offending variables are included in the model – in this example, the effect of object size on detection probability could be 'explained' by the model. Therefore, it is important to include all variables affecting detection probability in the MR model. If unobserved or unrecorded variables affect detection probability, correlation in detection probabilities may persist even when the effects of all recorded variables are modelled (i.e. 'unmodelled heterogeneity' remains).

A useful indication of dependence in detections lies in the comparison of the shapes of the MR model and the DS model. If detections are independent, then we expect the shapes of these detection functions to be the same (i.e. we expect the proportions of duplicate detections to decrease as perpendicular distance increases at the same rate that the number of unique detections decreases with increasing perpendicular distance). A difference in the shapes of the MR and DS detection functions indicates dependence in detections. If the MR model falls off more slowly than the DS model, this indicates detections between observers become more positively correlated as distance increases. Point independence (PI) is designed to deal with this phenomenon. We describe it below and contrast it to 'full independence', which is typical of MR models and can be used with MRDS models too. We also briefly describe a generalization of PI, called 'limiting independence', due to Buckland, Laake & Borchers (2010).

POINT INDEPENDENCE AND FULL INDEPENDENCE

As explained above, if some variables that affect detection probability are not included in the model, this results in detection probabilities that are not independent – a phenomenon that has long been recognized in the MR literature (Seber 1982). MR models sometimes deal with this by introducing random effects in detection (or capture) probability models (e.g. Burnham 1972; Pledger 2000; Dorazio & Royle 2003). MRDS models could do the same (although this has not yet been done), but MRDS models have an advantage over MR models that can be exploited to deal with the problem in a different way: the distribution of distances (of detected and undetected objects) can be assumed known on DS surveys (and is assumed known in conventional DS theory), and this allows the shape of detection functions to be estimated without MR data.

In the case of randomly placed line transects, distances are uniformly distributed, by design. (After accounting for the geometry, similar ideas lead to a triangular distribution for points.) A consequence of this is that the shape of the histogram of detection distances is (aside from random variation) identical to the shape of the detection function on line transect surveys. Therefore, the shape of the detection function can be estimated without MR data – which is not possible on MR surveys proper (because they lack an explanatory variable such as distance, with known distribution). The difference between this shape and the shape of the duplicate proportion distribution contains information about unmodelled heterogeneity, and the extent of any unmodelled heterogeneity can almost be estimated from the difference between the two shapes. In fact, it cannot be estimated without knowing what the unmodelled heterogeneity is at some point, and this is where 'PI' comes in. When detection probability is one for all objects, unmodelled heterogeneity must be zero because there is by definition no heterogeneity in detection probability. A PI model assumes that there is no unmodelled heterogeneity (i.e. that there is independence) at a given point (typically at perpendicular distance zero) and then uses the difference between MR and DS detection function shapes to model the increase in dependence as distance increases (see later examples). The PI assumption is incorporated by using the DS model to obtain the shape of the detection function and the MR model to estimate the probability of detection on the trackline (i.e. the intercept) – by assumption, there is no unmodelled heterogeneity on the trackline. Laake & Borchers (2004) coined the term 'PI', but Laake (1999) initially developed the model under the name of 'trackline conditional independence'. The DS model has the same form as the models fitted in conventional DS (Buckland *et al*. 2001) or multiple covariate DS (Marques & Buckland 2004).

Full independence (FI) models assume that there is no dependence (no unmodelled heterogeneity) at any distance and that the MR estimator is an unbiased estimator of detection probability – clearly a more stringent assumption than PI. There are two varieties of FI model: both assume no unmodelled heterogeneity, but one uses only the duplicate proportion data, while the other also uses the assumption of uniformly distributed distances and the data on the change in detection frequency as distance increases, to inform estimates of detection function shape. The former is just a particular variety of the MR model developed by Huggins (1989) – one that includes distance as an explanatory variable. We refer to it as an MR FI model. The latter incorporates the DS assumption of uniform object distribution in the vicinity of the sampler, and we refer to it as an MRDS FI model. Laake, Dawson & Hone (2008) discuss further the difference between MR FI and MRDS FI models.

Full independence models are simpler and have fewer parameters than PI models and, if the FI assumption holds, they would be preferable. However, it is often very difficult to be sure that this assumption holds. Limiting independence models (Buckland, Laake & Borchers 2010) use the MR and DS shapes in the same way as PI, but assume that there is no dependence only when detection probability reaches one, which it may not do, even at distance zero. Limiting independence models were found by Buckland, Laake & Borchers (2010) to be useful for diagnosing whether FI or PI assumptions were reasonable. However, they found that strong dependence between observers' detection probabilities can lead to unreliable estimation using limiting independence models and these models are not implemented in program DISTANCE.

MODEL OPTIONS

Central to MRDS analyses are the assumptions made about the nature of independence of detections between observers in the MR model and the distribution of distances in the DS model. In a conventional DS model, distance is assumed to be uniformly distributed, and it is only the rate at which the probability of detection away from the trackline changes that is of concern; the intercept of the model [i.e. $g(0)$] is assumed known and fixed at one. Incorporating the MR component allows the probability of detection on the trackline to be estimated in an MRDS model. If the distribution of distance cannot be assumed known, then both the probability of detection on the trackline and the probability of detection away from the trackline are estimated from the MR model. The only FI model implemented in DISTANCE at present is the MR FI model. This involves only a MR model. By contrast, a PI model (also implemented in DISTANCE) requires both a DS and a MR model. MRDS FI models, which assume both FI and a known distribution of distances, such as those described in Buckland, Laake & Borchers (2010) and Laake *et al*. (2011), are not yet incorporated into DISTANCE. Table 1 summarizes the models used depending on the assumptions made.

Double-observer configurations

A key consideration of a MR survey is the observer configuration, and with two observers (or two observer platforms), two search configurations are possible. When they search independently of each other, this is referred to as an independent observer (IO) configuration. An alternative configuration is one in which there is only one-way independence; Laake & Borchers (2004) called this a trial configuration, but it is also known as BT mode after Buckland & Turnock (1992) who first proposed it. A third, removal configuration will not be considered here, but it is often used with bird surveys (e.g. Farnsworth *et al*. 2002).

IO CONFIGURATION

In an IO configuration, the two observers search independently of each other. Detections by each observer serve as trials for the other, in which the outcome is either a 'success', corresponding to detection by the other observer, or a 'failure', if the other observer does not detect the object. Thus, the responses (detections of objects) are binary (success or failure), and the detection functions (the probabilities of success) can be modelled as logistic functions, using the method of Huggins (1989) who estimated capture probabilities in MR surveys. Huggins (1989) incorporated individual and environmental covariates into the logistic function, and using a similar approach, Buckland *et al*. (1993) included perpendicular distance as one of the possible covariates.

An IO configuration is useful when objects are unlikely to have moved in response to the survey platform between detection by one observer and detection by the other observer. Strictly, all DS methods require objects to be stationary as if a 'snapshot' was taken at the time of the survey. Conventional DS models are reasonably robust to low levels of movement (Turnock & Quinn 1991), but the robustness of MRDS models to movement remains un-investigated. When there is movement and each observer records a different distance to

Table 1. Summary of the models used depending on whether point independence (PI) or full independence (FI) is assumed and whether or not objects must be assumed to be uniformly distributed

Independence assumption	Must assume uniform distribution of animals	Model used
FI	No	MR only
FI	Yes	MRDS[1]
PI	Yes	MRDS

DS, distance sampling; MR, mark–recapture.
[1]The models in this row are not in DISTANCE; see Buckland, Laake & Borchers (2010) or Laake *et al*. (2011) for details.

duplicates, it is common practice to take the first distance as the object's distance as this will be closer to the object's original position. A more satisfactory approach would be to develop models that incorporate movement, but this is not straightforward and remains to be done.

Another potential problem with (single- and) double-observer surveys is that changes in availability of the object of interest can introduce bias (e.g. Heide-Jørgensen *et al.* 2010). For example, if the observers are in a fast-moving airplane when an animal is above-ground, or at the surface, and hence available to one observer, then it will also be available to the other observer; likewise, some animals will be unavailable to both observers. If availability is ignored, the overall probability of detection will be overestimated – it will be an estimator of detection probability conditional on the animal being available – and abundance will be underestimated because it will tend to be an unbiased estimate of the abundance of available animals only. The converse can also happen, with an animal being available to be detected by one observer making it less available for another observer; for example, in a marine environment, if one observer is an acoustic 'observer' and the other is a visual observer, then an animal under water is available to the acoustic observer and less available (or unavailable) to the visual observer (depending on its depth underwater). Bias due to availability is removed if the observers search for objects at times that are sufficiently different that availability for one observer is uncorrelated with availability for the other observer (Hiby 1999). There is, however, a trade-off: correlation is reduced by having a long time between observers searching the same area, but the greater the separation time the more difficult it is to identify duplicates. Trial configuration can help with this issue.

TRIAL CONFIGURATION

The function of one of the observers (who we will call observer 2, or the 'tracker') in a trial configuration is simply to generate trials for the other observer (observer 1, also called the 'primary observer'). The successes and failures of the primary observer to detect the trials set up by the tracker (i.e. animals detected by the tracker) generate binary data from which the detection function of the primary observer can be estimated. No attempt is made to estimate the tracker's detection function and so it is of no consequence if the tracker misses other animals while following (or 'tracking') one of these 'trial' animals. The tracker can therefore search far ahead of the primary observer without compromising duplicate identification (because tracking an animal makes duplicate identification for that animal relatively easy). Searching far ahead introduces a separation between the times animals are first available for observer 2 and first available for observer 1 to detect. This helps reduce correlation due to availability – and will remove it altogether if the time separation is sufficiently long. How long 'sufficiently long' is depends on the animal availability process: if the mean availability cycle time (the mean time from becoming available until next becoming available) is short, a shorter separation will be required to achieve independence than if the mean availability cycle is long. Separating the observers' search areas in this way with IO configuration is usually infeasible because it makes duplicate identification too difficult.

Even without such separation, duplicate identification is less error-prone with trial configuration, because only one decision about duplicate status needs to be made at any time (whether or not the tracked animal has been seen by the primary) and the tracker is following the animal in question. With IO configuration, each observer may have to focus on multiple animals at any one time, none of which is being carefully tracked. Laake & Borchers (2004) discussed these issues in more detail.

The trial configuration can also help reduce bias due to responsive movement. The idea is that the tracker searches a region sufficiently far ahead that objects are unlikely to have reacted to the observer's presence before being detected. By using the perpendicular distances of the trial detections at the time the tracker detects them when estimating the primary observer's detection function, we get a detection function estimate for the primary that is unaffected by responsive movement (providing there was no response prior to the tracker detecting animals). The tracker's search region must be sufficiently wide that objects outside of it could not enter the region searched by the primary; otherwise, object density (or abundance) will be estimated with positive bias. The primary must act independently of the tracker, but the tracker can be aware of primary detections (in order to facilitate duplicate identification) without compromising unbiased estimation of the primary detection function. In this case, detections by the primary cannot serve as a set of trials for the tracker because the tracker is aware of detections of the primary. Difficulties may arise in duplicate identification in a high-density region or if animals are not continuously available. For example, 20% of harbour porpoise detections considered to be possible duplicates by Hammond *et al.* (2013) could not be classified by them as definitely being duplicates (see Table A2 in their supplementary material). In some situations, it may be helpful to have a third person assessing duplicate status.

RESPONSIVE MOVEMENT

A trial configuration is often used when responsive movement is anticipated; here, the tracker looks sufficiently far ahead to detect objects before they have responded, as described above. However, the PI model is untenable if objects move in response to the presence of observers (or survey platform). This is because PI models use the shape of the DS model (more specifically, how this differs from the shape of the MR model) to infer the degree of correlation in detection probability as perpendicular distance increases and to infer the shape of the detection function. With movement, the shape of the DS model obtained from the primary detections will incorporate both the effects of responsive movement and the decline in detection probability due to increasing perpendicular distance; this will lead a PI model to biased inference about the degree of correlation and shape of the detection function, and estimates of detection probability and abundance will be biased as a result. The effects of responsive movement and unmodelled heterogeneity cannot be separated (for more details, see Cañadas, Desportes & Borchers 2004; Borchers *et al.* 2006). Obviously, responsive movement will not occur if the objects being detected are stationary, or if the observers move so quickly that there is too little time for the objects to move between detections, as is the case on many aerial surveys. If responsive movement is anticipated, then a MR FI model may be more appropriate because it does not use the assumption of uniform animal distribution. It uses only the proportions of duplicates at various distances to estimate detection probability as a function of distance (and other explanatory variables).

When there may be responsive movement on MRDS surveys, the analyst has to decide between two unsatisfactory choices: if PI is assumed, estimates of abundance may be biased due to movement; and if FI is assumed, estimates may be biased because there is unmodelled heterogeneity. It is a judgement call as to which is best in this circumstance – the MRDS data cannot help. The effects of responsive movement are illustrated in our cetacean case study below.

Example analyses

The analysis methods described above are available as an R (R Core Team 2012) package called mrds (Laake *et al.* 2013) and so can be accessed directly via the R environment, but this does require some understanding of R. However, the R package can now be accessed via DISTANCE (Thomas *et al.* 2010), and this provides an accessible route to these analysis options for those not familiar with R. We illustrate the use of an IO configuration using a survey of deer and elk faecal pellets (Jenkins & Manly 2008); a trial configuration is illustrated using data collected during a cetacean survey where one species of interest exhibited responsive movement (Cañadas, Desportes & Borchers 2004). We do not reanalyse these data here, and we merely use the data to illustrate the analysis methods. All analyses were performed in DISTANCE v6.1 Beta 1 (Thomas *et al.* 2010) using MRDS version 2.0.6 (Laake *et al.* 2013), and the DISTANCE project for Example 1 is available as Supporting Information S3.

PREPARATORY ISSUES

The reader is referred to the DISTANCE online manual for help with preparation of MRDS data as this is slightly different to that required for conventional DS data (also see Appendix S2 in Supporting Information). Prior to importing the data into DISTANCE, a preliminary examination of the data is recommended, for example to assess sample size. Understanding the data before fitting a detection function is particularly useful to identify potential assumption violations, for example, by plotting the distribution of distances with a large number of bins. If factor variables are being considered as potential covariates, then it may be necessary to combine factor levels using knowledge about which levels are likely to have similar detection functions (Marques *et al.* 2007).

For each unique object detected, two records are required in the 'Observation' data layer; one record for observer 1 and one for observer 2. A field called 'observer' denotes the observer (1 or 2), and a field called 'detected' indicates whether the observer detected the object or not (1 or 0, respectively). The perpendicular distance between the pair of records for each object should be the same – this is straightforward if only one observer saw the object – the information recorded by one observer is repeated for the other observer. Inserting this information for duplicates may not be as straightforward because the observers may have recorded different perpendicular distances. A scatterplot of observer 1's distances vs. observer 2's distances from duplicate detections could be used to check for any systematic bias in the measurements. When these differences in distance are likely to be due to measurement error, rather than due to movement between duplicate detections, a pragmatic approach is suggested, for example using the average perpendicular distance. With a trial configuration, where there could have been responsive movement between the tracker and the primary detections, perpendicular distances from the tracker should be used – the tracker should have detected the objects before any responsive movement. Borchers *et al.* (1998b) dealt with differences in group size estimation between observer 1 and observer 2 during a trial configuration survey; assuming observer 2 recorded more reliable group sizes than observer 1, they estimated a factor from duplicate detections to correct bias in observer 1 estimates.

EXAMPLE 1: SURVEY USING AN IO CONFIGURATION

An IO configuration was used during a survey of deer and elk faecal pellet groups conducted in Olympic National Park, USA, during the spring of 2001 and 2002 (Jenkins & Manly 2008). Two-stage stratified random sampling was used to distribute 4060 sampling units (400 m by 400 m grid cells) throughout the park, and data were collected from 102 sampling units. Two transects were chosen at random from a subsample of four 200 m, parallel line transects, located about 25 m apart, in each sampling unit. Observers worked in pairs; each observer in the pair surveying different transects as observer 1 and then switching transects to search as observer 2. Observers recorded the distance of the faecal group along the trackline, perpendicular distance from the faecal group to the trackline, species, the number of pellets and pellet clumps (a clump comprised of 5 or more pellets compressed together), pellet condition and ground vegetation cover. The observers determined duplicates by comparing records and any ambiguities were resolved by observers revisiting the location. We do not explore the full range of variables available in these data, which would be necessary for a complete analysis to model heterogeneity (for that see Jenkins & Manly 2008); instead, we fit simple models to illustrate the methods described earlier.

Observer 1 detected 1094 faecal groups, observer 2 detected 1102 groups, and there were 816 duplicates giving 1380 unique detections (Table 2). The distributions of perpendicular distances for each observer are shown in Fig. 1 along with the duplicate detections.

Table 2. Number of detections of faecal pellet groups [Example 1; independent observer (IO) configuration] and common dolphin groups (Example 2; trial configuration) by each observer. In Example 2, detections have been truncated at a perpendicular distance of 560 m (0·3 nmiles), and observer 1 is the primary and observer 2 is the tracker

Number of detections	Example 1	Example 2
Detected by observer 1	1094	74
Detected by observer 2	1102	63
Duplicates	816	50
Unique detections	1380	87

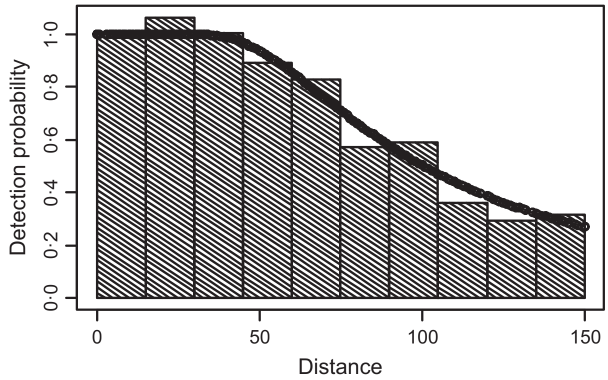

Fig. 2. Distance sampling (DS) model fitted assuming that detection is certain on the trackline [$g(0) = 1$] and overlaid onto the scaled histogram of perpendicular distances (cm) of all unique detections of faecal pellets.

Point independence assumption

To implement a model with the PI assumption, both a DS model and an MR model need to be specified. The DS model is fitted to the perpendicular distance distribution of all unique detections assuming that detection on the trackline was certain, and here, a simple hazard rate form was chosen for the detection function (Fig. 2). We refer the reader to Marques *et al.* (2007) for information on including explanatory variables into the DS model. [With an IO configuration, all detected objects are included in the DS model, whereas with a trial configuration, only objects detected by primary (observer 1) are included.]

The MR model used here included perpendicular distance and a factor variable that categorized the number of pellets into four group sizes (very small, small, medium and large) (Fig. 3). The histograms in Fig. 3 are the empirical estimators of the conditional detection functions; the heights of the histogram bins in Fig. 3 are obtained from the number of duplicates divided by the number of each observer's detections within each distance bin shown in Fig. 1 (i.e. Fig. 3a is derived from Figs 1b and 3b is derived from Fig. 1a, but note, for presentation purposes, different bin widths between Figs 3 and 1). From the fitted MR model, the probability of detection on the trackline by an observer, given that it was detected by the other observer [denoted by $p_{j|3-j}(0)$, $j = 1$ or 2], was 0·795 (CV = 0·021). Note that 'observer' can be included in the model as an explanatory variable, so $p_{1|2}(0) \neq p_{2|1}(0)$, but in this case, it was not selected by Akaike's Information Criterion (Akaike 1973). The probability of detection on the trackline by at least one observer, averaged over all covariates, $p(0)$, was estimated to be 0·942 (CV = 0·010).

With the PI assumption, the overall detection probability function is obtained by combining the shape of the detection function estimated from the DS model and the intercept parameter obtained from the MR model (Fig. 4a, Table 3). The probability of detection obtained from the DS model [i.e. assuming $g(0) = 1$] was 0·692 (CV = 0·032), and multiplying this by our estimate of $p(0)$, 0·942 (CV = 0·010), resulted in overall probability of detection of 0·652 (CV = 0·033).

Full independence assumption

If the FI assumption had been chosen, the DS model would not be required and the MR model would be used to estimate both the probability of detection on the trackline (which is the intercept of the detection function) and the probability of detection away from the trackline (which gives the shape of the detection function). Figure 4b shows the fitted model under the FI assumption (which in DISTANCE is an MR FI model)

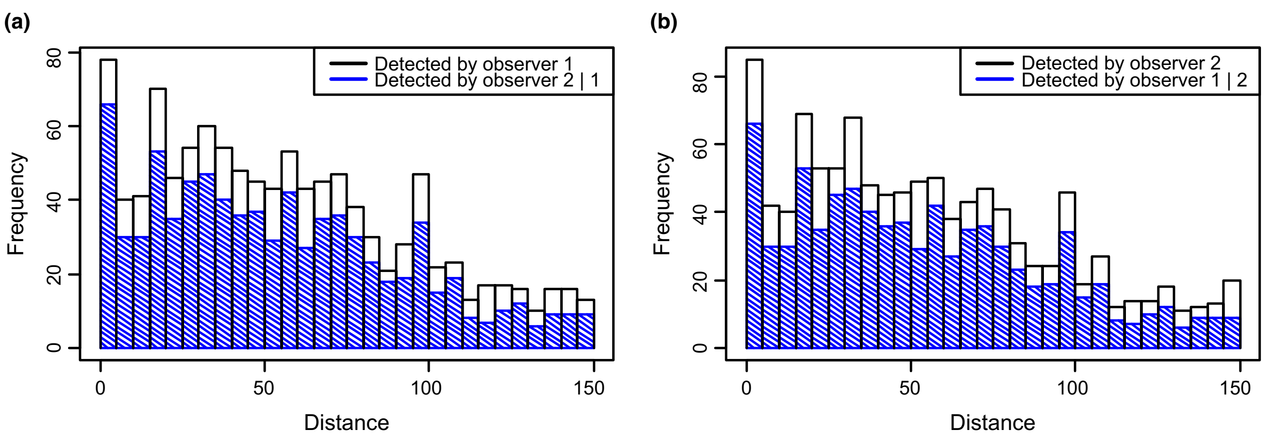

Fig. 1. Histograms of perpendicular distances (cm) of detections recorded by (a) observer 1 and (b) observer 2 during the faecal pellet survey (observers had a tendency to record distances to the nearest 5 cm). The shading indicates duplicate detections.

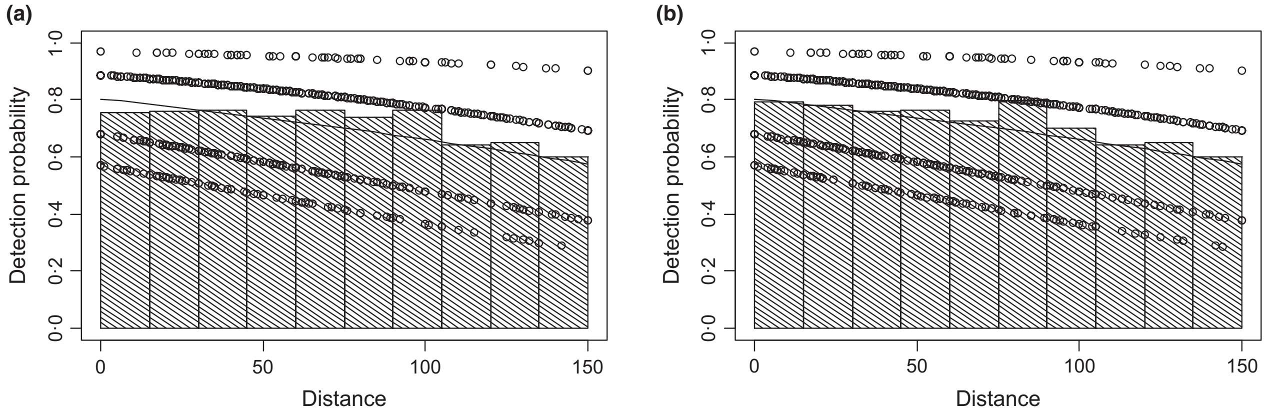

Fig. 3. Conditional detection functions from the faecal pellet survey for (a) observer 1 given detection by observer 2 and (b) observer 2 given detection by observer 1, and the fitted MR model averaged over pellet size class (solid line). The dots are the estimated detection probability for individual detections (large pellet class at the top and very small at the bottom).

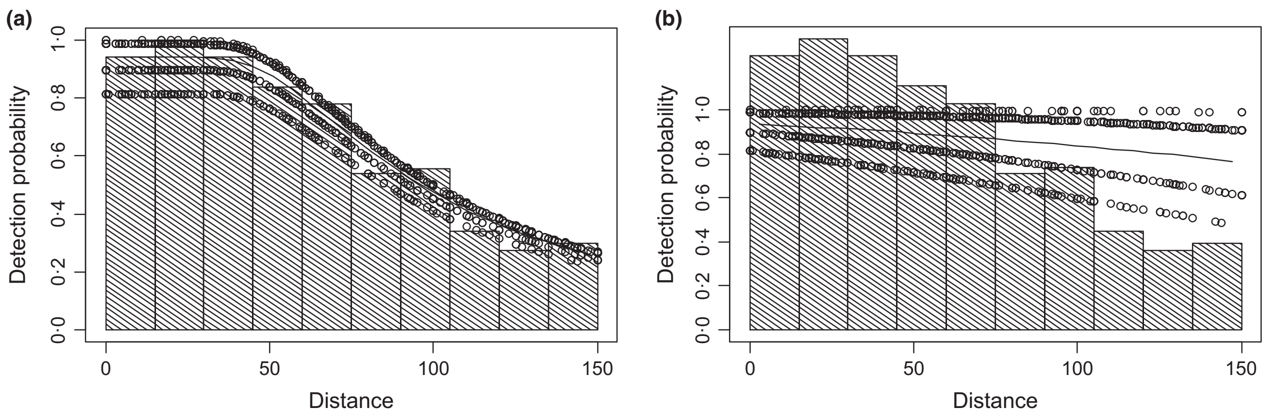

Fig. 4. Fitted MRDS model under the (a) point independence assumption (solid line) and (b) full independence assumption overlaid onto the scaled distribution of perpendicular distances (cm) of all unique detections of faecal pellets. The dots are estimated detection probabilities for individual detections.

Table 3. Probabilities of detection obtained from the distance sampling (DS) and Mark–recapture (MR) models (averaged over all covariates where appropriate). CVs are given in parentheses, and a dash indicates that the probability was not applicable. The notation $p_{j|3-j}(0)$ (j = 1 or 2) denotes the probability of detection on the trackline by observer j given detection by observer 3 − j; $p_{1\cup 2}$ (0) is the probability of detection on the trackline for both observers combined

	Example 1: faecal pellets		Example 2: pilot whales	
	Point independence		Full independence	
Probability	Model used	Estimate	Model used	Estimate
Probability of detection assuming $g(0) = 1$	DS model	0·692 (0·032)	–	–
$p_{1\|2}$ (0)	MR model	0·795 (0·021)	MR model	0·796 (0·106)
$p_{2\|1}$ (0)	MR model	0·795 (0·021)	–	–
$p_{1\cup 2}$ (0)	MR model	0·942 (0·010)	–	–
Overall probability of detection	MRDS	0·652 (0·033)	MR model	0·772 (0·107)

using the same MR model as used previously; the overall probability of detection from this model was 0·862 (CV = 0·017), which was substantially larger than the estimate from the PI model. Note that while the fit of the PI model to the distribution of distances of detected pellet groups is good (Fig. 4a), the fit of the FI model to this distribution is very bad (Fig. 4b) even though the conditional detection function model fits the duplicate proportions well (Fig. 3). The lack of fit of the FI model, evident in Fig. 4b, is a substantial indicator that the FI model is inadequate. In fact, it was this symptom of model inadequacy that led to the development of PI (see Laake 1999; Laake & Borchers 2004; Buckland, Laake & Borchers 2010). In this example, the PI assumption is more appropriate: there was no issue with responsive movement and so no reason to doubt that the shape of the histogram of perpendicular distances (Fig. 2) reflects the shape of the detection function.

EXAMPLE 2: SURVEY USING A TRIAL CONFIGURATION

The analysis of a trial configuration is illustrated using a cetacean survey conducted from a ship around the Faroe Islands in 1995 (data available with permission from the Faroese Museum of National History); the focus of the survey was the long-finned pilot whale, but data were collected on all species encountered and of interest here are detections of common dolphins (Cañadas, Desportes & Borchers 2004). The primary observers (observer 1) searched with naked eye for marine mammals within 1 km (0·5 nmile approximately) of the ship and 90° either side of the trackline; the trackers (observer 2) searched an area ahead of the primary observers (*c.* 1 km ahead of the vessel) with 7 × 50 binoculars. One tracker searched a sector 60° either side of the trackline, while another tracker searched up to 90° either side of the trackline. Once detected by the trackers, animals were followed until they were detected by the primary observers or passed abeam. The primary observers were visually and audibly isolated from the trackers; a third observer on the tracker platform was in contact with both observer teams and determined duplicate status.

A truncation distance of 560 m (0·3 nmiles) was chosen by Cañadas, Desportes & Borchers (2004) which left 74 groups of dolphins detected by the primary, 63 groups detected by the tracker and 50 groups detected by both (Fig. 5) for a total of 87 unique detections (Table 2). With a trial configuration, only the detection probability of the primary is of interest, but prior analysis suggested substantial movement of animals towards the ship by the time they were detected by the primary (Cañadas, Desportes & Borchers 2004). As a consequence, the distribution of distances recorded by the primary (Fig. 5a) no longer just reflects the shape of the detection function, but reflects a combination of detectability and responsive movement. If animals are attracted to a survey vessel, as in this case, the shape of the primary distance distribution will have more of a peak near perpendicular distance zero than the true shape of the detection function. For example, if detection probability was constant over the whole range of perpendicular distances searched by the primary (i.e. the detection function was flat), the distribution of distances of detected objects would still be peaked because attractive movement has led to there being more objects to detect close to the trackline than far from it. We therefore use a FI model to analyse these data.

The number of trials generated by the tracker and the number of duplicates are shown in Figure 5b, from which the empirical conditional detection function was obtained (Fig. 6). We fitted the MR model selected by Cañadas, Desportes & Borchers (2004), which included perpendicular distance, Beaufort sea state and group size as explanatory variables (Fig. 6). From this model, the probability of detection on the trackline by the primary observer, given detection by the tracker, was estimated to be 0·796 (CV = 0·11).

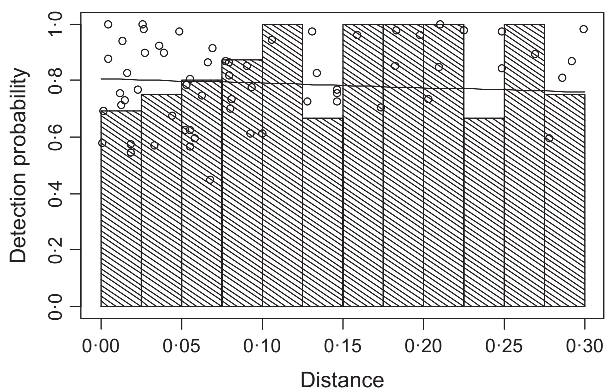

Fig. 6. The conditional detection function for observer 1 (primary) given detection by observer 2 (tracker) and fitted MR model for the common dolphin data averaged over covariates in the model (solid line). The dots are estimated detection probabilities for individual detections. Perpendicular distances are in nmiles.

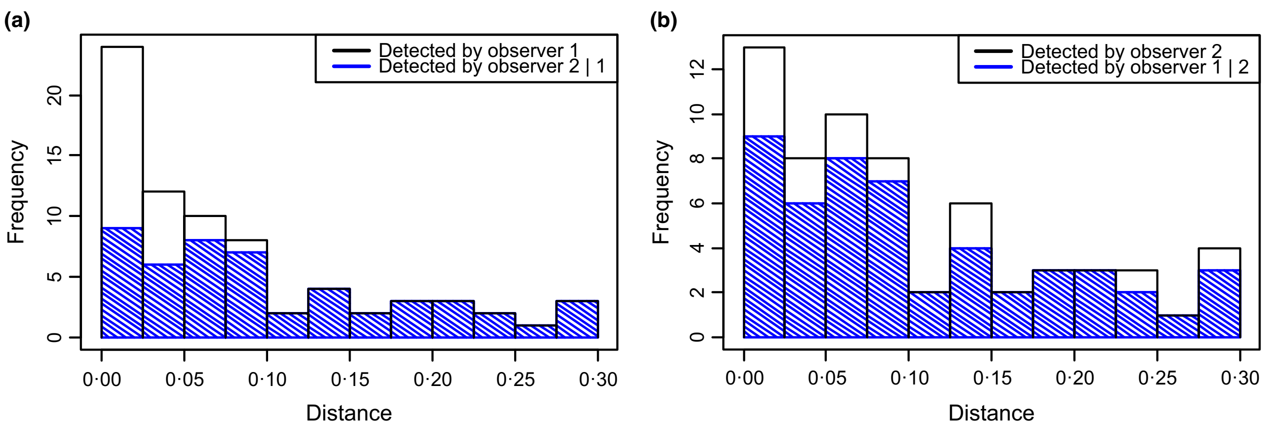

Fig. 5. Histograms of perpendicular distances (nautical miles and truncated at 0·3 nmiles which is 560 m) of common dolphin groups recorded by (a) observer 1 (primary) and (b) observer 2 (tracker). The shading indicates duplicate detections.

A FI model (Fig. 7b) involves only an MR model (and no DS model), and the overall probability of detection by the primary was estimated to be 0·772 (CV = 0·11). With the PI model (using a hazard rate form for the DS model, Fig. 7a), the overall probability of detection by the primary was 0·178 (CV = 0·29), which is less than a quarter of the estimate obtained under FI. Just as in the previous example, there is a difference in the shape of the detection function fitted to primary detections (Fig. 5a) and the conditional detection function (Fig. 6). However, in the previous example, this difference could be explained by dependence between detections and so covariates could be included into the MR model to explain the heterogeneity of detections. In this example, it may be that the lack of fit evident in Fig. 7b is due to both responsive movement and the violation of the FI assumption, and without additional information, it is impossible to say whether it is one, or both, of these reasons. Hence, preference for a FI or PI model is partly a subjective judgment: if responsive movement is the main problem, then FI should be used; if violation of the FI assumption is the main problem, then PI is preferable because it has less restrictive assumptions. In this particular example, Cañadas, Desportes & Borchers (2004) believed that responsive movement was the major problem, and therefore, the estimates of detection probability from FI model were used to estimate density and abundance.

Discussion

Implementing a double-observer configuration increases the complexity of the survey protocol and subsequent data

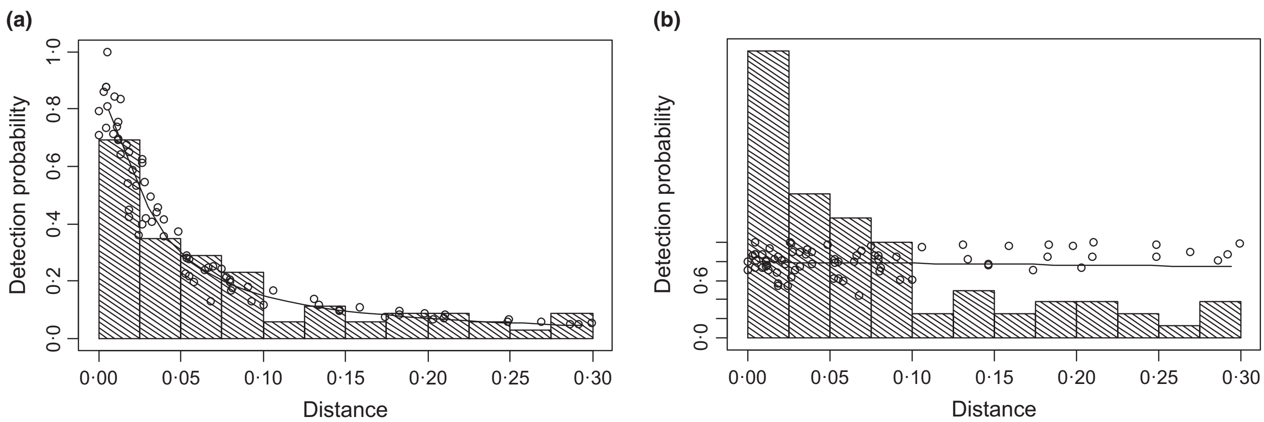

Fig. 7. Fitted MRDS model for the common dolphin data under (a) the point independence assumption and (b) the full independence assumption. The MRDS model (solid line) is overlaid onto the scaled histogram of primary distances. The dots are estimated detection probabilities for individual primary detections. Perpendicular distances are in nmiles.

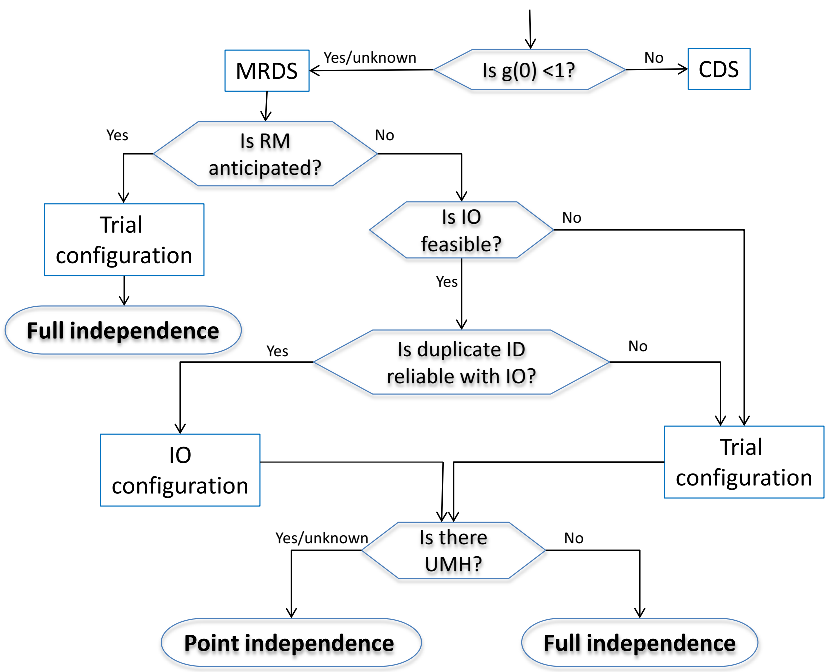

Fig. 8. Decision tree summarizing the survey types, observer configurations and analysis options available (CDS, conventional distance sampling; MRDS, mark–recapture distance sampling; RM, responsive movement; IO, independent observer configuration; ID, identification; UMH, unmodelled heterogeneity).

management. However, the benefit of being able to estimate detection on the trackline, or check that it is indeed one (or close to one), is clearly important. With two observers, different observer configurations give flexibility in search protocol, which can be chosen to suit the type of survey and species of interest. Program DISTANCE (Thomas *et al.* 2010), which is widely used for the analysis of conventional DS data, provides an accessible tool for the analysis of double-observer data, making it easier for the user to assess the important assumptions and obtain the best possible estimates of density and abundance. The flow chart in Fig. 8 provides a useful reference to both the survey methods and analysis options that are available.

Different assumptions can be made regarding the data generation process (e.g. whether or not it involved responsive movement), and which assumptions are most appropriate can be assessed by comparing model fits, along with knowledge of the survey and the characteristics of the object of interest. Unbiased estimation using PI requires that duplicate detections are independent along the trackline only, whereas FI requires that detections are independent at all distances. Although it is less restrictive than FI, PI is untenable if there is responsive movement before detection and, in this case, it may be preferable to assume FI. Buckland, Laake & Borchers (2010) showed the PI assumption could be weakened further, by assuming that as the detection probability tended to one, the dependence between detections tended to zero, which they called 'limiting independence'. Between the two extremes of limiting independence and FI, there is a range of models of intermediate independence, and Buckland, Laake & Borchers (2010) developed methods to assess whether the FI or PI are reasonable assumptions to make.

Knowledge of the object of interest is essential so that the appropriate observer configuration can be implemented. In the first example given here, the data were collected using IO configuration and analysed under a PI assumption. This was appropriate because there was no problem with responsive movement and dependence in the detections between observers could be explained by including the relevant covariates in the MR model. The analysis indicated that, individually, the observers were detecting 80% (CV = 0·02) of objects on the trackline and combined, they were detecting 94% (CV = 0·01) of objects on the trackline. The second example was more problematic; a trial configuration was implemented during the survey and knowledge of the species' behaviour, and the difference in the shape of the DS and MR detection functions indicated that responsive movement could be biasing PI estimates, and therefore, FI was assumed. This is a stringent assumption to make, but the alternative PI assumption risked underestimating the detection probability, and hence overestimating abundance, because dolphins had been attracted to the vessel by the time the primary observers had detected them, and the attraction was believed to have been in response to the survey vessel.

The methods we described here all relate to line transect data; however, these MRDS methods can also be applied to point transects, and we refer the reader to Laake *et al.* (2011) for this. We hope that this study, along with Laake *et al.* (2011) and Laake, Dawson & Hone (2008) together with the availability of DISTANCE, will promote the use of MRDS methods to produce reliable estimates of abundance from MRDS surveys. For experienced R users, the package mrds (Laake *et al.* 2013) is available to download from the R-project website (cran.r-project.org). Double-observer methods have been used predominantly in marine applications, but as our examples have demonstrated, surveys involving double observers are also applicable for terrestrial surveys where detection on the trackline is imperfect.

Acknowledgements

Thanks are due to the Faroese Museum of Natural History, particularly D. Bloch and B. Mikkelsen for allowing us to use the common dolphin data and G. Desportes, coordinator and leader of the cruise. Thanks are also due to E. Rexstad for his encouragement and comments, B. Jacq for providing graphical design expertise, and P. Griffin and three anonymous reviewers for their valuable comments. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the US Government or other institutions conducting this study.

Data Accessibility

The data used in Example 1 are available as a DISTANCE project as in Appendix S3 and at http://distancesampling.org/Distance/example-projects/MEE_Burtetal_Example1.zip. The data used in Example 2 are available with permission from the Faroese Museum of Natural History (http://savn.fo/00534/).

References

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *International Symposium on Information Theory*, 2nd edn (eds B.N. Petran & F. Csàaki), pp. 267–281. Akadèemiai Kiadi, Budapest, Hungary.

Barker, R. (2008) Theory and application of mark-recapture and related techniques to aerial surveys of wildlife. *Wildlife Research*, **35**, 268–274.

Borchers, D.L., Zucchini, W. & Fewster, R.M. (1998a) Mark-recapture models for line transect surveys. *Biometrics*, **54**, 1207–1220.

Borchers, D.L., Buckland, S.T., Goedhart, P.W., Clarke, E.D. & Hedley, S.L. (1998b) Horvitz-Thompson estimators for double-platform line transect surveys. *Biometrics*, **54**, 1221–1237.

Borchers, D.L., Laake, J.L., Southwell, C. & Paxton, C.G.M. (2006) Accommodating unmodelled heterogeneity in double-observer distance sampling surveys. *Biometrics*, **62**, 372–378.

Buckland, S.T., Laake, J.L. & Borchers, D.L. (2010) Double observer line transect methods: levels of independence. *Biometrics*, **66**, 169–177.

Buckland, S.T. & Turnock, B.J. (1992) A robust line transect method. *Biometrics*, **48**, 901–909.

Buckland, S.T., Breiwick, J.M., Cattanach, K.L. & Laake, J.L. (1993) Estimating population size of the California gray whale. *Marine Mammal Science*, **9**, 235–249.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling*. Oxford University Press, Oxford.

Buckland, S.T., Borchers, D.L., Johnston, A., Henrys, P.A. & Marques, T.A. (2007) Line transect methods for plant surveys. *Biometrics*, **63**, 989–998.

Burnham, K.P. (1972) *Estimation of population size in multiple capture-recapture studies when capture probabilities vary among animals*. PhD thesis, Oregon State University, Corvallis, Oregon.

Cañadas, A., Desportes, G. & Borchers, D.L. (2004) The estimation of the detection function and $g(0)$ for short-beaked common dolphins (*Delphinus delphis*), using double-platform data collected during the NASS-95 Faroese survey. *Journal of Cetacean Research and Management*, **6**, 191–198.

Chapman, D.G. (1951) Some properties of the hypergeometric distribution with applications to zoological censuses. *University of California Publications in Statistics*, **1**, 131–160.

Dorazio, R.M. & Royle, J.A. (2003) Mixture models for estimating the size of a closed population when capture rates vary among individuals. *Biometrics*, **59**, 351–364.

Farnsworth, G.L., Pollock, K.H., Nichols, J.D., Simons, T.R., Hines, J.E. & Sauer, J.R. (2002) A removal model for estimating detection probabilities from point-count surveys. *The Auk*, **119**, 414–425.

Focardi, S., Isotti, R. & Tinelli, A. (2002) Line transect estimates of ungulate populations in a Mediterranean forest. *Journal of Wildlife Management*, **66**, 48–58.

Hammond, P.S., Benke, H., Berggren, P., Borchers, D.L., Buckland, S.T., Collet, A. *et al.* (1995) Distribution and abundance of the harbour porpoise and other small cetaceans in the North Sea and adjacent waters. LIFE 92-2/UK/027.

Hammond, P.S., Macleod, K., Berggren, P., Borchers, D.L., Burt, M.L., Cañadas, A. *et al.* (2013) Distribution and abundance of harbour porpoise and other cetaceans in European Atlantic shelf waters. *Biological Conservation*, **164**, 107–122.

Heide-Jørgensen, M.P., Laidre, K.L., Simon, M., Burt, M.L., Borchers, D.L. & Rasmussen, M. (2010) Abundance of fin whales in West Greenland in 2007. *Journal of Cetacean Research and Management*, **11**, 83–88.

Hiby, A.R. (1999) The objective identification of duplicate sightings in aerial survey for porpoise. *Marine Mammal Survey and Assessment Methods* (eds G.W. Garner, S.C. Amstrup, J.L. Laake, B.J.F. Manly, L.L. McDonald & G.G. Robertson), pp. 137–148. Balkema, Rotterdam.

Huggins, R.M. (1989) On the statistical analysis of capture experiments. *Biometrika*, **76**, 133–140.

Jenkins, K.J. & Manly, B.F.J. (2008) A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. *Journal of Applied Ecology*, **45**, 1339–1348.

Laake, J.L. (1999) Distance sampling with independent observers: reducing bias from heterogeneity by weakening the conditional independence assumption. *Marine Mammal Survey and Assessment Methods* (eds G.W. Garner, S.C. Amstrup, J.L. Laake, B.J.F. Manly, L.L. McDonald & G.G. Robertson), pp. 137–148. Balkema, Rotterdam.

Laake, J.L. & Borchers, D.L. (2004) Methods for incomplete detection at distance zero. *Advanced Distance Sampling* (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 108–189. Oxford University Press, Oxford.

Laake, J., Dawson, M.J. & Hone, J. (2008) Visibility bias in aerial survey: mark--recapture, line-transect or both? *Wildlife Research*, **35**, 299–309.

Laake, J.L., Collier, B.A., Morrison, M.L. & Wilkins, R.N. (2011) Point-based mark-recapture distance sampling. *Journal of Agricultural, Biological and Environmental Statistics*, **16**, 389–407.

Laake, J., Borchers, D., Thomas, L., Miller, D. & Bishop, J. (2013) *mrds: Mark--Recapture Distance Sampling (mrds)*. R package version 2.1.4. http://CRAN.R-project.org/package=mrds.

Lincoln, F.C. (1930) Calculating waterfowl abundance on the basis of banding returns. *United States Department of Agriculture Circular*, **118**, 1–4.

Marini, F., Franzetti, B., Calabrese, A., Cappellini, S. & Focardi, S. (2009) Response to human presence during nocturnal line transect surveys in fallow deer (*Dama dama*) and wild boar (*Sus scrofa*). *European Journal of Wildlife Research*, **55**, 107–115.

Marques, F.F.C. & Buckland, S.T. (2004) Covariate models for the detection function. *Advanced Distance Sampling* (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 31–47. Oxford University Press, Oxford.

Marques, T.A., Thomas, L., Fancy, S.G. & Buckland, S.T. (2007) Improving estimates of bird density using multiple-covariate distance sampling. *The Auk*, **124**, 1229–1243.

Miller, D.L., Burt, M.L., Rexstad, E.A. & Thomas, L. (2013) Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution*, **4**, 1001–1010.

Petersen, C.G.J. (1896) The yearly immigration of young plaice into Limfjord from the German Sea. *Report of the Danish Biological Station*, **6**, 1–48.

Pledger, S. (2000) Unified maximum likelihood estimates for closed capture-recapture model using mixtures. *Biometrics*, **56**, 434–442.

Plumptre, A.J. (2000) Monitoring mammal populations with line transect techniques in African Forests. *Journal of Applied Ecology*, **37**, 356–368.

R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, URL http://www.R-project.org.

Schnupp, M.J., Hernández, F., Redeker, E.J., Bryant, F.C., Rusk, J.P., Demaso, S.J. *et al.* (2013) An electronic system to collect distance-sampling data during helicopter surveys of northern bobwhite. *Wildlife Society Bulletin*, **37**, 236–245.

Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*. Macmillan, New York.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. & Burnham, K.P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, **47**, 5–14.

Turnock, B.J. & Quinn, T.J. II (1991) The effect of responsive movement on abundance estimation using line transect sampling. *Biometrics*, **47**, 701–716.

Walter, M.J. & Hone, J. (2003) A comparison of 3 aerial survey techniques to estimate wild horse abundance in the Australian Alps. *Wildlife Society Bulletin*, **31**, 1138–1149.

Wegge, P. & Storaas, T. (2009) Sampling tiger ungulate prey by the distance method: lessons learned in Bardia National Park, Nepal. *Journal of Animal Conservation*, **12**, 78–84.

Received 27 February 2014; accepted 1 October 2014
Handling Editor: Nick Isaac

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. An introduction to distance sampling and mark–recapture methods.

Appendix S2. Running MRDS analysis in Distance and R: a tutorial.

Appendix S3. Data used in Example 1 set up as a Distance project.