A Likelihood Approach to Estimating Animal Density from Binary Acoustic Transects

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SUMMARY.   We propose an approximate maximum likelihood method for estimating animal density and abundance from binary passive acoustic transects, when both the probability of detection and the range of detection are unknown. The transect survey is purposely designed so that successive data points are dependent, and this dependence is exploited to simultaneously estimate density, range of detection, and probability of detection. The data are assumed to follow a homogeneous Poisson process in space, and a second-order Markov approximation to the likelihood is used. Simulations show that this method has small bias under the assumptions used to derive the likelihood, although it performs better when the probability of detection is close to 1. The effects of violations of these assumptions are also investigated, and the approach is found to be sensitive to spatial trends in density and clustering. The method is illustrated using real acoustic data from a survey of sperm and humpback whales.

KEY WORDS: Abundance; Animal density; Binary time series; Maximum likelihood estimation; Passive acoustic surveys; Second-order Markov approximation; Spatial Poisson process.

1. Introduction

Estimating absolute density and abundance of wild animals from survey data is vitally important to assess the viability of populations and estimate probability of extinction, manage human impacts, and determine removal quotas of exploited species. The task is particularly challenging when there is positive probability that some animals will remain undetected over the course of the survey (Thompson, 2002). The methods commonly used in this situation for animal populations fall into two broad categories: mark–recapture (see, e.g., Seber, 1982) and distance sampling (Buckland et al., 2001), although sometimes the methods are combined (Borchers, Zucchini, and Fewster, 1998; Buckland et al., 2004). For large, very elusive populations (such as some cetaceans), mark–recapture may be impractical, due mainly to the very low probability of recapture, but also to time or cost constraints, impossibility of identifying individuals using marks that persist over long time periods, etc. The analysis of surveys using distance sampling on the other hand requires the researcher to record the distance from the transect line to each detected animal or group of animals. The recorded distances give information on the detection function (probability of detection as a function of distance), which in turn allows conversion of the detection rate into estimates of absolute density (Buckland et al., 2001, 2004). However, many land- and sea-dwelling animals are better detected acoustically than visually. Although distance sampling can be used in acoustic surveys (Marques et al., 2009), this is rarely done as it is often difficult, impossible, or prohibitively expensive to determine distances from the transect line to individual animals or groups of animals.

Without determinations of distance from the transect line, the commonly used method of distance sampling cannot be employed. Thus, until recently, acoustic surveys (sometimes in conjunction with sightings) have been mainly used to examine trends in relative density over time or correlations with environmental variables (Jaquet, Whitehead, and Lewis, 1996; Norris, McDonald, and Barlow, 1999; Nichols, Thomas, and Conn, 2009), but rarely to estimate absolute density.

In addition, it is often impossible to determine from vocalizations the exact number of animals or groups present. Estimation of density from binary presence/absence data is challenging. Royle and Nichols (2003) discuss a method for estimating density from visual presence/absence data from "occupancy surveys" in which the same location is visited on more than one occasion.

Recently, Whitehead (2009) introduced a method-of-moments procedure for estimating absolute density from binary acoustic survey data, in which only the presence/absence of animals or groups is recorded at a set of fixed "listening stations" along a line. This procedure assumes that animals or groups in a region or stratum are uniformly distributed in space according to a homogeneous Poisson process, and exploits information in the sequential pattern of detections to also estimate the range of detection and probability of vocalization. (Vocalizations are assumed to be detectable with certainty out to the range of detection.) The idea is that if the distance between listening stations along a transect is less than the range of detection, then animals have more than one opportunity to be heard. Then if a positive listening station (at which animals are heard) is usually followed by another

positive station, this suggests that the same animal is being heard more than once, and this information can be used to estimate the range of detection. The fact that animals vocalize at some times and not others is an added complication. Here we extend the method-of-moments procedure to an approximate maximum likelihood (ML) method for estimating density when both the range of detection and probability of detection are unknown.

Section 2 outlines the assumptions and develops the likelihood. Section 3 examines the performance of the method when the assumptions are satisfied. Section 4 examines the performance when assumptions are violated and in Section 5 we compare the proposed method to existing methods for estimating animal density. In Section 6, we analyze real data on sperm and humpback whales. Finally in Section 7, we discuss the findings and future work.

2. Assumptions

Consider a binary passive acoustic survey, in which a researcher travels along a single transect, and stops at intervals to listen for vocalizations of the species of interest. The n points at which the researcher stops and listens are referred to as "listening stations." These define discrete points in space and also in time, such that the researcher is present at listening station t at time t, for $t = 1, 2, \ldots, n$. At each listening station, the researcher records the binary response $Y_t = 1$ if she/he hears any vocalizations from the species of interest and $Y_t = 0$ otherwise.

To develop the likelihood, we make the following simplifying assumptions:

(1) Individual animals are distributed in space according to a homogeneous Poisson process with density α. Individuals do not move, or move slowly relative to the observer.
(2) The probability that an individual animal vocalizes and is detected at time t is μ, for $t = 1, 2, \ldots, n$.
(3) Individuals can be detected if they are within a range of r units of the listening station.
(4) Detections are independent between individuals at a given listening station.
(5) Detections are independent between listening times for a given animal.
(6) Listening stations are spaced at equal intervals a known distance of d units apart. (The requirement of equal intervals is easily relaxed, as shown in the Appendix.)

To summarize the first three assumptions, if an animal is inside the "listening circle" of radius r whose centroid is at listening station t, then it will be detected at time t with probability μ. Note that the three parameters (α, μ, and r) are assumed to be constant over the course of the survey. In contrast to distance sampling, we do not allow detectability to be a function of distance; rather we assume that it remains constant over a circle of radius r centered at the observer, and is 0 outside this circle. The effects of departures from these assumptions will be evaluated using simulations in Section 3. We assume throughout that our main interest lies in estimating α, the density of animals per unit area.

2.1 *Likelihood*

When listening circles overlap, the binary variables Y_t, $t = 1, 2, \ldots, n$, are not independent. Thus we write the likelihood as a product of conditional probabilities,

$$L(\alpha, \mu, r) = p(y_n \mid y_{n-1}, y_{n-2}, \ldots, y_2, y_1)$$
$$\times p(y_{n-1} \mid y_{n-2}, \ldots, y_2, y_1) \ldots p(y_3 \mid y_2, y_1) p(y_2, y_1),$$

where, for example, $p(y_t \mid y_{t-1}, y_{t-2}) = \Pr(Y_t = y_t \mid Y_{t-1} = y_{t-1}, Y_{t-2} = y_{t-2})$. The conditional probabilities are intractable in general so we make the assumption that conditioning on only the two previous values is sufficient. The approximate likelihood using this second-order Markov assumption is

$$L(\alpha, \mu, r) = p(y_1, y_2) \prod_{t=3}^{n} p(y_t \mid y_{t-1}, y_{t-2})$$

$$= p(y_1, y_2) \prod_{t=3}^{n} \left\{ \frac{p(y_{t-2}, y_{t-1}, y_t)}{p(y_{t-2}, y_{t-1})} \right\}, \quad (1)$$

where $p(y_{t-2}, y_{t-1}) = P(Y_{t-2} = y_{t-2}, Y_{t-1} = y_{t-1})$ and $p(y_{t-2}, y_{t-1}, y_t) = P(Y_{t-2} = y_{t-2}, Y_{t-1} = y_{t-1}, Y_t = y_t)$ are joint probabilities.

Given our assumptions, the probabilities do not depend on t and so we can write $P(Y_{t-1} = i, Y_t = j)$ as P_{ij} for $t = 2, \ldots, n$, where i and j take values 0 or 1. Similarly, we can write $P(Y_{t-2} = i, Y_{t-1} = j, Y_t = k)$ as P_{ijk} for $t = 3, \ldots, n$, and where i, j, k take values 0 or 1. The likelihood is then proportional to

$$L(\alpha, \mu, r) = P_{00}^{(1-y_1)(1-y_2)} P_{01}^{(1-y_1)y_2} P_{10}^{y_1(1-y_2)} P_{11}^{y_1 y_2}$$

$$\times \prod_{i=0,1} \prod_{j=0,1} \prod_{k=0,1} \left(\frac{P_{ijk}}{P_{ij}} \right)^{n_{ijk}}, \quad (2)$$

where n_{ijk} is the number of triplets with $y_{t-2} = i$, $y_{t-1} = j$, and $y_t = k$. Simulation results, such as those presented in Section 3, show that the second-order Markov approximation is reasonable for many values of the parameters.

It follows from our assumptions that the probability that animals will be heard at a single listening station, P_1, is $1 - \exp(-a\mu)$, where $a = \alpha \pi r^2$ (Whitehead, 2009). The probabilities P_{ij} and P_{ijk} involve the function

$$O(d, r) = \begin{cases} \dfrac{2}{\pi} \left(\arccos\left(\dfrac{d}{2r} \right) - \dfrac{d}{2r} \sqrt{1 - \left(\dfrac{d}{2r} \right)^2} \right) & \dfrac{d}{r} \leq 2, \\[2em] 0, & \dfrac{d}{r} > 2 \end{cases}$$

the proportion of the area of a circle which is in the intersection of two circles both of radius r, whose centroids are separated by a distance d. Using this function, the probability of hearing animals at one station, but not at the following station is $P_{10} = (1 - e^{-(1-\mu+K\mu)a\mu})e^{-a\mu}$, where $K = 1 - O(d, r)$ (Whitehead, 2009).

Derivations of the P_{ijk} involve conditioning on the number of animals present in different regions of the three listening circles. We use capital letters to index listening circles and numbers to index time. The researcher is assumed to be at
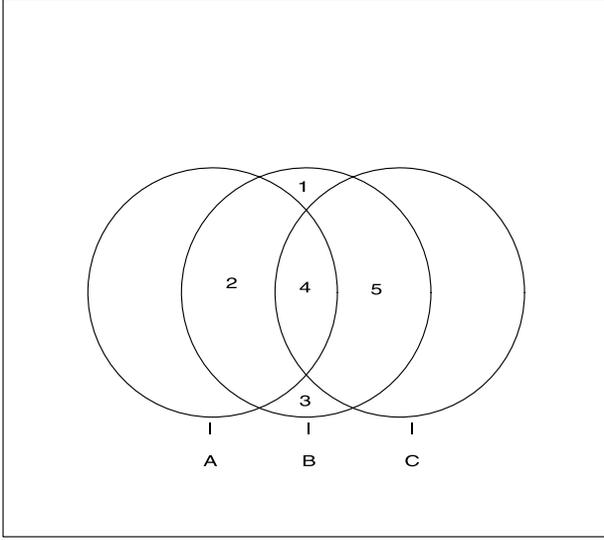
Figure 1. Three listening circles A, B, and C, with partitions of the circle B.

the centroid of listening circle A at time 1, circle B at time 2, circle C at time 3, etc., as shown in Figure 1. The figure shows the situation where $d/r \leq 1$ so that there is an intersection of the three circles (region 4). When $1 < d/r \leq 2$ both circle A and circle C intersect with circle B, but not with each other. When $d/r > 2$ there is no intersection among the circles and the results at the three listening stations are independent.

We denote by X_γ the number of animals within circle γ for $\gamma = A, B, \ldots$. Recall that animals are assumed to be essentially immobile, so time is not explicitly indexed. It follows from the assumptions given above that $X_\gamma \sim \text{Poisson}(a)$ where $a = \alpha \pi r^2$. We denote by $V_{\gamma t}$ the number of animals that vocalize and are detected in listening circle γ at time t for $t = 1, 2, \ldots$. Then, as is well known (see for instance Ross, 2000), $V_{\gamma t} \sim \text{Poisson}(a\mu)$. Finally, we denote by $V_{(R)t}$ the number of animals that are detected in region R at time t, where R is a region determined by intersecting circles. The distribution of $V_{(R)t}$ is $\text{Poisson}(A(R)\mu)$ where $A(R)$ is the area of region R.

Consider three successive listening circles at three successive listening times $t-2$, $t-1$, and t. Because probabilities do not depend on t, we can without loss of generality label the circles as A, B, and C, as shown in Figure 1, and the times as 1, 2, and 3. Note that animals in the intersection of the three circles (region ABC, labeled as region 4 in Figure 1) have three opportunities to be detected, whereas those in the intersection of two circles but not in the third (for instance region $AB\backslash C$, labeled as region 2 in Figure 1), have two opportunities to be detected, and those in regions 1 and 3 have one opportunity to be detected. We will condition on x, the number of animals in circle A, y the number of animals in region AB and z the number of animals in region $B\backslash A$, and then sum over x, y, and z, to give the required probabilities of detecting animals in regions A, B, and C. In the process, we will make use of the following principles: (1) the number of detections in nonoverlapping regions are independent and (2) given

the number of animals in a region, the number of detections at different times are conditionally independent. An intuitive explanation for (2) is that, given that we know some animals are present in a region, the fact that some are detected at time 1 gives no additional information about whether some are detected at time 2. Then

$$P_{100} = P(V_{A1} > 0, V_{B2} = 0, V_{C3} = 0)$$
$$= P(V_{A1} > 0, V_{(AB)2} = 0, V_{(B\backslash A)2} = 0, V_{(ABC)3} = 0,$$
$$V_{(BC\backslash A)3} = 0, V_{(C\backslash B)3} = 0)$$
$$= \sum_{x=0}^{\infty} \sum_{y=0}^{x} \sum_{z=0}^{\infty} P(V_{A1} > 0, V_{(AB)2} = 0, V_{(B\backslash A)2} = 0,$$
$$V_{(ABC)3} = 0, V_{(BC\backslash A)3} = 0 \,|\, x, y, z)$$
$$\times P(V_{(C\backslash B)3} = 0) P(X_A = x, X_{AB} = y, X_{B\backslash A} = z)$$
$$= \sum_{x=0}^{\infty} \sum_{y=0}^{x} \sum_{z=0}^{\infty} P(V_{A1} > 0 \,|\, x)$$
$$\times P(V_{(AB)2} = 0 \,|\, y) P(V_{(B\backslash A)2} = 0 \,|\, z)$$
$$\times P(V_{(ABC)3} = 0 \,|\, y) P(V_{(BC\backslash A)3} = 0 \,|\, z)$$
$$\times P(V_{(C\backslash B)3} = 0)$$
$$\times P(X_A = x) P(X_{AB} = y \,|\, X_A = x) P(X_{B\backslash A} = z).$$

With two exceptions (discussed below), the probabilities involved follow directly from the following facts:

(1) $(V_{A1} \,|\, X_A = x) \sim Binomial(x, \mu)$,
(2) $(V_{(AB)2} \,|\, X_{AB} = y) \sim Binomial(y, \mu)$,
(3) $(V_{(B\backslash A)2} \,|\, X_{B\backslash A} = z) \sim Binomial(z, \mu)$,
(4) $V_{(C\backslash B)3} \sim Poisson(Ka\mu)$,
(5) $X_A \sim Poisson(a)$,
(6) $(X_{AB} \,|\, X_A = x) \sim Binomial(x, 1-K)$, and
(7) $X_{B\backslash A} \sim Poisson(Ka)$.

To obtain $P(V_{(ABC)3} = 0 \,|\, X_{AB} = y)$, consider a single animal known to be in region AB. Either the animal is in $AB\backslash C$, shown as region 2 in Figure 1 (in which case it cannot be heard at time 3) or it is in ABC (region 4 on the figure), in which case it is not heard at time 3 with probability $1 - \mu$. Thus the probability that the animal is not heard at time 3 is

$$K_1 = \frac{A2 + A4(1-\mu)}{A24}, \qquad (3)$$

where $A24$ is the proportion of the area of a circle that is in region AB and equals $O(d, r)$, $A4$ is the proportionate area of region ABC and equals $O(2d, r)$ and $A2$ is the proportionate area of $AB\backslash C$ and equals $O(d, r) - O(2d, r)$. After simplification, K_1 can be expressed as

$$K_1 = 1 - \frac{\mu O(2d, r)}{O(d, r)}.$$

Given that there are y animals in region AB, the probability that none are heard at time 3, $P(V_{(ABC)3} = 0 \,|\, X_{AB} = y)$, is then K_1^y.

Similarly, to calculate $P(V_{(BC\backslash A)3} = 0 \,|\, z)$, consider a single animal known to be in region $B\backslash A$. Either the animal is in region 1 or 3 in Figure 1 (in which case it cannot be detected

at time 3) or it is in region 5 (in which case it is detected at time 3 with probability μ). Then the probability that the animal is not detected at time 3 is

$$K_2 = \frac{A1 + A3 + A5(1 - \mu)}{A135}, \qquad (4)$$

where $A135$ is the proportionate area of the region $B \backslash A$ and equals $1 - O(d, r)$, $A5$ is the proportionate area of the region in circle C but not in circle A and equals $O(d, r) - O(2d, r)$, and $A1 + A3$ is the area of circle B that is neither in A nor C and equals $A135 - A5 = 1 - 2O(d, r) + O(2d, r)$. After simplification,

$$K_2 = 1 - \frac{\mu\{O(d, r) - O(2d, r)\}}{1 - O(d, r)}.$$

Given that there are z animals in region $B \backslash A$, the probability that none are heard at time 3, $P(V_{(BC \backslash A)3} = 0 \,|\, z)$, is then $K_2{}^z$.

Evaluating all terms gives

$$P_{100} = \sum_{x=0}^{\infty} \sum_{y=0}^{x} \sum_{z=0}^{\infty} (1 - (1 - \mu)^x)(1 - \mu)^y (1 - \mu)^z K_1^y K_2^z$$

$$\times\, e^{-\mu a K} \binom{x}{y} (1 - K)^y K^{x-y} \frac{e^{-a} a^x}{x!} \frac{e^{-Ka} (Ka)^z}{z!}$$

and summing over x, y, and z gives $P_{100} = e^{C + K_2 K a (1 - \mu)} (e^{\delta_1} - e^{\delta_2})$ where $C = -a(1 + K(1 + \mu))$, $\delta_1 = a(1 - \mu)K_1(1 - K) + Ka$, and $\delta_2 = a(1 - \mu)^2 K_1(1 - K) + Ka(1 - \mu)$. Note that this is a refinement of the original expression given in Whitehead (2009), in which conditioning was on the sum $y + z$ rather than on y and z separately. The derivation above must be modified slightly when $1 < d/r \leq 2$ so that there is no three-way intersection of the listening circles, but the expression for P_{100} is unchanged. Similar arguments show that

$$P_{110} = P(V_{A1} > 0, V_{B2} > 0, V_{C3} = 0)$$

$$= \sum_{x=0}^{\infty} \sum_{y=0}^{x} \sum_{z=0}^{\infty} P(V_{A1} > 0 \,|\, x)$$

$$\times\, P(V_{B2} > 0 \,|\, y, z)$$

$$\times\, P(V_{(BC)3} = 0 \,|\, y, z) P(V_{(C \backslash B)3} = 0)$$

$$\times\, P(X_{AB} = y \,|\, X_A = x) P(X_A = x) P(X_{B \backslash A} = z)$$

$$= \sum_{x=0}^{\infty} \sum_{y=0}^{x} \sum_{z=0}^{\infty} (1 - (1 - \mu)^x)$$

$$\times\, (1 - (1 - \mu)^{y+z})(AA)^y (BB)^z e^{-\mu a K}$$

$$\times\, \binom{x}{y} (1 - K)^y K^{x-y} \frac{e^{-a} a^x}{x!} \frac{e^{-Ka} (Ka)^z}{z!}$$

and summing over x, y, and z gives $P_{110} = e^{C + K_2 K a} (e^{\delta_{11}} - e^{\delta_{12}}) - P_{100}$ where $\delta_{11} = a K_1(1 - K) + Ka$, and $\delta_{12} = a(1 - \mu)K_1(1 - K) + Ka(1 - \mu)$. Given P_1, P_{10}, P_{100}, and P_{110}, all other probabilities in the likelihood can be found by subtraction.

The second-order Markov approximation gives a likelihood (equation (1)) which is (apart from a term for the first two observations) proportional to the product of four binomial likelihoods. Each binomial depends on a different conditional probability, which corresponds to whether or not animals were

detected at the previous two listening stations. The data can therefore be condensed into the results for the first two stations and the eight counts corresponding to the number of detections and nondetections given the four possible results at the previous two stations, as in equation (2). An examination of the four conditional probabilities of detection reveals that they are distinct for $d/r < 1$ (i.e., when three or more listening circles overlap), that three are distinct for $1 < d/r < 2$ (i.e., when only two circles overlap), and that all four become equal for $d/r \geq 2$ (i.e., when no listening circles overlap). For $1 < d/r < 2$, the conditional probability of detecting an animal in a listening circle (say C) when none was detected in the previous circle (B) is not altered by the outcome in the circle before that (A). However, when an animal was detected at circle B, the probability of detection at circle C is lower when an animal was also detected at circle A, because it is then more likely that the animal is in the intersection of the listening circles A and B and therefore undetectable at station C. Consequently the method is able to estimate the three parameters of the model (α, r, and μ) for $d/r < 2$, although difficulties will occur as d/r approaches 2.

The likelihood can be maximized by any standard nonlinear optimizer. We used the function `nlminb` in R, Version 2.7.0, (R Development Core Team, 2009), which does not require derivatives. Inference about the parameters can be based on profile likelihood intervals or on the asymptotic normality of the maximum likelihood estimates (MLEs). We used transformations to constrain the parameter estimates to allowable values. In particular, we used a logistic transformation to constrain $\hat{\mu}$ to lie between 0 and 1, and a generalized logistic transformation $glogit(x) = 100/(1 + \exp(-(x)))$ to constrain $\hat{r}$ to lie between 0 and 100, which was deemed to be a reasonable upper limit for the species considered. Finally, we re-parameterized the likelihood using $\log(\alpha r^2)$ to deal with high correlation between $\hat{\alpha}$ and $\hat{r}$.

3. Bias under Standard Assumptions

To test the ability of our method to estimate density under the standard assumptions listed at the beginning of Section 2, we conducted numerous simulations in R. The locations of animals in space were generated according to a Poisson process with density α per unit area over a rectangular study area and animals were assumed to remain at this location for the duration of the simulation. A sequence of n listening stations were located at equally spaced intervals of length d along a transect bisecting the study area. Individual animals within a distance r of the researcher at time t were detected with probability μ, independently of other animals or previous detections. For each time t, $t = 1, 2, \ldots, n$, we recorded y_t, which equaled 1 if at least one animal was within distance r of listening station t, and was detected at time t, and 0 otherwise.

The percentage relative bias (PRB) in $\hat{\alpha}$ under one set of standard assumptions is shown in Figure 2. Here the true values of the parameters are $\alpha = 0.001$, $\mu = 0.9$, and $r = 10$. PRB is defined as $(\text{mean}(\hat{\alpha}) - \alpha_0)/\alpha_0 \times 100\%$, where $\hat{\alpha}$ is the MLE and α_0 is the true value of the parameter. The distance between listening stations, d, and hence the number of overlapping circles, is allowed to vary over the values $d = 3.4, 4, 5, 6.8,$ and 10 which corresponds to 6, 5, 4, 3, and 2 overlapping circles, respectively. The number of listening
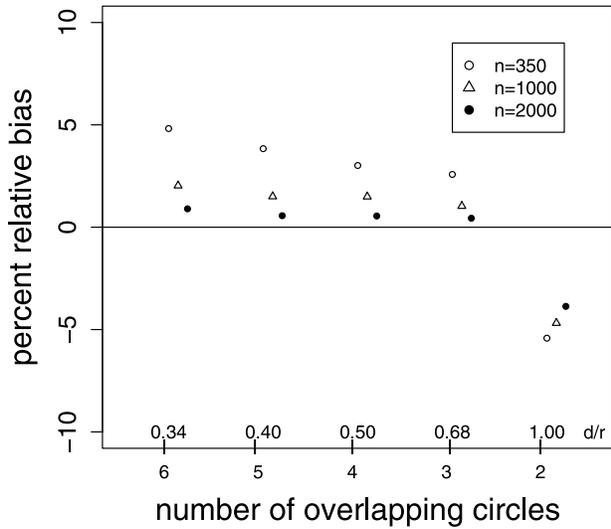
Figure 2. Percentage relative bias of $\hat{\alpha}$ under standard assumptions, with $\alpha = 0.001$, $r = 10$, and $\mu = 0.9$, which corresponds to $P_1 = 0.246$.

stations n varied over the values 350, 1000, and 2000. Figure 2 is based on 10,000 simulated data sets. Points with the same value of d but different values of n have been moved slightly in the horizontal direction for clarity of display. Note that

bias decreases abruptly as n increases from 350 to 1000, then levels off as n increases from 1000 to 2000.

Figure 3 shows contour plots of absolute PRB in $\hat{\alpha}$, as the expected proportion of positive listening stations P_1 and d/r vary, for various values of μ. Here absolute PRB is defined as $|\,(\text{mean}(\hat{\alpha}) - \alpha_0)/\alpha_0\,| \times 100\%$, where $\hat{\alpha}$ is the MLE and α_0 is the true value of the parameter. Figure 4 similarly shows contour plots of the coefficient of variation (CV) of $\hat{\alpha}$ expressed as a percentage, defined as $\sqrt{\text{var}(\hat{\alpha})}/\alpha_0 \times 100$. These plots are based on 400 points equally spaced in the P_1 and d/r plane, where the value of each point is calculated based on 1000 iterations, with $r = 10$ and the number of listening circles $n = 1000$.

Here we can see that the method performs well when μ is 1, as a large approximately circular area of the plot centered at $d/r = 1$ and $P_1 = 0.4$ has a CV less than 15% and in this area the absolute bias is less than 10%. For $\mu = 0.4$, the CV is always greater than 15%, and reaches its minimum at values of d/r near 0.8 and $P_1 = 0.25$. As μ decreases, the estimate of the density of animals becomes less reliable, because an animal that is present and within range might remain undetected, even though listening stations overlap and the animal has several opportunities to be heard. In this situation, it becomes difficult to separate information about the density α and the range of detection r. The probability that animals will be detected at any listening station, P_1, also affects the performance of the method. The CV increases as P_1 approaches
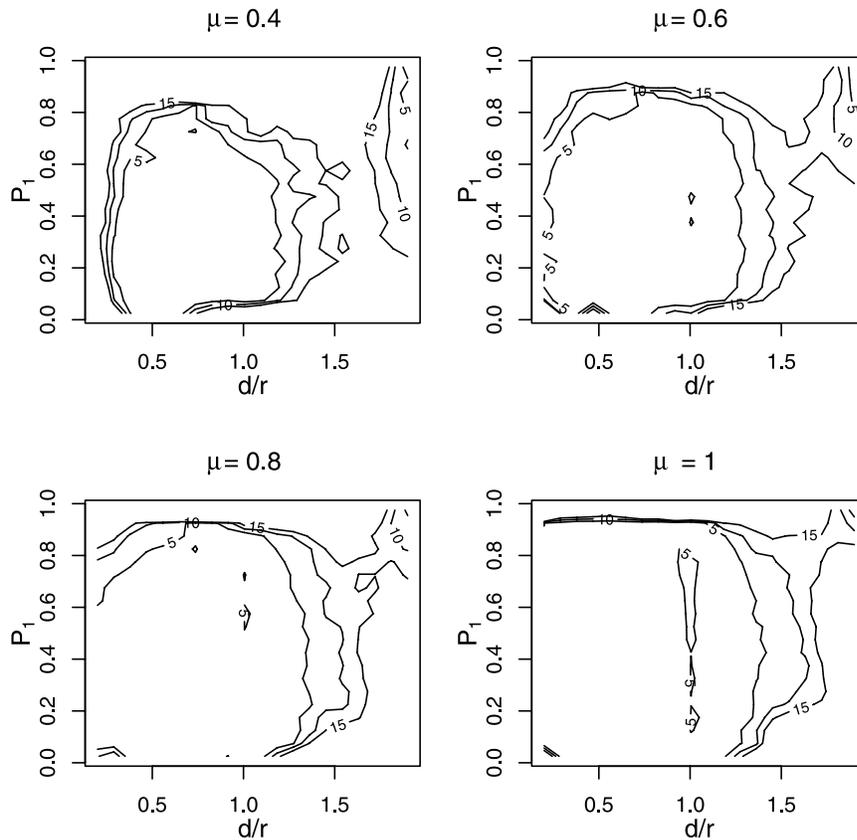
Figure 3. Contour plot showing absolute value of PRB in $\hat{\alpha}$, as P_1 and d/r vary, for various values of μ, with $r = 10$, and the number of listening circles $n = 1000$.
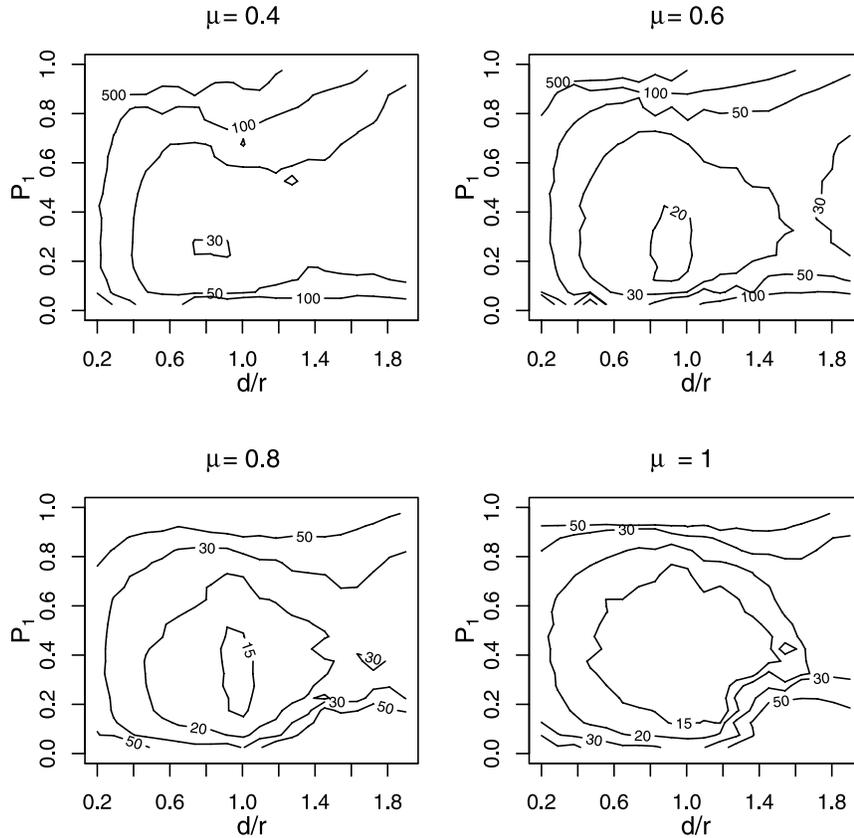
Figure 4. Contour plot showing CV of $\hat{\alpha}$ expressed as a percentage, as P_1 and d/r vary, for various values of μ, with $r = 10$, and the number of listening circles $n = 1000$.

0; for instance, for $\mu > 0.6$ and $d/r = 1$, the CV can be greater than 20% for $P_1 < 0.1$. Also, the CV increases more rapidly as P_1 approaches 1.0; for instance, for $\mu = .8$ and $d/r = 1$, CV is greater than 15% for $P_1 > 0.5$. Intuitively, if the number of positive listening stations is zero, one or all of α, μ, or r could be zero, but we would not be able to determine which one. Similarly, if the expected proportion of listening stations that are positive, P_1, is nonzero but very small, then we are not able to separately estimate the three parameters with any reliability. The same problem arises if all or most of the listening stations are positive. The quantity P_1 can be estimated as the proportion of listening stations at which animals were heard, and so is available to the researcher once data are collected, or can be estimated in advance of data collection from pilot data or previous studies.

4. Bias under Violation of Assumptions

We examined the effects of departures from the standard assumptions via simulation across various scenarios. Each scenario has $\alpha = 0.001$ (except scenarios 6 and 7, where α changes systematically), $\mu = 0.9$, $d = 5$, $r = 10$. This gives $P_1 = 0.25$ and $d/r = 0.5$, which are settings of the parameters where the method performs well when assumptions are satisfied. Each of the following scenarios has $n = 1000$ listening stations and was investigated separately with 10,000 simulated data sets:

(1) The standard assumptions given in Section 2 are satisfied.
(2) The distance between stations varies according to a normal distribution with mean d and standard deviation 1, i.e., a $N(5,1)$ distribution.
(3) The range of detectability varies between individuals, according to a $N(r, 0.2r)$ distribution, but is constant over time for a single individual. This could occur for instance if larger individuals make louder vocalizations.
(4) The range of detectability varies over time, according to a $N(r, 0.2r)$ distribution but is constant for all individuals at that time. This situation could occur in the field because of, for instance, different background noise or local environmental conditions.
(5) The range of detectability varies across individuals and across time according to a $N(r, 0.2r)$ distribution. This could occur for instance if individuals change orientation over time, and signal strength varies with changing orientations.
(6) The density of individuals increases linearly from zero to twice the standard density of $\alpha = 0.001$ along the transect line.
(7) The density of individuals increases linearly from half the standard density of $\alpha = 0.001$ to 1.5 times the standard density along the transect line.

Table 1
PRB and CV expressed as a percentage of $\hat{\alpha}$ under various scenarios of assumption violations

Scenario	1	2	3	4	5	6
PRB	1.34	0.21	−3.28	9.64	6.77	−22.95
CV	18.21	17.98	17.60	20.33	19.68	14.51
Scenario	7	8	9	10	11	12
PRB	−4.95	17.66	5.33	−2.78	1.54	3.52
CV	16.97	21.24	18.90	18.45	18.05	16.94

(8) Individuals avoid one another; no pairs of individuals are closer to one another than r units.
(9) Individuals avoid one another; no pairs of individuals are closer to one another than $r/2$ units.
(10) Individuals are attracted to one another; no individual is further than $5r$ units from another individual.
(11) The probability of detection at different stations is not constant, but rather uniformly distributed in (0.8,1).
(12) The probability of detection, μ, decreases with distance from the listening station according to the function $\mu = \exp\left(-(dist/r)^5\right)$, where $dist$ is the distance from the individual to the listening station. This function drops gradually from 1 at a distance of 0 from the listening station, to approximately 0.4 at a distance of 10, and continues to drop as distance increases.

Results are depicted in Table 1, which shows the PRB of $\hat{\alpha}$ and its CV (expressed as a percentage) by scenario number. In most cases, the relative bias is less than 10%. The exceptions (scenarios 6 and 8) are both rather serious violations of the homogeneous Poisson assumption.

We also investigated the behavior of the method under nonsystematic spatial aggregation. To do so, we conducted simulations where individuals were distributed according to a Neyman–Scott process as follows: first, primary individuals were generated over a very large rectangular space according to a Poisson process with intensity 0.001. For each primary individual, the number of extra individuals in that cluster was generated according to a Poisson distribution with a mean between 0 and 4. The locations of these extra individuals were distributed in space about the primary individual according to a bivariate normal distribution with mean 0 and standard deviation, which varied between 1 and 40. As above, $\mu = 0.9$, $d = 5$, $r = 10$, and $n = 1000$. To avoid edge effects, only approximately the center tenth of the original rectangular area was used in estimating the parameters. The results are shown in Figure 5, where we have used the square root scale on the horizontal axis to focus attention on the area of the plot where the absolute bias increases beyond 10%. This plot is based on 240 points distributed across the plane, where the value of each point is calculated based on 1000 simulated data sets. Our simulations indicate that when the mean number of extra individuals is less than 0.14, the number of individuals is underestimated by less than 10%. As the standard deviation of the location of extra individuals increases, the distribution of individuals becomes more like the Poisson process, and the absolute magnitude of the bias decreases.

5. Comparisons to Existing Methods

The method developed in this article is designed for situations where distances to individual animals cannot be measured or the exact number of animals which vocalize cannot be determined. However, there may be some situations where it is possible, but expensive, to determine distances to individual animals. In that case, conventional distance sampling (CDS) should be used to estimate density. How much information would be lost by using the approximate ML method presented in this article? To compare the approximate ML method to CDS, we generated 1000 simulated data sets, each along a single transect with $\alpha = 0.001$, $\mu = 1$, $d = 5$, $r = 10$, and $n = 300$, under the standard assumptions outlined in Section 2. We chose $\mu = 1$ to correspond to the assumption of perfect detectability along a transect line which is made in CDS. For the CDS estimates, we recorded perpendicular distances from each animal to the transect and used the DISTANCE 5.0 software (Thomas et al., 2010) with a uniform detection function and truncation distance of 10 units. For the ML method, we recorded only whether any animals were present in each listening circle.

Our ML procedure had similar absolute relative bias compared to CDS, but exhibited higher variability. The ML estimator had a relative bias of −0.7% and CV of 28.2%, whereas the CDS estimator had a relative bias of 0.7% and CV of 18.4%, where the results are expressed as a percentage of the true value of α. The smaller variability associated with CDS is not surprising given that CDS uses more information, namely the exact number of animals and their distance to the transect.

Compared to the method of moments (MOM) procedure presented in Whitehead (2009), the ML procedure presented here has smaller relative bias and variability under standard assumptions. Our simulations, using the same conditions specified above, showed the MOM estimator had a relative bias of 3.1% and CV of 32.7%, which is larger than the ML estimator's relative bias of 0.7% and CV of 28.2%. Again this is not surprising, as the ML estimator makes additional assumptions about the distribution of the data, whereas the MOM makes assumptions only about the first few moments of the distribution.

6. Examples

To illustrate our methodology, we use data from an acoustic transect survey reported in Whitehead (2009), which was collected in the southern Sargasso Sea. A hydrophone towed from a 12.5 m sailing vessel was monitored every half hour for about 1 minute and researchers recorded whether or not they heard humpback whale (*Megaptera novaeangliae*) songs and/or clicks from groups of sperm whales (*Physeter macrocephalus*). The $n = 332$ listening stations were spaced at a mean distance of 5.88 km (CV = 0.16). Distances between stations were calculated using GPS records. For the following analyses, we assume that the listening stations are equally spaced at a distance of 5.88 km.

Sperm whales usually occur in groups of 15–20 individuals, composed of females and immature males, whereas single males traveling alone are rarely encountered. As stated earlier, for species that occur in groups, the method presented here can estimate the number of groups per unit area, which

Percent bias in estimating number of individuals
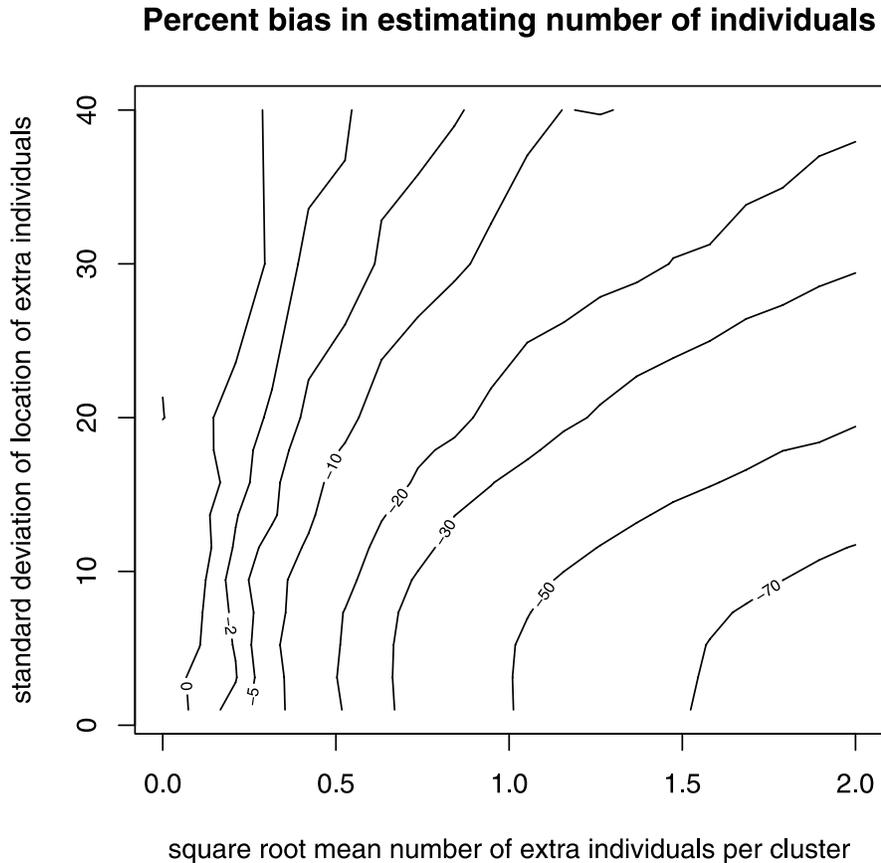
Figure 5. Contour plot showing percentage bias in estimating number of individuals from a Neyman–Scott process, as a function of the square root mean number of extra individuals per cluster and the standard deviation of the location of extra individuals.

can be augmented with information about group size to give an estimate of the density of individuals.

6.1 *Sperm Whales*

Sperm whales were heard at 28 out of 332 listening stations (8.4%). The data are in the form of counts: 279, 11, 11, 1, 3, 9, 9, 7 representing n_{000}, n_{100}, n_{001}, n_{101}, n_{010}, n_{110}, n_{011}, n_{111}, respectively, and with $y_1 = y_2 = 0$. We find the MLE of density is $\hat{\alpha} = 0.00036$ groups of whales per km^2, with 95% profile likelihood interval of (0.000160, 0.000736). The MLE of the probability that a group of whales is detected during any listening, $\hat{\mu}$, is 0.897 with 95% profile likelihood interval (0.64, 1.00). Similarly, the MLE of the radius of detection is $\hat{r} = 9.288$ km with 95% profile likelihood interval of (6.95, 15.14). With a correction for group size, the estimate of density is reasonable for this species (Whitehead, 2009).

6.2 *Humpback Whales*

Humpback whales were heard at 148 of the Sargasso Sea stations (44.6%), far more often than for sperm whale groups, suggesting that their density is higher, they call more often, and/or the radius over which they can be detected is larger. The data are in the form of counts: 92, 32, 32, 26, 31, 27, 27, 63 representing n_{000}, n_{100}, n_{001}, n_{101}, n_{010}, n_{110}, n_{011}, n_{111}, respectively, and with $y_1 = y_2 = 0$. We find the MLE of density is $\hat{\alpha} = 0.000336$ whales per km^2 with 95% profile likelihood

interval of (0, 0.00286). The MLE of the probability that an individual whale is detected during any listening is $\hat{\mu} = 0.365$ with a 95% profile likelihood interval of (0.213, 0.580). The MLE of the radius of detection is $\hat{r} = 39.515$ km with a 95% profile likelihood interval of (11.8, ∞). Joint profile likelihood regions for α and r indicate a strong nonlinear association between these two parameter estimates. This data set is apparently more challenging than the previous one. The profile confidence limits for α and r are wide and one sided. As shown in simulations, the estimated value of μ is near the limit of the method's usefulness. With $d = 5.88$, an estimated value for d/r is 0.151, which according to Figures 3 and 4, puts the data in an area where the method does not perform well (bias over 15% and CV over 100%).

7. Discussion

The approximate ML method developed in this article is designed for the problem of estimating density of animals from presence/absence data, in the situation where not all animals are likely to be detected, and when the probability of detection and range of detection are unknown. The method is designed for situations where distance sampling and mark–recapture methods are not feasible. Presence/absence data clearly have a lower information content than the data required for distance sampling, where not only the number of animals, but

also the distance from an observer to each individual animal must be determined. Similarly, presence/absence data contain less information than mark–recapture data, but the methods developed here do not require animals to be recaptured or reidentified, which can be difficult with elusive species.

To accommodate presence/absence data, we made strong assumptions about the distribution of animals in space, as have previous authors (e.g., Royle and Nichols, 2003), namely that animals are distributed in space according to a homogeneous Poisson process. When good estimates of distances from an observer to individual animals can be obtained, then distance sampling will usually be superior. However, for acoustic data, this may entail prohibitive costs (e.g., from arrays of hydrophones as in Lewis et al., 2007) or be impossible.

The likelihood was developed under assumptions that are explicitly stated in Section 2. For the mathematical derivation of the model, we assumed that animals do not move, but in practice, random movements that are slow relative to the observer would cause little bias. Movements by individuals in one direction would be compensated for by movements of other individuals in the opposite direction. More problematic is the situation in which animals systematically move in response to the observer, for instance following the observer as she/he moves along the transect, as this could potentially bias the estimation of all three parameters. The same issues are a concern in distance sampling (see Buckland et al., 2001). Although the sea is of course three dimensional, we used two-dimensional circles as a model for sound propagation when developing the likelihood. For marine animals that vocalize close to the surface, such as humpbacks, this model is realistic, whereas for those that vocalize at depth, the model is a simplification. However, because sound bounces off the ocean surface and thermoclines in ways which cannot easily be measured, this model is a workable approximation to a complicated reality. Our method assumes that the probability of detection is constant over a circle of radius r, then drops to 0. Although possibly unrealistic, our simulations show this approximation works well in practice.

We found that our method is robust to some violations of the assumptions used to derive the likelihood, but is sensitive to the Poisson assumption. This is concerning, as deviations from a homogeneous Poisson process are likely to occur in the field. If animals are likely to occur in clusters, then the method will need to be augmented with supplementary information on the mean number of animals per cluster. We are currently investigating methods for diagnosing deviations from the homogeneous Poisson assumption. When $d/r < 1$ so that three or more listening circles intersect, the approximate likelihood function is essentially the product of four binomial likelihoods. The fact that the four conditional probabilities of detection are distinct for $d/r < 1$ suggests that it may be possible to extend the model to include an extra parameter. This parameter could be chosen to detect overdispersion or departures from the assumption of a constant mean for the Poisson distribution of the number of animals (i.e., homogeneity).

The model developed here can likely be improved. For instance, a hierarchical model, where the true location of animals is treated as a hidden state, may allow relaxation of the assumption of a homogeneous Poisson process for animal locations. A Bayesian procedure for estimating the parameters of similar models is described in detail by Royle and Dorazio (2008).

Other avenues for investigation include the application of Bayesian methods because researchers will often have some prior knowledge about the range of detection and/or probability of vocalization and detection. The method can easily be modified to allow for varying known distances between listening stations (see Appendix). However, nonlinear transects and noncircular listening areas may introduce complicated geometries in the overlapping listening circles, and the likelihood will need to be modified accordingly. Other possibilities for further investigation include introduction of covariates, use of multiple transects and stratified estimators, and nonparametric estimates of standard errors. Extensions to the model could allow the probability of vocalization to vary systematically, depending on previous vocalizations of the same or neighboring animals, and examine the effect of heterogeneity of the detection function.

We envisage that the ML method for dependent binary data introduced here will be used mostly with acoustic data. However, it could also be used when the method of detection is by olfactory or chemical means. In these situations, distance from the animal to the observer is even harder to determine than with acoustic surveys, and so CDS is unlikely to be useful when estimating density. If visual data are available, then CDS may be preferred. However, our method will be an appealing option for visually elusive animals that can be detected acoustically (such as some birds, bats, and cetaceans) or by other means (perhaps olfactory detection of some terrestrial mammals).

Our method can easily be applied to archived data such as described in Jaquet et al. (1996), as long as listening stations are spaced at less than twice the range of detection. For future surveys, our simulations (see Figures 3 and 4) suggest that, in the absence of knowledge about μ, a general recommendation is to take d/r between 0.8 and 1.0. Because r will be unknown, one would have to make an educated guess based on a literature review or pilot survey. Furthermore our simulations suggest that about 1000 listening stations will give good precision, and if necessary several transects can be combined to reach this number.

When animals occur in groups, as in the sperm whales, our method can estimate the number of groups. An external estimate of group size can then be used to estimate density of individuals. As pointed out by a reviewer, for many species, the probability that an individual vocalizes will depend on group size. This can possibly be accommodated with a covariate recording group size. As discussed in Whitehead (2009), if animals can remain quiet while the listener passes through several listening stations, then a correction based on independent data would need to be incorporated.

To assess the status of wildlife populations, and manage human impacts, we need estimates of absolute density and abundance, rather than relative abundance or trends. For instance, two of the five criteria required by the International Union for Conservation of Nature (IUCN) for listing a species as "Critically endangered," "Endangered," or "Vulnerable" explicitly require absolute population estimates rather than trend data (IUCN, 2008). Elusive species that are hard to observe visually because of their habitats or habits often lack

absolute abundance estimates, because of the difficulty of assessing distances to individual animals, and thus applying distance sampling, or the impossibility of applying mark–recapture methods. The methods developed in this article give absolute estimates of density and abundance using presence/absence data. They will be particularly useful for species in which individuals are detected acoustically, and may also be effective for other nonvisual modes of detection.

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Appendix

In this Appendix, we outline the derivation of the likelihood when the distances between listening stations are variable and known. Suppose that the distance between listening stations at times t_1 and t_2 is d_{t_1,t_2}. Then we can use the likelihood as given in equation (1), where now the probabilities depend on t so we write $P(Y_{t-2} = i, Y_{t-1} = j) = P_{ij}^{t-1}$, and $P(Y_{t-2} = i, Y_{t-1} = j, Y_t = k) = P_{ijk}^t$, where i, j, and k take values 0 or 1. Then $P_{10}^{t-1} = (1 - e^{-(1-\mu+\mu K_{t-1})a\mu})e^{-a\mu}$, where $K_{t-1} = 1 - O(d_{t-2,t-1}, r)$. Then

$$P_{100}^t = \sum_{x=0}^{\infty}\sum_{y=0}^{x}\sum_{z=0}^{\infty}(1-(1-\mu)^x)(1-\mu)^y(1-\mu)^z K_1^y K_2^z$$
$$\times e^{-\mu a K_t}\binom{x}{y}(1-K_{t-1})^y K_{t-1}^{x-y}\frac{e^{-a}a^x}{x!}\frac{e^{-aK_{t-1}}(aK_{t-1})^z}{z!},$$

where K_1 is defined as in equation (3) but with $A24 = O(d_{t-2,t-1}, r)$, $A4 = O(_{t-2,t}, r)$, and $A2 = A24 - A4$; and where K_2 is defined as in equation (4) but with $A135 = 1 - A24 = 1 - O(d_{t-2,t-1}, r)$ and $A5 = A45 - A4 = O(d_{t-1,t}, r) - O(d_{t-2,t}, r)$ and $A1 + A3 = A135 - A5$. Other probabilities can be found by subtraction.