

# Statistical Approaches to the Analysis of Point Count Data: A Little Extra Information Can Go a Long Way<sup>1</sup>

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## Abstract

Point counts are a standard sampling procedure for many bird species, but lingering concerns still exist about the quality of information produced from the method. It is well known that variation in observer ability and environmental conditions can influence the detection probability of birds in point counts, but many biologists have been reluctant to abandon point counts in favor of more intensive approaches to counting. However, over the past few years a variety of statistical and methodological developments have begun to provide practical ways of overcoming some of the problems with point counts. We describe some of these approaches, and show how they can be integrated into standard point count protocols to greatly enhance the quality of the information. Several tools now exist for estimation of detection probability of birds during counts, including distance sampling, double observer methods, time-depletion (removal) methods, and hybrid methods that combine these approaches. Many counts are conducted in habitats that make auditory detection of birds much more likely than visual detection. As a framework for understanding detection probability during such counts, we propose separating two components of the probability a bird is detected during a count into (1) the probability a bird vocalizes during the count and (2) the probability this vocalization is detected by an observer. In addition, we propose that some measure of the area sampled during a count is necessary for valid inferences about bird populations. This can be done by employing fixed-radius counts or more sophisticated distance-sampling models. We

recommend any studies employing point counts be designed to estimate detection probability and to include a measure of the area sampled.

*Key words:* Detectability, distance sampling, double-observer, point counts, removal sampling.

## Introduction

Point count surveys are a popular method for sampling bird populations. Point counts can be conducted over a large area for very little cost compared with more intensive survey methods such as spot mapping or nest searching. In their basic design of timed bird counts they are also simple to conduct, requiring only knowledge of birds and their songs. However, analyses relying on data from point count surveys have been strongly criticized (e.g. Burnham 1981) because most implementations of point counts have a shortcoming: they are conducted without attempting to estimate or adjust for detection probability. Even though point counts are coming under increasing scrutiny (e.g. see Rosenstock et al. 2002, Thompson 2002), they are still used in many surveys (e.g., the North American Breeding Bird Survey [BBS], see Robbins et al. 1986). In a review of published reports in ornithological journals from 1989 to 1998, Rosenstock et al. (2002) found the most frequently employed technique to draw inferences about landbird abundance was unadjusted point counts. Most of the users of point counts are apparently unaware of the limitations on the inferences that may be appropriately drawn from such unadjusted counts (Barker and Sauer 1994).

Using unadjusted point counts to evaluate populations of landbirds requires a major assumption: that changes in the counts (e.g. between years or habitat types) reflect a difference in the true population of birds being sampled. However, counts are not censuses: the expected number of birds counted at a point is a product of the population size ( $N$ ) and the detection probability ( $p$ ), where the detection probability is the probability that a bird drawn randomly from the population within

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the sampled area will be detected by the observer. Thus differences between counts may reflect differences in the detection probability, differences in population size, or both.

Because the deficiencies in point counts have been well documented, a substantial amount of effort has been devoted to development of statistical methods to permit estimation of detection rates from point counts. Generally, these methods require collection of ancillary data during the count, and these additional data are used in the context of statistical models to estimate detection probabilities. Examples of these ancillary data include collection of distance information from the point to the bird, allowing for distance estimation of density (Buckland et al. 1993, 2001; Rosenstock et al. 2002), collection of counts by two observers at the same point and time allowing estimation of detection rates using capture-recapture methods (Nichols et al. 2000), and collection of counts divided into time intervals allowing application of removal methods (Farnsworth et al. 2002). These methods provide a variety of alternative approaches for estimating detectability, and incorporating these methods in logistically-efficient ways is a crucial challenge for investigators.

Another method recently proposed is a double-sampling approach (Bart and Earnst 2002). This method attempts to calibrate a quick survey method (e.g. point counts) by performing a census on a subsample of plots. Having a known population size on some plots allows for the estimation of detection probability. This probability can then be used to adjust counts from all the plots upon which the quick method was used. We feel the double-sampling approach is extremely effort intensive, and hence is not a comparable alternative method for counting birds in most habitats in which point counts are conducted. Performing a reliable census of a subsample of point counts would not be practical in most habitats such as forested areas where intensive nest-searching or territory mapping is very difficult and unlikely to provide a reliable census.

In this paper, we will discuss the methods available to deal with issues of detection probability and density from point count surveys. First, we define two of the important conceptual issues that often complicate estimation and analysis of point count data: (1) components of detection probability and (2) area sampled during point counts. For each method we will briefly address its strengths and weaknesses. Finally, we will explore the potential to combine methods and describe an example of combining distance and removal sampling to estimate density. We restrict the discussion to point count surveys designed to count breeding landbirds.

## **Components of Detectability**

In many point count surveys, most birds are detected by hearing songs or calls. In point count surveys of this type it may be useful to separate the overall detection probability into different components. In order for a bird to be recorded by an observer, the bird must vocalize audibly and this noise must be heard and recognized by the observer. We thus separate the components of detection probability into the probability a bird vocalizes ( $P_a$ ) and the probability it will be detected by the observer given that it vocalized ( $P_b$ ) such that the overall detection probability  $P = P_a \times P_b$ . We assume these two probabilities are independent.

## **Density Estimation**

In addition to separating these components of detection probability, area sampled during point count surveys is often an important complication in analysis of point counts. Often, the effective area sampled during point counts is vague, and observers tend to hear birds with varying efficiency. Although some estimation procedures explicitly estimate density of birds (e.g. distance sampling), other methods only estimate abundance. For all abundance estimation methods, differences in adjusted counts may reflect a difference in population size due to different amount of area sampled. For example, if point counts are conducted one year and repeated in a subsequent year and more birds are detected in the later year, it may reflect a greater detection radius in the later year and not a biologically meaningful increase in population size. In addition, many studies employing point counts are more interested in density of birds than abundance, and an important initial motivation of distance methods was to explicitly address this area surveyed issue by modeling detection as a function of distance from the point. Methods that do not include measures of distances to each bird should incorporate some measure of the area sampled as well as an estimate of detection probability.

## **Existing Methods**

### **Distance Sampling**

Distance sampling is a well-established framework for estimating detection probability and density from count data (Buckland et al. 1993, 2001). As applied to point counts, distance sampling theory models the detection probability as a monotonically declining function of distance. The probability a bird is detected when located at distance  $r$  from the point is described by the detection function  $g(r)$ . Distance sampling requires a number of assumptions. For example it assumes that birds are not affected by the presence of the observer. This method also normally requires the assumption that

all birds at the center of the point are detected [i.e. that  $g(0) = 1$ ].

The observer records the distance to all birds detected during a limited-interval count (e.g. 5 min). All observations are then pooled across many count locations to identify the specific shape of the detection function  $g(r)$  that is most appropriate. Akaike's Information Criterion (Burnham and Anderson 1998) may be used to choose the most parsimonious model for  $g(r)$  from several potential curves. Combining the total number of birds detected with the detection function leads to an estimate of density and an estimate of the variance. The theoretical underpinning of this method is well understood and will not be explored in detail here (for details on curve-fitting see Buckland et al. 1993, 2001).

Although distance sampling has been around for quite some time, many investigators have not adopted it as a field technique (Rosenstock et al. 2002). One obstacle preventing its widespread use appears to be the perception that measuring distances to birds is too difficult in many field situations. This can be overcome to some degree by assigning birds detected to distance categories instead of measuring actual distances (for recommendations see Buckland et al. 1993, 2001; Rosenstock et al. 2002).

However, a more serious problem with using distance sampling for point count surveys occurs when  $g(0) \neq 1$ . In many habitats where the majority of birds are detected by sound such as high-canopy forests the probability of detecting a bird at the center of the count circle may be substantially less than one. A bird directly over the head of an observer still must vocalize and be heard (and identified) to be recorded during a point count. Using the components of detection probability discussed above, distance sampling should work well for modeling the probability a bird is detected given that it sings ( $P_b$ ) as a function of distance from the observer, but distance sampling does not directly address the first component of detection probability, the probability a bird vocalizes audibly ( $P_a$ ).

### **Double-Observer Method**

Based on the work done by Cook and Jacobson (1979) with aerial surveys, Nichols et al. (2000) designed a procedure to estimate detection probability during point counts by using two observers. One observer is designated the primary and the other the secondary. The primary conducts a point count normally. The secondary is aware of the birds detected by the primary and records any additional birds that were missed by the primary. The two observers alternate roles during successive point counts. Every bird that is detected by the secondary provides information about the detection probability of the primary observer, and by switching

roles, the technique allows for estimation of the detection probability of each observer. These observer-specific detection probability estimates can then be used to estimate the combined detection probability for both observers during a point count and the associated variance (for details see Nichols et al. 2000).

A similar approach using mark-recapture framework with two (or more) independent observers is also possible (discussed in Pollock et al. 2002). These double-observer approaches (independent and dependent) to estimation of detection probability only deal with the second component of detection probability discussed above (probability bird is detected given that it sings,  $P_b$ ). Using two observers allows estimation of how many birds of those available to be counted (vocalizing audibly) are missed but does not directly address the birds that are missed because they did not vocalize during the count.

The double-observer method estimates detection probability, but this should still be combined with a measure of the area sampled. The double-observer method estimates bird abundance by adjusting counts based on detection probability. If the area sampled is different between counts, these adjusted counts may obscure a real change in bird density. For example if a disturbance such as forest clearing had the combined effects of decreased bird density and increased detection radius (by removing barriers to sound travel), point counts before and after the disturbance may show no difference. This can be overcome by using fixed-radius point counts where a change in bird density will be reflected in estimates of bird abundance within the count circle (see Nichols et al. 2000).

### **Removal Sampling**

The removal sampling framework is based on the idea that as the population of animals being sampled is depleted by removing individuals, the decrease in new animals being caught provides an estimate of the total number of animals originally present (Moran 1951). In its simplest form, the detection probability is assumed to be equal for all animals and constant throughout a series of trapping episodes. As originally conceived, animals were caught and killed, reducing the population available to be caught. The next trapping episode thus is expected to catch fewer animals because the population is smaller but the probability of capture is the same.

As applied to point counts, this method treats birds detected as removed from the population of birds available for initial detection (for details see Farnsworth et al. 2002). In this method, the count period is divided into several time intervals. As birds are detected in one time interval, they are considered "removed" from the

population of birds being sampled in subsequent intervals. One advantage of this approach is that, under an assumption that every bird has some *a priori* probability  $>0$  of vocalizing during the sample period, it can estimate the number of birds missed during the count including those that did not vocalize. In this way, the estimate of detection probability derived from the removal method is the product of the two components of detection probability ( $P = P_a \times P_b$ ).

Without some measure of the area sampled during a point count, this method will be vulnerable to the same confounding effects of detection radius and density discussed above. However, this can be overcome by using fixed-radius counts to estimate density (for details see Farnsworth et al. 2002). Another way to estimate density is by combining the ideas of removal sampling and distance sampling into one unified procedure (see below).

## Emerging Syntheses

With the increased awareness of the shortcomings of unadjusted point counts, improved counting techniques are required that permit estimation of detection probability. Though available for some time, distance sampling is becoming more widely used. In addition, double-observer and removal sampling have recently been adapted to point counts. There is considerable work to be done to combine several of these methods into a unified approach to estimation of bird density. Here we present a method that combines distance and removal sampling. Combining removal and distance sampling allows a detection function to be used that does not require  $g(0) = 1$ .

We consider only the simplest possible case: a count divided into two time-intervals of equal length and every bird detected identified as within a fixed radius or beyond a fixed radius from the observer. In theory a combined method may include any number of time intervals and distance categories and fit any of a number of curves for the detection function, but here we provide only a simple example and will use the half-normal function to model the decline in detection probability with increasing distance.

The rationale for this method is as follows. A bird may only be detected if it vocalizes, but the probability it will be detected given that it vocalizes decreases with increasing distance from the observer. The probability a bird vocalizes within a time-interval is  $P_a$ , and the probability a bird is detected given that it vocalizes is  $P_b$ . The overall detection probability is the product of these two independent probabilities:  $P = P_a \times P_b$ . The probability a bird is detected given that it sings ( $P_b$ ) is a

function of distance from the observer ( $r$ ). In the simple case discussed here we define

$$P_b = \exp\left(\frac{-r^2}{\sigma^2}\right)$$

where  $\sigma$  is a parameter with units of distance (e.g. meters) describing how quickly  $P_b$  declines from 1 with increasing distance from the observer. Thus the overall detection probability is:

$$P = P_a \exp\left(\frac{-r^2}{\sigma^2}\right)$$

With two time-intervals and two distance categories, there are four sufficient statistics, defined as  $X_{ij}$  = number of birds first recorded in the  $i$ th distance category during the  $j$ th time interval. For example  $X_{11}$  is the number of birds detected within the radius  $r_1$  of the observer during the first time-interval. Having a count divided into at least two time intervals allows for the estimation of  $P_a$ , and classifying birds detected into at least two distance categories allows for estimation of the decline in  $P_b$  with increasing distance. *Appendix 1* derives the equations necessary for these estimators as well as an estimator for density from these parameters.

The assumptions of this particular model are as follows:

1. Birds are not moving during the count period.
2. The probability a bird vocalizes is the same for all birds and constant throughout the count period.
3. Birds are assigned to the proper distance category.
4. Birds are counted without mistakes (properly identified and no double-counting).

## Example

In 2000, we conducted 824 point counts along established BBS routes. For each count we recorded all birds detected during three minutes, separated into those initially detected in the first 1½ min and those first detected in the final 1½ min. Each bird detected was identified as being within 50 m of the observer or beyond 50 m. In addition each bird recorded was noted as being detected by sight or by sound. For this example, we consider the three most frequently recorded bird species detected by ear, Red-eyed Vireos (*Vireo olivaceus*), American Robins (*Turdus migratorius*), and American Crows (*Corvus brachyrhynchos*).

Among the three species analyzed, Red-eyed Vireo was the most frequently recorded ( $X_{..} = 676$ ) and had the highest estimated density ( $\hat{D} = 0.35$  birds per ha; *table 1*). American Crow was the next most frequently

**Table 1**— Counts and estimates of model parameters and density ( $D$ ) for three most frequently detected species during 824 point counts separated into two time intervals and two distance categories. Parameter  $P_a$  represents the probability a bird vocalizes during one time interval and  $\sigma$  reflects the decline in detection probability with increasing distance from the observer. Larger  $\sigma$  corresponds to slower decline in detectability (i.e. louder vocalization).

Species	$X_{11}$	$X_{12}$	$X_{21}$	$X_{22}$	$\hat{P}_a \pm \hat{SE}$	$\hat{\sigma} \pm \hat{SE}$ (m)	$\hat{D}$ (Ha <sup>-1</sup> )
Red-eyed Vireo	183	38	321	134	1.00 ± 0.04	71 ± 3	0.35
American Robin	134	34	186	86	0.97 ± 0.05	65 ± 3	0.28
American Crow	23	8	392	136	0.92 ± 0.06	183 ± 17	0.18

detected species ( $X_{..} = 559$ ), but its estimated density ( $\hat{D} = 0.18$  birds per Ha) was lower than the less frequently-recorded American Robin ( $X_{..} = 440$ ;  $\hat{D} = 0.28$  birds per Ha). This was due to the greater estimate of the parameter  $\sigma$  for American Crow ( $\sigma_{\text{crow}} = 183\text{m}$  and  $\sigma_{\text{robin}} = 65\text{m}$ ). Vocalizations of American Crows can be heard at a greater distance than vocalizations of American Robins.

This example demonstrates one potential way removal sampling and distance sampling may be combined. The model described here was necessarily simple due to the limitations of having only four sufficient statistics. Future efforts should include more time intervals and distance categories and attempt to relax some model assumptions. For example the assumption that the probability an undetected bird will vocalize is constant throughout the count period is probably not valid because if there is heterogeneity within the population of birds being sampled with regard to singing frequency, the birds singing most consistently will be more likely to be detected in the first time interval. More time intervals and distance categories will improve the precision of estimates.

## Discussion and Recommendations

Point counts will undoubtedly remain a standard method for sampling many bird species because they are easy to implement. A small number of trained observers can record birds over a large area at a very low cost. If inferences are to be drawn about populations of these bird species beyond mere presence/absence information, auxiliary information should be collected. A little extra information recorded about the birds detected during counts can go a long way to improving the inferences one can make about bird populations. When designing a study using point counts, the investigator(s) should incorporate ways to estimate detection probability and measure the area sampled.

Point counts can estimate detection probability by having two observers or by separating the count period

into intervals and recording in which interval a bird is first detected. Having more than one observer conducting counts at the same time may have the additional advantage of minimizing errors in species identification because each observer may provide a check on the other's identification of species. Similarly, having two observers each estimating distances to birds detected will provide a measure of the precision of these estimates. If counts are divided into intervals, we recommend having at least three intervals of equal length. Having three or more intervals allows the model to incorporate heterogeneity in the probability of vocalizing ( $P_a$ ) as demonstrated by Farnsworth et al. (2002). To avoid violating assumption 1 (that birds are not moving during the count), investigators may want to use counts of short duration (e.g. 3 min). The model framework can be applied to counts divided into intervals of different length (Farnsworth et al. 2002), but the mathematical formulations are simpler with equal time intervals.

In addition, counts should be designed to include a measure of the area sampled or the distance to each bird detected. If fixed-radius counts are used, the size of the radius must be chosen such that a bird that vocalizes within the radius can be detected by the observer. Too large a radius will mean that birds near the edge (farthest from the point, but within the radius) will have very low, perhaps zero probability of detection even if they vocalize. Too small a radius will unnecessarily reduce the number of birds used in analyses. Most point count surveys are designed to count many different species at the same time. Some of the species recorded will have loud vocalizations and some faint vocalizations. In such situations, it may be useful to assign birds detected into several distance categories. This would allow data to be analyzed as fixed-radius counts of different size for different species. Of course assigning birds detected into many distance categories also allows for analyses that model the decline in detection probability with increasing distance from the point such as distance sampling and the hybrid model described here.

Overall we recommend future point count surveys to record the additional information necessary to apply these existing and emerging statistical models. The best way to apply these principles will depend on the needs and goals of specific projects, but we offer the following rules of thumb to help design new count protocols. (1) Separate the count period into three or more time-intervals of equal length. (2) Record the distance to each bird detected. This may be done by assigning each bird detected into one of several (e.g. four) distance categories. For example, we recommend a ten-minute count separated into five intervals of two min each with birds identified as first detected in one of these distance categories: 0 – 25 m, 25 – 50 m, 50 – 100 m, and >100 m from the point. Such counts could be performed with one observer or could employ the double observer frame-work by having the primary observer conduct the count as above and the secondary observer record additional birds not detected by the primary observer. The above distance categories are provided as a suggestion designed to provide easily conducted counts that are appropriate for a variety of species (with loud and faint vocalizations). Focused studies targeting particular species may benefit from different distance categories.

We agree with the many recent recommendations to stop using unadjusted point counts for drawing inferences about landbird populations. There are now several methodological approaches to estimation of detection probability that should provide estimates of avian abundance and density superior to those based on unadjusted counts. These model-based approaches include distance sampling, multiple observers and temporal removal modeling. Unlike distance sampling and multiple observers, the temporal removal approach permits estimation of detection probability in a manner that includes the probability that a bird in the sampled area vocalizes. Combination methods that include two or more of the above approaches are currently under development and should provide additional modeling flexibility and estimator robustness as demonstrated here. We believe that avian ecologists should avoid using unadjusted point counts in favor of model-based methods such as those described here. We look forward to the next several years, as avian ecologists gain experience with these methods and biometricians develop a suite of methods and associated inference procedures. We expect such efforts to yield increased knowledge of avian population dynamics and increased ability to make wise management and conservation decisions.

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### Appendix 1

The expected number of birds counted during the  $j$ th time interval ( $X_{.j}$ ) within a ring defined as the area between the distance  $r$  and  $r + dr$  from the observer may be expressed as:

$$E(X_{.j}) = N_r p (1 - p)^{j-1} = DA_r p (1 - p)^{j-1}$$

$$= D\pi \left[ (r + dr)^2 - r^2 \right] P_a \exp\left(\frac{-r^2}{\sigma^2}\right) \left[ 1 - P_a \exp\left(\frac{-r^2}{\sigma^2}\right) \right]^{j-1}$$

where  $N_r$  is the population of birds within the ring,  $A_r$  is the area of the ring, and  $D$  is the density of birds. The probability a bird is detected in the time interval is  $p$ , which is a function of the probability a bird vocalizes ( $P_a$ ) that declines with increasing distance from the observer according to the parameter  $\sigma$ . If  $dr$  is very small relative to  $r$ , then  $dr^2$  can be ignored yielding:

$$E(X_{.j}) = D\pi 2r P_a \exp\left(\frac{-r^2}{\sigma^2}\right) \left[ 1 - P_a \exp\left(\frac{-r^2}{\sigma^2}\right) \right]^{j-1} dr$$

The  $i$ th distance category is defined as the ring formed between the distances  $r_{i-1}$  and  $r_i$  (with  $r_0 = 0$ ) from the observer. Thus the expected number of birds counted within the  $i$ th distance category during the  $j$ th time interval is:

$$E(X_{ij}) = \int_{r_{i-1}}^{r_i} D\pi 2r P_a \exp\left(\frac{-r^2}{\sigma^2}\right) \left[ 1 - P_a \exp\left(\frac{-r^2}{\sigma^2}\right) \right]^{j-1} dr$$

This model will work for any number of time intervals and distance categories. In the following example, we consider only the simple case with two time intervals and two distance categories: (1) from the observer to  $r_1$  and (2) from  $r_1$  to  $\infty$ . The expected value of the number of birds counted in the first time interval within  $r_1$  of the observer ( $X_{11}$ ) is:

$$E(X_{11}) = \int_0^{r_1} D\pi 2r P_a \exp\left(\frac{-r^2}{\sigma^2}\right) dr = D\pi P_a \sigma^2 \left[ 1 - \exp\left(\frac{-r_1^2}{\sigma^2}\right) \right]$$

and the expected value for the number of birds counted in the first time interval beyond  $r_1$  of the observer ( $X_{21}$ ) is:

$$E(X_{21}) = D\pi P_a \sigma^2 \left[ \exp\left(\frac{-r_1^2}{\sigma^2}\right) \right]$$

The expected values of the number of birds counted in the second time interval ( $X_{12}$  and  $X_{22}$ ) are:

$$E(X_{12}) = D\pi P_a \sigma^2 \left[ 1 - \exp\left(\frac{-r_1^2}{\sigma^2}\right) + P_a \frac{\exp\left(\frac{-2r_1^2}{\sigma^2}\right)}{2} - \frac{P_a}{2} \right]$$

$$E(X_{22}) = D\pi P_a \sigma^2 \left[ \exp\left(\frac{-r_1^2}{\sigma^2}\right) - P_a \frac{\exp\left(\frac{-2r_1^2}{\sigma^2}\right)}{2} \right]$$

The expected total number of birds detected during the entire count ( $X_{..}$ ) is the sum of the four expected values above:

$$E(X_{..}) = D\pi P_a \sigma^2 \left[ 2 - \frac{P_a}{2} \right]$$

In order to estimate the parameters  $P_a$  and  $\sigma$ , we must find the conditional probabilities of each of the four sufficient statistics. We do this by finding the probability a bird is a member of  $X_{ij}$  given that it is a member of  $X_{..}$ . The advantage of this is that the unknown parameter  $D$  can be removed from the equations (to be calculated later). The result is:

$$\pi_{11} = P(y \in X_{11} | y \in X_{..}) = \frac{1 - \exp\left(\frac{-r_1^2}{\sigma^2}\right)}{2 - \frac{P_a}{2}}$$

$$\pi_{12} = P(y \in X_{12} | y \in X_{..}) = \frac{1 - \exp\left(\frac{-r_1^2}{\sigma^2}\right) + \frac{P_a}{2} \exp\left(\frac{-2r_1^2}{\sigma^2}\right) - \frac{P_a}{2}}{2 - \frac{P_a}{2}}$$

$$\pi_{21} = P(y \in X_{21} | y \in X_{..}) = \frac{\exp\left(\frac{-r_1^2}{\sigma^2}\right)}{2 - \frac{P_a}{2}}$$

$$\pi_{22} = P(y \in X_{22} | y \in X_{..}) = \frac{\exp\left(\frac{-r_1^2}{\sigma^2}\right) - \frac{P_a}{2} \exp\left(\frac{-2r_1^2}{\sigma^2}\right)}{2 - \frac{P_a}{2}}$$

The conditional multinomial probability density function is:

$$f(X_{11}, X_{12}, X_{21}, X_{22}) = \frac{X_{..}!}{X_{11}! X_{12}! X_{21}! X_{22}!} (\pi_{11})^{X_{11}} (\pi_{12})^{X_{12}} (\pi_{21})^{X_{21}} (\pi_{22})^{X_{22}}$$

The values for  $P_a$  and  $\sigma$  that maximize the following likelihood function

$$L(P_a, \sigma | X_{11}, X_{12}, X_{21}, X_{22}) \propto (\pi_{11})^{X_{11}} (\pi_{12})^{X_{12}} (\pi_{21})^{X_{21}} (\pi_{22})^{X_{22}}$$

represents the maximum likelihood estimates for these two parameters. Program SURVIV may be used to find these maximum likelihood estimates with associated estimates of their variances. These estimates of  $P_a$  and  $\sigma$  may then be combined with  $X_{..}$  and the total number of counts conducted ( $n$ ) to estimate density ( $D$ ):

$$\hat{D} = \frac{X_{..}}{n\pi\hat{\sigma}^2\left(2\hat{P}_a - \frac{\hat{P}_a^2}{2}\right)}$$

If  $\hat{\sigma}$  is represented in meters, then  $\hat{D}$  above will have units birds per m<sup>2</sup>. Converting this estimate of density to birds per Ha is thus:

$$\hat{D} = \frac{X_{..}}{n\pi\hat{\sigma}^2\left(2\hat{P}_a - \frac{\hat{P}_a^2}{2}\right)} \times 10,000$$