

A Conceptual Guide to Detection Probability for Point Counts and Other Count-based Survey Methods¹

D. Archibald McCallum²

Abstract

Accurate and precise estimates of numbers of animals are vitally needed both to assess population status and to evaluate management decisions. Various methods exist for counting birds, but most of those used with territorial landbirds yield only indices, not true estimates of population size. The need for valid density estimates has spawned a number of models for estimating p , the ratio of birds detected to those present. Wildlife biologists can be assisted in evaluating these methods by appreciating several subtleties of p : (1) p depends upon the duration of the count, (2) p has two independent components, *availability* of cues and *detectability* of cues, (3) detectability is a function of both the *conspicuousness* of cues (e.g., vocalizations, conspicuous movements) and the *abundance* of cues, and (4) discontinuous production of cues lowers availability, which has a direct and sometimes profound effect on p . Two recently-updated methods of estimating p , double-observer sampling and distance-sampling, are better suited to estimating detectability, while two others, double sampling and removal sampling, are better suited to estimating availability. While none of the four offers a complete solution at present, hybrids are under development, and a technique that can yield estimates of availability and detectability from survey data may be available in the near future.

Key words: abundance of cues, availability, bird survey, census, conspicuousness, detectability, detection probability, distance sampling, double sampling, double-observer sampling, index ratio, point count, removal sampling.

Introduction

Unlike most fish, insects, and nocturnal mammals, birds are typically surveyed without capturing or marking individuals. A number of passive sampling techniques, e.g., spot-mapping, line transects, and point counts, are commonly used for estimating numbers of birds. A complete taxonomy of sampling and analytical methods is given by Thompson (2002). The accuracy and precision of most techniques currently used to count birds has been questioned, because of their failure to provide estimates of detection probability (Nichols et al. 2000, Bart and Earnst 2002, Farnsworth et al. 2002, Rosenstock et al. 2002, Thompson 2002).

Detection probabilities are used to account for “birds present but not detected” on surveys (Thompson 2002: 19). The importance of estimating detection probabilities for bird counts has long been recognized (Burnham 1981), but 95 percent of recent avian population studies surveyed by Rosenstock et al. (2002) relied on unadjusted counts (called “indices”) for analysis and comparison. This practice assumes, tacitly or otherwise, that detection probability is constant across the entire sample (Thompson 2002). It is now widely suspected that this assumption is violated in a number of ways (Thompson 2002). If so, comparisons of index data obtained at different times and places may lead to erroneous conclusions. Adoption of new survey methods that accurately estimate detection probabilities would alleviate this concern.

The recent flurry of publications on detection probability (Nichols et al. 2000, Buckland et al. 2001, Bart and Earnst 2002, Rosenstock et al. 2002, Farnsworth et al. 2002, and especially Thompson 2002) suggests that changes in sampling techniques may be imminent. These authors advance four largely independent methods for estimating detection probabilities, but an independent comparison of them is not available.

The purpose of this paper is to assist biologists and managers in understanding the concepts underlying detection probability and to help them select from among these new methods for estimating detection probability for vocalization-based counts. Unlike the quite proper development of estimation techniques in the statistically focused publications that introduce these techniques, this survey will define a small set of heuristic parameters that will be used to describe and distinguish the methods, leading to recommendations based on logical and empirical considerations.

¹A version of this paper was presented at the **Third International Partners in Flight Conference, March 20-24, 2002, Asilomar Conference Grounds, California.**

²Applied Bioacoustics, P.O. Box 51063, Eugene, OR 97405. E-mail: arch@appliedbioacoustics.com.

The Meaning of P

If the goal of a sampling technique is to estimate the number, N , of individuals present in an area from a sample count, C , of that area, (See Appendix for table of parameters and symbols.), the expected value of the count is given by $E(C) = Np$, where p is the “detection probability” (Nichols et al. 2000, Farnsworth et al. 2002) or “index ratio” (Bart and Earnst 2002). Use of C (raw count data) to estimate the change in N over time (i.e., trend), requires the “proportionality assumption” (Thompson 2002) that a trend in p does not exist (J. Bart, pers. com). Populations in different areas and populations counted with different methods cannot be compared quantitatively with indices (i.e., C values) (Bart and Earnst 2002). In order to make inferences from count data without “discomfort with the knowledge that such inferences depend upon untested assumptions” (Nichols et al. 2000: 394), it is necessary to estimate N , preferably with methods that are grounded in statistical theory (Thompson 2002).

The standard form of such an estimate is given by

$$\hat{N} = \frac{C}{\hat{p}} \tag{1}$$

(Nichols et al. 2002, equation 4). These parameters apply to the birds of a sex, species, area, or indeed any group that has a common value of p (Nichols et al. 2000). P is the probability of detecting a typical individual. It can be thought of as the average detection probability of all the individuals that reside in the area being surveyed, although is it never estimated in this way. Instead, it is estimated from population parameters. \hat{D} , the estimated population density, can be calculated as \hat{N}/A , where A is the area in which counts were made.

All of the above is uncontroversial mathematically. The real issue is how to obtain the estimate \hat{P} of the parametric detection probability p , so the estimate \hat{N} can be calculated. The four methods reviewed here estimate p in different ways. The following points are helpful in understanding p , and thereby recognizing the differences in estimation methods.

1. p is specific to the duration of the count

The single holistic parameter p incorporates a variety of causes of non-detection, including the bird’s being silent during the count, attenuation of signal(s), masking of a song by ambient physical noise, the sounds of non-target animals (e.g., insects), noise made by the observer(s), and ascribing the sound to the wrong species. Regardless of the sources of p , its expected value is C/N (Nichols et al. 2000), where C is the count obtained in a count of duration m . It follows that p

varies with C , and therefore any value of p is specific to the duration m of the count period used to obtain C . *Figure 1* is a standard accumulation curve that shows the cumulative number of individuals, C , detected for any amount of effort, e.g., minutes (m) spent counting. According to this uncontroversial relationship, C is expected to be slightly higher in a 5-min point count than it is in a 3-min point count, and considerably higher in 2 hr of observation. The practice of sampling until the cumulative count of individuals in an area levels off is merely an empirical way to maximize detection of all birds present (but the longer the count period, the greater the likelihood of over counting, see below).

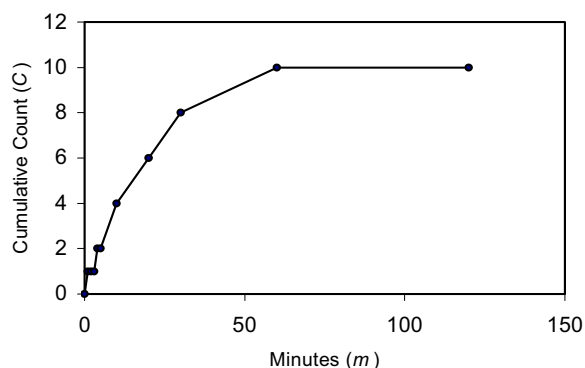


Figure 1—Hypothetical cumulative count (C) of individuals as a function of effort, e.g., minutes (m), in any kind of monitoring program. Detection probability, $p = C/N$, increases with effort (e.g., total person-minutes) until all individuals are counted.

The curve in *Figure 1* has the general form $p_m = 1 - (1 - p_{1m})^m$, where m is the duration of the count, p_m is estimated by C/N for counts of that duration, and p_{1m} is the detection probability for a 1-min count. For example, if $C/N = 0.5$ for 3-min counts, p_{1m} is 0.207. Once p_{1m} has been found, p_m for count periods of any duration, m , can be calculated, and applied as a correction factor to counts of that duration. This approach requires independent knowledge of N in the count areas in which p_m is estimated, as obtained with double sampling methods (Bart and Earnst 2002).

2. For aural surveys, p must estimate both “availability” and “detectability”

Although detectability of birds is a potentially a function of a number of factors, it is useful for aural surveys to subdivide p into two main components (Farnsworth et al. 2002):

$$p = p_s p_{d_s} \tag{2}$$

where p_s is the probability that an average bird sings (or produces some other detectable cue) and p_{d_s} is the probability it is detected, given that it sings. Recogniz-

ing the distinction between these two component probabilities, “availability” and “detectability,” plays a central role in evaluating the four methods (see below). The next two sections explain each of these probabilities.

3. Detectability: Only one detection is required to count an individual

Unlike intensive survey methods, (e.g., territory-mapping, nest-finding protocols), “rapid survey” methods (e.g., point counts, line transects) define a single detection of an individual as sufficient to count that individual. Further detections of that individual do not change *C*. Indeed, count periods are intentionally made brief to minimize the possibility of double-counting of an individual (e.g., Buckland et al. 2001). So, detectability ($p_{d|s}$) is actually the probability that a bird will be detected *at least once* during its active periods. Therefore

$$p_{d|s} = 1 - (1 - p_{1d})^s \tag{3}$$

where p_{1d} is the probability of detecting an average cue; and *s* is the number of cues, i.e., songs or other detectable acts, it actually produces during the count period.

Conspicuousness. p_{1d} is a measure of conspicuousness, i.e., it captures reductions in detectability due to the following four factors:

Amplitude of the vocalizations of the average individual. Amplitude diminishes as the square of the distance between the source and the detector, so detectability is strongly influenced by distance and correlated factors, such as sound blocking structures.

Auditory acuity of the observer. Acuity is frequency-dependent in all humans, and is greatest at 1-2 kHz, below the frequencies of most bird sounds. One reason that *p* differs among species is the varying degree to which the birds’ sounds fall outside this 1-2 kHz band. Moreover, individual humans vary in both general acuity and frequency response (Emlen and DeJong 1981). Obviously, *p* is observer-specific for these reasons, even if not for others.

Attentiveness of the observer. Because point counts are typically conducted in real time, i.e., the observer cannot rewind and hear or see any cues a second time, it is standard practice for an observer to attempt to focus on a single singer, identify it, and then move on to another. This means that the listening time of the observer is divided among all the singers, some of which will be missed if they cease vocalizing before the observer has a chance to attend to them.

Masking of focal sounds by other sounds, including ambient noise, speech of the observer and any assist-

ants present, vocalizations of other species, and vocalizations of non-focal individuals of the focal species.

High amplitude mitigates the other three causes. If a sound is loud, it is more likely to be noticed and more likely to mask other sounds than to be masked. Amplitude is directly related to distance, while the other three factors come into play because of the low amplitude of sounds from distant sources.

Abundance of Cues. Parameter *s* is the number of cues produced during a count period, independent of their intensity. High singing rates (*s/m*) mitigate all four causes of non-detection, by giving the observer multiple opportunities to make the single detection that is needed to count an individual.

Equation (3) quantifies the intuitive relationship between singing rate and the likelihood of detecting an individual. The good news from this equation is that even inconspicuous cues (low p_{1d}) can result in detection when they are numerous (high *s*). For example, $p_{1d} = 0.2$, as one might find during an intense dawn chorus, translates to $p_{d|s} = 0.996$, with a realistic *s* of 25, or five songs per min in a 5-min count period. Equation 3 also shows why the dawn chorus may not be the optimal time to conduct a survey. Singing rates (*s/m*) tend to be highest at this time, and owing to correlation of *s* among individuals, masking by other individuals may reduce p_{1d} , offsetting the advantage of high *s*. Figure 2 shows these trade-offs graphically.

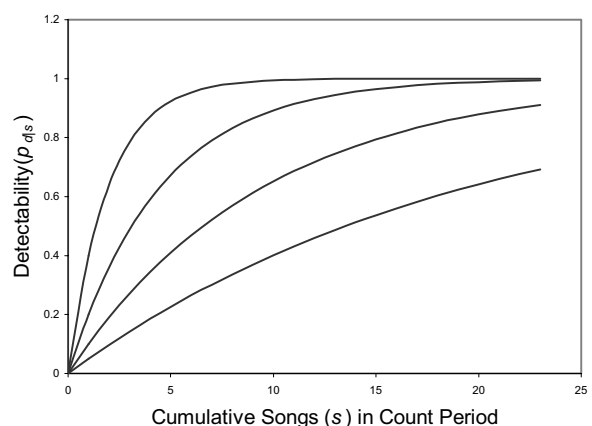


Figure 2—Probability of detecting an individual at least once during a count period as a function of the abundance of cues (e.g., the cumulative number of songs it sings, *s*), and the conspicuousness of a cue (i.e., the probability of detecting it once, p_{1d}). Each curve represents a different level of conspicuousness. A horizontal line anywhere on this graph crosses combinations of conspicuousness and cue abundance (i.e., p_{1d} and *s*) that yield identical detectability ($p_{d|s}$).

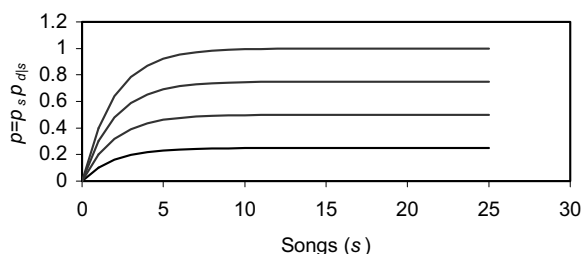


Figure 3—The joint effects of availability and detectability on detection probability (p). Conspicuousness (p_{1d}) is 0.40 in all cases. The top curve is identical to the top curve in Figure 2. The other curves show the effects of lower availability on overall detection, as singing males acquire mates and sing less often.

4. Availability: The overlooked component of detection probability.

Availability, the probability that a bird produces any cue at all during a count period, is often <1 , and low availability may be the most serious cause of non-detection. Surveyors use scheduling to mitigate the low incidence of singing in the middle of the day, or late in the breeding season, but optimal timing is not possible for every sample. A correction for low availability due to time of day, season, or pairing status would greatly improve the accuracy of count data. Nonetheless, p has been estimated as though it were a single parameter until recently. Buckland et al. (2001) briefly referred to availability, but did not include it as an independent parameter in their model. Farnsworth et al. (2002) were the first to do this.

Equation 3 and Figure 2 show that the probability of detecting an individual bird increases as its song production, s , increases. This is, however, not the whole story. If songs are evenly distributed across the time period in which a survey may be taken, s should be a good predictor of detection. But, if songs are clumped in time, i.e., delivered in bouts, silent intervals between bouts may be long enough to completely overlap a standard count period. The resulting reduction in p_s has a serious impact on overall detection, p (fig. 3). Substituting equation 3 in equation 2, we have

$$p = p_s (1 - (1 - p_{1d})^s) \tag{4}$$

Because p_s is independent of p_{dis} (Farnsworth et al. 2002) and is free to vary from 0 to 1, there is no necessary correlation between singing rate s/m and the overall value of p . There may, however, be an empirical correlation between singing rate and p_s , (e.g., Scott et al., in prep.), and this deserves further study.

Comparison and Evaluation of Models

The double-observer (Nichols et al. 2000), double-sampling (Bart and Earnst 2002), distance sampling (Buckland et al. 2001), and removal (Farnsworth et al. 2002) models have been proposed as methods for estimating p . Consumers (e.g., wildlife biologists) need criteria for choosing among these methods. The heuristic decomposition of detection probability, p , into several independent components makes it easier to compare and evaluate these methods. To be sufficient for estimating p , a method must explicitly or implicitly estimate the parameters of equations 2-4.

Double-Observer Method

The double-observer method obtains an estimate of p by comparing the numbers of birds detected by two observers, who count the birds in the same area at the same time. The second observer records the data for the primary observer, and at the same time is expected to detect additional birds that are missed by the primary observer. The method proposed for point counts is an adaptation of a technique originally designed for visual surveys from an aerial platform (Cook and Jacobson 1979). It is a member of a family of “multiple-platform” techniques (Buckland et al. 2001).

In actuality, the double-observer method (Nichols et al. 2000) produces an estimate of p_{dis} that incorporates the effects of observer skill, inattention, and noise of all kinds. The method offers no means of estimating p_s , and so tacitly assumes that $p_s = 1$. The authors who applied it to point count data have subsequently endorsed this interpretation (Farnsworth et al. 2002). It therefore should be used only in situations in which this assumption can be met.

Distance Sampling

Distance sampling uses the fall-off in detections with distance to model a distance-detection function for plots with preset dimensions. The plot may be sampled from fixed points or a transect line. This function is estimated from the estimated distances to the first detection of each individual per species. The distance-detection function is used to estimate a detection probability, which is construed (Buckland et al. 2001:37, equation 2.2) to be p , as defined here. Density, D , is estimated directly from p and A . \hat{N} is calculated as $\hat{D} * A$.

Distance sampling was developed to deal with the effect of distance on *visibility* during ship-borne and airborne line-transect surveys of cetaceans. The line-transect theory has been extended, with appropriate

modification for differences in geometry, to “point transects,” which are sets of variable circular plot surveys (Ramsey and Scott 1979, Reynolds et al. 1980), with updated estimation methods (Buckland et al. 2001).

Although distance sampling has been proposed for surveying territorial songbird populations (Buckland et al. 2001, Rosenstock et al. 2002), this recommendation comes with a number of caveats and disclaimers. A very clear assumption of the method is that all animals present at distance = 0 are detected. Leaving aside the very real possibility that the observer’s presence may bias detection or even the presence of animals at close distances, this assumption tacitly requires that $p_s = 1$, i.e., that all animals present perform detectable acts during the survey period. The detection probability estimated by the distance method is therefore $p_{d|s}$, not p .

When cues are discrete, e.g., bird song, the assumption of perfect detectability at distance = 0 may be difficult to meet. This can be mitigated by increasing the time at the point. But, “the objects around a point should be located at an instant in time” (Buckland et al. 2001:147). These authors recommend a “snapshot” preceded by a few minutes of locating individuals and followed by a few minutes to confirm their presence at the time of the snapshot. If birds are counted throughout the period, as is typical in point counts, an upward bias in the estimate of numbers results.

Incidentally, if the recommended snapshot is essentially instantaneous, does it estimate $p_{d|s}$ or p_{1d} , in the terminology of this paper (see equation 3)? Actually, the two are equal when $s = 1$, as is the case in an instantaneous sample. Moreover, because the estimate of C is also instantaneous, the constant ratio of C and p discussed above is not violated.

Bout structure also poses problems. When “periods of detectability [are] interspersed with periods of unavailability” the distance method produces an estimate that is the product of density and the proportion of birds available for detection [i.e., p_s] at any given time (Buckland et al. 2001:189). This is a second way of saying that the distance method estimates $p_{d|s}$, not p . In such circumstances, e.g., whales that dive for long periods or songbirds that are silent for periods longer than the standard counting period, an independent estimate of p_s is required.

An alternative to conventional distance sampling is “cue counting,” in which distance is estimated to every cue (song or other detectable event) rather than every animal. In this case, movement of the bird is not a problem, as long as all cues are counted. The detection function is estimated as with distance sampling, and the estimate of D requires an independent estimate of cue

rate, which is s/m in the terminology of this paper. This is a possible area of research (Buckland et al. 2001). Potential difficulties are detecting and measuring distances to all the cues in a chorus of songbirds, and high variance in the cue rate owing to bout structure (see above).

Despite these difficulties, distance sampling does offer a potential solution to a major problem of point counts. The probability of detecting a single song, p_{1d} , is a function of the amplitude of the song and related factors (see above). Because amplitude decreases as the square of distance increases, each bird would have a different p_{1d} . A method is needed to account for p_{1d} for the entire population, and the distance method would appear to meet this need.

Double Sampling

The double-sampling model was developed for waterfowl monitoring and has been adapted to the monitoring of breeding populations of upland birds (Bart and Earnst 2002). Unlike the other three models, double-sampling does not attempt to estimate p from the data to which it will be applied as a correction factor. A set of “rapid surveys,” such as line-transects or variable circular plot counts, is taken as usual. In a random subset of the rapid survey plots, other workers conduct “intensive surveys,” i.e., true censuses of all N individuals present. The estimate of p obtained from the ratio C/N in the intensive plots may then be used as the estimate of p for the rapid surveys.

To date, the main empirical shortcoming of this method is that it has not yet been applied to point-centered rapid surveys. The rapid surveys performed by Bart and Earnst (2002) involved area search, rather than aural sampling, in tundra (i.e., treeless) study plots, where the attenuation of a bird’s signal with distance was a negligible problem. These relatively long “rapid” surveys in areas with relatively low bird density and high visibility made masking and inattention insignificant issues. But, application of double-sampling to aurally based point counts in areas with more complex vegetation will require an estimate of $p_{d|s}$. It may be that an adequate estimate of $p_{d|s}$ can be obtained with the distance method.

Intensive surveys of birds typically include nest searches and territory mapping. Territory mapping is essential to determine whether the territory centroid is on or off the measured intensive plot, and must be done just outside as well as inside the plot for this reason (Bart and Earnst 2002). Although highly desirable, intensive study plots can be expensive to census. Bart and Earnst (2002) provided estimators of cost, and a

routine for optimizing allocation of effort to intensive and rapid plots.

Removal Sampling

In developing their removal model, Farnsworth et al. (2002) explicitly set out to overcome the shortcomings of the double-observer and distance methods by accounting for p_s as well as $p_{d|s}$. This is a large step in the right direction. Their approach relies on the logic of removal sampling, in which the probability of trapping another individual declines as individuals are removed from a closed, finite population. The method of Farnsworth et al. (2002) relies on “virtual” removal. They divide a point count period into sequential segments, and record the number of birds first detected in each segment. The decline in new detections over the duration of the count is used to estimate p_s . The computational gambit that permits an estimate of p_s without knowing N is division of the N birds into one *ad hoc* subgroup in which all birds are detected and another in which some are detected. This assumption is relaxed in some reduced models.

Despite providing the first explicit decomposition of detection probability into availability and detectability, the model of Farnsworth et al. (2002) estimates only availability. Nevertheless, this model makes it possible to reanalyze old data sets that are subdivided temporally and produce an estimate of detection probability.

More recently, Farnsworth et al. (this volume) have added a distance component to their removal model, as suggested by Farnsworth et al. (2002). They estimate detectability ($p_{d|s}$) by dividing the count circle into two or more concentric rings, and assigning the first detection of each individual that is counted to one of these rings. This practice yields an estimate of detectability for the entire circle that is corrected for the fall-off in detectability with distance. This “binning” of the data into concentric rings is an acceptable alternative to estimating the distance to each bird as long as birds are accurately assigned to rings (Buckland et al. 2002, Farnsworth et al. 2002).

Farnsworth and colleagues are seeking a method that can be applied retrospectively to point count data that were binned into time intervals and distance rings. For example, Ralph et al. (1995) recommended recording data separately for sequential 3-, 2-, and 5-min segments of a 10-min point count, so the results can be compared to BBS results, which are based on 3-min point counts, and other data sets. Similarly, the recently adopted protocol in the U. S. Pacific Northwest (Huff et al. 2000) recommends subdividing detections into at least two distance rings. Many data sets may therefore

yield estimates of availability and detectability if this removal-distance method proves reliable.

Because this method is intended to estimate both availability and detectability from actual count data, without the expense of double-sampling, managers will follow its development with great interest. A few cautions are therefore in order.

The cues produced by territorial birds are often delivered in bouts of intense singing separated by intervals of total silence. This bout structure is a challenge for the removal method. Availability is estimated from changes in activity during count periods. In the most likely case, a 5-min count divided into 3-min and 2-min segments, some segment of the population must stop or start producing cues during that short interval. Availability will be overestimated as 1.0 if all individuals present are either silent or active throughout the 5-min count period. The longer are the bouts and interbout intervals, the greater this problem becomes. The proportion of the N individuals that must start or stop producing cues in order to yield an accurate estimate of availability is therefore a question that must be addressed.

Adding the distance method to the removal method is exactly what is needed to estimate detectability. But the requirement that the count be taken at an instant in time (see above) poses a problem for the method of Farnsworth et al. (this volume), which relies on changes in activity during a count period to estimate availability. Buckland et al. (2001, see discussion above) recommend sandwiching a “snapshot” between brief periods, in which active birds are accounted for, to obtain the instantaneous count. Perhaps such a “snapshot” can be taken during each of the time segments, thereby yielding the estimate of availability without compromising the estimate of detectability. This issue illustrates well the heuristic value of distinguishing between availability and detectability.

In summary, concern about this method does not center on the use of concentric distance rings, which is a well-understood alternative to estimating distance to each bird, but instead on the applicability of the distance method, in any form, to point counts that rely on aural cues. Nevertheless, because the removal-distance method is conceptually adequate (i.e., it recognizes the independence of availability and detectability) and mathematically rigorous, it deserves thorough study, with the hope that it proves robust to the caveats expressed above.

Conclusions

In conclusion, all four methods reviewed appear logically valid, when their stated and unstated assumptions are met. The currently predominant method for surveying songbirds, rapid aural point counts, will seldom meet all the assumptions or requirements of any of these methods. In their current forms, the double-observer and distance-sampling methods are better suited to estimating detectability, while the double-sampling and removal methods are better suited to estimating availability. Although incomplete at the time of this writing, all four of the new methods probably yield less-biased indices than raw point counts (Bart and Earnst 2002). A hybrid of two, three, or all four of these methods is the likely outcome of further development in this fast-moving field.

Acknowledgments

Discussions with B. Peterjohn and K. Pardieck about estimating detection probabilities from tape recordings inspired this paper. I thank the authors listed below for advancing the field with their penetrating insights. G. Johnson, J. Bart, B. Walker, and C. J. Ralph kindly reviewed the manuscript and provided much needed feedback

Literature Cited

- Bart, J. and S. Earnst. 2002. **Double sampling to estimate density and population trends in birds.** *Auk* 119: 36-45.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. **Introduction to distance sampling: Estimating abundance of biological populations.** Oxford, UK: Oxford University Press.
- Burnham, K. P. 1981. **Summarizing remarks: Environmental influences.** *Studies in Avian Biology* 6: 324-325.
- Cook, R. D. and J. O. Jacobosen. 1979. **A method for estimating visibility bias in aerial surveys.** *Biometrics* 35: 735-742.
- Emlen, J. T. and M. J. DeJong. 1981. **The application of song detection threshold distance to census operations.** *Studies in Avian Biology* No. 6: 346-352.
- Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. **A removal model for estimating detection probabilities from point-count surveys.** *Auk* 119: 414-425. Estimating density from point-count surveys: theory with applications.
- Farnsworth, G. L., J. D. Nichols, J. R. Sauer, S. G. Fancy, K. H. Pollock, S. A. Shriner, and T. R. Simons. This volume. **Statistical approaches to the analysis of point-count data: a little extra information can go a long way.**
- Huff, M. H., K. A. Bettinger, H. L. Ferguson, M. J. Brown, and B. Altman. 2000. **A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon.** Gen. Tech. Rep. PNW-GTR-501. Portland, OR; Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 39 p.
- Nichols, J. T., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. **A double-observer approach for estimating detection probability and abundance from point counts.** *Auk* 117: 393-408.
- Ralph, C. J., J. R. Sauer, and S. Droege. 1995. **Monitoring bird populations by point counts.** Gen. Tech. Rep. PSW-GTR-129. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- Ramsey, F. L. and J. M. Scott. 1979. **Estimating population densities from variable circular plot surveys.**, In: R. M. Cormack, J. P. Patil, and D. S. Robson, editors. *Sampling biological populations.* Fairland, MD: International Cooperative Publishing House; 155-181.
- Reynolds, R. T., J. M. Scott, and R. M. Nussbaum. 1980. **A variable circular-plot method for estimating bird numbers.** *Condor* 82: 309-313.
- Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. **Landbird counting techniques: Current practices and an alternative.** *Auk* 119: 46-53.
- Scott, T. A., P.-Y. Lee, G. Greene, and D. A. McCallum. This volume. **Singing rate and detection probability: an example from the Least Bell's Vireo (*Vireo belli pusillus*).**
- Thompson, W. T. 2002. **Toward reliable bird surveys: accounting for individuals present but not detected.** *Auk* 119: 18-25.

Appendix 1. Detection Probability Cheat Sheet

Parameters discussed in this paper, and their algebraic symbols, if used.

Symbol	Parameter
A	Area. The measured area of a survey area.
C	Count. The number of individuals detected by some survey method in a single count area, or group of such areas.
D	Density. The number of resident individuals per unit area. \hat{D} is often estimated as \hat{N} / A , but it is the primary output of the distance method.
M	Time. As used here, the number of minutes in a single point count or other sample.
N	Population size. The number of individuals, or males, or other category of interest, that reside in a survey area. If the area is small, e.g., a point count circle, care must be taken to account for home ranges that are not wholly included in the area. One approach to this problem is to consider an individual a resident of a survey area if the centroid of its territory or home range lies inside the boundaries of the area (Bart and Earnst 2002). \hat{N} is an estimate of N that is calculated from estimates of other parameters. It is the primary output of the double observer and double sample methods.
p	Detection Probability. The likelihood that a typical (average) individual residing in a survey area will be detected at least once during a survey period. Synonym of Index Ratio. \hat{P} is an estimate of p that is produced by all four methods described in this paper.
p_{dis}	Detectability. The likelihood that at least one cue (a behavior that is physically detectable by the means employed in the survey) is detected during the count period of m minutes.
p_s	Availability. The likelihood that an individual residing in a survey area produces a cue during the survey period.
p_{ld}	Conspicuousness. The absolute energy content of a cue, at the survey point, discounted by the conspicuousness of competing cues. The probability that an average cue is detected.
S	Cue Abundance. The number of cues available for detection during a survey period. High cue abundance mitigates the effect of low conspicuousness.
s/m	Cue Rate. The number of cues occurring per unit time.
s/m	Song Rate. The number of songs occurring per unit time. A special case of Cue Rate.
	Cue. Any discrete behavior (e.g., a song, a display flight) that can be used, with appropriate equipment, to detect a bird. When evidence of the presence of a bird comes in packets, rather than continuously, each packet is a Cue.