VISIBILITY BIAS IN AERIAL SURVEYS: A REVIEW OF ESTIMATION PROCEDURES

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Abstract: Aerial surveys are often used to estimate the density of

wildlife populations. A common problem is underestimation of population

density due to animals being missed. This visibility bias can be quite

serious and in this paper we review various methods of attempting its

estimation. A variety of methods based on comparison with ground counts,

use of a subpopulation of marked animals, mapping with multiple observers,

line transect sampling, and multiple counts on the same areas are considered.

All of the methods are model based and the various model assumptions are

discussed and compared.

Aerial surveys are often used to estimate the population size of many large birds, large terrestrial mammals, and marine mammals. Sometimes they are used in conjunction with other methods of estimation, and sometimes by themselves, either by choice or necessity. One thing that is almost always true, as it is with other methods, is that the entire population is not enumerated by the survey. This results in what is termed "visibility bias". This bias results from observers missing animals because of fatigue, bad weather conditions, or animals being just generally difficult to sight from aircraft. For example, animals may be under cover, blend into the surrounding landscape, or be a long distance from the line of flight.

It can be said, then, that beyond the logistics and dangers of flying large transects or quadrats precisely, the principal difficulty in using aerial censuses lies in estimating the visibility bias, so that a correction factor can be used to adjust the population count or estimate. There are several approaches available for accomplishing this task, and most of them will be discussed in this paper in varying degrees of detail. Taking a methods approach to this topic, the discussion of the approaches to dealing with this bias will be broken down into those involving ground counts, those involving marked animals, those utilizing multiple observers in the same aircraft, the utilization of line transect methods, and other models that use multiple counts over the same tracts. In addition, procedures for dealing with animals occurring in groups will be discussed.

METHODS

Complete Ground Counts

Using total ground surveys, in addition to the aerial surveys, is probably the most simple method, mathematically speaking, and, if two very important assumptions are met, one of the most accurate. Seber (1982; 456)

cited Jolly (1969) for pointing out that if 1) X_i is an accurate count

of the population of strip i, Y_i is an aerial count of strip i, and 2), p

is the probability of an animal being spotted from the plane, and is the

same for all animals, then $E[Y_i | X_i] = pX_i$, and p can be estimated by

$\bar{y}/\bar{x}$, where $\bar{y}$ is the mean Y over all i in the subsample, where a ground

count is done. The correction factor in this case is $\bar{x}/\bar{y}$. If $\bar{y}'$ is

the average aerial count over the entire sample of transects, and n^* is

the total number of transects included in the study area, and n and n'

are the number of transects in the subsample and sample, respectively,

then the estimate for the population size is

$$\hat{N} = \frac{n^* \bar{y}'}{\hat{p}} = \frac{n^* \bar{x} \bar{y}'}{\bar{y}} \quad .$$

This approach can be viewed as an example of double sampling

(Cochran 1977, p. 343). The variance of $\hat{N}$ is included in an appendix

for completeness.

A problem here is that the ground count is often not an accurate one. To deal with this complication, Seber (1982:456) cited other ways of obtaining that accurate count, such as photography, infrared scanning, ultraviolet photography, or conspicuous tags.

In a study cited by Jolly (1969), both sighting and photography were used to count and verify the number of domestic cattle in several areas in Africa, where photography took the place of the ground count. The methods used and resulting counts and estimates of p can be found in Table 1. It is obvious that visibility of the animals was quite good in this case. Using this information, and a set of typical subsample and sample sizes, Jolly (1969) generated standard error estimates for $\hat{N}$, $\bar{x}$, and $\bar{x}'$, which are found in Table 2. S.E.$(\hat{N})$ was arrived at as indicated previously, S.E.$(\bar{x})$ is the standard error that would result if no sampling would be done beyond the subsample size indicated, and S.E.$(\bar{x}')$ is the standard error that would result if ground counts would be done on every transect in the sample.

Noting the similarity between S.E.$(\hat{N})$ and S.E.$(\bar{x}')$, Jolly (1969) made the very important observation that only a little precision would be lost when ground counts would be done on only a few transects, compared to the case where ground counts would be done on the entire sample of transects. This particular example seems to infer that more energy should be devoted to doing aerial counts in these studies, with a minimum number of ground counts.

The assumption that p is equal for all animals in the strip can cause problems, but there are situations where it is approximately true. Unfortunately, ground counts are very costly, and sometimes an accurate count of an area simply cannot be obtained, so other methods must be found.

Incomplete Ground Counts

In situations where animals that are spotted can be mapped, and thus individually identified both by the aerial and ground observer, the ground count can still be used without assuming that it is a complete count.

The approach here is to utilize the two sample capture-recapture (Petersen) estimate, which assumes that (i) the number of animals seen by the two observers are independent, (ii) the probability of spotting any animal is the same for each particular observer, but can vary between observers, (iii) there is perfect matching, i.e., there are no errors in mapping so that it is clear which animals are seen by either one or both of the observers, and (iv) the population is closed. This approach was used by Henny et al. (1974), and Henny and Anderson (1979) on osprey nests and by Magnusson et al. (1978) on crocodiles. Since only one of the observers was in the air, this method yielded one estimate of probability of sighting from the air. This estimate then yielded a correction factor that could be applied to larger areas of the homogeneous habitat. It should be noted that Magnusson et al. (1978) actually utilized Chapman's (1951) modification of the Petersen estimate, which we also recommend. We find that

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m + 1)} - 1$$

where $\hat{N}$ = population size estimate,

n_1 = number seen by the first observer (e.g., the aerial observer),

n_2 = number seen by the second observer (e.g., the ground observer),

and m = number seen by both observers.

Note that $\hat{N}$ is unbiased if $(n_1 + n_2) > N$. Seber's (1982:60) estimate of $V(\hat{N})$ was used which is

$$\hat{V}(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m)(n_2 - m)}{(m + 1)^2(m + 2)} \quad ,$$

and is also unbiased when $(n_1 + n_2) > N$.

To illustrate with an actual example we consider one of Henny and Anderson's (1979) studies, which was an aerial survey of active osprey nests on rock cliffs of the Midriff Islands. In this survey a total of 51 nests were seen from the air (n_1), 63 were seen from the ground (n_2), and 41 were seen from both vantage points (m). This yields an estimate of the population size, $\hat{N}$ = 78.24, with standard error, S.E.$(\hat{N})$ = 3.11, and an estimated aerial visibility rate of $\hat{p}_1 = n_1/\hat{N} = 51/78.24 = 0.65$ or 65%. The proportional standard error in this case is only about 4%.

A brief discussion of the assumptions is now given.

(i) The independence assumption should be no problem, since the two observation methods were quite different, with no communication between observers.

(ii) With regard to the second assumption, since some animals are usually simply harder to see than others, the assumption of equal probabilities often will not hold, and a negative bias in $\hat{N}$ will usually result. On the other hand, according to Seber (1982:86), if the two methods of "capture" are completely independent, the heterogeneity tends to be offset, since the same pattern of sightability is not encountered.

(iii) Henny and Anderson (1979) mentioned no problem with matching nests between air and ground observation .

(iv) The closure assumption is usually not a problem in this case, unless there are a lot of animals on the fringes of the study area, or there is a long period between the aerial and ground counts.

This approach is a very enticing alternative, although sometimes any kind of ground count is either cost prohibitive or impossible to do. In addition, for many mobile animals mapping will not permit individual identification and this method cannot be implemented. For these reasons other methods often must be used.

Marked Subpopulation

Another situation where the Petersen estimator can be used is when a marked subpopulation of the population is available and can be distinguished from the air.

Rice and Harder (1975) carried out a detailed helicopter assisted mark and recapture study on white-tailed deer in Ohio. The marked deer had clearly visible collars attached. The authors concluded that most assumptions were valid in their study. The only obvious concern is the practical one of cost. It is very expensive to capture and mark deer.

Recently scientists have begun to use radio-telemetry to obtain their known subpopulation of marked animals. In a recent article Packard et al. (1985) describe the use of radio-telemetry to estimate visibility bias for manatees in Florida. We believe that this approach will become much more frequent as the cost of telemetry equipment comes down and the equipment becomes more efficient; however it will not always be possible to tell whether or not you have counted a radio-tagged animal from the air. Furthermore there will always be practical limitations on the number of radio-tagged animals available so that resulting estimates will be very variable. For example, Packard et al. (1985) only had 7 radio-tagged manatees in their study.

Mapping By Multiple Observers

Two Independent Observers

The Petersen estimate can also be used when the two observers are in the same plane. A modification of this approach was used by Grier et al. (1981) on eagle nests. The problem with using this approach here is that since both observers are looking from the same vantage point, even if they do not communicate it is not likely that their observations will be independent, and since the methods of sighting are the same, any heterogeneity in sighting probabilities will not be offset.

Seber (1982:87) pointed out how drastically heterogeneity can affect the accuracy of $\hat{N}$. Let B represent the bias coefficient of the estimate, where $E(\hat{N}) = NB$. If p is uniformly distributed over the interval [c,d], where ($0 <= c <= d <= 1$), and $w = c/d$, then B = 1, 27/28, 27/31, and 3/4 when w = 1, 1/2, 1/5, and 0 respectively. It can be seen that when the distribution is spread out, the bias is more extensive, and when some of the probabilities are very small, the bias can be as much as 1/4 of the true value, and could be even more severe if the probabilities are concentrated near 0. It should also be noted that the bias is always in the negative direction in this case.

Two Dependent Observers

The Removal Method

An alternative approach that eliminates the need for lack of communication between observers is the two-sample removal method (Seber 1982:318). The assumptions for this model are that i) the population is closed, ii) the sighting probability is constant for each animal, and iii) the sighting probability is constant between observers. The maximum likelihood estimates for this model are:

$$\hat{N} = \frac{n_1^2}{n_1 - n_2} \quad ,$$

$$\hat{V}(\hat{N}) = \frac{n_1^2 n_2^2 (n_1 + n_2)}{(n_1 - n_2)^4}$$

$$\hat{p} = 1 - [n_2/(n_1 + 1)],$$

$$\hat{v}(\hat{p}) = \frac{n_2(n_1 + n_2)}{n_1^3}$$

where $\hat{N}$ = estimate of population size,

n_1 = number of animals observed by the first observer,

n_2 = number of animals observed by the second observer, but not by the first,

$\hat{p}$ = probability of an animal being recorded (the formula for this is an approximately unbiased version of the ML estimate).

This approach is also susceptible to heterogeneity in sighting probabilities (Seber 1982:322). In fact, if p is uniformly distributed, the percent bias in the removal estimate is the same as the percent bias in the Petersen estimate, for a given range of p values. In addition, in this case the variance is underestimated by as much as one third when the p values are uniformly distributed over the [0,1] interval (Seber 1982:322).

Cook and Jacobsen Extension

Cook and Jacobsen (1979) developed an extension of this model, where the assumption of homogeneous sighting probabilities is replaced by the assumption that the sighting probabilities are identically distributed random variables with a mean p. To offset the difference in sighting skill between the two observers, the design calls for them to switch roles halfway through the study. An additional assumption with this design is that the probability of a given observer recording an animal is the same, whether he is the primary or secondary observer. This may not be realistic, but it is necessary for the model to be usable, and it holds well enough most of the time (Cook and Jacobsen 1979).

The terms used in this model are as follows:

a_i = probability that an animal is recorded by observer i, i = 1,2,

N_j = total number of animals in the jth half of the sampled area,

N = total number of animals in the whole sampled area,

X_{ij} = total number of animals recorded by observer i in the jth

half of the sampled area,

f_j = known sampling fraction for the jth half of the sample area,

b_j = f_j/f , where $f = f_1 + f_2$,

p = probability that an animal is recorded, $p = 1 - (1-a_1)(1-a_2)$.

Two distributions were used in estimating the parameters a_1, a_2, p,

and N. One was a joint binomial distribution of X_{11}, X_{22}, X_{12} and X_{21},

and the other was a multinomial distribution with equal cell probabilities.

Both of these approaches yielded identical maximum likelihood estimates

$$\hat{a}_1 = \frac{X_{11}X_{22} - X_{12}X_{21}}{X_{11}X_{22} + X_{22}X_{21}} \quad ,$$

$$\hat{a}_2 = \frac{X_{11}X_{22} - X_{12}X_{21}}{X_{11}X_{22} + X_{11}X_{12}}$$

The numerators here are the same, and if they are 0, while $X_{ij} > 0$, i = 1,2,

j = 1,2, then the probabilities cannot be estimated separately. Using the

multinomial model,

$$V(\hat{a}_1) = \frac{a_1(1-p)(1-b_1 p)}{X..a_2(1-a_2)b_1 b_2} \quad ,$$

$$V(\hat{a}_2) = \frac{a_2(1-p)(1-b_2 p)}{X..a_1(1-a_1)b_1 b_2} \quad ,$$

$$\text{cov}(\hat{a}_1, \hat{a}_2) = \frac{1-p}{X..b_1 b_2}$$

The maximum likelihood estimates for the other parameters of interest are

$$\hat{p} = 1 - \frac{X_{12}X_{21}}{X_{22}X_{11}} \quad ,$$

$$\hat{N} = X_{..}/f\hat{p} \quad ,$$

$$V(\hat{p}|X_{..}) = \frac{(1-p^2)p}{X_{..}} \left(\frac{1}{a_1 b_1} + \frac{1}{a_2 b_2} + \frac{1}{a_2(1-a_1)b_1} + \frac{1}{a_1(1-a_2)b_2} \right) \quad ,$$

$$V(\hat{N}) = N[X_{..}V(\hat{p}|X_{..})/fp^3 + (1 - fp)/fp] \quad .$$

Cook and Jacobsen (1979) applied their model to studies of moose and deer, and used one study of white-tailed deer as an example. They did their observations on groups of animals, where the number in a group was easy to see, once the group was sighted. Table 3 contains the number of groups of three different sizes recorded. The data were analyzed by the techniques previously described, and the results are in Table 4.

The data were also analyzed using the standard removal model mentioned earlier (Seber 1982:318). The formulas were expressed in the terminology of Cook and Jacobsen (1979), yielding

$$\hat{N}_1 = \frac{X_{11}^2}{X_{11} - X_{21}} \quad ,$$

and a similar formula for $\hat{N}_2$. Recall that the crucial assumption here that distinguishes it from the approach of Cook and Jacobsen (1979) is that the two observers are equal in skill. This is hard to achieve, but it is feasible to approximate it. The formula for the variance of $\hat{N}_1$, reexpressed, is

$$\hat{V}(\hat{N}_1) = \frac{X_{11}^2 X_{21}^2 (X_{11} + X_{21})}{(X_{11} - X_{21})^4}$$

and a similar formula for $V(\hat{N}_2)$. $V(\hat{N})$ is calculated by

$$\frac{\hat{V}(\hat{N}_1) + \hat{V}(\hat{N}_2)}{f^2}$$

It can be seen in Table 4 that the removal estimates of N for the deer data are almost equal to those that Cook and Jacobsen arrived at, suggesting that in this example the two observers had equal sighting probabilities. The removal variance estimates, however, are considerably · lower, especially with larger group size. This is because there are fewer parameters to estimate in this model.

We can compare efficiencies of the Petersen and removal estimates, assuming the sighting probabilities are the same for both observers and all animals. In this case

$$\frac{V(\hat{N}_p)}{V(\hat{N}_r)} = \frac{Nq^2/p^2}{Nq^2(1+q)/p^3} = \frac{p}{1+q} < 1$$

where $\hat{N}_p$ = the Petersen estimate,

  $\hat{N}_r$ = the Removal estimate,

  $q = 1 - p$.

We can see from this that the Petersen estimate is more efficient than the removal estimate, especially for small values of p (Seber 1982:324). For instance, when p = .6, .4, and .2, then the above ratio is 3/8, 2/7, and 1/6, respectively. Note that the removal method will also be more efficient than that of Cook and Jacobsen (1979), as we discussed earlier.

As a summary for these three approaches, it is fair to say that the Petersen estimate is the best one to use if the assumption of independent observers holds, but because both observers are in the same plane this is a rarity. The alternative would be to use the removal method if the observers can be considered to have the same probability of sighting an animal, implying equal skill, fatigue level, and so on. If this is not true, then Cook and Jacobsen's (1979) model would be appropriate. Of course there is still the assumption that the probability of an observer sighting an animal is the same, regardless of his or her role, as primary or secondary observer.

The Line Transect Sampling Procedure

A completely different approach to the estimation of visibility bias involves using the line transect sampling model for aerial surveys where lines are flown. This approach requires that distance (usually perpendicular distance) from the line is recorded for each animal detected. It is assumed that all animals present on the line are detected and that the probability of sighting an animal is a decreasing function of its distance from the line.

The line transect sampling model has been developed fully in a wildlife monograph by Burnham et al. (1980), and therefore only a very brief treatment will be presented here. The detection function, $g(y)$, is defined as the probability of sighting an animal located at a perpendicular distance y from the line. Note that the assumption of all animals on the line being sighted implies that $g(0) = 1$. The sample of perpendicular distances sighted $y_1, y_2, \cdots, y_n$ form the basis of estimating the visibility bias.

The density estimate is given by

$$\hat{D} = \frac{n\,\hat{f}(0)}{2L}$$

where n is the number of animals seen, L is the line length, and

$f(y) = g(y)/\int_0^\infty g(y)\,dy$ is the probability density function of the

perpendicular distance data. Therefore $\hat{f}(0)$ is an estimator of the

probability density function at zero. The form of this estimator depends

on the form of the detection function. No variance formulas are given here,

because they too depend on the form of the function. For an example with

an exponential detection function we have $\hat{f}(0) = 1/\bar{y}$

the reciprocal of the mean perpendicular distance. Burnham et al. (1980)

discussed a variety of forms of the detection function and their corresponding

density estimators. They finally settled on a Fourier series detection function

as a flexible form which provides an estimator of density with good properties.

The line transect sampling model can be viewed as a method of adjusting

for visibility bias where the bias is assumed to be completely due to incomplete

sightings increasing with distance away from the transect line. Unfortunately

in a substantial number of aerial surveys the assumption of one hundred

percent visibility on the line may not be justified. For example, Burnham et al.

(1980:76) discussed a large aerial survey on porpoise. They found that for

small schools of porpoise the probability of sighting on the line was less

than one hundred percent. If the visibility on the line is, say, eighty

percent, this will induce a negative bias on the density estimate, so that

it is only eighty percent of the true density.

To our knowledge the intriguing prospect of combining the line transect

method with a method which uses the Petersen estimate has not been tried.

We believe that future research could look at this combination.

Multiple Counts

When the population of interest cannot be mapped, the usual approach is to do multiple counts over the same transect or quadrat, and attempt to get the estimates from this collection of counts.

Routledge (1982) evaluated the use of the method of bounded counts (Robson and Whitlock 1964), where the multiple counts are ordered, such that $X(1) < X(2) \ldots < X(m)$. Since using $X(m)$ as the estimate almost always produces a negative bias, N is estimated as $\hat{N} = X(m) + [X(m) - X(m-1)]$, which is unbiased if the X_i's are independently and uniformly distributed between 0 and N, or if m = the number of counts is "large". The $(1-\alpha)\%$ confidence interval derived for this case was $N_L = X(m)$ and $N_U = X(m) + [X(m) - X(m-1)][1 - \alpha] / \alpha$. Routledge (1982) pointed out that m can realistically only be 5 to 10, and that often is not large enough, and the uniform distribution is unrealistic for these censuses.

Routledge's (1982) conclusion was that unless almost complete coverage can be counted on in an aerial survey, the method of bounded counts is too unreliable to be trusted. We also do not believe this approach is likely to be useful.

Another approach to multiple counts using the same method is to use the binomial distribution directly (Seber 1982:457 ; Caughley and Goddard 1972). A transect is flown over several times and the sample mean and variance, $\bar{x}$ and s^2 , are computed. Assuming a binomial distribution of X (probability of sighting an animal is equal for all animals on all occasions), then $E(\bar{x}) = Np$ and $E(s^2) = Np(1-p)$, where N is the population size and p is sightability. From here estimates can be derived,

$$\hat{N} = \frac{\bar{x}^2}{\bar{x}-s^2} \quad , \text{ and } \quad \hat{p} = 1 - \frac{s^2}{\bar{x}} \quad .$$

This approach is very simple, but as Caughley and Goddard (1972) pointed out, individuals do not necessarily have the same sightability, and due to weather, time of day, observer skill, etc., p will change between occasions.

Even if p was the same throughout, the estimate of N is heavily dependent on the binomial distribution assumption, and not robust to variation from this. Looking at the denominator of the estimate, if the distribution of X varies from the binomial, the variance of the random variable will grow, and the denominator will quickly go to zero, producing large positive bias on N, and negative bias on p.

A method of estimation to use when p varies was derived from the relationship between s^2 and $\bar{x}$ when p is constant, which is $s^2 = \bar{x} - (1/N)\bar{x}$ (Caughley and Goddard 1972 ; Seber 1982:457). This is a parabola that cuts the $\bar{x}$-axis at 0 and at N. Though this relationship does not hold true when p varies, Caughley and Goddard (1972) argued that the regression of s^2 on $\bar{x}$ must still cut the x-axis at 0 and N, because the counts cannot be less than 0, nor greater than N (assuming no double counts). The authors claimed that the relationship is likely to be quadratic and of the form $s^2 = k[\bar{x} - (1/N)\bar{x}^2]$, where k is a coefficient of deviation from the binomial. The technique here is to take multiple censuses using two different methods, with all other variables held constant. This results in two equations, with k and N as the only unknowns, and these can be solved for. The assumption here is that k is the same for both equations, and is characteristic of the distribution of survey counts over the whole study (Caughley and Goddard 1972). The stability of the estimates were investigated by computer simulation, using four conditions of variability in sighting probabilities. The estimates that resulted were always within two standard errors of true size.

Routledge (1981) criticized the model that Caughley and Goddard (1972) proposed on several points. First, he claimed that they gave no justification

for assuming that k would not vary with method. Second, even if k was equal for both methods, Routledge (1981) claimed that the simulation they did had problems: 1) 100 surveys were done at each level, which is unrealistic, and it still had a coefficient of variation of 10%. 2) In each case, the higher survey efficiency value or mean was 71%, which is too high for most species. When the highest efficiency was lowered to 50%, negatively biased estimates resulted, with sporadic extremely large or negative values. In the same vein, with levels of sightability of 50% and 20%, 800 surveys per level would be required to get 95% coverage in a confidence interval. We do not believe this approach will be useful.

Caughley et al. (1976) put forth another method utilizing multiple counts, using different methods. He asserted that for areas that must be sampled (instead of total counts), the true density is estimated as the y-intercept of a regression of the observed density per sampling unit on plane speed (S), height (H), and transect width. We have $\hat{D} = b_0 + b_1 S + b_2 H + b_3 T$, where $\hat{D}$ is the density observed from the air under a given set of conditions and b_0 is an estimate of the true density. Seber (1982:457) noted that caution should be observed when extrapolating the relationship to 0. He also noted that the model ignores variation in observer fatigue, weather conditions, and other factors. Both of these points are very important ones, and we believe that this method is not likely to be useful either.

Animals in Groups, Complete Ground Counts

Cook and Martin (1974) developed a method for estimating visibility bias where animals occur in groups. They derived a function, based on the assumption that the probability of sighting a group increases monotonically (with group size) to 1. The function arrived at was $p(x) = 1 - q(q^x)$, where q = the probability of missing a single animal, and x = group size - 1.

The assumptions involved in this model are 1) that animals occur in quadrats in groups of varying sizes, 2) that each animal has a probability, P_i, of being observed, and that the P_i's are independent and identically distributed random variables with mean $\bar{P}$, 3) that if one member of a group is observed, the whole group is observed with certainty. In addition, it is assumed that each member of a group must be independently missed, in order to miss the whole group. This assumption is really unrealistic (Cook and Jacobsen 1979 ; Samuel and Pollock 1981).

Samuel and Pollock (1981) offered an alternative sighting function, with two parameters:

$$p(x) = 1 - ae^{-bx} ,$$

where a = probability that a single animal is missed,

b = rate at which the function approaches the asymptote 1.

Both models were applied to a pooled data set of three months of sea otter censusing (Cook and Martin 1974). The function can only be fit if there is a ground census as well, and it is assumed that the ground census is complete. The proportions seen from the air in areas where ground censuses were taken were calculated $\hat{p} = y/n$ (y = air count, n = ground count), and their variances were computed, assuming a binomial distribution. Nonlinear regression was used to fit the models.

The results showed that the observed probabilities and those predicted by the asymptotic regression model were similar, but those predicted by the Cook and Martin model were quite dissimilar. Comparisons of the residual sums of squares and a partial F test showed the Samuel and Pollock model to be better at fitting the sea otter data ($P > .0005$) (Samuel and Pollock 1981).

Figure 1 shows the actual points and those predicted by the two models, and further illustrates that the 2-parameter model provided a better fit. Correction factors can be obtained by inverting the predicted probabilities, and their 95% confidence limits.

We believe that the question of grouped animals needs a lot of attention. Some of the other methods used in this paper might be extended to this case.

DISCUSSION

As has been shown, there are many different methods for estimating population sizes and visibility bias correction factors, and many different approaches have been taken toward developing methods. It would be difficult to try to rank all of them, because their assumptions are different, and different ones are used in different circumstances. A few general comments can be offered, however.

Statistically, the best technique to employ is a total ground count, or some other method that totally enumerates a subsample of the population. By comparing this with the aerial count an accurate assessment of the visibility bias is obtained for that subsample. In this case any sampling error stems from slight variations between transects of the subsample and the rest of the study area, and not from within the transects used in the ground count. Unfortunately this method is often either impractical or cost prohibitive, or both.

When complete ground counts cannot be assured, the assumption of completeness can be relaxed if the animals seen can be mapped accurately from both the ground and the air. In this case the two sample capture-recapture estimate is used. By mapping, the number of animals spotted by both observers can be determined, and the fact that two different methods of observation are being used maintains the independence of the two observers, and helps to offset heterogeneity in the sightability of the animals.

If the cost of marking animals directly or by using radio-tags is not prohibitive capture-recapture approaches may be very useful. We believe that estimation of visibility bias by radio tags will increase in the next few years.

When any ground count is infeasible, but the animals can still be mapped from the plane, there are three feasible approaches using two observers in the plane that have reasonably good properties. The two sample capture-recapture approach can be used here, and is the most efficient of the three approaches, but its assumption of independence of observers is usually violated, and it is also vulnerable to heterogeneity in sighting probabilities. The removal method does not require the assumption of independence of observers, but assumes not only homogeneity of animal sightabilities for one observer, but also between observers. The method of Cook and Jacobsen (1979) allows for differences between observers, and to some extent between animals, but it is the least efficient of the three approaches. All of these factors should be weighed in deciding which of the approaches to use in this case.

Another approach that can be very useful, and whose theory is well developed, is the line transect approach. However, the assumption that all animals on the transect line are seen is crucial to using this approach, so the survey should be designed in such a way that the line is quite visible and observers instructed to concentrate on sighting near the line. In areas of heavy cover or animals diving below the surface of water, even in a well designed study, it may be impossible to sight all animals on the line. As we concentrate on aerial surveys we come to slightly different conclusions than the recent article by Burnham and Anderson (1984). We believe their faith in the line transect approach is not justified in many aerial surveys.

Other methods that have been mentioned that utilize multiple counts over the same areas are the method of counded counts (Robson and Whitlock 1964),

a binomial model and extension of that (Caughley and Goddard 1972), and a multiple regression approach (Caughley 1977). All of these methods have major flaws, and will not usually prove to be very helpful.

There have been a couple of models utilized to deal with animals that occur in groups, where a complete ground count is again utilized (Cook and Martin 1974 ; Samuel and Pollock 1981). Both models assume that the probability of spotting a group of animals increases monotonically to 1 with the size of the group, and Cook and Martin's model (1974) assumes that each animal in a group must be missed independently for the group to be missed, which is unrealistic. The model by Samuel and Pollock (1981) was the better fitting model when both were applied to some sea otter data, but there is much work left to be done in this area.

The methods that have been presented here are not the only approaches dealing with visibility bias in aerial surveys, but they represent the main body of recent work. Not only is there a variety of statistical models to choose from, but there are many ways to apply the methods in the field.

Something that should be mentioned here is that the use of helicopters tends to reduce the magnitude of visibility bias, since they are more maneuverable, they can move slower, their forward visibility is greater, and they are safer to fly at lower altitudes, in comparison to fixed-wing aircraft. There are other advantages, but a big disadvantage is that they are also extremely expensive to use (Kufeld et al. 1980).

Another problem which should be mentioned is the danger of using a correction factor determined in one study under one set of conditions for another study under different conditions. For example, Packard et al. (1985) emphasize that manatee visibility varies due to habitat, observer experience and weather conditions. On the other hand in many studies the costs or practicability may dictate that the only correction factor available is from another study.

To conlude, as with many other techniques for estimating parameters of wildlife populations, the question here should not be which one of those mentioned here is the best, but which one is the best one to be used, given the population, the species, the habitat, the budget, and the use to which the estimate will be put.

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Table 1. Proportion (p) of domestic cattle detected by aerial survey of two areas in East Africa (Jolly 1969).

Location	Subsample Size n	Aerial Mean $\bar{y}$	Actual Mean $\bar{x}$	$\hat{p}$
Kaputie	26	51.5	52.3	0.984
Samburu	76	70.6	75.3	0.937

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Table 2. The standard errors of the estimated mean population size per unit ($\hat{\bar{N}}$), for the subsample "accurate" mean ($\bar{x}$), and for the estimate obtained if accurate counts had been made on all units of the main sample ($\bar{x}'$), resulting from three sets of typical sample (n') and subsample (n) sizes, for two locations in East Africa (Jolly 1969).

Location	n'	n	S.E.($\hat{\bar{N}}$)	S.E.($\bar{x}'$)	S.E.($\bar{x}$)
	20	4	5.6	5.4	12.1
Kaputie	50	10	3.5	3.4	7.7
	50	5	3.6	3.4	10.8
	20	4	12.0	11.4	25.6
Samburu	50	10	7.6	7.2	16.2
	50	5	7.9	7.2	22.9

Table 3. White-tailed deer aerial census data, Red Deer,
Alberta, 1977-78. (Cook and Jacobsen 1979).

Group Size	First Half		Second Half		Total
	Primary Observer	Secondary Observer	Primary Observer	Secondary Observer	
1	8	4	5	3	20
2	8	4	15	5	32
3	5	2	10	2	19

Table 4. Comparison of estimates of parameters and standard errors for the 1977-78 Alberta deer survey by the Cook and Jacobsen (1979) approach and by the Removal approach.

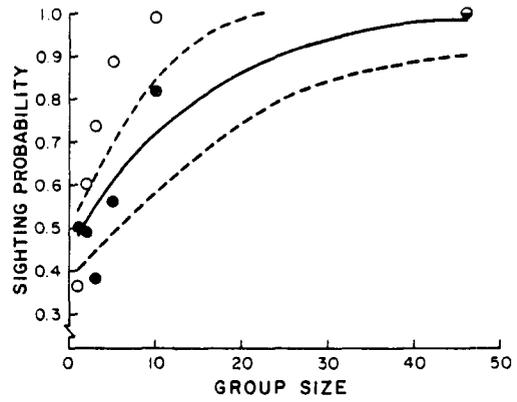| Group Size	Cook and Jacobsen				Removal	
	$\hat{p}$	S.E.$(\hat{p}\|x)$	$\hat{N}$	S.E.$(\hat{N})$	$\hat{N}$	S.E.$(\hat{N})$
1	.70	.286	74.7	33.79	74.41	33.10
2	.83	.134	100.4	21.61	100.52	20.10
3	.92	.089	54.0	11.30	54.39	9.56

Fig.1 Comparison of asymptotic regression model (—) with 95% confidence bands (—) to pooled sea otter census data (●) and Cook and Martin model (○). Note that (◉) indicates that (●) and (○) occur together.

APPENDIX

Here we present the variance equation for the estimator based on a complete ground count given on P3.

$$\text{Var}(\hat{N}) = (n^*)^2 \{ (\tfrac{1}{n'} - \tfrac{1}{n^*}) s_x^2 + \tfrac{1}{\hat{p}^2} \; (\tfrac{1}{n} - \tfrac{1}{n'}) \; s_e^2 \},$$

$$\text{S.E.} \; (\hat{p}) = \sqrt{\frac{s_e^2}{n\bar{x}^2}}$$

where

$$s_e^2 = s_y^2 - 2\hat{p} \, s_{xy} + \hat{p}^2 s_x^2$$

$$s_x^2 = \frac{1}{n-1} \{ \sum_{r=1}^{n} x_r^2 - \frac{(\sum_{r=1}^{n} x_r)^2}{n} \}$$

$$s_y^2 = \frac{1}{n-1} \{ \sum_{r=1}^{n} y_r^2 - \frac{(\sum_{r=1}^{n} y_r)^2}{n} \}$$

$$s_{xy} = \frac{1}{n-1} \{ \sum_{r=1}^{n} x_r y_r - \frac{\sum_{r=1}^{n} x_r \sum_{r=1}^{n} y_r}{n} \}$$