when natural mortality is not replaced by harvest. This is possible because the harvested population is permitted to regain its more productive state in the interval and because advantage is taken of the cumulative net gain in population size. Still greater yields might be achieved by age-selective hunting designed to preserve annually the most productive breeding stock. Annual culling practices employed in Great Britain and continental Europe thus produce greater yields on an annual basis than can be achieved by the nonselective methods of hunting employed in North America.

Although no distinction was made between sexes in the foregoing, the increased yields obtained are the result of effects on the abundance and age structure of the most productive age-classes of females. Thus, periodic harvest of females and annual harvest of males may produce almost the same results. However, periodic harvest of males also takes advantage of a cumulative gain in numbers available to the hunters at the start of each hunting period. Furthermore, as mean age and body size are increased during the closed periods, biomass yield and the quality of the hunt may be improved by periodically hunting both sexes. In cases where hunters normally take a disproportionately large number of juveniles, periodic harvest should improve yields even more than if hunting is not selective; productivity (and thus juvenile density) should be higher, and population age structure should be less affected by hunting.

These advantages could be partially offset by the possibility that populations managed for periodic harvest may accommodate less total hunting effort than those managed for annual yields. This would be true if animals become more vulnerable when hunted less frequently, so that the same total yield might be taken by fewer hunters. Also, large numbers of hunters may be required to reduce the enlarged population to the base level in one season. Thus, unless hunting is spread out across a lengthy season by regulations, unacceptable or unattractive concentrations of hunters may result in a reduction in recreational quality. A management program based on periodic harvests may be more acceptable from the hunter's point of view when alternative places to hunt each year are abundant.

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Received for publication January 28, 1971.

IMPROVING THE ESTIMATES FROM INACCURATE CENSUSES

GRAEME CAUGHLEY, School of Biological Sciences, University of Sydney, Sydney, Australia

JOHN GODDARD, F.A.O., Luangwa Valley Project, Chipata, Zambia[1]

Abstract: Most counts of animals are underestimates of the true total, because some animals are not seen during the census. This is particularly true of an aerial census. A method is presented for estimating the number of animals in an area from several counts, each of which underestimates the true total. It requires a mean and a variance from sets of counts obtained at two levels of survey efficiency. An estimate of true numbers is obtained by solving a pair of simultaneous equations describing a parabolic relationship between mean and variance. Computer simulations suggest that the estimate is stable whether sightability is constant or variable between individuals and whether individual sightabilities remain constant or vary between survey occasions. A worked example utilizes counts of black rhinoceros (*Diceros bicornis*).

In this paper, we draw attention to a source of bias present in almost all enumerations obtained by direct counting and suggest ways in which an estimate of true numbers can be obtained from these biased counts.

As an illustration, we take the imaginary example of a population of elephants living on a lightly timbered island. The usual method of census in this case calls for flying over all parts of the island and counting the elephants. But at any one time, a number of elephants will be standing under trees and will therefore not be detected. If we carry out this census several times we will obtain a set of totals, but although we can present the highest of these as an estimate of minimum numbers, we have no way of knowing what proportion of the true total the estimate represents. This problem appears in almost all direct enumerations.

We thank A. C. Hodson, University of Sydney, and L. L. Eberhardt, Battelle Memorial Institute, for criticizing a previous draft of this paper.

BINOMIAL MODEL

If all individuals in a population share a common probability, p, of being seen, and p is constant from one occasion to the next, an accurate estimate of the true total, n, is easily calculated. Since in this example all animals were sampled at each count, insofar as they were searched for, each animal can be characterized as seen or not seen. We have an estimate only of the number in the first category. The proportion seen estimates p but its value is unknown. The counts may each be regarded as coming from a binomial distrbution (Simpson et al. 1960: 124–129, 154–156) resulting from n independent trials, each trial having probability p of success in seeing a given animal. The mean, $\bar{x}$, of the several counts is therefore related to the true total by

$$E(\bar{x}) = np,$$

and the observed variance, s^2, of the counts estimates the variance of the binomial distribution such that

$$E(s^2) \simeq np\,(1-p).$$

These two equations in combination can be used to estimate the total number of animals in the area as

$$n = \frac{\bar{x}^2}{\bar{x} - s^2} \qquad (1)$$

and the mean proportion of these seen per count as

$$p = 1 - \frac{s^2}{\bar{x}}. \qquad (2)$$

[1] Editor's note: John Goddard died in Luangwa Valley, Zambia, July 8, 1971.

Equation (2) was first developed by Seierstad et al. (1967) to estimate the efficiency of survey counts. Equation (1) was derived by Hanson and Chapman (Hanson 1967: 240–241) as a direct estimator of population size.

GENERAL MODEL

Although the binomial model is fine in theory, its basic assumption—the constancy of p—makes it unrealistic in practice. We can think of situations in which p would be the same over several counts, but these cases are rare and special. In practice, p usually has two sources of variability. First, individuals are likely to have intrinsically different sightabilities, and p will therefore be a random variable with its own distribution. Second, mean sightability is likely to fluctuate, between counts, consequent on differences in weather, time of day, viewing conditions, and skill of observers. Mean p will therefore also have its own distribution. Variability can be reduced by tight experimental design, but there usually remains a residual puddle resisting all efforts to drain it. Any variability in the probability of being seen will expand the observed variance of counts beyond that of the binomial variance, thereby resulting in an overestimate of population size by equation (1); or no estimate at all if variance is greater than the mean. Consequently, we sought an elaboration of the simple binomial model that would give an estimate of population size even when p differed between individuals and fluctuated between counts.

The variance of a binomial distribution has a simple relationship to the mean:

$$np(1-p) = np - np^2$$
$$= np - (1/n)(np)^2,$$

or in terms of the observed mean and variance,

$$s^2 = \bar{x} - (1/n)\bar{x}^2. \quad (3)$$

Equation (3) is a disguised version of the general equation for a parabola—

$$y = a + bx + cx^2.$$

The parabola symbolized by equation (3) is simplified by having the coefficient a equal to zero, b to unity, and c to minus the reciprocal of population size. This is another way of saying that the parabola relating variance on the y-axis to mean on the x-axis cuts the x-axis at the origin and again at the true population size. Here, then, is a second way of solving n when p is constant for a given method of counting. If we collect a number of counts by each of two methods—for example, by making one set from 800 feet altitude and the other from 200 feet—we would obtain two means and two variances. By fitting a parabola through the origin to these two mean-variance points, an estimate of n is obtained as the value at which the parabola cuts the x-axis. Of course, we would not do this because a simpler solution is provided by equation (1), but the relationship suggests a method by which n can be solved when p is not constant for a given method of observation.

Under field conditions, the distribution of counts obtained by one method of survey will reflect both the distribution of individual sightabilities at any one occasion and the distribution of viewing conditions between occasions. Irrespective of the form of the resultant distribution of survey counts, a regression of their variance on mean must cut the x-axis at zero and again at n. No count can be less than zero or greater than n, and hence a mean of zero or of n implies zero variance. The distribution of counts being a result of two probability distributions in combination, is likely to share with the binomial distribution a parabolic relationship between variance and mean. If

Table 1. Results of censuses of 100 animals simulated by computer under differing conditions of sightability.

Model	Sightability Varies Between: Methods	Individuals	Occasions	$\hat{N}$	$\hat{s}$	SE	$\hat{k}$
1	Yes	No	No	100.17	8.91	1.79	0.99
2	Yes	No	Yes	101.43	9.24	1.85	7.59
3	Yes	Yes	No	101.87	13.97	2.79	1.06
4	Yes	Yes	Yes	103.98	10.87	2.17	6.88

this is so, the trend will vary from the parabola describing the binomial case only by an increase or decrease in height above the x-axis.

A formula can therefore be written for the general case as

$$s^2 = k[\bar{x} - (1/n)\bar{x}^2], \quad (4)$$

where k is a coefficient of deviation from binomial variance. When $k = 1$, the observed variance is the same as the binomial variance, and the formula reduces to equation (3). A greater value of k indicates more variance than would be expected in the binomial case. If we have counts obtained at two levels of survey efficiency, we can write a pair of equations in the form of equation (4) and solve simultaneously for k and n.

SIMULATION TESTS

The stability of the estimate of population size was investigated by simulating censuses in a CDC 6600 computer under four sets of conditions that might be met in the field:

1. For a given method of survey, all individuals have the same sightability on all occasions.
2. For a given method of survey, all individuals have the same sightability at any one occasion, but this common sightability varies between occasions according to variations in weather.
3. For a given method of survey, sightabilities differ between individuals, but the distribution of these is the same on each occasion.
4. For a given method of survey, sightabilities differ between individuals, and the mean and the variance of the distribution of sightabilities vary between occasions in response to variation in weather.

The estimates of population size, calculated by equation (4) for a population of 100 individuals, are shown in Table 1. The estimate for each model is a mean of 25 estimates resulting from simulations described later. In each case, the estimate is within two standard errors of the *true* population size, indicating that statistical bias, if present, is not large enough to be detected by these simulations. It can be tentatively concluded that this method of estimating population size will cope with the range of situations represented by the four models.

WORKED EXAMPLE

We illustrate this method with Goddard's (1967) counts of black rhinoceros in the area centered on the Olduvai Gorge, Tanzania. He presented the results of 18 aerial censuses of a population known, from careful ground counting, to contain 69 animals. These data are not entirely appropriate to this method of analysis, because they were not collected by two different methods. We have been forced into using time of day as the characteristic dividing two sets of counts. Goddard gave 18 totals, the highest of which represents only 50 percent of the true total. In an attempt to hold constant all the variables except time of day, we rejected two censuses, one made mainly from 900 feet (all others were from a much lower altitude) and one made from a helicopter. (Fixed-wing aircraft were used for the remainder.) Considerable variability between censuses still exists in weather, air speed, number of observers, and time spent counting, but we hope this is spread evenly across the division we will make according to time of day.

Two sets of data were extracted from the 16 counts. The first comprises the censuses begun before midday—four counts with a mean of 16.7 and a variance of 33.0. The second comprises counts begun after 4:00 PM—eight counts with a mean of 25.4 and a variance of 41.7. The selection left four additional counts, from the intermediate period, which were not used in the analysis.

Binomial variances are always smaller than the mean. Since variance is greater than mean for both sets of counts, equations (1) and (3) will not estimate true numbers. A solving can, however, be made by equation (4) whose use does not presuppose constancy of p.

To facilitate calculations, equation (4) is used in the form

$$\bar{x} = s^2(1/k) + \bar{x}^2(1/n)$$

to give, in this case,

$$\begin{cases} 25.4 = 41.7(1/k) + 25.4^2(1/n) \\ 16.7 = 33.0(1/k) + 16.7^2(1/n). \end{cases}$$

Multiplying the first by 33.0 and the second by 41.7 yields

$$\begin{cases} 838 = 1{,}376(1/k) + 21{,}290(1/n) \\ 696 = 1{,}376(1/k) + 11{,}630(1/n) \end{cases}$$

from which, by subtraction,

$$142 = 9{,}661(1/n)$$

and $\qquad n = 68$ rhinoceroses.

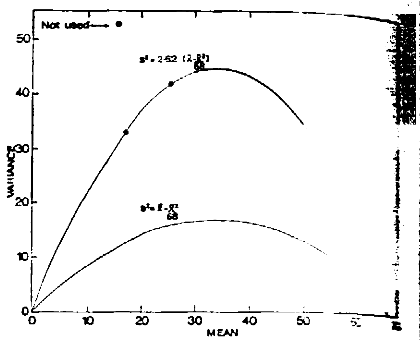

Fig. 1. The upper parabola relates variance and mean of counts obtained by two different methods. The lower parabola gives the relationship to be expected if probability of sighting is constant for a given method.

By substituting this value of n in either equation, k can be solved as 2.62. The parabola relating variance to mean is therefore

$$s^2 = 2.62\bar{x} - 0.0385\bar{x}^2.$$

This parabola, fitted to the two mean-variance estimates, and a parabola calculated from equation (3) showing the trend of variance on mean to be expected had p been constant for a given method of census are shown in Fig. 1.

DISCUSSION

The closeness of the estimated population size (68) to the true population size (69) is largely fortuitous. It should not be interpreted as a tribute to the accuracy of the method. Fig. 1 includes a third point, not used in calculating the parabola, representing the variance and mean of the four censuses begun between midday and 3:45 PM. It is well off the curve. Further, if the 16 counts had been ranked by time of day and simply divided into the first and second sets of eight observations, the resultant estimate of population size would have been only 49. We consider that these discrepancies reflect the fact that the census was not designed with this method in mind. It therefore contains variation that would have been controlled in a design appropriate to this analysis.

This analysis requires that variability accruing from sources other than from the difference between the two methods of census must be spread equally between the two methods. For instance, if altitude of observation is chosen to differentiate the two methods, the time of day, weather, season, and number of observers should be held as close to constancy as conditions permit. Where constancy cannot be achieved, the variability of each influence should be equalized between the two methods. Unless this is done, k will differ between methods, and the estimate of population size will be inaccurate.

Since the shooting of a parabola through two points to hit a third point requires accurate estimates of the two sighting points, we recommend that each should represent no less than 10 counts.

The main utility of this method is likely to be the calculation of correction factors that can be applied to extensive surveys. We know that, regardless of viewing conditions, most aerial censuses of game animals return underestimates (Gilbert and Grieb 1957, Bergerud 1963, Goddard 1967, Caughley 1969, Watson et al. 1969*a*, *b*), but we seldom have more than a hazy appreciation of the extent of the bias. This method can be used to estimate true density in small areas, and this estimate divided by the density that is measured by a routine aerial survey can be used as a correction factor for aerial surveys of larger areas with the same kind of habitat.

Although this method has been discussed mainly in the context of aerial surveys, since this was the specific problem that faced us when we were seeking a solution, the method is quite general and can be used to estimate birds in forests, leaves on trees, insects in grass, and similar populations.

EXPLANATION

Each computer model is a simulation of repeated surveys of a population of 100 animals counted at two levels of sightability. Sightability at the lower level has a parameter mean of 0.2857, and at the higher level, 0.7143. For a given model, 100 surveys were simulated at each of the two levels of sightability, the process being repeated five times to give five estimates of the mean and variance of counts at each level. Mean and variance of each low sightability trial were combined with those of each high sightability trial to give 25 estimates of population size by equation (4). Although these estimates are not fully independent, their mean and standard error should allow a check on statistical bias.

The four models were simulated as follows:

1. The number counted at a single survey was a variate drawn at random from a binomial distribution with the defined parameter mean sightability. Naylor et al. (1966:109) give a simple method of generating these variates.

2. The number counted at a single survey was a variate drawn at random from a binomial distribution whose p at each survey was drawn at random from a beta distribution with the defined parameter mean.

3. Individual sightabilities were drawn as random variates from a beta distribution with the defined parameter mean. An individual was recorded as seen during a survey if its sightability was greater than a random number drawn from a rectangular distribution bounded by 0 and 1.

4. Individual sightabilities were variates drawn at random from a beta distribution.

At each survey, this distribution was defined by a mean that was itself drawn as a random variate from a beta distribution with the defined parameter mean. Individuals were judged as seen or not seen in the same way as for the previous model.

Beta variates of models 2 and 3 were drawn from distributions with variances of 0.0136 at both high and low sightability. The variances of the beta distributions in model 4 averaged the same value.

As a check on the models, censuses of 50 and 150 animals were simulated under the same conditions as those listed. Apart from the expected shift of the estimates, the results are consistent with those given in Table 1.

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Received for publication November 16, 1970.

BRIEFER ARTICLES

SAGE GROUSE WINTER MOVEMENTS AND HABITAT USE IN CENTRAL MONTANA[1]

ROBERT L. ENG, Department of Zoology and Entomology, Montana State University, Bozeman
PHILIP SCHLADWEILER, Montana Fish and Game Department, Bozeman

Abstract: Movements and habitat use by sage grouse (*Centrocercus urophasianus*) were studied in central Montana during the winters of 1965–66 and 1966–67. Two and three female sage grouse were radio-equipped and tracked during the two respective winters. Winter ranges of the five instrumented females ranged from approximately 2,615 to 7,760 acres. A 4-square-mile primary study area, containing over half of the relocations of the five instrumented birds, was separated into two big sagebrush (*Artemisia tridentata*) canopy cover classes on 16-inch: 1-mile aerial photographs. Fifty-five percent of the primary study area was in the more dense (over 20 percent canopy coverage) and 45 percent in the less dense (under 20 percent canopy coverage) category. Observed use of the two canopy coverage classes was significantly ($P < 0.01$) different, a decided preference for the more dense stands being indicated. The characteristics of central Montana sage grouse winter areas (large expanses of dense sagebrush with little if any slope) make them prime targets of sagebrush control programs. Removal of sagebrush from these areas would greatly reduce their capacity to support wintering sage grouse.

Sage grouse habitat has been declining for many years, primarily through the removal of sagebrush (Patterson 1952:281). With aerial application of herbicides becoming commonplace, this trend has accelerated. In 1965, a 10-year project was initiated by the Montana Fish and Game Department and the U. S. Department of the Interior, Bureau of Land Management, to determine the ecological effects of sagebrush removal. In the winters of 1965–66 and 1966–67, we studied the distribution and habits of sage grouse as related to sagebrush densities to determine habitat requirements during this season.

We acknowledge the assistance of D. B. Pyrah, S. R. Bayless, and N. S. Martin of the Montana Fish and Game Department in trapping and making observations. M. P. Meyer, School of Forestry, University of Minnesota, developed a technique for separating the primary study area into sagebrush canopy classes.

[1] A joint contribution from the Department of Zoology and Entomology, Montana State University, Bozeman, and the Game Management Division, Federal Aid Projects W–105–R–1, 2, Montana Fish and Game Department. Published as Journal Series No. 287, Montana Agricultural Experiment Station.

STUDY AREA

This study was conducted in central Montana approximately 15 miles southwest of the town of Winnett. The gently sloping upland on the north side of Pike Creek was selected because of its known history of winter use by sage grouse. This area is in the southern portion of the Yellow Water Triangle, the vegetation of which is described by Bayless (1969). During the periods of study, snow depths ranged from 0 to 10 inches in 1966 and 0 to 6 inches in 1967. Temperature extremes were –15 to 53 F and –12 to 65 F during the two respective study periods (U. S. Dept. Commerce, 1966, 1967).