

ESTIMATING DENSITY FROM SURVEYS EMPLOYING UNEQUAL-AREA BELT TRANSECTS

Author(s) :Stephen V. Stehman and Daniel W. Salzer Source: Wetlands, 20(3):512-519. 2000. Published By: The Society of Wetland Scientists DOI: <u>http://dx.doi.org/10.1672/0277-5212(2000)020<0512:EDFSEU>2.0.CO;2</u> URL: <u>http://www.bioone.org/doi/full/10.1672/0277-5212%282000%29020%3C0512%3AEDFSEU</u> %3E2.0.CO%3B2

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

ESTIMATING DENSITY FROM SURVEYS EMPLOYING UNEQUAL-AREA BELT TRANSECTS

Stephen V. Stehman

SUNY College of Environmental Science and Forestry 320 Bray Hall Syracuse, New York, USA 13210 E-mail: svstehma@mailbox.syr.edu

> Daniel W. Salzer The Nature Conservancy of Oregon 821 S.E. 14th Avenue Portland, Oregon, USA 97214 E-mail: dsalzer@tnc.org

Abstract: Fixed-width belt transects employed in surveys of irregular shaped regions will differ in length and, therefore, in area. When estimating density from such a sample, the unequal transect areas must be taken into account. A density estimator dividing the mean number of objects (e.g., plants or animals) per transect by the mean transect area is recommended. An alternative estimator, the mean density per transect, is applicable for equal-area transects but often has undesirable properties for unequal-area transects. The recommended density estimator is identified as a ratio estimator, and its standard error is derived from ratio estimation theory.

Key Words: consistent estimation, quadrat sampling, ratio estimator, systematic sampling

INTRODUCTION

Quadrat sampling is a standard approach for estimating density, numbers, biomass, and other characteristics of a population (Mueller-Dombois 1974, Greig-Smith 1983, Bonham 1989, Krebs 1989), and belt or strip transects represent a special case of quadrat sampling. For sampling relatively rare organisms, belt transects offer a practical, easy-to-implement sampling protocol that may yield more precise estimates than, for example, square meter quadrats. The general problem of determining appropriate quadrat size and shape has received much attention in ecology. No single quadrat size or shape is universally best (Krebs 1989:64). A practical advantage of rectangular quadrats is "increased facility with which the quadrat can be studied" (Kershaw 1973:32) including diminished trampling of the vegetation and ease of dividing up the quadrat for counting (Greig-Smith 1983:28). Belt transects offer enhanced precision if a gradient is present and the transects are aligned parallel to this gradient (Schreuder et al. 1993:294). Kershaw (1973:32), Greig-Smith (1983:28), and Barbour et al. (1999:218) similarly note the potential of smaller variance achieved by rectangular quadrats relative to square quadrats if the long axis of the rectangular plot is placed parallel to the major environmental gradient. A potential disadvantage of belt transects is that the perimeter-to-area ratio is high, requiring more decisions on plot boundary or edge individuals compared to circular and square quadrats.

Descriptions of quadrat sampling typically focus on equal-area quadrats. In practice, if fixed-width belt transects are selected and the study region's natural shape is irregular rather than rectangular, then the belt transects will not be equal length or equal area. For example, suppose the objective is to estimate characteristics of a population of rare plants found within a riparian floodplain (Figure 1). These characteristics may include the number and density of plants, seed production and biomass per unit area, and number of flowers per plant. In Figure 1, the sample transects are located systematically along the stream and oriented perpendicular to a common baseline. Once the starting point of a sample transect is located, the field crew traverses the complete transect. Extending the transects the full width of the floodplain results in the transects being unequal in length and area. At issue is how to analyze the data resulting from the unequal-area transects shown in Figure 1. Two approaches to estimate density may occur to practitioners. One is to estimate density as a ratio estimator of the mean number of plants per transect divided by the mean area per tran-



Figure 1. Systematic sample of belt transects traversing an irregular-shaped region determined by a floodplain.

sect (or, equivalently, the total number of plants counted divided by the total area sampled). Alternatively, density could be calculated for each sampled transect and then these individual transect densities averaged. The primary purpose of this article is to justify the ratio estimator as the more appropriate estimator.

ESTIMATING DENSITY

The following notation will be used. Let Y = total number of objects in the population, A = total area of the study region, and D = Y/A = density (e.g., number of plants or animals per unit area). D, Y, and A are parameters, and a census would reveal the value of each parameter. One way to view such a census, and at the same time to motivate the sampling protocol, is to partition the region into N belt transects, with each transect oriented perpendicular to a common baseline. For each transect, define $y_u =$ number of objects in transect u, and $a_u =$ area of transect u. Then $Y = \sum_{u=1}^{N} y_u$, $A = \sum_{u=1}^{N} a_u$, and density is

$$D = Y/A = \sum_{u=1}^{N} y_{u} / \sum_{u=1}^{N} a_{u}, \qquad (1)$$

where $\sum_{u=1}^{N}$ denotes summation over all N transects.

Because resources are rarely available for a census, we obtain a sample of *n* transects employing either a simple random or systematic selection protocol. The sample-based estimator of density is denoted \hat{D} , and the estimators of *Y* and *A* are denoted \hat{Y} and \hat{A} . The density estimator is then

$$\hat{D} = \frac{\hat{Y}}{\hat{A}} = \frac{N\bar{y}}{N\bar{a}} = \frac{\bar{y}}{\bar{a}},\tag{2}$$

where $\bar{y} =$ sample mean number of objects per transect, and $\bar{a} =$ sample mean transect area. \hat{D} is called a ratio estimator because it is a ratio of two estimated totals, \hat{Y} and \hat{A} (or equivalently, a ratio of two sample means). The numerator $\hat{Y} = N\bar{y}$ and denominator $\hat{A} =$ $N\bar{a}$ are unbiased estimators of the parameters Y and A. \hat{D} is not an unbiased estimator of D, but the bias is small if the number of sample transects, n, is large. Särndal et al. (1992:251) suggest that bias is negligible if n > 20, and Cochran (1977:sec. 6.8) provides detailed theory on bias.

Estimating density based on "standardizing" individual transects to account for unequal transect area may be posed as an alternative to \hat{D} . That is, each transect is standardized to the number of objects on a per-unit-area basis (e.g., plants per m²), $d_u = y_u/a_w$ and then these individual transect densities are averaged to obtain $\bar{d} = \sum_s d_u/n$, where \sum_s indicates summation over the sample transects. Comparing average density to the ratio estimator raises the question of whether unequal transect areas should be accounted for at the individual transect level, as in \bar{d} , or at the aggregate sample level, as in \hat{D} . The consistency criterion provides a statistical basis for the decision.

STATISTICAL PROPERTIES OF THE DENSITY ESTIMATORS

By definition, an estimator is consistent if it equals the population parameter when the sample size, n, equals the population size, N (Cochran 1977:21). In practical terms, consistency ensures that we are estimating the population parameter of interest. That is, if a census of the target population were available and we applied the sample-based estimation formula to the census data, we would obtain the exact value of the parameter. A rationale for recommending \hat{D} instead of \overline{d} is that these estimators are consistent for different parameters. \hat{D} is consistent for the parameter D, and \bar{d} is consistent for the parameter $\overline{D} = \sum_{\mu=1}^{N} d_{\mu}/N$, the mean density of the population of N transects (Appendix A). Because density is defined as the total number of plants per unit area, D = Y/A, \overline{D} is the preferred estimator because it is consistent for D. Further, D does not depend on the partition of the study region into transects, whereas \overline{D} is dependent on this partition. That is, if the study region is partitioned differently by choosing a different transect width, the parameter \overline{D} may change, but D will remain the same. Because the partition of the region into N transects is a structure imposed by the sampling protocol and not a characteristic of the population, the dependence of \overline{D} on the partitioning argues against \overline{D} as a biologically relevant parameter and accordingly against the use of \bar{d} as an estimator of D. D and \bar{D} are the same if all Ntransects are equal area, so \overline{d} and \hat{D} are equivalent if transects are equal length. Consequently, standardizing for transect area on an individual transect basis is justified for equal-area transects, but this standardization does not generalize to the unequal-area case.

The estimated variance of \hat{D} , denoted $\hat{V}(\hat{D})$, is derived from standard ratio estimation theory. $\hat{V}(\hat{D})$ may be computed via two algebraically equivalent forms,

$$\hat{\mathbf{V}}(\hat{D}) = \frac{1}{\bar{a}^2} \left(\frac{N-n}{N} \right) \frac{s_e^2}{n}$$
 (Thompson 1992:61), (3)

where $s_e^2 = \sum_{s} (y_u - \hat{D}a_u)^2 / (n - 1)$, or

$$\hat{\mathbf{V}}(\hat{D}) = \frac{(1 - n/N)}{n\bar{a}^2} (s_y^2 + \hat{D}^2 s_a^2 - 2\hat{D}s_{ya})$$

(Cochran 1977: eqn. 6.13), (4)

where s_y^2 and s_a^2 are the sample variances of y and a, respectively, and

$$s_{ya} = \left(\sum_{s} a_{u}y_{u} - n\bar{a}\bar{y}\right) / (n-1)$$

is the sample covariance between *a* and *y*. $\hat{V}(\hat{D})$ is an approximation valid for large samples. A sample size of 30 is usually sufficiently large to justify this approximation (Cochran 1977:153 and sec. 6.9). The approximation may be adequate for smaller sample sizes (see next section) if the distribution of transect areas is nearly symmetric or if the correlation between *a* and



Figure 2. Plant locations and study region for Population 1 used in the simulations (sample transects are oriented perpendicular to the long axis of the figure).

y is close to 1. The standard error, $SE(\hat{D}) = \sqrt{\hat{V}(\hat{D})}$, is used to construct a confidence interval for the parameter *D* via the formula

$$\hat{D} \pm t^* \text{SE}(\hat{D}) \tag{5}$$

where t^* is a percentile from the t-distribution with n - 1 degrees of freedom. A numerical example is presented in Appendix B.

SIMULATION STUDY OF ESTIMATOR PROPERTIES

Some simulation results illustrate properties of the density estimators and the variance estimator of \hat{D} . Two populations representing different field scenarios are investigated (Figures 2 and 3, Table 1). Population 1 has only two transect lengths (20 m and 40 m), so the coefficient of variation of transect area, CV(a), is small (28%). The low density of plants in the center region results in a low correlation between *a* and *y* ($\rho = 0.12$). Population 2 has a higher correlation between *a* and *y* ($\rho = 0.67$), and, because of the greater variability in transect lengths, Population 2 has a higher CV(*a*) of 57%.

The simulation results (Table 2) are based on 10,000 simple random samples of each sample size (*n*) from each population. The estimates, \hat{D}_k , \bar{d}_k , and $\hat{V}(\hat{D}_k)$ are calculated for each sample, where the subscript *k* denotes the *k*th sample in the simulation. For each sample size and population, the simulation results are used to compute the approximate bias of the estimator, \hat{D} ,

Bias
$$(\hat{D}) = \sum_{k=1}^{10,000} \hat{D}_k / 10,000 - D,$$
 (6)

which measures the degree to which the estimator \hat{D} differs, on average over the possible samples, from the parameter D. Relative bias, $\text{Bias}(\hat{D})/D$, is reported in Table 2.

The variance of \hat{D} is approximated by the formula

$$V(\hat{D}) = \sum_{k=1}^{10,000} (\hat{D}_k - E(\hat{D}))^2 / 10,000,$$
(7)



Figure 3. Plant locations and study region for Population 2 used in the simulations (sample transects are oriented perpendicular to the horizontal axis).

where $E(\hat{D}) = \sum_{k=1}^{10,000} \hat{D}_k/10,000$ is the expected value of \hat{D} . $V(\hat{D})$ represents the true precision of the density estimator. Because in the simulation study we know the entire population, we can approximate $V(\hat{D})$ closely via simulation. In practice, $V(\hat{D})$ is estimated from the sample data using $\hat{V}(\hat{D})$. We also computed mean square error (MSE),

$$MSE(\hat{D}) = V(\hat{D}) + [Bias(\hat{D})]^2,$$
 (8)

which combines bias and variance into a single summary measure. The estimator possessing the smaller MSE is preferred. Root mean square error (RMSE), the square root of MSE, re-scales MSE to units of density (e.g., number per m²). The bias, variance, and RMSE of \bar{d} are obtained using formulas (6), (7), and (8), with \hat{D}_k replaced by \bar{d}_k , the average density computed from sample k. To facilitate comparisons between \hat{D} and \bar{d} , Table 2 shows the ratio of root mean square errors, RMSE(\bar{d})/RMSE(\hat{D}). When this ratio exceeds 1, \hat{D} is preferred over \bar{d} .

Lastly, we evaluated the bias of the variance estimator $\hat{V}(\hat{D})$ and the properties of confidence intervals for D constructed using $\hat{V}(\hat{D})$. Bias of $\hat{V}(\hat{D})$ is approximated by

Bias[
$$\hat{V}(\hat{D})$$
] = $\sum_{k=1}^{10,000} \hat{V}(\hat{D}_k)/10,000 - V(\hat{D}).$ (9)

Relative bias, $\text{Bias}[\hat{V}(\hat{D})]/V(\hat{D})$, is reported in Table 2 to scale bias by the quantity targeted for estimation, $V(\hat{D})$. Confidence interval coverage is determined by computing a 95% confidence interval for *D* from each sample *k*,

$$\hat{D}_k \pm t^* \mathrm{SE}(\hat{D}_k),\tag{10}$$

and finding the proportion of samples in the simulation for which D is contained in the confidence interval. The resulting observed coverage should be close to the 95% nominal level.

Sampling theory reported for the ratio estimator assumes large sample size, so these simulation results are particularly useful to illustrate properties of the ratio estimator and its estimated variance for the small sample sizes sometimes employed in practice. Estimator properties vary by population, so examining two populations obviously does not exhaust the full range of estimator behaviors. The simulation approach could be applied to new populations constructed to represent specific conditions expected in any given application.

RESULTS OF THE SIMULATION STUDY

The simulation results confirm the theoretical prediction that the bias of \hat{D} is small. The absolute value of the relative bias of \hat{D} is less than 2% (0.02) for all sample sizes evaluated and less than 0.5% (0.005) for all cases when $n \ge 15$ (Table 2). As expected from the consistency criterion, \overline{d} is not a good estimator of D, and relative bias is much higher for \overline{d} than \hat{D} for both populations. Because \bar{d} is consistent for \bar{D} , the relative bias of \bar{d} is approximately $(\bar{D} - D)/D$, so \bar{d} overestimates D in Populations 1 and 2 by about 7% and 13%, respectively (for other populations, \bar{d} may underestimate D). The bias of \bar{d} for these two populations is large enough to be of concern in practice. Whereas sampling theory ensures that the bias of \hat{D} decreases as *n* increases, the bias of \overline{d} does not shrink with increasing n.

The RMSE comparison of the estimators generally favors \hat{D} . For the small sample sizes, n = 5 and n =10, \bar{d} has a slight advantage over \hat{D} for Population 1, but for $n \ge 15$ in Population 1 and all sample sizes in Population 2, \hat{D} is the preferred estimator. The RMSE advantage of \hat{D} is greater in Population 2 than Popu-

Table 1. Description of the populations used in the simulation study.

	Size	Population Total		Coefficient of Variation (%)			Density	Average Density
Popn.	(N)	Y	Α	у	а	Correlation	D = Y/A	$ar{D}$
1	600	7000	5000	86.2	28.3	0.12	1.40	1.50
2	1000	5050	5050	79.9	57.2	0.67	1.00	1.13

	Relat	ive Bias	Ratio of	Relative Bias of Ŷ (<i>D̂</i>)	Observed Coverage (Nominal 95%)
n	ā	Ď	Root Mean Square Errors*		
Population 1					
5	0.077	0.017	0.971	-0.068	90.8
10	0.077	0.011	0.990	-0.026	91.6
15	0.067	-0.001	1.002	-0.025	91.7
20	0.073	0.004	1.022	-0.033	92.8
25	0.070	-0.001	1.039	0.020	93.8
30	0.072	0.002	1.057	-0.006	93.6
50	0.069	-0.002	1.113	-0.009	93.9
Population 2					
5	0.139	0.010	1.903	-0.074	92.9
10	0.137	0.005	2.044	-0.013	93.8
15	0.129	0.000	2.089	-0.015	93.6
20	0.131	0.001	2.149	-0.005	94.0
25	0.132	0.002	2.211	-0.025	94.0
30	0.133	0.002	2.308	-0.006	94.3
50	0.130	0.000	2.492	-0.014	94.6

Table 2. Properties of density estimators for simple random sampling of n transects from each of two populations (for each sample size, the simulation results are based on 10,000 samples).

* Value shown is RMSE of \overline{d} divided by RMSE of \hat{D} ; ratios exceeding 1 are cases in which \hat{D} is preferable to \overline{d} when evaluated on this criterion.

lation 1 because of the higher correlation between a and y in Population 2.

The variance estimator $\hat{V}(\hat{D})$ generally underestimates the true variance, $V(\hat{D})$, with the most severe underestimation being the relative bias of -0.074(-7.4%) observed for n = 5 of Population 2. For $n \ge 1$ 10, the largest absolute value of relative bias is 3.3%, and the relative bias of $\hat{V}(\hat{D})$ generally decreases as sample size increases. The observed confidence interval coverage is 92.8% or higher when n > 15 for Population 1 and 92.9% or higher for all sample sizes in Population 2. Because $\hat{V}(\hat{D})$ underestimates variance, the observed confidence interval coverage is below the nominal 95% (i.e., the confidence intervals tend to be too narrow), but as the sample size increases, coverage approaches 95%. For the two populations shown, performance is good even at these relatively small sample sizes. Theory presented earlier suggests that good performance is generally assured for sample sizes greater than 30. For a highly skewed distribution of transect areas and/or a low correlation between a and y, a larger sample size may be needed for the variance approximation to work well. More detailed guidelines are difficult to specify, but again, simulation can be used to evaluate empirically the variance approximation for any hypothesized population one might expect to encounter in practice.

ESTIMATING OTHER POPULATION CHARACTERISTICS

Suppose the objective is to estimate characteristics such as number of flowers, biomass, or seed production. These characteristics may be of interest in several forms: 1) as population totals, 2) on a per-unit-area basis, or 3) on a per-plant basis. The unequal transect areas need not be incorporated in the first and third cases, and ratio estimation is applicable to all three cases.

First consider estimating a population total. Let z_u denote the value of the characteristic recorded on transect u (e.g., biomass) and $Z = \sum_{u=1}^{N} z_u$ denote the population total. An unbiased estimator of Z is $\hat{Z} = N\bar{z}$, with estimated variance

$$\hat{\mathbf{V}}(\hat{Z}) = N^2 (1 - n/N) s_z^2 / n,$$
 (11)

where s_z^2 is the sample variance of *z*. Transect area, a_u , is not used in the formula for the estimated total, \hat{Z} . If the total area of the study region, *A*, is known, a ratio estimator of the population total, $\hat{Z}_R = A\hat{Z}/\hat{A}$, may be more precise than the unbiased estimator \hat{Z} . The condition under which \hat{Z}_R is preferred is $\rho > (1/2)CV(a)/$ CV(z), where ρ is the correlation between *y* and *z*, and CV(z) and CV(a) are the coefficients of variation for *z* and *a* (Särndal et al. 1992:250).

When estimating characteristics on a per-unit-area

basis, the ratio estimator approach used to estimate density, \hat{D} , is applicable. The estimator of the mean per unit area is $\hat{R} = \hat{Z}/\hat{A} = \bar{z}/\bar{a}$. The variance of \hat{R} is estimated by (3), with \hat{D} replaced by \hat{R} , and y_u replaced by z_u .

To estimate characteristics on a per-plant basis (e.g., mean biomass per plant), a ratio estimator is used. For example, if z_u = biomass measured on transect u and x_u = number of objects observed in transect u, the parameter representing mean biomass per plant is M = Z/X, where $X = \sum_{u=1}^{N} x_u$. Then the estimator of M is $\hat{M} = \hat{Z}/\hat{X} = \bar{z}/\bar{x}$, and the variance is estimated by equation (3) or (4) with \hat{D} replaced by \hat{M} , y_u replaced by z_u , and a_u replaced by x_u . Transect area (a_u) is not directly incorporated in the ratio estimator \hat{M} .

DISCUSSION

Assumptions

Few assumptions are required to justify the density estimator \hat{D} or to derive its properties. Estimating density or other characteristics of a population within a defined spatial region is a sampling problem in which design-based inference is often invoked. Design-based inference (Hansen et al. 1983) is the framework typically discussed in sampling texts (Cochran 1977, Särndal et al. 1992, Thompson 1992, Schreuder et al. 1993). The attributes of the population elements are viewed as fixed constants, not random variables (Särndal et al. 1992:34), and variation is attributed to the randomization of the sample selection protocol. Cochran (1977:8) states that the mathematical form of the frequency distribution of the measurements or observations obtained on the sampling units is not assumed known, "so that the approach might be described as model-free or distribution-free." Similarly, Gregoire (1998:1431) notes that design-based inference is "free of any assumptions" about the statistical distribution of the observed values. Consequently, the validity of the ratio estimator and its variance estimator does not require assuming that the variables measured are normally distributed, that each observation has equal variance, or that objects are randomly distributed in space. The assumption-free character of design-based inference extends to spatial autocorrelation. In design-based inference, "spatial correlation is an irrelevant issue" (Gregoire 1998:1433) because no assumption of independent observations is invoked in the derivation of estimators or their properties. De Gruijter and ter Braak (1990) and Stehman and Overton (1996) provide additional discussion of spatial autocorrelation and design-based inference.

Although a statistical model provides the underlying rationale for the ratio estimator \hat{D} , "The basic properties (approximate unbiasedness, validity of the variance formulas, etc.) are not dependent on whether the model holds" (Särndal et al. 1992:227). The more closely this statistical model represents the population being sampled, the better the precision of the estimator. However, even if the model fits poorly, the density estimator is still consistent for D, and the variance and confidence interval formulas derived for the ratio estimator still apply.

Simple Random versus Systematic Sampling

Transects may be selected via simple random or systematic sampling. The consistency property of \hat{D} holds under either design, so the criteria for deciding between the two designs are ease of implementation, precision, and variance estimation. Advantages of systematic sampling are that it is easy to implement and often results in better precision than simple random sampling (Greig-Smith 1983). However, if the sample transects are selected via a systematic design, then even for large *n*, the variance estimator for \hat{D} may be biased. Usually, the true systematic sampling variance is smaller than the estimated variance obtained from (3) or (4). Consequently, confidence intervals are "conservative" (i.e., too wide) and actual coverage is higher than the specified nominal confidence level. Whether the systematic sampling variance estimator is in fact badly biased is rarely known with certainty in a particular application. Therefore, if a variance approximation is considered unacceptable, systematic sampling should not be chosen. For many applications, a variance approximation is adequate, so avoiding systematic sampling because it does not allow unbiased variance estimation is usually not warranted.

SUMMARY

Belt transects provide a sampling protocol that is practical to implement in the field and results in precise estimates if the transects are oriented with their long axis parallel to a strong environmental gradient. Even if the precision advantage gained by employing belt transects is small relative to alternative quadrat sizes and shapes, easy implementation may translate into greater area sampled per unit of time and, consequently, enhanced precision. In those situations in which belt transects are selected and the transects differ in area, a density estimator dividing the mean number of objects per transect by the mean transect area, \hat{D} , is recommended over the average of the individual transect densities, \overline{d} . \hat{D} is statistically consistent for the parameter representing population density, D, whereas \overline{d} is not consistent for D. Recognizing \hat{D} as a ratio estimator provides the link to standard sampling theory and the derivation of the standard error and approximate bias of \hat{D} . The standard error and confidence interval formulas associated with \hat{D} were demonstrated to perform well in the simulation study, even for relatively small sample sizes. Similar good performance for small sample sizes is not ensured for other populations, but the simulation approach provides a mechanism for evaluating other populations. Sampling theory justifies use of the ratio estimator and its variance estimator for larger sample sizes.

ACKNOWLEDGMENTS

We thank Chip Harvey, Terry Kimes, Nathan Rudd, Peter Smallidge, and John Willoughby for their comments on an early version of the article, and Philip Dixon for valuable suggestions on a later draft. We acknowledge Associate Editor James Reinartz's helpful requests for clarifications during several stages of revision.

LITERATURE CITED

- Barbour, M. G., J. H. Burk, W. D. Pitts, F. S. Gilliam, and M. W. Schwartz. 1999. Terrestrial Plant Ecology (3rd edition). Addison Wesley Longman, Inc., New York, NY, USA.
- Bonham, C. D. 1989. Measurements for Terrestrial Vegetation. John Wiley, New York, NY, USA.
- Cochran, W. G. 1977. Sampling Techniques (3rd edition). John Wiley, New York, NY, USA.
- De Gruijter, J. J. and C. J. F. Ter Braak. 1990. Model-free estimation from spatial samples: A reappraisal of classical sampling theory. Mathematical Geology 22:407–415.
- Gregoire, T. G. 1998. Design-based and model-based inference in survey sampling: appreciating the difference. Canadian Journal of Forest Research 28:1429–1447.
- Greig-Smith, P. 1983. Quantitative Plant Ecology (3rd edition). University of California Press, Berkeley, CA, USA.
- Hansen, M. H., W. G. Madow, and B. J. Tepping. 1983. An evaluation of model dependent and probability sampling inferences in sample surveys. Journal of the American Statistical Association 78:776–807.
- Kershaw, K. A. 1973. Quantitative and Dynamic Ecology (2nd edition). William Clowes & Sons Limited, London, UK.
- Krebs, C. J. 1989. Ecological Methodology. Harper Collins, New York, NY, USA.
- Mueller-Dombois, D. 1974. Aims and Methods of Vegetation Ecology. John Wiley, New York, NY, USA.
- Särndal, C. E., B. Swensson, and J. Wretman. 1992. Model-Assisted Survey Sampling. Springer-Verlag, New York, NY, USA.
- Schreuder, H. T., T. G. Gregoire, and G. Wood. 1993. Sampling Methods for Multiresource Forest Inventory. John Wiley, New York, NY, USA.
- Stehman, S. V. and W. S. Overton. 1996. Spatial Sampling. p. 31– 63. In S. L. Arlinghaus and D. A. Griffith (eds.) Practical Handbook of Spatial Statistics. CRC Press, Inc., New York, NY, USA.

Thompson, S. K. 1992. Sampling. John Wiley, New York, NY, USA.

Appendix A: Consistency of the Density Estimator, \hat{D}

The proposition that $\hat{D} = \hat{Y}/\hat{A}$ is consistent for the parameter D = Y/A is established by noting that for a census (n = N), $\hat{Y} = N\bar{y} = N\sum_{u=1}^{N} y_u/N = Y$, and $\hat{A} = A$ (for the same reason that $\hat{Y} = Y$). Consequently, $\hat{D} = D$ when the sample size equals N, satisfying the definition of a consistent estimator. If \bar{d} is computed from a census, we obtain $\bar{d} = \sum_{u=1}^{N} d_u/N = \bar{D}$, establishing \bar{d} as consistent for \bar{D} . \bar{d} is not consistent for D except when $\bar{D} = D$ (e.g., transect areas are equal).

Appendix B: Numerical Example

To illustrate application of the formulas for estimating density and the associated standard error, we use sample data from a monitoring study of flowering pale white larkspur (Delphinium leucophaeum (Greene)), a rare plant locally abundant along the Willamette River near Portland, Oregon. The region defining the spatial boundary of this population extended from the river to an abrupt forest edge. Sample transects were oriented perpendicular to the river, and the transects differed in length because the distance from the river to the forest edge varied depending on the transect starting location. The study region can be partitioned into N = 150 transects each 1 m wide. A sample of n = 20 transects was selected, and $y_{\mu} =$ number of plants and a_u = area (m²) was recorded for each sampled transect, *u* (Table 3).

For this sample, the estimated density is $\hat{D} = \bar{y}/\bar{a} = 21.45/28.395 = 0.7554$. To estimate the variance of \hat{D} , create the column $e_u = y_u - \hat{D}a_u$, and then compute $s_e^2 = \sum_s (y_u - \hat{D}a_u)^2/(n-1) = 7908.975/19 = 416.262$. Substituting into equation (3), the estimated variance is then

$$\hat{\mathbf{V}}(\hat{D}) = \frac{1}{\bar{a}^2} \left(\frac{N-n}{N} \right) \frac{s_e^2}{n} = \frac{1}{28.395^2} \left(\frac{150-20}{150} \right) \frac{416.262}{20} = 0.0224,$$

and the standard error of \hat{D} is SE(\hat{D}) = $\sqrt{0.0224}$ = 0.1496. Equivalently, we could compute the estimated variance using equation (4). The required covariance term is

$$s_{ya} = \left(\sum_{s} a_{u}y_{u} - n\bar{a}\bar{y}\right) / (n-1)$$

= [13789.30 - 20(28.395)(21.45)]/19
= 84.623, and

Transect			<u>^</u>	
<i>(u)</i>	\mathcal{Y}_u	a_u	$e_u = y_u - \hat{D}a_u$	$a_u y_u$
1	0	22.0	-16.6188	0.0
2	22	27.0	1.6042	594.0
3	1	33.0	-23.9282	33.0
4	12	38.4	-17.0074	460.8
5	4	41.0	-26.9714	164.0
6	21	45.0	-12.9930	945.0
7	77	34.0	51.3164	2618.0
8	27	34.0	1.3164	918.0
9	4	41.0	-26.9714	164.0
10	23	31.0	-0.4174	713.0
11	19	37.0	-8.9498	703.0
12	63	42.0	31.2732	2646.0
13	55	30.5	31.9603	1677.5
14	39	30.0	16.3380	1170.0
15	17	27.0	-3.3958	459.0
16	7	3.0	4.7338	21.0
17	18	13.0	8.1798	234.0
18	3	12.0	-6.0648	36.0
19	12	14.0	1.4244	168.0
20	5	13.0	-4.8202	65.0

Table 3. Sample data for n = 20, 1 *m* wide belt transects in a monitoring study of pale white larkspur.

The summary statistics needed to compute the estimates are: $\bar{y} = 21.45$, $s_y^2 = 463.3132$, $\Sigma_s a_a y_a = 13789.30$, $\bar{a} = 28.395$, $s_a^2 = 141.5942$.

$$\hat{\mathbf{V}}(\hat{D}) = \frac{(1 - n/N)}{n\bar{a}^2} (s_y^2 + \hat{D}^2 s_a^2 - 2\hat{D} s_{ya})$$

$$= \frac{(1 - 20/150)}{20(28.395)^2} [463.3132 + 0.7554^2(141.5942) - 2(0.7554)(84.623)]$$

$$= 0.0224.$$

The total area of the study region is A = 5897 m², so the estimated population size is $\hat{D}A = 0.7554(5897)$ = 4454.6 plants with a standard error of $A*SE(\hat{D}) =$ 5897(0.1496) = 882.2.

Manuscript received 18 February 1999; revisions received 19 August 1999 and 10 April 2000; accepted 23 May 2000.