ESTIMATING POPULATION SIZE WITH CORRELATED SAMPLING UNIT ESTIMATES

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Abstract: Finite population sampling theory is useful in estimating total population size (abundance) from abundance estimates of each sampled unit (quadrat). We develop estimators that allow correlated quadrat abundance estimates, even for quadrats in different sampling strata. Correlated quadrat abundance estimates based on mark–recapture or distance sampling methods occur when data are pooled across quadrats to estimate, for example, capture probability parameters or sighting functions. When only minimal information is available from each quadrat, pooling of data across quadrats may be necessary to efficiently estimate capture probabilities or sighting functions. We further include information from a quadrat-based auxiliary variable to more precisely estimate total population size via a ratio estimator. We also provide variance estimators for the difference between or the ratio of 2 abundance estimates, taken at different times. We present an example based on estimating the number of Mexican spotted owls (*Strix occidentalis lucida*) in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico, USA. Owl abundance for each quadrat was estimated with a Huggins 4-pass mark–resight population estimator, but with initial capture and resighting probabilities modeled in common across all sample quadrats. Pooling mark–resight data across quadrats was necessary because few owls were marked on individual quadrats to estimate quadrat-specific capture probabilities. Model-based estimates of owl abundance for each quadrat necessitated variance estimation procedures that take into account correlated quadrat estimates. An auxiliary variable relating to topographic roughness of sampled quadrats provided a useful covariate for a ratio estimator.

JOURNAL OF WILDLIFE MANAGEMENT 67(1):1–10

Key words: Arizona, closed population estimation, finite population sample theory, Huggins estimator, mark–recapture, mark–resight, Mexican spotted owl, New Mexico, program MARK, ratio estimator, *Strix occidentalis lucida.*

Sound wildlife resource management requires credible information on wildlife population status. Such information frequently is difficult to obtain because many wildlife species are secretive and not easily counted. Consequently, a need exists for estimators that provide unbiased estimates of population size and have reduced variances due to use of available auxiliary information. Here, we consider a population of size N distributed over an area that is divided into a set of U quadrats (notation generally follows Thompson et al. 1998). The objective is to estimate abundance when only a sample of quadrats can be surveyed. Quadrat populations are assumed to be closed during the estimation process. Further, we assume that not all animals on the sampled quadrats are counted, thus requiring quadrat population estimates to be corrected for probability of detection of the animals counted.

Estimation of wildlife population size in situations where the entire wildlife population cannot be sampled involves 2 phases (Thompson et al. 1998). The first phase involves finite population sampling theory (e.g., Cochran 1977, Thompson 1992) where a population of interest is defined and a sample of units is selected from a sampling frame. The second phase involves obtaining estimates of population abundance on the selected units. Because the animals on the selected units are not detected with a probability equal to 1, estimation of the size of wildlife populations is considerably more difficult than the usual finite sampling problems in which the variable of interest can be determined exactly for each sampled unit.

Two primary approaches are available for obtaining unbiased estimates of population size of a wildlife population on a sampling unit when animals are not detected with probability 1: distance sampling (Buckland et al. 1993) and re-encounters of marked animals (reviewed by Thompson et al. 1998). Both methods involve the estimation of nuisance parameters (i.e., probability of detection) to correct a count of animals observed. For determining animal abundance over large areas, both methods are employed with finite population sample theory to estimate animal abundance (Thompson et al. 1998). In addition, both meth-

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ods frequently use auxiliary information to improve estimates of the nuisance parameters and hence improve the estimates of population abundance. For example, cluster size commonly is used to improve distance sampling estimates of population size, whereas quadrat-specific or individual covariates such as gender, age, or breeding status commonly are used to improve mark–encounter population estimates (Huggins 1991).

Finite population sampling theory includes numerous techniques that are useful in improving the estimates of population size (abundance) of wildlife populations. Most notable for the scenario described here are stratification and ratio estimators that incorporate auxiliary information, both of which improve the precision of the population estimate.

Skalski (1994) combined basic finite population sampling plans with mark–recapture population size estimation on sampled quadrats to obtain estimators of total population size and corresponding variances. We provide 3 extensions to the work of Skalski (1994). First, we incorporate auxiliary information into the estimation of population size via a ratio estimator. Second, we allow correlated quadrat abundance estimates because our proposed estimators incorporate auxiliary information across quadrats to produce improved estimates within quadrats. Third, we provide variance estimators for both the difference between and ratio of 2 abundance estimates obtained from our estimator at different sampling times on the same quadrats.

We only consider a stratified random sampling of quadrats. Our estimation process requires that some method is used that provides, at least approximately, unbiased estimators of individual sampled quadrat abundance and their corresponding variances and covariances. As described above, the most commonly applied approaches to achieve this requirement are re-encounters of marked animals and distance sampling.

As an example, we estimate the number of Mexican spotted owls within a given area using mark–recapture (resight) techniques to obtain required quadrat estimates. The area was divided into quadrats because efficient mark–recapture data collection for owls was deemed feasible on an individual quadrat basis but not the area as a whole. However, the mark–resight data available separately by quadrat failed to provide reliable individual quadrat estimates because only a small number of owls were marked on any quadrat. Pooled quadrat data were used to obtain model-based estimates, by quadrat, of initial capture and resighting probabilities, that depended on quadrat covariates. Then individual quadrat abundance estimates were made. Quadrat estimates were expanded via a ratio estimator into total area abundance estimate. Quadrat abundance estimates were correlated, requiring use of the variance estimation procedures given in this paper. As suggested above, distance sampling (Buckland et al. 1993) provides another example of a method where estimates of population size from sampling units are correlated when a common sighting function is estimated with data pooled from all sampled units.

DEVELOPMENT OF THE ESTIMATOR

Auxiliary information is commonly used to obtain an improved estimator (reduced variance) of abundance. We incorporate auxiliary information in the sampling design, first attempting to stratify quadrats into homogeneous groups, and second into the estimation process via ratio estimation. The following notation will help identify how the problem of interest differs from the standard use of ratio estimation with stratified sampling as given by Cochran (1977) or Thompson (1992). The quadrats are stratified into L strata where U_h is the number of quadrats in stratum h, (h = 1, ..., L). Total population size can be written as

$$N = \sum_{h=1}^{L} \sum_{q=1}^{U_h} N_{hq} = \sum_{h=1}^{L} N_h ,$$

where N_{hq} is the number of animals of interest on quadrat q of stratum h, (q = 1, ..., U_h), and N_h is the number of animals in stratum h. A stratified random sample, sampling without replacement, is selected with $u_h \geq 2$ quadrats selected from the U_h quadrats in stratum h. The sample size of at least 2 quadrats in each stratum facilitates variance estimation. Next, we assume an auxiliary variable, x, is available whose value on each sampled quadrat can be determined and whose total, X_h, also is known for all U_h units in stratum h. Let X_{hq} be the value of the auxiliary variable on quadrat q of stratum h. Then

$$X_h = \sum_{q=1}^{U_h} X_{hq} .$$

We also define the ratio, R_h, to be equal to N_h/X_h. The stratified, separate ratio estimator of population size (Cochran 1977) can be written as

$$\hat{N} = \sum_{h=1}^{L} X_h \left(\frac{\sum_{q=1}^{u_h} N_{hq}}{\sum_{q=1}^{u_h} X_{hq}} \right).$$

In our problem, as in cases considered by Skalski (1994), the population size of each sample quadrat is unknown. We assume that it is possible to obtain an unbiased estimate of abundance for each sampled quadrat and an approximately unbiased estimator of the variances and covariances of the quadrat abundance estimators. To estimate N, it is only necessary to estimate, unbiasedly, the abundance of the combined u_h sampled units. However, an abundance estimate for each sampled quadrat is needed for variance estimation.

Our estimator of N is written as

$$\hat{N}_R = \sum_{h=1}^{L} X_h \left(\frac{\sum_{q=1}^{u_h} \hat{N}_{hq}}{\sum_{q=1}^{u_h} X_{hq}} \right) = \sum_{h=1}^{L} X_h \hat{R}_h = \sum_{h=1}^{L} \hat{N}_h. \quad (1)$$

Thus, we have replaced the unknown abundance N_{hq} in the estimator $\hat{N}$ by $\hat{N}_{hq}$, an unbiased estimator of N_{hq}. We are using a separate ratio estimator in each stratum. Note that the expected value of $\hat{N}_R$ holding the sample of quadrats fixed is the estimator $\hat{N}$. If the population sizes of sampled quadrats were estimated independently of one another, then the estimator (1) would be classified as a stratified, 2-stage, separate ratio estimator. Standard variance estimation procedures (Cochran 1977) for such estimators can be readily modified to incorporate the use of mark–recapture or mark–resight techniques in obtaining individual quadrat estimates. Our development includes the needed modifications as a special case.

We consider the more general case in which the quadrat abundance estimates may be correlated, even for sample quadrats in different strata. Such a sampling plan has been identified as a 2-phase sampling plan (Sarndal et al. 1992). Although general expressions for the variance and variance estimators are given in Sarndal et al. (1992) for 2-phase sampling plans, details need to be worked out for specific cases. Instead, we obtain the needed results for our specific estimator (1) by applying standard statistical techniques.

The estimator $\hat{N}_R$ has the same expectation as the stratified, separate ratio estimator $\hat{N}$ whose properties are stated by Cochran (1977). The estimator is biased, but the bias decreases as the u_h ($h = 1, ..., L$) all are increased. If the bias in each stratum is of the same sign, the cumulative bias over all strata is of concern.

The derivation of both an approximate variance and variance estimator for $\hat{N}_R$ is outlined in the Appendix. The variance of $\hat{N}_R$ can be written as

$$\mathrm{Var}(\hat{N}_R) = \sum_{h=1}^{L} \mathrm{Var}(\hat{N}_h) + \sum_{h \neq h'}^{L} \sum_{h'=1}^{L} \mathrm{Cov}(\hat{N}_h, \hat{N}_{h'}), \quad (2)$$

where Var(.) indicates variance of the enclosed estimator and Cov(.,.) indicates covariance between the 2 enclosed estimators. Thus, the sum of all the estimated variance and covariance components gives an estimator of the variance of $\hat{N}_R$. The estimators of $\mathrm{Var}(\hat{N}_h)$ and $\mathrm{Cov}(\hat{N}_h, \hat{N}_{h'})$, $h \neq h'$, are given by Appendix Equations 8 and 6, respectively.

Alternatively, the variance of $\hat{N}_R$ can be written as the sum of 2 parts associated with sampling in 2 phases. The first-phase variance component is the variance due only to quadrat sampling, that is, when a sample of quadrats is taken and the population size on each sampled quadrat is known. The second-phase variance component is the variance due to estimating the population size of interest on the sampled quadrats. The relative size of the 2 components may be helpful in deciding on future allocation of resources between the 2 phases. Formulas for estimating the 2 variance components are given by Appendix Equations 9 and 10.

Confidence interval construction can be approached in several ways. First, if the number of quadrats sampled is large, then a standard large sample approach would be to construct an interval for the population size N as $\hat{N}_R \pm z_{1-\alpha/2}\sqrt{\hat{\mathrm{V}}\mathrm{ar}(\hat{N}_R)}$, where $z_{1-\alpha/2}$ is the $1-\alpha/2$ quantile of the standard normal distribution. Because the distribution of $\hat{N}_R$ generally will be skewed to the right, the following procedure, based on a logarithmic transformation, tends to have actual confidence level coverage closer to nominal than the standard large sample procedure. The interval is given as $\hat{N}_R[\exp(\pm z_{1-\alpha/2}\hat{\mathrm{C}}\mathrm{V}(\hat{N}_R))]$, where $\hat{\mathrm{C}}\mathrm{V}(\hat{N}_R) = \sqrt{\hat{\mathrm{V}}\mathrm{ar}(\hat{N}_R)}/\hat{N}_R$. If the number of quadrats is small, particularly for the strata that contribute a large part of the overall estimated variance, then replacement of $z_{1-\alpha/2}$ by the corresponding Student's t quantile where the degrees of freedom are calculated will give a better result. The degrees of freedom could be calculated following Cochran (1977:96) for stratified sampling where the second phase variance contribution is ignored.

Table 1. Distribution of quadrats and characteristics of the 2 strata used to estimate the population size of Mexican spotted owls in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico, USA, 1999.

Stratum (h)	Stratum area (A_h)(km^2)	Area sampled $\left(\sum_{h=1}^{u_h} a_h\right)$(km^2)	Total quadrats (U_h)	Quadrats sampled (u_h)	TIN ratio – 1 (X_h)
Low	10,046.39	271.81	390	5	9.80417
High	35,384.26	1,231.40	593	20	3.13968
Total	45,432.65	1,505.21	983	25	12.94385

COMPARISON OF ABUNDANCE AT TWO TIME POINTS

Either the difference or the ratio of abundance at 2 times may be useful in studying change in population size. Let N and M refer to abundance at the 2 times. We assume the same stratified sample of quadrats is used both times. Then an estimator of the variance of the difference $\hat{N} - \hat{M}$ is

$$\widehat{\text{Var}}(\hat{N} - \hat{M}) = \widehat{\text{Var}}(\hat{N}) + \widehat{\text{Var}}(\hat{M}) - 2\,\widehat{\text{Cov}}(\hat{N}, \hat{M}),$$

and an estimator of the variance of the ratio $\hat{R} = \hat{M}/\hat{N}$ is

$$\widehat{\text{Var}}\left(\frac{\hat{M}}{\hat{N}}\right) = \frac{\widehat{\text{Var}}(\hat{M}) + \hat{R}^2\,\widehat{\text{Var}}(\hat{N}) - 2\,\hat{R}\,\widehat{\text{Cov}}(\hat{N}, \hat{M})}{\hat{N}^2}.$$

An estimator of the covariance between the 2 population size estimators is given by Appendix Equation 11. If 2 estimates of population size are obtained by implementing completely independent surveys for the 2 times, then the covariance terms in the 2 preceding variance estimators are omitted.

Standard, large sample, confidence intervals with nominal confidence levels take the form (Estimate $\pm z_{1-\alpha/2}\widehat{\text{SE}}$) where $\widehat{\text{SE}}$ is obtained as the square root of the appropriate estimated variance.

EXAMPLE

Our example illustrating use of these estimators is based on a pilot study evaluating methods for monitoring populations of Mexican spotted owls (Ganey et al. 1999). Twenty-five quadrats in 2 strata (representing high and low expected density, based on elevation) were surveyed for Mexican spotted owls (Table 1) in the Upper Gila Mountains Recovery Unit (U.S. Fish and Wildlife Service 1995). Located owls were captured, uniquely color-banded, and resighted on subsequent survey passes (n = 4). In brief, to estimate the total number of Mexican spotted owls in the Recovery Unit (N) and the standard error, SE($\hat{N}$), we first used capture–recapture data from the 4 surveys of the sampled quadrats to estimate initial capture probabilities (p) for each quadrat. Second, we used the estimates of p to correct the observed counts of banded owls and unbanded owls to estimate the number of owls (N_{hq}) for each quadrat. The variance–covariance matrix of these estimators also was estimated. Finally, we estimated the total number of owls (N), and its standard error, in the Recovery Unit by the use of a ratio estimator applied separately for each strata. The value of the auxiliary variable (an index of topographic roughness) had been determined for each quadrat (n = 983; Table 1) in the entire area.

In the first step, we used the capture–recapture data from banded owls on the 11 quadrats where owls were banded and subsequently resighted to estimate p, the probability of capture on a given trapping occasion. To estimate p, we used a closed capture–recapture modeling procedure developed by Huggins (1989, 1991) that is implemented in program MARK (White and Burnham 1999). The goal at this stage was to estimate the p as precisely as possible because the sampling variance of the p contribute to the sampling variance of $\hat{N}_R$. In addition to p, the probability of recapture (c) also can be estimated, adding an additional parameter to be modeled. In standard closed capture–recapture models, maximum likelihood estimation is used to estimate both p and N simultaneously (Otis et al. 1978), i.e., the resulting estimates from standard closed capture–recapture models represent the joint maximum likelihood estimates. The Huggins models differ from the standard models in that only p and c are modeled with N being estimated as a derived parameter (i.e., N is computed algebraically from p). The primary advantage of the Huggins model is that covariates specific to the individual animal can be incorporated into the estimator. Also, the Huggins estimator provides more reasonable estimates of SE($\hat{N}$) for small samples such as we encountered than the asymptotic (large sample) variance used for the maximum likelihood estimator.

Thus, our initial efforts centered around modeling the capture–recapture data to obtain parsimonious estimates of p. To estimate p, we ran 26 closed-capture models in program MARK. In this set of models, we modeled the effects on p of sex, road access to the quadrat, occasion-specificity, and behavioral response to initial capture (i.e., inclusion of the recapture parameter c in the model). We used a bias-corrected version of Akaike's Information Criterion, AIC_c (Akaike 1973, Hurvich and Tsai 1995, Burnham and Anderson 1998) to rank models, with the best model having the lowest AIC_c. The best model was $p = c_{T + roadless + sex}$, which constrained p equal to c, and had a linear occasion effect (T), an effect of roadless quadrats versus quadrats with roads, and a sex effect on the p. The linear occasion, roadless, and sex effects were all negative and different from 0 (β_T = –0.350, 95% CI = –0.637, –0.063; $\beta_{roadless}$ = –1.614, 95% CI = –2.742, –0.486; β_{sex} = –0.983, 95% CI = –1.764, –0.203). This model indicated that capture probabilities declined over occasions in a linear fashion, roadless quadrats had lower capture probabilities than quadrats with roads, and that females had lower capture probabilities than males. Rather than using the p solely from this model, we estimated Akaike weights for each model (Buckland et al. 1997, Burnham and Anderson 1998) which represented the likelihood of a specific model as the best model to explain this particular dataset, relative to the other models examined in our set of models. We then used Akaike weights to derive a weighted mean estimate of capture probabilities (p_i; i.e., the p_i were model averaged) for each occasion for each sex and within roaded and unroaded quadrats across all models (see Stanley and Burnham 1998*a*,*b*). These weighted estimates of p_i had estimated standard errors that included a variance component due to model uncertainty (Buckland et al. 1997, Burnham and Anderson 1998). Thus, we ended up with 16 estimates of p, 1 for each of 4 occasions times 2 types of quadrats (roaded vs. unroaded) and for each sex. We then estimated an overall probability of detection of an owl (p^*) for each of the quadrats as

$$p^* = 1 - (1 - \hat{p}_1)(1 - \hat{p}_2)(1 - \hat{p}_3)(1 - \hat{p}_4).$$

For a few quadrats where only 2 or 3 survey passes were completed, appropriate p estimates were set equal to 0 (i.e., $\hat{p}_3 = \hat{p}_4 = 0$). Using the estimated covariance matrix $\hat{\text{V}}\text{ar}(\hat{p})$, where $\hat{p}$ denotes the vector of initial capture probabilities across occasions and quadrats, we computed the variance–covariance matrix, $\hat{\text{V}}\text{ar}(\hat{p}^*)$, for the probability of detection on each quadrat using the delta method (Seber 1982). The estimates of p^* were used to correct the number of owls banded (plus the additional number of unbanded owls known to exist) on each of the 25 quadrats as

$$\hat{N}_i = \frac{M_{t+1,i}}{\hat{p}_i^*},$$

where i indexes quadrat and $M_{t+1,i}$ is the number of owls observed on the quadrat (both banded and unbanded; see Ganey et al. 1999). On each quadrat, we estimated N_i separately for males and females. Thus, we had 50 estimates (2 estimates for each of the 25 quadrats) of N_i. Again, the delta method (Seber 1982) was used to compute the variance–covariance matrix of the 50 estimates of N_i where the $M_{t+1,i}$ were considered constant or fixed at observed values, as well as the variance–covariance matrix for the estimated total number of owls (males plus females) on each of the 25 quadrats, and the estimated density for each of the 25 quadrats (Table 2).

Using the methods described in this paper, the estimate of population size for the recovery unit was computed using a covariate that provided auxiliary information about each quadrat. The covariate used was based on the ratio of true surface area to the planar area (true surface area/planar area) for each quadrat, which provides an index of topographic roughness. Surface area, or the true area that lies within each quadrat, was calculated by developing triangulated irregular networks (TIN) for each quadrat using U.S. Geological Survey Digital Elevation Models. Because the ratio of surface area to planar area (hereafter referred to as TIN ratio) always will be ≥1, we subtracted 1 from the ratio (i.e., the final covariate = TIN ratio – 1) to set the minimum value equal to 0. We used TIN ratio – 1 as an auxiliary variable in the ratio estimator because it was highly correlated with $\hat{N}_{hq}$, Pearson's coefficient = 0.847 for the combined strata, 0.923 for the high stratum, and 0.379 for the low stratum.

Using the ratio estimator based on TIN ratio – 1, the estimate of population size for the recovery unit [$\hat{N}_{RU}$ = 2,172.8, $\hat{\text{SE}}(\hat{N}_{RU})$ = 519.6] had a coefficient of variation (CV) equal to 24% (Table 3). If the sampling variance of $\hat{N}_{hq}$ is ignored (Table 3), the CV is reduced to 16%. The lowest achiev-

Table 2. Estimated total population size (males and females combined) for each of 25 quadrats surveyed for Mexican spotted owls in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico, USA, 1999. (H = expected high-density stratum, L = expected low-density stratum).

Quadrat (q)	Area (a_{hq}) (km^2)	Owls observed	Estimated population	$\hat{SE}(\hat{N}_{hq})$	Estimated density	$\hat{SE}(\hat{D}_{hq})$	TIN ratio – 1 (X_h)
H01	43.68	0	0.00	0.00	0.00	0.00	0.005532
H02	61.15	6	6.38	0.29	0.10	0.00	0.032071
H03	46.45	0	0.00	0.00	0.00	0.00	0.004690
H04	76.40	2	2.13	0.10	0.03	0.00	0.004225
H07	59.60	1	1.01	0.01	0.02	0.00	0.007503
H08	55.66	2	2.13	0.10	0.04	0.00	0.006042
H09	54.88	0	0.00	0.00	0.00	0.00	0.002569
H11	57.92	0	0.00	0.00	0.00	0.00	0.019724
H12	63.20	2	2.13	0.10	0.03	0.00	0.010574
H13	66.77	2	2.13	0.10	0.03	0.00	0.012682
H14	68.09	0	0.00	0.00	0.00	0.00	0.014146
H16	69.03	8	8.82	0.52	0.13	0.01	0.036742
H17	62.32	2	2.13	0.10	0.03	0.00	0.017425
H18	66.86	4	9.52	4.35	0.14	0.07	0.043160
H19	49.94	0	0.00	0.00	0.00	0.00	0.002242
H20	71.01	1	1.01	0.01	0.01	0.00	0.039831
H21	72.80	17	32.08	13.16	0.44	0.18	0.094638
H22	52.45	7	12.21	5.10	0.23	0.10	0.034828
H23	66.26	5	5.27	0.20	0.08	0.00	0.027315
H24	66.93	15	15.90	0.69	0.24	0.01	0.054178
L01	40.89	0	0.00	0.00	0.00	0.00	0.023609
L02	66.14	0	0.00	0.00	0.00	0.00	0.003028
L03	68.53	0	0.00	0.00	0.00	0.00	0.023073
L05	44.97	0	0.00	0.00	0.00	0.00	0.040615
L06	51.28	1	1.11	0.10	0.02	0.00	0.034768

able CV based on using TIN ratio – 1 is 14% where just the raw counts of owls (M_{t+1}) are used in the ratio estimator of $\hat{N}_q$ with no adjustment of these counts by p*. The difference in the standard errors for the naive estimate and $\hat{N}_{RU}$ are substantial, and point to the impact of quadrat H21 in particular, but also H22 and H18 to some extent, in greatly increasing the variance of the estimate when detection probability corrections were applied. These quadrats had some of the lowest detection probabilities (Ganey et al. 1999), and hence much larger variances for $\hat{N}_{hq}$. These 3 quadrats contribute 99.6% of the variance to the term

$$\sum_{h=1}^{2}\sum_{i=1}^{u_h} \hat{\text{V}}\text{ar}(\hat{N}_{hq}).$$

Table 3. Results of estimating the density and population size of Mexican spotted owls for the low- and high-density strata in the Upper Gila Mountains Recovery Unit (not including tribal lands), Arizona and New Mexico, USA, in 1999. TIN ratio – 1 was used as the ratio covariate. Shown (in order) are estimates (1) incorporating all variance components; (2) incorporating variance due to adjustment of raw counts by capture probabilities; and (3) based on raw counts of owls observed on quadrats (), with no correction for owls not detected.

Population estimate	Stratum	Stratum population ($\hat{N}$)	$\hat{SE}(\hat{N})$	CV (%)
$\hat{N}_h$ (all components)	High	2,144.9	518.1	24.2
	Low	27.9	25.7	92.1
	Recovery Unit	2,172.8	519.6	23.9
$\hat{N}_h$ (without Var($\hat{N}_{hq}$))	High	2,144.9	341.9	15.9
	Low	27.9	25.7	92.1
	Recovery Unit	2,172.8	342.8	15.8
M_{t+1}(raw counts)	High	1,543.3	220.6	14.3
	Low	25.1	23.1	92.0
	Recovery Unit	1,568.4	221.8	14.1

A Quattro Pro® spreadsheet demonstrating the calculations for the above example plus 2 additional auxiliary covariates (quadrat area and TIN Ratio minus 1 raised to a power) is provided at <http://www.cnr.colostate.edu/~gwhite/OwlEstimator.htm>.

MANAGEMENT IMPLICATIONS

Quadrat-specific estimates of owl population size could not be obtained without modeling capture probabilities across quadrats. However, these quadrat-specific estimates are now correlated, with this correlation induced by the model of capture probabilities. When the sampling variance and covariance of estimates of population size for each quadrat are ignored in computing the variance of the total population size, a biased variance estimate results. In most cases, the resulting estimate will underestimate the true variance, as was evident in our example. This results in population estimates that appear more precise than they actually are, which may in turn lead to unfounded management decisions. For example, underestimating variance could lead to a conclusion that a population change had occurred between 2 points in time, when a more accurate estimate of variance would result in a conclusion of no detectable change. The estimators we presented here correct this bias, and allow for the proper estimation of total population size with finite population sampling used with estimates from each sampling unit. In addition, use of the ratio estimator with appropriate covariate(s) improves precision of the estimator, partially compensating for the effect of considering all variance components.

ACKNOWLEDGMENTS

This work was funded through an agreement between the U.S. Forest Service, Rocky Mountain Research Station, and Colorado State University (RJVA #00-133). The pilot study on Mexican spotted owls was funded by the Southwestern Region, U.S. Forest Service. More than 50 field assistants collected the data used in the example. J. Jenness conducted the spatial analyses resulting in TIN ratios, and S. Arundel developed the quadrat sampling frame.

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Received 23 October 2001.
Accepted 20 May 2002.
Associate Editor: Brennan.

APPENDIX

The derivation of both an approximate variance and variance estimator for $\hat{N}_R$ is outlined. Our estimator of N is written as

$$\hat{N}_R = \sum_{h=1}^{L} X_h \frac{\sum_{q=1}^{u_h} \hat{N}_{hq}}{\sum_{q=1}^{u_h} X_{hq}} = \sum_{h=1}^{L} X_h \hat{R}_h = \sum_{h=1}^{L} \hat{N}_h . \quad (1)$$

The variance of $\hat{N}_R$ can be written as

$$\text{Var}\,(\hat{N}_R) = \sum_{h=1}^{L} \text{Var}\,(\hat{N}_h) + \sum_{h \neq h'}^{L} \sum_{h'=1}^{L} \text{Cov}(\hat{N}_h, \hat{N}_{h'}), \quad (2)$$

where Var(.) indicates variance of the enclosed estimator and Cov(.,.) indicates covariance between the 2 enclosed estimators. First, we estimate each variance and covariance component separately. Then, the sum of all the estimated components gives an estimator of the variance of $\hat{N}_R$.

Now, as in (1), write $\hat{N}_h = X_h \hat{R}_h$. Let B_h be the specific set of u_h quadrats selected from stratum h, $h = 1, ..., L$. Then we use conditional expectations to write

$$(\hat{N}_h) = X_h^2 \left[\text{Var}\left(\frac{\sum_{q=1}^{u_h} N_{hq}}{\sum_{q=1}^{u_h} X_{hq}} \right) + \text{E}(\text{Var}(\hat{R}_h \mid B_h)) \right].$$

The first term inside the brackets is the variance of a ratio estimator in simple random sampling. An expression for this first term is obtained by the use of the standard Taylor series approximation method (the delta method). The second term is the expected value (E) of the conditional variance $\hat{R}_h$ given B_h, i.e., variance of $\hat{R}_h$ holding units specified by B_h fixed. Thus, in this conditional variance, the denominator of $\hat{R}_h$ given B_h is a constant. Therefore,

$$\text{Var}(\hat{N}_h) \doteq X_h^2 \left[\frac{U_h - u_h}{U_h u_h} \frac{\sum_{q=1}^{U_h} (N_{hq} - R_h X_{hq})^2}{\bar{X}_h^2 (U_h - 1)} + \text{E}\left(\frac{1}{u_h^2 \bar{x}_h^2} \left(\sum_{q=1}^{u_h} \text{Var}(\hat{N}_{hq}) + \sum_{q \neq q'}^{u_h} \sum_{q'=1}^{u_h} \text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'}) \right) \right) \right], \quad (3)$$

where $\bar{X}_h = X_h / U_h$ and $\bar{x}_h = \sum_{q=1}^{u_h} X_{hq} / u_h$.

In terms of variance estimation, we do not need to evaluate the expected value for the second term in the variance expression. We need only replace the variance and covariance terms by their corresponding unbiased estimators to estimate unbiasedly the second term. However, to get an expression for variance $\hat{N}_h$, we approximate the expected value of the second term by an application of the Taylor series technique. Thus,

$$\text{Var}(\hat{N}_h) \doteq X_h^2 \left[\frac{U_h - u_h}{U_h u_h} \sum_{q=1}^{U_h} \frac{(N_{hq} - R_h X_{hq})^2}{\bar{X}_h^2 (U_h - 1)} + \frac{1}{u_h \bar{X}_h^2} \left(\sum_{q=1}^{U_h} \frac{\text{Var}(\hat{N}_{hq})}{U_h} + (u_h - 1) \sum_{q \neq q'}^{U_h} \sum_{q'=1}^{U_h} \frac{\text{Cov}(\hat{N}_h, \hat{N}_{h'})}{U_h (U_h - 1)} \right) \right]. \quad (4)$$

Next, we derive the covariance terms needed for (2). Again, write $\hat{N}_h = X_h \hat{R}_h$. Then, with $h \neq h'$,

$$\begin{aligned} \text{Cov}(\hat{N}_h, \hat{N}_{h'}) &= X_h X_{h'} \text{Cov}(\hat{R}_h, \hat{R}_{h'}) \\ &= X_h X_{h'} \left[\text{Cov}\left(\frac{\sum_{q=1}^{u_h} N_{hq}}{\sum_{q=1}^{u_h} X_{hq}}, \frac{\sum_{q'=1}^{u_{h'}} N_{h'q'}}{\sum_{q'=1}^{u_{h'}} X_{h'q'}} \right) + \text{E}\left(\text{Cov}(\hat{R}_h, \hat{R}_{h'} \mid B_h, B_{h'}) \right) \right]. \end{aligned}$$

Given stratified random sampling, the first term within the brackets is zero. A first-order Taylor series expansion of both $\hat{R}_h$ and $\hat{R}_{h'}$ is used to obtain

$$\begin{aligned} \text{Cov}(\hat{N}_h, \hat{N}_{h'}) &\doteq X_h X_{h'} \left[E\left(\text{Cov}\left(\frac{\sum_{q=1}^{u_h} (\hat{N}_{hq} - R_h X_{hq})}{u_h \bar{X}_h}, \frac{\sum_{q'=1}^{u_{h'}} (\hat{N}_{h'q'} - R_{h'} X_{h'q'})}{u_{h'} \bar{X}_{h'}} \middle| B_h B_{h'} \right) \right) \right], \quad h \neq h'. \quad (5) \\ &\doteq \sum_{q=1}^{U_h} \sum_{q'=1}^{U_{h'}} \text{Cov}(\hat{N}_{hq}, \hat{N}_{h'q'}) \end{aligned}$$

Let $\hat{\text{Cov}}(\hat{N}_{hq}, \hat{N}_{h'q'})$ be an unbiased estimator of $\text{Cov}(\hat{N}_{hq}, \hat{N}_{h'q'})$. Then we use (6) as an approximately unbiased estimator of $\text{Cov}(\hat{N}_h, \hat{N}_{h'})$, that is,

$$\hat{\text{Cov}}(\hat{N}_h, \hat{N}_{h'}) = X_h X_{h'} \left(\frac{\sum_{q=1}^{u_h} \sum_{q'=1}^{u_{h'}} \hat{\text{Cov}}(\hat{N}_{hq}, \hat{N}_{h'q'})}{u_h \, u_{h'} \, \bar{x}_h \, \bar{x}_{h'}} \right), \quad h \neq h'. \quad (6)$$

Note, that (6) uses a ratio estimator expansion for the covariance term.

Now we return to the estimation of $\text{Var}(\hat{N}_h)$. We need an estimator for the first term in the brackets of (3). Define the sample covariance operator $s_{(w_{hq}, v_{hq})}$ as

$$s_{(w_{hq}, v_{hq})} = \sum_{q=1}^{u_h} \frac{(w_{hq} - \bar{w}_h)(v_{hq} - \bar{v}_h)}{u_h - 1},$$

where $\bar{w}_h$ and $\bar{v}_h$ are the sample means of u_h pairs of sample values (w_{h1}, v_{h1}), ..., (w_{hu_h}, v_{hu_h}), respectively. Then, if the pairs $(w_{hq}, v_{hq})$are constants given the quadrats hq, $q = 1, ..., u_h$, the expected value of $s_{(w_{hq}, v_{hq})}$ is given as

$$S_{(w_{hq}, v_{hq})} = \sum_{q=1}^{U_h} \frac{(w_{hq} - \overline{W}_h)(v_{hq} - \overline{V}_h)}{U_h - 1},$$

where $\overline{W}_h$ and $\overline{V}_h$ are the stratum means of U_h pairs of values (w_{h1}, v_{h1}), ..., (w_{hU_h}, v_{hU_h}). Note, $s_{(w_{hq}, w_{hq})} = s^2_{(w_{hq})}$ and $S_{(w_{hq}, w_{hq})} = S^2_{(w_{hq})}$.

Consider,

$$\sum_{q=1}^{u_h} \frac{(\hat{N}_{hq} - \hat{R}_h X_{hq})^2}{u_h - 1} = s^2_{(\hat{N}_{hq})} + \hat{R}_h^2 s^2_{(X_{hq})} - 2\hat{R}_h s_{(\hat{N}_{hq}, X_{hq})}. \quad (7)$$

Then,

$$\text{E}\left(s^2_{(\hat{N}_{hq})}\right) = \text{E}\left[\text{E}\left(\frac{\sum_{q=1}^{u_h} \hat{N}_{hq}^2 - u_h \tilde{n}_h^2}{u_h - 1} \,\Big|\, B_h\right)\right]$$

$$= \text{E}\left(\frac{\sum_{q=1}^{u_h}\left(N_{hq}^2 + \text{Var}(\hat{N}_{hq})\right) - u_h\left(\bar{n}_h^2 + \text{Var}(\tilde{n}_h | B_h)\right)}{u_h - 1}\right)$$

$$= \text{E}\left(s^2_{(N_{hq})} + \sum_{q=1}^{u_h} \frac{\text{Var}(\hat{N}_{hq})}{u_h} - \sum_{q \neq q'}^{u_h} \sum_{q'=1}^{u_h} \frac{\text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'})}{u_h(u_h - 1)}\right)$$

$$= S^2_{(N_{hq})} + \sum_{q=1}^{U_h} \frac{\text{Var}(\hat{N}_{hq})}{U_h} - \sum_{q \neq q'}^{U_h} \sum_{q'=1}^{U_h} \frac{\text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'})}{U_h(U_h - 1)},$$

where

$$\bar{n}_h = \sum_{q=1}^{u_h} \frac{N_{hq}}{u_h} \text{ and } \tilde{n}_h = \sum_{q=1}^{u_h} \frac{\hat{N}_{hq}}{u_h}.$$

Standard practice in approximating the expected value of (7) is equivalent to replacing $\hat{R}_h$ by R_h before applying the expectation operator to the right hand side. Thus,

$$\text{E}\left(\sum_{q=1}^{u_h} \frac{(\hat{N}_{hq} - \hat{R}_h X_{hq})^2}{u_h - 1}\right) \doteq S^2_{(N_{hq})} + \sum_{q=1}^{U_h} \frac{\text{Var}(\hat{N}_{hq})}{U_h} - \sum_{q \neq q'}^{U_h} \sum_{q'=1}^{U_h} \frac{\text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'})}{U_h(U_h - 1)}$$

$$+ R_h^2 S^2_{(X_{hq})} - 2R_h S_{(N_{hq}, X_{hq})}$$

$$\doteq \sum_{q=1}^{U_h} \frac{(N_{hq} - R_h X_{hq})^2}{U_h - 1} + \sum_{q=1}^{U_h} \frac{\text{Var}(\hat{N}_{hq})}{U_h} - \sum_{q \neq q'}^{U_h} \sum_{q'=1}^{U_h} \frac{\text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'})}{U_h(U_h - 1)}.$$

Or an approximately unbiased estimator of $\sum_{q=1}^{U_h} \frac{(N_{hq} - R_h X_{hq})^2}{U_h - 1}$ is given by

$$\sum_{q=1}^{u_h} \frac{(\hat{N}_{hq} - \hat{R}_h X_{hq})^2}{u_h - 1} - \sum_{q=1}^{u_h} \frac{\hat{\text{Var}}(\hat{N}_{hq})}{u_h} + \sum_{q \neq q'}^{u_h} \sum_{q'=1}^{u_h} \frac{\hat{\text{Cov}}(\hat{N}_{hq}, \hat{N}_{hq'})}{u_h(u_h - 1)}.$$

Then, from (3), we obtain

$$\hat{\text{Var}}(\hat{N}_h) = X_h^2 \left[\frac{U_h - u_h}{U_h u_h \bar{x}_h^2}\left(\frac{\sum_{q=1}^{u_h}(\hat{N} - \hat{R}_h X_{hq})^2}{u_h - 1} - \frac{\sum_{q=1}^{u_h} \hat{\text{Var}}(\hat{N}_{hq})}{u_h} + \sum_{q \neq q'}^{u_h} \sum_{q'=1}^{u_h} \frac{\hat{\text{Cov}}(\hat{N}_{hq}, \hat{N}_{hq'})}{u_h(u_h - 1)}\right) + \frac{1}{u_h^2 \bar{x}_h^2}\left(\sum_{q=1}^{u_h} \hat{\text{Var}}(\hat{N}_{hq}) + \sum_{q \neq q'}^{u_h} \sum_{q'=1}^{u_h} \hat{\text{Cov}}(\hat{N}_{hq}, \hat{N}_{hq'})\right)\right].$$

Or

$$\hat{\text{Var}}(\hat{N}_h) = \frac{X_h^2}{\bar{x}_h^2}\left[\frac{U_h - u_h}{U_h u_h} \frac{\sum_{q=1}^{u_h}(\hat{N}_{hq} - \hat{R}_h X_{hq})^2}{(u_h - 1)} + \frac{\sum_{q=1}^{u_h} \hat{\text{Var}}(\hat{N}_{hq})}{U_h u_h} + \frac{u_h(U_h - 1)}{U_h(u_h - 1)} \sum_{q \neq q'}^{u_h} \sum_{q'=1}^{u_h} \frac{\hat{\text{Cov}}(\hat{N}_{hq}, \hat{N}_{hq'})}{u_h^2}\right]. \quad (8)$$

Substitution of (6) and (8) for the corresponding terms in (2) gives an estimator of the variance of $\hat{N}_R$.

Alternatively, the variance of $\hat{N}_R$ can be written as the sum of 2 parts associated with sampling in 2 phases. The first-phase variance component is the variance due only to quadrat sampling, that is, when a sample of quadrats is taken and the population size on each sampled quadrat is known. The second-phase variance component is the variance due to estimating the population size of interest on the sampled quadrats. The relative size of the 2 components may be helpful in the allocation of resources between the 2 phases. The first-phase variance component, the variance of the expected value of $\hat{N}_R$ holding the quadrats selected in the first phase of sampling fixed, $\mathrm{Var}(\hat{N})$, is estimated as

$$\hat{\mathrm{Var}}(\hat{N}) = \sum_{h=1}^{L} X_h^2 \left[\frac{U_h - u_h}{U_h u_h \bar{x}_h^2} \left(\frac{\sum_{q=1}^{u_h} (\hat{N}_{hq} - \hat{R}_h X_{hq})^2}{(u_h - 1)} - \frac{\sum_{q=1}^{u_h} \hat{\mathrm{Var}}(\hat{N}_{hq})}{u_h} + \sum_{q \neq q'}^{u_h} \sum_{q'=1}^{u_h} \frac{\hat{\mathrm{Cov}}(\hat{N}_{hq}, \hat{N}_{hq'})}{u_h(u_h - 1)} \right) \right]. \quad (9)$$

The second-phase variance component, or the conditional variance of $\hat{N}_R$ holding the quadrats selected in the first phase of sampling fixed, Var $(\hat{N}_R |$ phase 1), is estimated as

$$\hat{\mathrm{Var}}\ (\hat{N}_R |\ \text{phase 1})$$

$$= \sum_{h=1}^{L} \frac{X_h^2}{u_h^2 \bar{x}_h^2} \left(\sum_{q=1}^{u_h} \hat{\mathrm{Var}}(\hat{N}_{hq}) + \sum_{h \neq h'}^{L} \sum_{h'=1'}^{L} \hat{\mathrm{Cov}}(\hat{N}_{hq}, \hat{N}_{hq'}) \right) + \sum_{h \neq h'}^{L} \sum_{h'=1'}^{L} X_h X_{h'} \left(\frac{\sum_{q=1}^{u_h} \sum_{q'=1}^{u_{h'}} \hat{\mathrm{Cov}}(\hat{N}_{hq}, \hat{N}_{h'q'})}{u_h u_{h'} \bar{x}_h \bar{x}_{h'}} \right). \quad (10)$$

Finally, consider 2 population size estimates at different times based on the same stratified random sample of quadrats. Let N and M refer to population size at the 2 times. Then an estimator of the covariance between the 2 abundance estimators is

$$\hat{\mathrm{Cov}}(\hat{N}, \hat{M}) = \sum_{h=1}^{L} \frac{X_h^2}{\bar{x}_h^2} \left(\frac{1}{u_h} - \frac{1}{U_h} \right) \sum_{q=1}^{u_h} \frac{\left[\hat{d}_{hq} \hat{d}_{hq}^* - \hat{\mathrm{Cov}}(\hat{N}_{hq}, \hat{M}_{hq}) \right]}{u_h - 1} + \sum_{h=1}^{L} \sum_{h'=1}^{L} \frac{X_h X_{h'}}{\bar{x}_h \bar{x}_{h'}} \sum_{q=1}^{u_h} \sum_{q'=1}^{u_{h'}} \hat{\mathrm{Cov}}(\hat{N}_{hq}, \hat{M}_{h'q'}), \quad (11)$$

where $\hat{d}_{hq} = \hat{N}_{hq} - \hat{R}_h X_{hq}$, $\hat{d}_{hq}^* = M_{hq} - \hat{R}_h^* X_{hq}$, and $\hat{R}_h^* = \hat{M}_h / X_h$.