

ESTIMATING SMALL MAMMAL ABUNDANCE ON FUELS TREATMENT UNITS IN SOUTHWESTERN PONDEROSA PINE FORESTS

Sarah J. Converse, Brett G. Dickson, Gary C. White, and William M. Block

In many North American forests, post-European settlement fire suppression efforts have resulted in the excessive accumulation of forest fuels and changes to the historic fire regime, thereby increasing the risk of catastrophic wildfires (Cooper 1960; Dodge 1972; Covington and Moore 1994). To reduce this risk, it is necessary to develop treatments that will remove excess fuels while moving forests toward historical structural conditions and disturbance intervals, an approach currently being attempted in southwestern ponderosa pine (*Pinus ponderosa*) forests (see Covington et al. 1997; Fulé et al. 2001). Both prescribed fire and mechanical fuel treatments have been used for restoration. However, it is not known if fire surrogates such as mechanical fuel treatment are sufficient to achieve historical forest structure in the place of fire, or how these treatments will affect ecosystem function.

The national Fire and Fire Surrogate (FFS) Program is a cooperative effort among federal land-management agencies, universities, and private organizations to investigate the impact of fire and fire surrogate treatments on forest ecology and fire risk (Weather- spoon and McIver, unpublished report). The FFS approach applies a similar study design and sampling scheme on 13 study areas across the United States. The study areas consist of three replicate blocks (study sites) divided into four treatments (units): control, thin, burn, and a thin/burn combination. In accordance with the national protocol, treatment effects will be examined for several response variables in the general areas of vegetation, fuels and fire behavior, soils,

entomology, pathology, and treatment costs and utilization economics. This paper focuses on a subset of the wildlife response variables outlined in the national protocol (Zack and Laundenslayer, unpublished report), namely small mammal abundance, and our subsequent modifications to this protocol.

After the 2000 trapping season, we were concerned that the trap densities outlined by the national protocol were inadequate for robust estimation of small mammal population sizes. We therefore conducted an analysis of pre-treatment data, including an analysis of an increase in trap effort implemented on a limited number of treatment units in 2001 to (1) allow a better assessment of the post-treatment effects of fire and fire surrogate treatments on small mammal populations, and (2) identify the potential limitations of our data to enable improvements to subsequent data collection efforts.

METHODS Study Areas

FFS Program study areas in the Southwest are located on the Coconino and Kaibab National Forests in Arizona, west of Flagstaff, and on the Santa Fe National Forest in New Mexico, west of Los Alamos. Each of these study areas includes three replicate blocks (study sites) of four ≥ 10 ha treatment units. Treatment types represented on each site are thin, burn, thin/burn combination, and no treatment activity (control). In Arizona, these sites are differentiated as Rudd Tank (RT with units 271–274) and Powerline (PL with units 321–324) on the Coconino

This file was created by scanning the printed publication.
Errors identified by the software have been corrected;
however, some errors may remain.

National Forest, and KA Hill (KA with units 1–4) on the Kaibab National Forest. In New Mexico, we identified sites as Virgin Mesa (VM with units A–D), Tusa's Tank (TT with units E–H), and Lake Fork (LF with units I–L). Each unit was equipped with a permanent grid system of 36 monumented points spaced 50 m apart and typically arranged in a 6 x 6 array, with some variations as necessitated by unit shape; all sampling was keyed to this grid system to facilitate cross-disciplinary analysis.

The Arizona study sites are located at 2100–2300 m elevation. These sites have a ponderosa pine forest type, and a Gambel oak (*Quercus gambelii*) understory in some areas. The New Mexico study sites are located at 2400–2600 m elevation, with a forest type of ponderosa pine and mixed conifer, including southwestern white pine (*Pinus strobiformus*), Douglas-fir (*Pseudotsuga menziesii*), Gambel oak, and aspen (*Populus tremuloides*).

Small Mammal Trapping

We conducted small mammal live-trapping on the Arizona study area during the summers of 2000 and 2001. The New Mexico study area was added to the study later than the Arizona study area and was first sampled during the summer of 2001. We conducted trapping in the vicinity of all 36 permanent points in the grid system (i.e., with 50 m trap spacing). We positioned traps within 3 m of a grid point, along small mammal trails, at the openings of burrow holes, and/or in proximity to downed woody debris. A large wood shingle was used to shade and insulate traps. We placed

a handful of cotton at the back of each trap and added approximately 20 mL of a bait mixture of rolled oats and chicken feed. A small amount of bait was also trailed into the entrance of each trap. We set traps during the afternoon hours and checked and reset all traps in the morning and late afternoon during the trapping session. We recorded the species, mass, age, sex, reproductive condition, and release condition for all animals captured. Animals were permanently marked with two unique ear tags. In general, we sampled two of the four units on each site during one of two 5-day trapping sessions on each study area (one session 4.5 days and one 5.5 days in 2000; Table 1).

To test the adequacy of the 50 m trap spacing prescribed by the national protocol, we expanded the trapping effort on two randomly selected Arizona units (RT 272 and PL 321, session 2) in 2001. On RT 272, we spaced traps 25 m apart by placing additional trap lines between the existing grid points, expanding the original grid from a 6 x 6 to an 11 x 11 array. Large Sherman live-traps were placed at all points (for a total of 121 traps) and extra-large Sherman live-traps were placed at all of the original grid points (for a total of 36 traps). Thus, 157 traps per 10 ha treatment unit were maintained in the expanded effort on this unit. On PL 321, the original 9 x 4 grid was expanded in a similar way, to a 17 x 7 grid, resulting in a total of 119 large Sherman traps and 36 extra-large Sherman traps.

Small Mammal Population Estimation

For species with relatively large sample sizes (> 30 individuals) we used the Huggins

Table 1. Trapping dates and units trapped during 2000 and 2001 in Arizona study area and during 2001 in New Mexico study area.

Study Area	Year	Session	Dates	Units Trapped
Arizona	2000	1	15 Aug–20 Aug	KA 2, 3; RT 272, 273; PL 321, 323
Arizona	2000	2	29 Aug–2 Sept	KA 1, 4; RT 271, 274; PL 322, 324
Arizona	2001	1	25 July–29 July	KA 1, 4; RT 271, 274; PL 322, 324
Arizona	2001	2	31 July–4 Aug	KA 2, 3; RT 272, 273; PL 321, 323
New Mexico	2001	1	7 Aug–11 Aug	VM A, B; TT F; LF I, L
New Mexico	2001	2	13 Aug–17 Aug	TT E, G, H; LF J, K
New Mexico	2001	2	14 Aug–18 Aug	VM C, D

closed-capture model (Huggins 1989, 1991) implemented in Program MARK (White and Burnham 1999; software available at www.cnr.colostate.edu/~gwhite/mark/mark.htm) to estimate the abundance of populations on each of the treatment units. The Huggins model generates estimates of initial capture rates (p_i , $i = 1, \dots, t$) and recapture rates (c_i , $i = 2, \dots, t$) for t occasions (10 occasions in our analysis) based on animal encounter histories and uses these rates to generate estimates of abundance. We chose the Huggins model because it appears to perform fairly well with small sample sizes (White 2002), and the traditional closed-capture model in Program MARK did not perform well on this data set. Program MARK employs model selection procedures (Burnham and Anderson 1998) based on Akaike's Information Criterion (Akaike 1973) corrected for small sample size (AICc) to select the most parsimonious model. We considered several candidate models, including models where p 's and c 's were not assumed to be equal, which allowed for estimation of a behavioral response to capture, and models where p 's and c 's were held constant, or were modeled as a function of trapping session, unit, or trapping effort (Arizona only—effort was higher in expanded grids in 2001). We used the estimates of abundance from the top AICc model in the model set, that is, the model with the highest AICc weight (Burnham and Anderson 1998). The Huggins model estimates abundance, based on capture rates, as

$$\hat{N} = \frac{M_{t+1}}{1 - (1 - p_1)(1 - p_2) \dots (1 - p_t)}, \quad (1)$$

where M_{t+1} is the number of unique individuals marked on a grid during t trapping occasions, i.e., the minimum known population size, and p_t is the estimate of initial capture rate for occasion t . We included adult animals from each sex in the abundance estimates and determined an animal's age class based on the mass recorded at initial capture.

RESULTS

Small Mammal Abundance

During the summers of 2000 and 2001, seven species were captured on the Arizona study area; five species were captured on the New Mexico study area during 2001 (Table 2). Two species on each study area contributed the majority of captures: the deer mouse (*Peromyscus maniculatus*) and gray-collared chipmunk (*Tamias cinereicollis*) in Arizona and the deer mouse and least chipmunk (*Tamias minimus*) in New Mexico. Large differences existed across the study sites in the number of captures and the proportion of captures belonging to each species (Table 3).

In general, we captured few individuals of any species at either study area. This resulted in abundance estimates ($\hat{N}$) with high variance and sample sizes (M_{t+1}) sufficiently robust to model the abundance of only three species: deer mouse (Arizona and New Mexico), gray-collared chipmunk (Arizona), and least chipmunk (New Mexico; Table 4).

Evaluation of Expanded Trapping Effort

To evaluate the utility of the expanded trapping effort, we compared capture rates and recapture rates on the Arizona expanded grids ($p(\text{expanded})$ and $c(\text{expanded})$, respectively) for deer mice and gray-collared chipmunks to those on the standard trapping grids ($p(\text{standard})$ and $c(\text{standard})$). The best-fitting model for gray-collared chipmunks was $\{p(\text{session}) c(\text{session})\}$ (p and c are different, and vary by trapping session); however, the next best fitting model was $\{p(\text{effort}) c(\text{effort})\}$ (p and c are different, and vary by trapping effort). Examining the p 's and c 's estimated under this model, we find that $p(\text{standard}) = 0.228$ (SE = 0.050, 95% CI: 0.145, 0.339) and $p(\text{expanded}) = 0.088$ (SE = 0.073, 95% CI: 0.016, 0.362); $c(\text{standard}) = 0.323$ (SE = 0.029, 95% CI: 0.269, 0.383) and $c(\text{expanded}) = 0.419$ (SE = 0.048, 95% CI: 0.329, 0.515). Capture rates appear to have declined with increased effort, whereas

Table 2. Common names, scientific names, and four-letter codes for small mammal species captured on the FFS study areas during the summers of 2000 and 2001.

Common Name	Scientific Name	Species Code
Mexican vole	<i>Microtus mexicanus</i>	MIME
Mexican woodrat	<i>Neotoma mexicana</i>	NEME
Brush mouse	<i>Peromyscus boylii</i>	PEBO
Deer mouse	<i>Peromyscus maniculatus</i>	PEMA
Golden-mantled ground squirrel	<i>Spermophilus lateralis</i>	SPLA
Gray-collared chipmunk	<i>Tamias cinereicollis</i>	TACI
Cliff chipmunk	<i>Tamias dorsalis</i>	TADO
Least chipmunk	<i>Tamias minimus</i>	TAMI

Table 3. Number of unique trapped individuals (M_{t+1}) for species captured on the Arizona and New Mexico study areas (NP = not present on study area).

Study Area	Year	Site	MIME	NEME	PEBO	PEMA	SPLA	TACI	TADO	TAMI
Arizona	2000	KA	0	1	0	20	0	7	2	NP
		RT	1	4	0	21	0	72	0	NP
		PL	0	4	0	19	1	26	0	NP
		Total	1	9	0	60	1	105	2	NP
Arizona	2001	KA	0	0	1	11	0	1	2	NP
		RT	0	2	0	22	2	54	1	NP
		PL	0	2	0	25	1	7	0	NP
		Total	0	4	1	58	3	62	3	NP
New Mexico	2001	VM	NP	1	5	16	0	NP	NP	0
		TT	NP	4	0	42	0	NP	NP	24
		LF	NP	0	5	25	4	NP	NP	7
		Total	NP	5	10	83	4	NP	NP	31

recapture rates appear to have increased, and the 95% confidence intervals overlap in both cases; thus the evidence based on gray-collared chipmunks is inconclusive. However, the capture and recapture rates from the deer mice, based on the best model $\{p(\text{effort}) = c(\text{effort})\}$, are clearly higher for the expanded grids ($p = c(\text{standard})$: 0.131 (SE = 0.022, 95% CI: 0.093, 0.181), $p = c(\text{expanded})$: 0.250 (SE = 0.031, 95% CI: 0.195, 0.316)). Additionally, sample sizes for deer mice were highest on the expanded grids (RT 272: $n = 12$; PL 321: $n = 11$).

DISCUSSION

An important feature of our approach to evaluating small mammal responses to fire and fire surrogate treatments in the context of this study is our use of robust estimates of

population size, rather than indices. The use of indices of abundance to evaluate impacts of forest management on small mammal populations is ubiquitous (e.g., Krefling and Ahlgren 1974; Brooks and Healy 1989; Kirkland et al. 1996; Schmid-Holmes and Drickamer 2001). Abundance indices generally take the form of minimum known population size, (i.e., M_{t+1}) or catch-per-unit-effort. These raw counts are the product of the parameter of interest ($\hat{N}$) and an encounter or detection probability (i.e., p), yet it is often assumed that these indices are tightly linked with true population size. To assume that these counts are consistent indicators of total abundance, it is necessary to assume that detection probabilities are constant over time and space, and over the species and or populations of interest. However, this un-

Table 4. Numbers of unique trapped individuals (M_{t+1}), estimated total number of individuals ($\hat{N}$), rounded to nearest integer), and standard errors (SE) for deer mice, gray-collared chipmunks, and least chipmunks. NP = not present on study area. Units in bold were trapped with an increased trap density in 2001.

Year	Site	Unit	PEMA			TACI			TAMI		
			M_{t+1}	$(\hat{N})$	SE	M_{t+1}	$(\hat{N})$	SE	M_{t+1}	$(\hat{N})$	SE
2000, AZ	KA	1	3	4	0.96	2	2	0.28	NP	NP	NP
		2	4	5	0.86	2	2	0.39	NP	NP	NP
		3	5	6	0.97	0	0	0	NP	NP	NP
		4	8	10	1.61	3	3	0.34	NP	NP	NP
	RT	271	5	6	1.25	20	21	0.90	NP	NP	NP
		272	3	3	0.74	19	20	1.26	NP	NP	NP
		273	4	5	0.86	19	20	1.26	NP	NP	NP
		274	9	11	1.72	14	15	0.75	NP	NP	NP
	PL	321	1	1	0.43	8	9	0.80	NP	NP	NP
		322	5	6	1.25	6	6	0.48	NP	NP	NP
		323	7	8	1.16	8	9	0.80	NP	NP	NP
		324	6	7	1.38	4	4	0.39	NP	NP	NP
2001, AZ	KA	1	1	1	0.67	1	1	0.24	NP	NP	NP
		2	4	5	1.39	0	0	0	NP	NP	NP
		3	2	3	0.96	0	0	0	NP	NP	NP
		4	4	5	1.19	0	0	0	NP	NP	NP
	RT	271	3	4	1.19	10	10	0.74	NP	NP	NP
		272	12	13	0.93	18	30	13.86	NP	NP	NP
		273	2	3	0.96	4	7	3.58	NP	NP	NP
		274	5	7	1.58	22	23	1.28	NP	NP	NP
	PL	321	11	12	0.88	2	3	2.07	NP	NP	NP
		322	5	7	1.58	3	5	2.83	NP	NP	NP
		323	6	8	1.75	2	2	0.34	NP	NP	NP
		324	3	4	1.19	0	0	0	NP	NP	NP
2001, NM	VM	A	1	1	0.75	NP	NP	NP	0	0	0
		B	1	1	0.75	NP	NP	NP	0	0	0
		C	3	3	0.48	NP	NP	NP	0	0	0
		D	11	12	0.88	NP	NP	NP	0	0	0
	TT	E	13	14	1.01	NP	NP	NP	6	8	1.63
		F	9	12	2.72	NP	NP	NP	8	10	1.93
		G	9	10	0.78	NP	NP	NP	8	10	1.93
		H	11	12	0.93	NP	NP	NP	2	3	0.89
	LF	I	3	4	1.37	NP	NP	NP	0	0	0
		J	9	10	0.83	NP	NP	NP	2	3	0.89
		K	9	10	0.83	NP	NP	NP	5	6	1.47
		L	4	6	1.62	NP	NP	NP	0	0	0

tested assumption is certainly false in many instances (Nichols 1992; Anderson 2001). In this work, we calculated $p(\text{deer mice}) = 0.131$ and $p(\text{gray-collared chipmunks}) = 0.228$, i.e., gray-collared chipmunks had nearly twice the capture probability of deer mice. If we had caught 20 individuals of each of these species in a hypothetical capture grid in our study area and used an index of abundance, we would have concluded that the species were equally common. However, based on our calculated capture rates, it can be seen that deer mice would be much more abundant on this hypothetical grid. Also, we might imagine that capture rates of a given species may change in response to forest management. If habitat improves substantially after a treatment, individuals may need to move shorter distances to meet their foraging requirements, thereby lowering capture rates. If an index of abundance is used in such a case, conclusions about the response of small mammal populations to treatments will be confounded with behavioral responses to the treatment. Therefore, it is critical that investigators not rely on indices of abundance to evaluate the impacts of forest management treatments on small mammal populations. Rather, we strongly recommend that investigators take the approach we have taken here; that is, estimate true abundance in an environment such as Program MARK, which computes associated estimates of precision and employs an objective model selection procedure.

We made a number of changes to the national FFS protocol to best sample the small mammal populations at the Southwest study areas, while still collecting the data in a way that will facilitate comparisons across study areas. An initial concern with the national FFS protocol involved the number of traps placed at each grid point. The national protocol called for the placement of one extra-large Sherman live-trap and one Tomahawk #201 live-trap at all grid points. Prior to trapping in 2000, because larger members of the southwestern small mammal community are few, we modified the national protocol and placed one large

Sherman live-trap at all grid points and one extra-large Sherman live-trap at every other grid point.

A second concern with the national protocol involved the spacing of traps on the small mammal trapping grids at 50 m. This spacing is much greater than the 10–15 m trap spacing more typically employed in small mammal studies (Jones et al. 1996). Potential problems arising from this arrangement may include (a) undersampling of populations as animals using the matrix between traps are not captured, with associated small sample sizes, resulting in difficulties in the modeling of abundance; and (b) low capture and recapture rates, resulting in imprecise estimates of abundance (Otis et al. 1978; White et al. 1982). Some members of the species found in the Southwest study area are capable of moving long distances; on several occasions we observed a tagged individual moving from one unit to a neighboring unit during a single trapping session. However, in general, it appears that in our study areas, large trap spacing will result in too few individuals captured within the trapping grid. Following the national protocol, sample sizes and capture-recapture rates on our study grids did not provide reasonable measures of pre-treatment small mammal community structure. Because precision of population size estimates in mark-recapture studies is closely linked with capture probabilities, our power to detect post-treatment effects in the FFS study will be a function of the precision of estimates of the response variable of interest, in this case, population size, and therefore power will depend on capture probabilities. Increased trapping effort on the RT 272 and PL 321 grids in 2001 increased the sample size and capture-recapture rates for the deer mouse. With adequate resources, we anticipate implementing the expanded grid design of 2001 in upcoming field seasons and on both study areas. Our modified protocols will allow us to capture more individuals and will allow us to more accurately characterize population abundance, before and after treatments are implemented. We suggest

that other FFS wildlife investigators consider our modifications to the national protocol and assess the most effective way to capture, analyze, and estimate the local variation in small mammal populations.

Future statistical modeling efforts in this research will focus on obtaining more robust estimates of abundance for species with small sample sizes. One possible approach will involve a combined analysis of all species so that information on capture probabilities, e.g., over time, will be more robust and the use of capture information for species with large sample sizes will be used to estimate the abundance of species with smaller sample sizes.

Additionally, as the FFS data collection efforts in the southwestern study areas continue, multiple years of data analyzed in Pollock's robust design framework (Kendall et al. 1995, 1997) will provide larger sample sizes, thereby improving estimates of abundance. In addition to better estimates of abundance on an annual basis, the robust design model allows for estimation of survival rates and movement rates between years. Understanding how these rates change in response to fuels treatments will allow us to better understand the mechanisms driving wildlife response to fire and fire surrogates in southwestern ponderosa pine forests.

ACKNOWLEDGMENTS

Funding for this research was provided by the interagency Joint Fire Sciences Program, administered in the southwestern study areas by C. Edminster, USDA Forest Service Rocky Mountain Research Station. K. Covert, L. Doll, J. Jenness, R. Lopez, K. Nodal, and B. Strohmeier assisted in data collection. Special thanks to T. Sisk for early planning and advice. Additional logistical support was provided by the USDA Forest Service Rocky Mountain Research Station, and the Department of Fishery and Wildlife Biology at Colorado State University. We thank two reviewers for their comments on an earlier draft of this manuscript.

LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory*, edited by B. N. Petrov and F. Csaki, pp. 267–281. Akademiai Kiado, Budapest.
- Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* 29: 1294–1297.
- Brooks, R. T., and W. M. Healy. 1989. Response of small mammal communities to silvicultural treatments in eastern hardwood forests of West Virginia and Massachusetts. In *Management of amphibians, reptiles, and small mammals in North America: Proceedings of the symposium*, July 19–21, 1988, technical coordinators R. C. Szaro, K. E. Severson, and D. R. Patton, pp. 313–318. Flagstaff, AZ. U.S. Forest Service General Technical Report, RM-166, Fort Collins CO.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: A practical information-theoretic approach*. Springer-Verlag, New York.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs* 30: 129–164.
- Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure and resource conditions: Changes since Euro-American settlement. *Journal of Forestry* 92: 39–47.
- Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. *Journal of Forestry* 95 (4): 23–29.
- Dodge, M. 1972. Forest fuel accumulation—A growing problem. *Science* 177: 139–142.
- Fulé, P. Z., A. E. M. Waltz, W. W. Covington, and T. A. Heinlein. 2001. Measuring forest restoration effectiveness in reducing hazardous fuels. *Journal of Forestry* 99 (11): 24–29.
- Huggins, R. M. 1989. On the statistical analysis of capture-recapture experiments. *Biometrika* 76: 133–140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47: 725–732.
- Jones, C., W. J. McShea, M. J. Conroy, and T. H. Kunz. 1996. Capturing mammals. In *Measuring and monitoring biological diversity: Standard methods for mammals*, edited by D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster, pp. 115–155. Smithsonian Institution Press, Washington DC.
- Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22: 751–762.

- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78: 563-578.
- Kirkland, G. L., Jr., H. W. Snoddy, and T. L. Amstler. 1996. Impact of fire on small mammals and amphibians in a central Appalachian deciduous forest. *American Midland Naturalist* 135: 253-260.
- Krefting, L. W., and C. E. Ahlgren. 1974. Small mammals and vegetation changes after fire in a mixed conifer-hardwood forest. *Ecology* 55: 1391-1398.
- Nichols, J. D. 1992. Capture-recapture models. *Bioscience* 42: 94-102.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monograph* 62: 1-135.
- Schmid-Holmes, S., and L. C. Drickamer. 2001. Impact of forest patch characteristics on small mammal communities: A multivariate approach. *Biological Conservation* 99: 293-305.
- White, G. C. 2002. Discussant: The use of auxiliary variables in capture-recapture modeling: An overview. *Journal of Applied Statistics* 29: 103-106.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement): 120-138.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Report LA-8787-NERP, Los Alamos NM.