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ESTIMATION OF ANIMAL ABUNDANCE WHEN CAPTURE PROBABILITIES ARE LOW AND HETEROGENEOUS

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Abstract: Obtaining reliable estimates of abundance or relative abundance under conditions of low numbers of captures and recaptures is crucial to properly assess population status of species that are of management concern; however, these characteristics make estimation difficult. We applied the commonly used jackknife (Burnham and Overton 1978, 1979) and moment (Chao 1988) estimators of abundance to capture-recapture data from northern flying squirrel (*Glaucomys sabrinus*) populations that had low ($\bar{p} \cong 0.10$), heterogeneous, capture probabilities and low densities (approx 2 squirrels/ha). The jackknife estimator selection procedure, higher-order jackknife estimators, and moment estimator were sensitive to the number of trapping occasions. These estimators tended to have low precision. Comparisons of estimators suggested specific, lower-order jackknife estimators performed well. Monte Carlo simulations corroborated results from field data. The moment estimator tended to have low bias, but the high root mean square error made the estimator less reliable than lower-order jackknife estimators. First- and second-order jackknife estimators tended to be the most reliable (low bias and precise) estimators when the number of trapping occasions (t) was $\geq$12. However, confidence interval coverage (% replications in which the constructed confidence interval included true N) was low with the first-order jackknife estimator, reflecting the negative bias of the variance estimator. We improved confidence interval coverage by an ad hoc adjustment to the variance estimator; coverage with the adjusted estimator approached the nominal 90% level at t $\geq$ 12. Reliable estimates of abundance can be achieved under conditions often encountered in field studies (small N and low, heterogeneous, capture probabilities) with lower-order jackknife estimators, a modification of the variance estimator for the first-order jackknife estimator, and $\geq$12 trapping occasions.

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Estimation of abundance is central to basic and applied ecology, but is problematic for populations with low densities and for species with low capture probabilities that vary among individuals (heterogeneity; Otis et al. 1978). These characteristics are common in studies of vertebrate populations (Chao 1989, Hammond 1990, Hallett et al. 1991). Estimation of abundance of such species or populations, however, is critical in assessing their status.

Otis et al. (1978) and White et al. (1982) cautioned against using model-based estimators of abundance when capture probabilities or sample sizes are low. Unfortunately, many studies of animal abundance fail to meet their suggested minimum number of different individuals observed (n = 25) and minimum capture probabilities ($\bar{p} > 0.30$, when $N \leq 100$). When field data fail to meet these criteria, the number of distinct individuals captured (enumeration, S) is often used to estimate abundance or relative abundance ($\widehat{rel} = S_l/S_m$, where $rel = N_l/N_m$, and l and m denote different populations in either space or time). Enumeration is a biased estimator of abundance when $\bar{p} < 1.0$ (Nichols 1986) and is often a biased estimator of relative abundance because capture probabilities frequently differ spatially and temporally, as well as among species (Nichols and Pollock 1983, Nichols 1986). Bias is greater when a small proportion of the population is captured, which occurs when capture probabilities and number of trapping occasions are low (Hilborn et al. 1976). In comparative studies in which few individuals were captured, some investigators (e.g., Carey et al. 1992, Witt 1992) have estimated abundance us-

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ing S for some populations and model-based estimators for other populations, a method that can lead to Type I statistical errors (Rosenberg et al. 1994*a*).

We evaluated the performance of the set of jackknife estimators and its estimator-selection procedure, the moment estimator, and S, the enumeration estimator, with field data and Monte Carlo simulations. We applied these estimators to data from northern flying squirrel populations that had low ($\bar{\bar{p}} \cong 0.10$), heterogeneous, capture probabilities and low densities (approx 2.0 squirrels/ha; Rosenberg 1991). We then simulated populations with parameters estimated from field data to investigate behavior of the estimators with known population characteristics.

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METHODS

Estimator Descriptions

The generalized jackknife model for estimating population size (Burnham and Overton 1978, 1979) was reported to yield reliable estimates when capture probabilities were heterogeneous and the population was assumed closed during the sampling period (Otis et al. 1978). Furthermore, the model was robust to departures of other sources of variation in capture probabilities (Otis et al. 1978). The jackknife model included a set of estimators (k orders, k = 1, 2, 3, 4, 5) that were linear functions of the capture frequencies (f_i; the no. of animals observed i times, $i = 1, 2, \ldots, t$, where t is the no. of consecutive trapping occasions) such that

$$\hat{N}_{jk} = S + \sum_{i=1}^{k} \alpha_{ik} f_i,$$

where $\hat{N}_{jk}$ was estimated population size from the jackknife estimator of the kth order, and α_{ik} were the coefficients computed for each kth order and ith capture frequency (Burnham and Overton 1979). In the simplest case, $k = 1$, and $\alpha_{ik} = (t - 1)/t$ (Burnham and Overton 1978). Bias was theoretically reduced with increasing k, but with an increase in sampling variance (Burnham and Overton 1979).

A procedure to select the kth-order jackknife estimator that reduces bias with a minimum increase in variance is desirable because the specific estimator that yields the most reliable estimate cannot be selected a priori; such a procedure was described by Burnham and Overton (1978:629, 1979:929). The procedure was a sequence of statistical tests to determine if expected values of $\hat{N}$ differed from 1 order to the next (e.g., H_0: $E[\hat{N}_{j2} - \hat{N}_{j1}] = 0$). The first order ($k = 1$) was compared with S, which was expected to have the greatest bias. If no statistical difference was found, then the lower-order estimator (in this case S) was used due to the anticipated increase in sampling variance as k increased. If the null hypothesis was rejected, the procedure was repeated with the next higher order (the max. order computed by Burnham and Overton [1978:629, 1979:928] was $k = 5$).

In some cases, the selected jackknife estimator was considerably biased when the number of recaptures was small (Otis et al. 1978:37). A moment estimator was proposed by Chao (1988) as an alternative to the jackknife estimator when many animals are captured only once. Estimates from the moment estimator of population size are computed as $\hat{N} = S + f_1^2/2f_2$ (Chao 1988: 296). Despite the availability of model-based estimators, enumeration estimators have often been used (Nichols and Pollock 1983). The number of distinct individuals captured, S, has been used as an estimator of abundance (e.g., Hilborn et al. 1976, Carey et al. 1992) and relative abundance (N_i/N_m; e.g., Lefebvre et al. 1982, Rosenberg et al. 1994*b*) despite performance normally inferior to model-based estimators (Nichols and Pollock 1983).

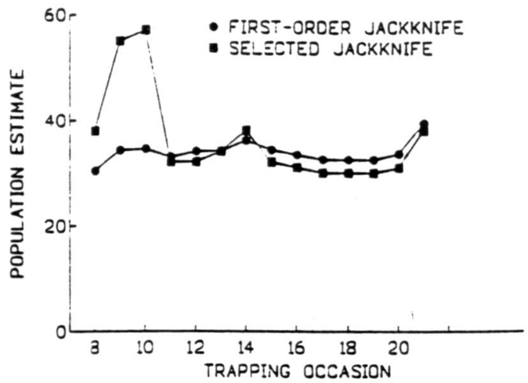

Fig. 1. An example of how stability of population estimators was computed from field data. We used the coefficient of variation (CV) of population estimates to measure stability, such that CV = $100(\mathrm{SE}[\hat{N}]/\bar{\hat{N}})$, where $\mathrm{SE}(\hat{N})$ was an empirical standard error of the population size estimated at 14 points in time (trapping occasions 8–12), and where

$$\bar{\hat{N}} = \sum_{t=8}^{21} \hat{N}_t/14,$$

and $\hat{N}_t$ is the estimated population size for trapping occasion t. The example shown here is from 1 northern flying squirrel population, with estimates given from the first-order jackknife estimator and from the selected jackknife estimator. In this example, the first-order jackknife estimator had a lower CV (CV = 1.5) than the selected jackknife estimator (CV = 6.6), due primarily to high estimates on trapping occasions 9 and 10.

Table 1. Distribution of capture probabilities (p) of simulated datasets for N = 40.

Group	$\bar{p}$[a]	No. of individuals assigned into p_i					
		p_1 = 0.05	p_2 = 0.10	p_3 = 0.15	p_4 = 0.20	p_5 = 0.30	p_6 = 0.50
1	0.07	27	13				
2	0.08	24	10	6			
3	0.12	18	11	5	3		3
4	0.14	9	14	5	5	7	

[a] $\bar{x}$ capture probability.

Field Studies

Field work was conducted in the Blue River and McKenzie Ranger districts, Willamette National Forest, Oregon. We compared flying squirrel abundance in 2 forest types by establishing trapping grids in 10 stands (Rosenberg and Anthony 1992). Each grid (approx 13 ha) consisted of 96–100 trapping stations spaced at 40-m intervals arranged in 10 × 10 to 16 × 6 arrays. We placed 2 baited live traps (41 × 13 × 13 cm) at each station. We eartagged squirrels with Monel tags. In 1988, we operated traps in 5 grids for 21 consecutive nights (occasions), and in the remaining 5 grids for 16 nights. In 1989, we trapped for 21 consecutive nights in all 10 grids. Thus, we sampled 20 "populations" (10 grids × 2 yr).

We compared $\hat{N}$ and its estimated standard error ($\widehat{\mathrm{SE}}[\hat{N}]$, except for S, which lacks a variance estimator) among the jackknife estimators (k = 1, 2, 3, 4, 5), the jackknife estimator chosen by the noninterpolated selection procedure of Burnham and Overton (1978, 1979), the moment estimator, and the enumeration estimator. In field studies and computer simulations, we modified estimators by making all estimates that were less than the number of individuals captured (S) equal to S; our procedure differed from that in Burnham and Overton (1979:932), which used the estimate from the $\hat{N}_{J1}$ (i.e., the first-order jackknife estimator), rather than S. We calculated the coefficient of variation (CV) for $\hat{N}$ from trapping occasion t = 8–21 to evaluate stability of population estimates in the 1989 field study (n = 10 populations; Fig. 1). We computed the CV for each population and estimator as CV = $100(\mathrm{SE}[\hat{N}]/\bar{\hat{N}})$, where $\mathrm{SE}(\hat{N})$ is an empirical SE of the population size estimated at 14 points in time (trapping occasions 8–21), and

$$\bar{\hat{N}} = \sum_{t=8}^{21} \hat{N}_t/(14),$$

where $\hat{N}_t$ is the population estimate for trapping occasion t. We did not statistically compare CV, $\hat{N}$, and $\widehat{\mathrm{SE}}(\hat{N})$ among estimators because of the correlated nature of the data. We excluded squirrels that died at first capture (1988, n = 11, 3.7%; 1989, n = 15, 5.0%) from analyses.

We tested homogeneity of capture frequencies among populations sampled in 1989 (21 trapping occasions) with a 10 (populations) × 3 (no. of capture frequency classes) contingency table. To avoid low expected values in frequency classes >2, we pooled the number of individuals captured ≥3 times into 1 class.

Computer Simulations

We used program GAUSS (Aptech Syst., Maple Valley, Wash.) for computer simulations. We established guidelines for simulation procedures from results of field data. We set population size at 40, and established 4 groups having different distributions of capture probabilities (Table 1) to resemble the various capture frequencies and percent recapture rates for squirrel populations sampled during 1988–89.

For comparison of abundance (N_i) and relative abundance (N_i/N_m), we made 2,000 replications of the simulated datasets for each cap-

Table 2. Mean total number of northern flying squirrels captured ($\bar{S}$) and percent captured *i* times. Values are from livetrapping on 10 grids, Willamette National Forest, Oregon, 1988–89.

	Grids			% of animals captured *i* times									
				i = 1		*i* = 2		*i* = 3		*i* = 4		*i* ≥ 5	
Year	t[a]	*n*	$\bar{S}$[b]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1988	16	5	29.6	56.1	3.3	21.9	2.8	8.6	2.1	8.6	0.6	4.6	0.4
				(44.8–60.0)[c]		(14.3–27.3)		(2.8–13.1)		(7.1–10.5)		(3.6–5.7)	
	21	5	25.4	39.8	6.0	30.6	6.3	14.0	2.2	8.1	3.0	7.6	2.6
				(22.6–60.0)		(16.7–52.6)		(5.3–27.0)		(0.0–16.7)		(0.0–16.1)	
1989	21	10	28.6	50.9	4.4	21.9	2.6	8.4	2.3	5.5	1.4	13.2	2.7
				(32.4–75.0)		(9.0–34.3)		(0.0–22.7)		(0.0–13.5)		(0.0–24.3)	

[a] No. of consecutive trapping occasions.

[b] $S = \sum_{i=1}^{t} f_i$, where f_i is the no. of individuals captured *i* times, *i* = 1, 2, . . . , t, in a single grid and year.

[c] Range.

ture probability distribution (Group = 1, 2, 3, 4; Table 1) and t (t = 6, 12, 21) combination. We adjusted, in an ad hoc fashion, the variance estimator of the first-order jackknife estimator to improve poor coverage (see Results). We maintained the general structure of the estimator, but increased the value of the single constant in the variance equation given by Burnham and Overton (1979:930), thus not altering the theoretical rationale for the variance estimator (Burnham and Overton 1978). The modified variance estimator followed the form

$$\widehat{\text{Var}}_{adj}(\hat{N}_{j1}) = \sum_{i=1}^{t} (a'_{ij1})^2 f_i - \hat{N}_{j1},$$

where $a'_{ij1} = \alpha_{ij1} + 1.5$, and $\alpha_{ij1} = (t - 1)/t$, rather than that developed by Burnham and Overton (1979) where $a_{ij1} = \alpha_{ij1} + 1.0$. For $i > 1$, $\alpha_{ij1} = 0$ (Burnham and Overton 1979), thus

$$\widehat{\text{Var}}_{adj}(\hat{N}_{j1}) = ([t - 1]/t + 1.5)^2 f_1 + (1.5)^2(S - f_1) - \hat{N}_{j1}.$$

For evaluation of abundance estimators, we computed the mean estimate ($\bar{\hat{N}}$), mean percent relative bias (MPRB = $100[\{\bar{\hat{N}} - N\}/N]$), and root mean square error:

$$\text{RMSE} = \left([1/R] \sum_{r=1}^{R} [\hat{N}_r - N]^2\right)^{1/2},$$

where R was the number of replications, and $\hat{N}_r$ was the population estimate for the rth replicate. Root mean square error ≥8 was considered unacceptably large (i.e., >20% of N, sensu Pollock et al. [1990:70] for CV). We also compared $\widehat{\text{SE}}$ and confidence interval coverage (at the 0.90 level) among the first 4 orders of the jackknife estimator.

For comparisons of estimator bias and precision in estimating relative abundance, we simulated 2 populations, each with a population size of 40. For the first population, we used the set of capture probabilities specified previously for Groups 1–4 (Table 1); however, for the second population, we doubled the capture probabilities in each group. For each estimator, we computed mean difference (MD) of $\hat{N}$ between populations such that

$$\text{MD} = (1/R) \sum_{r=1}^{R} (\hat{N}_{lr} - \hat{N}_{mr}),$$

where $\hat{N}_{lr}$ and $\hat{N}_{mr}$ were the population estimates for population l and m, respectively, for the rth replicate, and compared MD percent relative bias (MDPRB) and RMSE among estimators:

$$\text{MDPRB} = \left|\left(100[\text{MD}/N]\right)\right|, \text{ and}$$

$$\text{RMSE} = \left([1/R] \sum_{r=1}^{R} [\{\hat{N}_{lr} - \hat{N}_{mr}\} - 0]^2\right)^{1/2}.$$

RESULTS

Northern Flying Squirrel Populations

The distribution of capture frequencies (f_i) differed among flying squirrel populations (χ^2 = 32.6, 18 df, P < 0.025; Table 2). Many (≥39%) individuals were captured only once, with >70% of the individuals captured ≤2 times. This varied, and in 1 population approximately 24% of the captured squirrels were caught ≥5 times (Table 2).

As expected, estimates of population size and

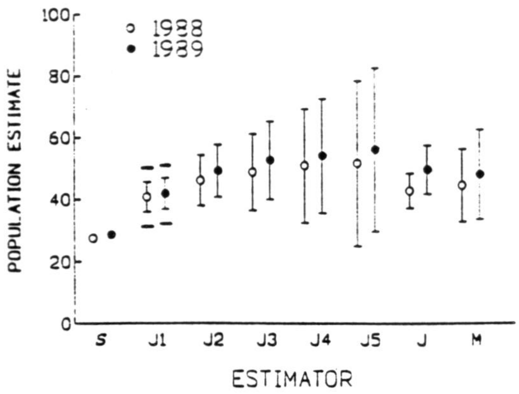

Fig. 2. Comparison of the mean estimated population size ($\bar{\hat{N}} \pm \widehat{SE}$) of 10 northern flying squirrel populations in 1988–89, Willamette National Forest, Oregon. Estimators compared were enumeration (*S*), first through fifth jackknife (J1–J5), the selected jackknife (J), and the moment (M). For all estimators except *S*, $\widehat{SE}$ was computed from variance estimators in Burnham and Overton (1978) and Chao (1988). The $\widehat{SE}$ from the adjusted variance estimator for J1, $\widehat{Var}_{adj}(\hat{N}_{J1}) = ([t-1]/t + 1.5)^2 f_1 + (1.5)^2(S - f_1) - \hat{N}_{J1}$, increased the $\widehat{SE}$ considerably ($\pm \widehat{SE}_{adj}[N_{J1}]$ indicated with bold lines). A variance estimator for *S* was not included.

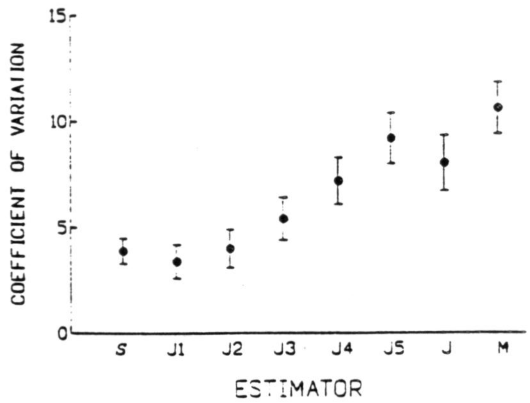

Fig. 3. Comparison of the mean coefficient of variation of population size estimates ($\overline{CV} \pm SE$) from 10 northern flying squirrel populations, Willamette National Forest, Oregon, 1989. The CV was computed from successive population estimates from 8 to 21 trap occasions, where $CV = 100(SE[\hat{N}]/\bar{\hat{N}})$, where $SE(\hat{N})$ was an empirical SE of population size estimated at 14 points in time (trapping occasions 8–21), and where

$$\bar{\hat{N}} = \sum_{t=8}^{21} \hat{N}_t/14,$$

and $\hat{N}_t$ was the estimated population size for trapping occasion t. We compared the enumeration (*S*), first through fifth jackknife (J1–J5), the selected jackknife (J), and the moment (M) estimators.

standard error varied among estimators for flying squirrel populations. Estimated population size and standard error increased for the first- through fifth-order jackknife estimators; the $\widehat{SE}$ from the adjusted first-order variance estimator was similar to the second-order $\widehat{SE}$. Population size estimates from the moment estimator were similar to first- and second-order jackknife estimators, but the $\widehat{SE}$ was similar to the third-order jackknife estimator (Fig. 2). The jackknife estimator chosen by the selection procedure varied with number of trapping nights. At t = 8, $k \leq 2$ was selected in 11 of 20 flying squirrel populations (grid-yr combinations). At t = 12, the first or second order was selected in 16 of 20 populations. By t = 21, $k \leq 2$ was selected in 13 of 15 populations (only 5 populations were sampled for 21 consecutive trapping occasions in 1988).

The stability of abundance estimates differed among squirrel populations and estimators. Coefficient of variation of $\hat{N}$, used to measure stability, ranged from 0.4 to 18.5%; $\overline{CV}$ ($\bar{x}$ of the 10 populations examined in 1989) ranged from 3.4 to 10.6% among estimators (Fig. 3). The moment, fifth-order, and selected jackknife estimates had higher $\overline{CV}$ than did the other estimators. First-order estimates had the lowest $\overline{CV}$, with slightly lower $\overline{CV}$ than estimates from the second-order jackknife estimator or the enumeration estimator (Fig. 3).

Simulated Populations

Abundance.—The most consistent patterns were related to the estimator and t (Table 3). All jackknife estimators were biased negatively at t = 6, except for orders 3–5 for the Group 4 distribution; these had low, positive bias. The moment estimator generally had moderately low, positive bias at t = 6, but consistently had high RMSE. Negative bias remained high for *S* in all simulated groups and for all t. Although bias was reduced considerably for *S* with increasing t, relative bias was consistently >10%. At t = 6, RMSE >8 were produced by all estimators except for the second-order estimator with Group 4 (highest $\bar{p}$). Bias generally decreased with increasing t for the first-order jackknife estimator and remained low for the moment estimator. At t ≥ 12, the moment estimator often was least biased, but RMSE was consistently high; only first- and second-order jackknife estimators were moderately precise and had low bias. By t = 21, all estimators except *S*, which had high negative bias and high RMSE, were positively biased. Higher-order jackknife estimators had greater bias and higher RMSE than lower-order estimators as t increased. In all groups, first-order jackknife estimators had low bias and the lowest RMSE at t = 21. Bias of the selected jackknife

Table 3. Bias and precision of the enumeration (S), jackknife, and moment estimators of absolute abundance. Results are from simulated data with 2,000 replications for each group-t combination.

			Estimator							
				Jackknife order						
Group[a]	t[b]	Statistic	S	First	Second	Third	Fourth	Fifth	Selected	Moment
1	6	MPRB[c]	−67.0	−44.3	−29.0	−19.0	−12.9	−9.9	−19.1	11.8
		RMSE[d]	26.9	18.4	13.4	11.2	10.6	10.7	13.4	30.6
	12	MPRB	−46.0	−13.6	5.0	15.5	21.3	24.9	10.5	12.8
		RMSE	18.6	7.6	8.2	12.8	17.2	21.2	15.9	21.1
	21	MPRB	−26.5	5.7	16.9	19.0	20.5	25.3	14.5	4.7
		RMSE	10.9	5.3	10.5	14.5	18.7	24.4	13.7	10.1
2	6	MPRB	−63.2	−39.2	−23.8	−14.1	−8.3	−5.6	−13.7	14.0
		RMSE	25.4	16.4	11.7	10.1	10.1	10.4	12.4	29.5
	12	MPRB	−42.0	−10.5	5.9	14.3	18.9	22.2	8.1	6.4
		RMSE	17.0	6.7	8.2	12.6	16.8	20.8	14.7	17.8
	21	MPRB	−23.7	5.7	14.8	16.7	19.6	26.2	12.8	3.4
		RMSE	9.8	5.1	9.7	13.5	17.9	24.2	12.5	9.8
3	6	MPRB	−54.5	−30.5	−16.4	−8.0	−2.9	−0.6	−9.1	6.0
		RMSE	22.0	13.1	9.3	8.9	9.7	10.3	11.7	23.7
	12	MPRB	−34.5	−5.8	7.5	13.7	17.1	20.1	8.1	4.0
		RMSE	14.0	5.4	8.2	12.2	16.0	19.9	13.6	14.5
	21	MPRB	−18.7	5.8	11.8	13.0	16.4	24.0	10.1	2.0
		RMSE	7.8	4.8	8.4	11.6	15.7	22.1	10.1	7.9
4	6	MPRB	−45.2	−17.9	−4.2	2.7	6.2	7.7	−1.7	2.0
		RMSE	18.3	8.6	7.0	8.8	10.6	11.5	10.8	17.7
	12	MPRB	−25.0	1.2	9.7	12.4	15.0	19.1	8.0	0.4
		RMSE	10.3	4.5	8.0	11.4	14.9	19.0	11.1	9.2
	21	MPRB	−12.0	6.7	8.6	9.7	14.7	24.5	9.1	1.8
		RMSE	5.2	4.4	6.8	9.5	13.9	21.2	9.1	7.1

[a] Each group contains a different distribution of capture probabilities (Table 1).
[b] No. of consecutive trapping occasions.
[c] $\bar{x}$ % relative bias.
[d] Root $\bar{x}$ square error.

estimator varied considerably with t and with group, but consistently had high RMSE (>8). At t = 21, the moment estimator had the lowest relative bias (<5%); however, RMSE tended to be relatively high (≥7).

Relative Abundance.—We found patterns of bias and RMSE similar to those found above when we investigated relative abundance of 2 simulated populations of equal size but different mean capture probabilities (Table 4). At t = 6, all estimators except the moment estimator tended to have high bias (Table 4); the moment estimator had the lowest relative bias, ranging from 0.9 to 7.0%. However, all estimators at t = 6 had consistently high (>8) RMSE. Bias was generally reduced for jackknife estimators at t = 12, but RMSE remained high, except for the first-order jackknife estimator with Group 4. Bias of the moment estimator remained low at t = 12, and RMSE was reduced, but remained >8. By t = 21, bias was generally low for all estimators except S, which had relatively high relative bias (9.2–18.9%) that decreased with increasing $\bar{p}$. The RMSE was consistently low for the first-order jackknife estimator, reasonably high for the moment estimator, and unacceptably high for higher-order and selected jackknife estimators. All estimators were generally least biased and most precise for Group 4, which had the highest $\bar{p}$.

Jackknife Order Selection.—The order selected by the jackknife-selection procedure changed with number of trapping occasions (Table 5). The first-order jackknife estimator was selected in >79% of replicates at t = 21; this percentage increased as $\bar{p}$ of groups increased (Table 5). Conversely, except for Group 4, other orders were selected more often when t = 6, especially the fifth-order jackknife estimator.

Confidence Interval Coverage.—Standard errors were underestimated for the first-order jackknife estimator and resulted in poor (0.0–62.6%) 90% confidence interval coverage for all t (Table 6). The adjusted variance estimator improved coverage and was usually consistent with the higher-order estimators, while $\widehat{SE}$ remained lower than $\widehat{SE}$ of higher-order jackknife estimators. At t ≥ 12, coverage was usually near or above the 90% (nominal) level for all estimators

Table 4. Bias and precision of the enumeration (S), jackknife, and moment estimators of relative abundance. Results are from simulated data of 2 populations with 2,000 replications for each group-t combination.

			Estimator							
				Jackknife order						
Group[a]	t[b]	Statistic	S	First	Second	Third	Fourth	Fifth	Selected	Moment
1	6	MDPRB[c]	22.4	30.7	32.5	31.9	30.8	30.1	29.7	7.0
		RMSE[d]	10.0	14.3	16.5	18.0	19.2	19.8	20.5	38.9
	12	MDPRB	24.2	21.3	10.6	0.5	4.8	5.7	2.9	9.6
		RMSE	10.4	10.9	11.5	15.6	20.9	26.4	19.1	24.8
	21	MDPRB	18.9	5.0	7.5	9.4	5.2	1.0	1.9	1.1
		RMSE	8.2	5.9	9.8	14.4	20.0	28.6	13.4	9.7
2	6	MDPRB	22.9	29.1	29.0	27.1	25.4	24.4	22.9	4.1
		RMSE	10.1	13.7	15.3	16.7	17.9	18.6	18.5	35.9
	12	MDPRB	22.7	17.7	7.7	0.1	2.7	2.5	4.2	3.6
		RMSE	9.8	9.6	10.7	15.0	20.1	25.8	17.9	20.1
	21	MDPRB	16.9	3.7	6.3	7.4	4.7	0.5	2.0	0.1
		RMSE	7.4	5.4	9.2	13.7	19.2	27.6	12.0	8.8
3	6	MDPRB	21.6	24.5	22.9	20.1	17.9	16.8	16.4	2.6
		RMSE	9.5	11.9	13.1	14.5	15.8	16.6	16.2	26.2
	12	MDPRB	19.5	12.6	3.5	1.7	2.6	0.9	2.9	0.9
		RMSE	8.5	7.9	9.8	13.9	18.5	23.5	15.0	14.9
	21	MDPRB	13.6	1.5	5.5	5.5	3.9	1.8	2.6	0.5
		RMSE	6.1	4.8	8.3	12.1	17.2	25.2	10.9	8.0
4	6	MDPRB	22.1	18.7	12.8	8.6	6.5	5.5	8.2	0.9
		RMSE	9.6	9.7	10.2	12.0	13.8	14.8	13.4	20.1
	12	MDPRB	15.9	5.1	2.4	4.5	4.1	3.0	0.2	1.5
		RMSE	7.0	5.6	8.7	12.6	16.8	21.9	12.1	10.0
	21	MDPRB	9.2	2.1	4.5	3.5	3.0	2.9	3.7	0.3
		RMSE	4.2	4.0	6.9	9.8	14.6	22.8	9.0	7.1

[a] Each group contains a different distribution of capture probabilities (Table 1).
[b] No. of consecutive trapping occasions.
[c] $\bar{x}$ difference % relative bias: MDPRB $= |100([1/R] \sum_{r=1}^{R} [\hat{N}_{lr} - \hat{N}_{mr}])/N|$, where R was the no. of replications and $\hat{N}_{lr}$ and $\hat{N}_{mr}$ were the population estimates for population l and m, respectively, for the rth replicate.
[d] Root $\bar{x}$ square error: RMSE $= ([1/R] \sum_{r=1}^{R} [(\hat{N}_{lr} - \hat{N}_{mr}) - 0]^2)^{1/2}$.

except the unadjusted first-order estimator. However, for Group 4 (highest $\bar{p}$) the $\widehat{SE}$ of the adjusted first-order jackknife estimator was underestimated at t = 21, which resulted in poor (40%) coverage.

DISCUSSION

Populations of northern flying squirrels had low densities and low, heterogeneous, capture probabilities that are similar to those of many vertebrate populations for which mark-recapture techniques are used to estimate population size (Eberhardt 1969, Chao 1989, Hammond 1990, Hallett et al. 1991). Under these conditions, enumeration is often used to estimate abundance. However, enumeration would have provided a poor estimate of abundance or relative abundance because temporal and spatial differences in capture probabilities, probabilities that are <1, exist in northern flying squirrel populations (Carey et al. 1991, Rosenberg 1991, Witt 1991). Simulations support this contention; the enumeration estimator had high bias and low precision in estimating abundance and relative abundance, as expected given the form of the estimator (Hilborn et al. 1976, Nichols and Pollock 1983, Nichols 1986).

Estimates of flying squirrel abundance, using selected and higher-order jackknife estimators and the moment estimator, were sensitive to number of trapping occasions. Therefore, assuming true population size did not change with each trapping occasion, as the almost consistent nonsignificant closure tests (Otis et al. 1978) suggested (Rosenberg and Anthony, unpubl. data), these estimators appeared unreliable. The first-order jackknife estimator provided the most stable estimates of flying squirrel abundance. Abundance estimates became more similar among estimators as number of trapping occasions increased, which resulted in higher num-

Table 5. Percent of replications each jackknife order was chosen by the selection procedure.[a] Results are from simulated data with 2,000 replications for each group-t combination.

Group[b]	t[c]	Jackknife order First	Second	Third	Fourth	Fifth
1	6	18.8	24.4	15.7	1.4	39.9
	12	38.3	40.0	11.6	3.8	6.4
	21	79.2	15.8	2.7	1.0	1.5
2	6	16.7	30.2	16.6	2.0	34.6
	12	51.2	33.1	7.5	3.9	4.4
	21	83.8	11.4	2.8	1.0	1.2
3	6	29.3	29.7	12.0	4.4	24.7
	12	63.1	25.1	4.8	3.3	3.8
	21	90.8	5.9	1.9	0.7	0.9
4	6	42.4	33.9	9.3	2.3	12.2
	12	83.5	11.0	2.2	1.1	2.3
	21	96.8	1.3	0.5	0.7	0.8

[a] Burnham and Overton (1978, 1979).
[b] Each group contains a different distribution of capture probabilities (Table 1).
[c] No. of consecutive trapping occasions.

Table 6. Mean estimated standard error (SE) and confidence interval coverage[a] (CIC) of the first 4 orders of the jackknife estimator[b] from simulated data with 2,000 replications for each group-t combination.

Group[c]	t[d]	Statistic	Jackknife order First	$First_{adj}$[e]	Second	Third	Fourth
1	6	SE	3.6	6.0	6.6	8.6	10.0
		CIC	2.6	13.9	42.7	71.9	78.5
	12	SE	4.0	6.9	9.0	13.5	18.2
		CIC	54.8	82.9	93.6	93.5	92.4
	21	SE	2.6	6.1	9.7	16.0	24.0
		CIC	55.2	96.1	91.0	93.8	93.7
2	6	SE	3.7	6.1	6.9	9.1	10.7
		CIC	4.0	21.3	60.0	83.9	88.1
	12	SE	3.7	6.6	9.0	13.6	18.7
		CIC	62.6	85.3	94.5	93.2	92.3
	21	SE	1.9	5.4	9.2	15.6	23.6
		CIC	40.4	94.0	91.7	95.0	95.2
3	6	SE	3.2	5.8	6.9	9.4	11.2
		CIC	12.4	36.0	71.9	89.1	92.9
	12	SE	2.6	5.8	8.4	13.3	18.5
		CIC	57.4	88.2	92.8	93.7	93.7
	21	SE	0.7	4.2	8.2	14.4	22.3
		CIC	8.3	87.0	90.3	95.3	95.4
4	6	SE	3.2	6.1	7.5	10.4	12.5
		CIC	37.4	67.0	89.2	93.9	94.4
	12	SE	1.2	4.9	8.1	13.5	19.4
		CIC	32.7	91.1	94.0	96.0	95.9
	21	SE	0.1	2.0	6.7	13.0	21.0
		CIC	0.0	40.0	91.6	96.6	96.2

[a] % replications in which the 90% CI included the true N.
[b] Burnham and Overton (1978, 1979).
[c] Each group contains a different distribution of capture probabilities (Table 1).
[d] No. of consecutive trapping occasions.
[e] $First_{adj}$ is the first-order jackknife estimator with the variance estimator adjusted: $\text{Var}_{adj}(\hat{N}_{j1}) = ([t-1]/t + 1.5)^2 f_1 + (1.5)^2(S - f_1) - \hat{N}_{j1}$, where f_1 is the no. of individuals captured only once, S is the no. of different individuals captured, and $\hat{N}_{j1}$ is the population size estimate from the first-order jackknife estimator.

bers of captures and recaptures. At t = 21, the jackknife-selection procedure usually chose the first-order estimator with flying squirrel data; we found a similar pattern with simulated data. This was not surprising because lower bias is expected when a larger proportion of the total population is captured, as occurs with a greater number of trapping occasions. In this respect, the estimator selection procedure performed well: lower-order estimators should be selected as t increases (Burnham and Overton 1979).

Results from analysis of computer-simulated data supported those from field investigations. First- and second-order jackknife estimators tended to be most precise and least biased of the jackknife estimators. Higher-order jackknife estimators ($k \geq 3$) and the selected order provided estimates with unacceptably large RMSE; these estimators appeared to be unreliable for estimating abundance or relative abundance under conditions we investigated. The first-order jackknife estimator generally performed well. However, when average capture probabilities and number of trapping occasions were low (Groups 1 and 2, t ≤ 12), the second-order estimator provided more accurate estimates than the first-order estimator. Chao (1988, 1989) found that when few animals were captured >2 times, the moment estimator was less biased than the selected jackknife estimator; however, precision of these estimators was low. Our conclusions are similar to those of Chao (1988, 1989) regarding the comparison of moment and selected jackknife estimators. However, we found the moment estimator to have similar, although typically lower bias, but greater variation than first- or second-order jackknife estimators. This was reflected in moment estimates that were sensitive to number of captures and recaptures, as Hallet et al. (1991) observed.

The jackknife estimator was frequently used to estimate population size (Greenwood et al. 1985; Chao 1989; Pollock et al. 1990:58; Hallett et al. 1991; Rosenberg and Anthony 1992, 1993*a*) and considered one of the most robust estimators for closed populations (Otis et al. 1978). The selected jackknife estimator was the one most often used and recommended by Otis et al. (1978) and White et al. (1982). Although the jackknife selection procedure provided an objective method for choosing a specific estimator, the order selected was sensitive to number of new captures and recaptures under conditions of small population size with low and heterogeneous capture probabilities. Performance of each of the 5 orders of the jackknife estimator was not compared in previous evaluations (Burnham and Overton 1978, 1979; Otis et al. 1978; Pollock 1982; Chao 1988, 1989; Menkens and Anderson 1988), probably because the objective nature of the selection procedure was desirable, and a method of choosing proper estimators on the basis of data structure was the procedure of choice (Burnham and Anderson 1992). However, in many biological applications sample sizes are inadequate for statistical procedures for selecting the least biased and most precise estimator (Menkens and Anderson 1988, Chao 1989). We recommend that the selection procedure for the jackknife estimator be used with caution, and attention should be paid to the particular jackknife estimator being used, especially in comparative studies. Our results suggest use of the first- or second-order jackknife estimator when population sizes are low and capture probabilities are low and heterogeneous.

Although confidence interval coverage is often low with the jackknife estimator (Otis et al. 1978:34; Chao 1988, 1989), the adjusted variance estimator (this study) for the first-order jackknife estimator improved its otherwise poor coverage, and we obtained the nominal 90% level in most cases, especially when the number of trapping occasions was ≥ 12. The ad hoc adjustment to the variance estimator was warranted by consistently low confidence interval coverage that we obtained with the unadjusted variance estimator. However, the adjusted variance estimator was negatively biased under conditions investigated with the Group 4 distribution of capture probabilities ($\bar{p} = 0.14$) at $t = 21$.

Field and simulation results indicated that <12 days are inadequate to provide reliable (low bias, high precision) estimates of absolute or relative abundance under conditions we investigated. Although the first- and second-order jackknife estimator provided reliable estimates at $t = 12$ for some capture probability distributions, the estimators typically were biased and imprecise at low t (<12). However, extensive trapping periods are prohibitive in terms of cost in many field studies, may increase trap mortality (Rosenberg and Anthony 1993*b*), and may increase the degree to which the closure assumption is violated. Investigators should use methods that increase the number of individuals captured and recaptured, thereby reducing the need for lengthy trapping periods. An increase in the number of traps per home range, both by a decrease in the interval between traps and an increase in the number of traps per station, may increase capture probabilities; this would allow the number of trapping occasions to be reduced. In addition, larger grid sizes should reduce the influence of immigration and emigration, as well as provide larger numbers of individuals in the sample. Furthermore, reducing sources of heterogeneity in capture probabilities would also improve parameter estimation (Otis et al. 1978, White et al. 1982), although this may be difficult for some species.

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