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**Small Mammal Estimates Using Recapture Methods,  
with Variables Partitioned<sup>1</sup>**

[With 5 Tables &amp; 1 Fig.]

Modifications and implementation of the model presented by Smith, Jorgensen & Tolley (1972) (*EM-1*) to estimate small mammal numbers and densities are described, along with some of the limitations. These modifications provide a practical model (*EM-2*) that can be used to estimate small mammal populations, while at the same time, partitioning the estimator variables. Estimates can be obtained with confidence statements without dense-line data, or for that matter, without a dense-line even included in the field design.

## I. INTRODUCTION

Historically, population ecologists have been concerned with estimating population parameters, such as distribution, population size, activity range, birth rate, death rate, age structure, density, biomass, etc. Before most of the parameters can be estimated, the number of organisms within a given area must be estimated by one of several possible methods that have been specifically designed to retain the population structure in its existing environment (Petersen, 1896; Lincoln, 1930; Schnabel, 1938; Hayne, 1949; Leslie & Chitty, 1951; Leslie, 1952; Jolly, 1963, 1965, and Smith, Jorgensen & Tolley, 1972). Although all of these proposed methods were designed to satisfy specific sampling problems, the method described by Smith *et al.*, 1972 (hereafter referred to as *EM-1*) provided the most complete partitioning of the variables that are inevitably confounded in estimates of population size. This paper provides the basis for implementing *EM-1* and is referred to as *EM-2*.

The field design and logic for the analytical method used to partition

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the variables confounding estimates are explained by Smith *et al.* (1972). The logic is clear and *EM-1* should be expected to provide reliable estimates of small mammal densities, if all of the assumptions are satisfied. Since the assumption of animal movement is not always satisfied and the general methods proposed are so restricted by this and other assumptions, a more robust model was required before the estimator could be very useful. Although fewer assumptions were required and *EM-2* could be more widely applied, it sacrificed some accuracy when the assumptions of *EM-1* were not completely satisfied.

This revised model (*EM-2*), with its redefinitions, is designed to provide estimates of mortality, trap avoidance, dispersal and population density when the dense-line yields no information about movement and/or the probability of trap avoidance is high from day  $j$  to day  $t$ . Also, it provides an estimate of the population size ( $N_i$ ), with the above variables partitioned when a dense-line is not even included in the field design (Fig. 1).

## II. ANALYTICAL METHODS

Perhaps the most elusive parameters effecting the response of estimators are the animal-trap relationships. Among these relationships is trap avoidance ( $\hat{Pa}_i$ ), which is stated as the probability of a marked animal being recaptured exactly  $i$  days after it was first caught, and estimated with:

$$\hat{Pa}_i = \left[ \sum_{j=1}^{t-i} \frac{A_{j, j+1}}{n_j} \right] / (t-i) \quad (1)$$

where:  $A_{ij}$  = the  $A_{ij}$  matrix described by Jolly (1963, 1965), and  
 $n_j$  = the number of animals caught on day  $i$ , that is the sample size on day  $i$ .

This estimate differs from a comparable estimate in *EM-1* ( $a_i$ ), but its use is even more essential since it controls how the marked animals on the grid, that were never recaptured, are partitioned before  $N_i$  is determined.

After  $\hat{Pa}_i$  has been determined, the probability that an animal left the grid after being captured can be estimated with:

$$\hat{Pl}_i = \left[ \sum_{j=1}^{t-i} \frac{lt_{i, j+1}}{n_j} \right] / (t-i) \quad (2)$$

where:  $lt_{ij}$  = a matrix containing the capture history of animals that left the grid. The  $lt_{ij}$  element is the number of grid residents that were last



caught on the grid on day  $i$ , then caught on the dense-line (if present) on day  $j$ , but subsequently disappeared.

The probability of death ( $\hat{P}d_i$ ) can now be determined with:

$$\hat{P}d_{i+1} = 1 - \sum_{j=1}^i \left( \hat{P}l_{t-j} + \hat{P}a_{t-j} \right) \tag{3}$$

This probability represents the likelihood that an animal caught on day  $i$ , and never observed again, is dead, providing that  $Pd_1=1$ . The number of animals that are not caught and assumed to be dead between day  $i$  and day  $t-1$  can be estimated with  $d_i=(g_i) (\hat{P}d_{i+1})$ . In this case,  $g_i$  is defined as the number of marked animals caught on day  $i$  that were not caught during the rest of the trapping period.

$$g_i = n_i - \sum_{j=i+1}^t A_{ij} \tag{4}$$

where:  $g_i = n_i$  less the number of grid residents caught on the dense-line when present) on the last trapping day, since grid residents may be caught on the dense-line on the last day.

Since it is not possible to determine precisely which days the  $d_i$  animals died on, it is necessary to estimate the number of marked animals assumed to be dead from day 1 to day  $t-1$  with:

$$\hat{M}D_i = \sum_{j=1}^i (d_j) (\hat{P}d_{t-i+j}) \tag{5}$$

Now that the number of dead animals ( $\hat{M}D_i$ ) can be estimated for day  $i$ , it is possible to estimate the number of marked animals on the grid at day  $i$  with:

$$\hat{M}_i = \sum_{j=1}^i (n_j + k_j - m_j - l_j - r_j) - \hat{M}D_i \tag{6}$$

where:  $k_j$  = the number of animals that immigrated to the grid and took up residency,  
 $m_j$  = the number of marked animals caught alive in the sample on day  $i$ ,  
 $l_j$  = the number of marked animals that left the grid on day  $i$ , and  
 $r_j$  = the number of animals that died in the traps on day  $i$ .

The number of animals moving onto the grid ( $k_i$ ) and the number of marked animals that move off the grid ( $l_i$ ) are determined with:

$$k_i = \sum_{j=1}^i kt_{ij} \quad (7)$$

$$l_i = \sum_{j=1}^i lt_{ij} \quad (8)$$

where:  $kt_{ij}$  = a matrix containing the capture history of animals that came onto the grid. The  $kt_{ij}$  element is the number of animals that were last caught on the dense line on day  $i$  that were subsequently caught on the grid on day  $j$  then caught at least once more on the grid, but then never again caught on the dense-line.

The probability of capture ( $\hat{\Phi}_i$ ) for marked animals can be estimated with  $(m_{i+1} + k_{i+1})/M_i$ ; thus, the population size ( $N_i$ ) on the grid can be estimated with:

$$EM-2_i = \frac{(n_{i+1} + k_{i+1})}{(m_{i+1} + k_{i+1})/M_i} \quad (9)$$

Changes in the population during the sampling (trapping) period may now be expressed as  $\Delta N_i = k_i + b_i - d_i - l_i$ , where  $b_i$  is the number born on day  $i$  plus some random fluctuations due to errors in estimating  $\hat{\Phi}_i$ . This might also be expressed as  $\Delta N_i = \hat{N}_i - \hat{N}_{i-1}$ , where  $\hat{N}_i = EM-2_i$ . The density of animals is then determined by taking the area contained within the grid and dividing it by  $\hat{N}_i$ .

As Smith *et al.* (1972) stated, estimates of population numbers should be accompanied by an appropriate confidence statement. The statement provided by them has been adopted as being the best, when modified such that  $k_j = 1$  when the dense-line is absent or when animals have not been detected to move onto the grid. Confidence for these estimates may then be obtained with:

$$p \left[ \frac{\hat{N}_i}{\hat{\Phi}_i + Z_{\alpha/2} \sqrt{\frac{\hat{\Phi}_i (1-\hat{\Phi}_i)}{k_{i-1}}}} \right] < N_i < \left[ \frac{\hat{N}_i}{\hat{\Phi}_i - Z_{\alpha/2} \sqrt{\frac{\hat{\Phi}_i (1-\hat{\Phi}_i)}{k_{i+1}}}} \right] = 1-\alpha \quad (10)$$

### III. METHODS

Field design for the grid and its accompanying dense-line are presented in Fig. 1. A more complete description of this design is provided by



Smith *et al.* (1972), but a brief illustration here is useful in explaining some of the experiments conducted to validate the estimator. Basically, data were gathered from a small mammal simulator where the variables could be controlled (Jorgensen, Smith & Scott, 1972). The estimator (equation 9) will be illustrated with a set of data obtained from the small mammal simulator described by Jorgensen, Scott & Smith (1972).

#### IV. RESULTS

Data from the simulator included in Table 1 were converted to an  $A_{ij}$  matrix (Table 2) for all animals caught on the grid. All other calculations

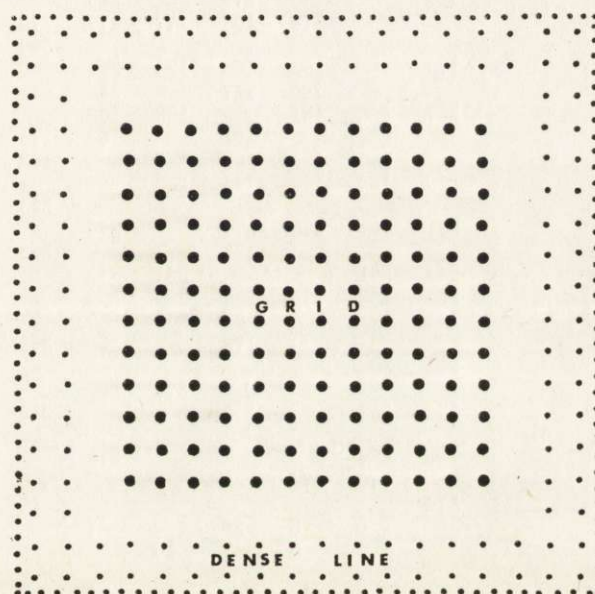


Fig. 1. Field design for the grid and its accompanying dense-line

are generated from this matrix, along with similar matrices for leaving the grid ( $lt_{ij}$ ) and coming onto the grid ( $kt_{ij}$ ). In this particular example animals did not move onto or from the grid; thus, the ( $lt_{ij}$ ) and ( $kt_{ij}$ ) matrices were all zeros and provided no input into  $\hat{M}_i$  (equation 6). Also, since the data were obtained from the simulator where population parameters could be controlled, the population was maintained stable at 49.

Results of this example are reported in Table 3. If one is interested in a single estimate for the 10 day trapping period, there are several strategies that might be used. First, is simply a matter of using the mean (54.2) which is questionable because of the dependence of each estimate on those preceding it. Secondly, a median (54) might also be used. This

Table 1  
 Capture data of one class, trap numbers greater than 144 are dense-line traps.

Animal number	Percent dense-line captures	Days caught with station number									
		1	2	3	4	5	6	7	8	9	10
1	1.00						168 <sup>a</sup>			300	
2	1.00					179	174	176	305	306	
3	1.00									165	
4	1.00			153						360	
5	1.00	158	295	158	158				161	159	
6	1.00			148	182	147		289		146	145
7	1.00		148	148		148	290	184		148	182
8	1.00	181			179		306		181	183	
9	1.00			178	183	177	177	175	179	176	178
10	1.00							300	167	167	
11	1.00	170		166	168	170	301			166	
12	1.00			169	167		168		168	168	
13	1.00	297	298	161		163	162		297	162	
14	1.00				301		169	170		171	169
15	1.00		183	183	183	183		183	180		
16	1.00	289	182	289	145	289	289			363	289
17	1.00							296			296
18	1.00	371		175	176		304		303	304	371
19	1.00				305			305	177	177	
20	1.00	294	361			361			293		
21	1.00	366	298	299	299	299	366		366		
22	1.00	185			185	306	185		187	187	183
23	1.00				173		368	301	301		368
24	1.00	365	364							365	365
25	1.00					370	369		369		
26	1.00	152	359		358			359			
27	1.00								364		
28	1.00						370				
29	1.00		370	374							
30	.67	374								374	
31	.00		8	8	20		7		8		8
32	.00			6	7	18				18	6
33	1.00								311		
34	.00		6	18	5				6		18
35	.00				13			2	13		
36	.00	9		22		9	21			22	21
37	1.00			313			198		196	196	200
38	.00		13			13					
39	.00	20	20		20	20				19	21
40	1.00	278						378	314		376
41	1.00		201		376	380		378	380		314
42	.00	17		30			15	29	17		
43	.00				21		21				
44	.00						23	11		36	
45	.00	29			17	29		30		17	
46	.00	15		27				26		26	
47	.00					46	47	34		33	
48	.00			28		39					
49	.00	31	43	43		43		43	30		
50	1.00	202	206	315	319	206					
51	1.00	382	382	211			382		382	318	384
52	.00		53		42					42	41
53	1.00				212	208		208			
54	.00	35		48	48	60				47	48

Table 1, continued

Animal number	Percent dense-line captures	Days caught with station number									
		1	2	3	4	5	6	7	8	9	10
55	1.00		320							320	
56	.00	55		55		55	42		55		56
57	1.00				215						
58	.00	62	61	50				52			
59	.20		44			56	56		68		416
60	.00	59							59	59	
61	.00		56	69				69			
62	.00			67	55	66					54
63	.00	62	62			61	61	61		73	
64	.00	67						67			
65	.00	72		72				84			
66	1.00	322	386		388					386	
67	.00	93		56		81		81			69
68	.00	75	76		83	76		76			
69	.00					83	83	70	83		83
70	1.00	220		220	218	222	218	220		214	218
71	.00				96				84		
72	.00		81	81	69					70	
73	.00			91					80		
74	.00		79	79		78	66				79
75	.50			390						84	
76	1.00			325			222				325
77	1.00			221	221	221	219	221			
78	1.00			389			389		387	389	325
79	.00		94	82	95		95		81		95
80	.00			86						85	
81	.00	88	88			88			88	88	89
82	1.00	222	220								
83	.00	106				96					
84	.00						108				96
85	.00	96	95	95			95		107		
86	.00				92			105		117	
87	.00	106	106	106			106	106			104
88	.00						119				
89	.00			107	106	118		118			106
90	.00					97		109			
91	1.00		328								
92	.00								101		
93	1.00								395		
94	.00								116	116	116
95	1.00	329		327			395		393		
96	.00	117	129	116	128			117		116	128
97	.00				117	140			130		
98	.00			128				128	129		
99	.00	144	131	131		119	131	130			131
100	1.00					334	332				
101	1.00			331						395	
102	.00			129			129		129	129	129
103	.00			125	136		137	138	125		
104	1.00					395	395			395	
105	1.00	241									
106	.00		129		129			139	140		
107	.00			121				133	133		
108	.00		135					136		135	
109	1.00	334	398	394	334		398		398		



Table 1, continued

Animal number	Percent dense-line captures	Days caught with station number									
		1	2	3	4	5	6	7	8	9	10
110	1.00	333	238		333			238			238
111	.00		142				130				
112	.00		141		129					142	
113	1.00	238	242			248					335
114	1.00		239								241
115	.50			136			407				
116	1.00						400			400	
117	1.00						414	415			414
118	1.00	405									
119	1.00	402		403				402	402		256
120	1.00		250		337	340	335			337	
121	1.00	248					248	337		248	250
122	1.00	266		265	346	346			265	267	346
123	1.00		286	416			249	285			285
124	1.00	262	264	265	263	260			263	265	
125	1.00		288		287		249			288	287
126	1.00		269					266			
127	1.00	282									282
128	1.00			266							
129	1.00		279	354							
130	1.00			288		288					
131	1.00			269							
132	1.00		282								
133	1.00	262									
134	1.00				267						
$n_i$		21	23	29	20	24	20	27	23	19	21

<sup>a</sup> Interpret as animal 1, caught in trap 168, on day six.

has the effect of eliminating extremes and may be considered if one can assume the population to be stable during the sampling period. One might logically assume that if the population is stable during the trapping period, the best estimate would be that provided by the most trapping data — the last day with an estimate. This is expected since it includes the most complete information concerning the probability of trap avoidance, death, and possibly leaving the grid. Consequently, if one standard day were selected, it would logically be the estimate for the ninth day.

$$p \left[ \frac{47}{.44 + 1.96 \sqrt{\frac{(.44)(1-.44)}{1}}} \right] < 47 < \left[ \frac{47}{.44 - 1.96 \sqrt{\frac{(.44)(1-.44)}{1}}} \right] = .95$$

$$p(33 < 47 < 88)$$

Eighteen simulation experiments were conducted, while holding the size constant and varying the size of home ranges and density, to further test the estimator's accuracy (Table 4). As far as the most reliable



estimate over the nine day period is concerned, estimates for all days departed significantly from the known population size except those for day nine. However, if experiment 15 were deleted from the analyses, estimates for days eight and nine both failed to depart significantly from the actual population size. If the population were stable, it is suggested that the mean and median might also be considered effective estimates.

Table 2

$A_{ij}$  matrix for the data provided in Table 1, along with the essential parameters for using the estimator (EM-2).

Trapping day (i)	$n_i$	$m_i$	$\hat{M}_i$	$A_{ij}$ Matrix									
				1	2	3	4	5	6	7	8	9	10
1	21	0	21		10	7	1	1	0	2	0	0	0
2	23	10	34			12	4	5	1	1	0	0	0
3	29	19	44				9	8	4	6	1	1	0
4	20	14	50					8	4	4	2	2	0
5	24	22	52						8	6	2	4	1
6	20	17	54							8	6	1	2
7	27	27	52								10	8	4
8	23	21	51									3	5
9	19	19	47										9
10	21	21	45										

Table 3

Parameters used in computing EM-2 as an estimator of small mammals.

Trapping day	Probabilities				Population estimates						
	$\hat{P}a_i$	$\hat{P}d_i$	$\hat{P}l_i$	$\hat{\Phi}_i$	$d_i$	$k_i$	$l_i$	$g_i$	$\hat{M}D_i$	EM-2 <sup>a</sup>	$N_i$
1	.00	1.00	.00	.48	.00	0	.00	0	.00	48	49
2	.00	1.00	.00	.56	.00	0	.00	0	.00	52	49
3	.00	1.00	.00	.32	.00	0	.00	0	.00	63	49
4	.03	1.00	.00	.44	.00	0	.00	0	.00	55	49
5	.04	.97	.00	.33	2.77	0	.00	3	.14	61	49
6	.11	.92	.00	.50	2.44	0	.00	3	1.32	54	49
7	.13	.81	.00	.40	3.43	0	.00	5	3.13	57	49
8	.26	.69	.00	.37	6.03	0	.00	14	5.71	51	49
9	.38	.43	.00	.44	.51	0	.00	10	9.52	47	49
10	—	.05	.00	.00	.00	0	.00	—	12.08	—	—

<sup>a</sup> Confidence limits on the ninth day estimate at the .95 level are  $p(33 < 47 < 88)$ .

The Chi-square test resulted in totals of 32.59 and 32.90 for the means and medians respectively; both being slightly larger than  $\chi^2$  for day eight (31.0), but appreciably greater than  $\chi^2$  for day nine (25.2).

Although one wouldn't expect the  $\chi^2$  values for any given experiment to be particularly low they can be used to determine which data sets result in extreme departures from known population size. The two

extreme departures in the 18 simulated experiments are no. 5 and 15. Although others are relatively high, reasonable estimates are usually available from one of the methods mentioned previously. There seems to be no reason for these infrequent wide departures, and they are most likely simply a matter of chance, and are rather difficult to identify unless the daily estimates are extremely erratic as is the case with expt. no. 5.

Table 4

Population estimates (*EM-2*) for 18 simulation experiments, along with  $\chi^2$  analyses of the results, for stable population.

Simulation expt. No.	Actual pop. size	Population estimates for each trapping day ( <i>i</i> ) <sup>a</sup>									Mean ( <i>x</i> )	Home range radius <sup>b</sup> (m)	Chi square
		1	2	3	4	5	6	7	8	9			
1	18	12	24	12 <sup>c</sup>	15	32	12	12	11	21	16.7	30	24.6*
2	18	6	5	10	17	49	16 <sup>c</sup>	17	16	15	16.7	30	75.5*
3	30	21	66	28 <sup>c</sup>	42	28	24	34	28	33	33.7	30	53.0*
4	30	20	41	34	25	28 <sup>c</sup>	35	31	22	27	29.2	30	11.8
5	36	65	61 <sup>c</sup>	125	87	68	32	31	36	40	60.5	30	362.9*
6	36	59	27	37 <sup>c</sup>	53	28	60	21	37	30	39.1	30	50.1*
7	17	14	16	21	14	18	16	25	17 <sup>c</sup>	18	17.7	44	6.1
8	17	20	19	15	17	16	19	20	18 <sup>c</sup>	17	17.8	44	1.8
9	35	57	40	42	42	37	38 <sup>c</sup>	36	34	32	39.7	44	18.0*
10	35	44	38	33	62	41	35 <sup>c</sup>	32	33	29	38.6	44	25.9*
11	49	41	48	68	60	59	53 <sup>c</sup>	55	48	49	53.4	44	14.2*
12	49	48	52	63	55	61	54 <sup>c</sup>	57	51	47	54.2	44	9.8*
13	13	19	24	18	15	15	15	20	17 <sup>c</sup>	16	17.6	54	20.6*
14	13	10	32	18	21	19 <sup>c</sup>	19	19	18	18	19.3	54	47.5*
15	16	30	35	32 <sup>c</sup>	31	35	33	34	32	31	32.6	54	156.1*
16	16	37	26 <sup>c</sup>	21	29	27	27	25	24	23	26.6	54	73.5*
17	43	64	51	59	61	55 <sup>c</sup>	57	54	52	49	55.8	54	38.7*
18	43	44	49 <sup>c</sup>	47	53	59	57	52	48	45	50.4	54	16.7*
Chi Square		148.1*		151.9*		60.0*		31.0*					
		126.2*	268.0*	143.5*	52.9*	25.2*							

<sup>a</sup> Estimates, using *EM-2* are not obtainable on the last day of a trapping period; thus, estimates are not listed for *i*=10.

<sup>b</sup> Home range radii were computed according to the methods described by Burge & Jorgensen (1973).

<sup>c</sup> Median.

\* Significant difference at the .95 level.

Natural populations probably do not usually remain stable during the trapping period, although change in the members may be rather subtle in either a positive or negative direction. Also, birth and death might compensate to the extent that the actual population fluctuates very little, if any. These presumed changes during the trapping periods were imposed on different populations at varying rates (Table 5). If one assumes the population size is changing, or even if the composition is

Table 5  
 Population estimates (EM-2) for 27 simulation experiments, along with  $\chi^2$  analyses of the results for populations experiencing birth and/or death during the trapping period.

Simulation expt., No.	Population estimates and actual population size (in parenthesis) for each trapping day (i) <sup>a</sup>										Birth rates <sup>c</sup>	Death rates <sup>c</sup>	Home range radius <sup>b</sup> m	Chi- square
	1	2	3	4	5	6	7	8	9	10				
1	3 (12)	8 (11)	8 (11)	7 (10)	21 (9)	10 (9)	6 (9)	6 (8)	5 (8)	5 (8)	.16	.72	30	28.0*
2	0 (18)	16 (18)	19 (19)	20 (19)	24 (20)	17 (20)	23 (20)	24 (22)	23 (22)	23 (23)	.49	.072	30	20.2*
3	32 (24)	20 (24)	31 (24)	23 (24)	20 (24)	28 (24)	26 (24)	25 (24)	22 (24)	22 (24)	.00	.00	30	7.1
4	0 (10)	14 (10)	13 (11)	17 (12)	17 (13)	17 (14)	15 (15)	24 (15)	22 (17)	22 (17)	.49	.00	44	22.8*
5	79 (18)	29 (16)	20 (14)	15 (12)	19 (10)	13 (9)	11 (8)	9 (7)	9 (6)	9 (5)	.00	.72	44	223.7*
6	31 (30)	43 (29)	47 (28)	39 (29)	36 (29)	38 (28)	41 (28)	37 (28)	37 (28)	37 (28)	.15	.072	44	40.2*
7	16 (14)	17 (14)	17 (14)	20 (14)	19 (14)	18 (13)	19 (13)	17 (13)	16 (13)	16 (13)	.00	.072	54	12.5
8	26 (21)	27 (21)	26 (22)	26 (23)	25 (23)	25 (23)	24 (23)	23 (23)	22 (23)	22 (23)	.16	.00	54	4.5
9	30 (19)	51 (18)	34 (18)	28 (17)	31 (17)	32 (18)	33 (20)	29 (20)	27 (18)	27 (18)	.50	.72	54	127.6*
10	4 (12)	8 (12)	10 (12)	21 (12)	16 (12)	11 (12)	11 (12)	21 (12)	12 (12)	12 (12)	.00	.00	30	22.0*
11	16 (18)	19 (18)	23 (18)	21 (18)	18 (18)	20 (18)	25 (19)	19 (19)	22 (19)	22 (20)	.16	.072	30	4.8*



Table 5, continued

Simula- tion expt., No.	Population estimates and actual population size (in parenthesis) for each trapping day (i) <sup>a</sup>										Birth rates <sup>c</sup>	Death rates <sup>c</sup>	Home range radius <sup>b</sup> m	Chi- square
	1	2	3	4	5	6	7	8	9	10				
12	33 (24)	24 (24)	24 (21)	27 (21)	25 (22)	31 (22)	23 (21)	22 (21)	15 (23)	23 (23)	.50	.72	30	12.6
13	16 (10)	13 (10)	14 (9)	11 (5)	8 (5)	6 (4)	11 (5)	5 (4)	9 (4)	3 (3)	.16	.72	44	31.0*
14	40 (18)	25 (19)	20 (20)	26 (20)	24 (20)	28 (20)	31 (22)	31 (22)	33 (25)	26 (26)	.49	.00	44	44.5*
15	52 (30)	37 (30)	36 (30)	42 (30)	38 (30)	37 (30)	34 (29)	31 (29)	29 (29)	29 (29)	.00	.072	44	28.5*
16	29 (14)	22 (15)	24 (15)	22 (17)	26 (17)	24 (20)	23 (19)	23 (19)	23 (19)	19 (19)	.49	.072	54	34.3*
17	31 (21)	19 (19)	18 (18)	18 (17)	15 (17)	12 (15)	10 (13)	11 (13)	9 (12)	10 (10)	.00	.72	54	7.4
18	32 (19)	35 (19)	38 (19)	35 (19)	34 (19)	39 (19)	49 (21)	42 (21)	41 (21)	21 (21)	.15	.00	54	165.1*
19	12 (12)	9 (12)	26 (13)	9 (13)	18 (15)	10 (15)	14 (15)	16 (15)	11 (15)	15 (15)	.16	.00	30	18.5*
20	26 (18)	27 (17)	17 (18)	15 (16)	11 (15)	13 (14)	11 (14)	22 (14)	8 (11)	8 (10)	.49	.72	30	16.7*
21	24 (24)	20 (23)	21 (23)	20 (22)	14 (22)	15 (22)	11 (22)	14 (22)	10 (22)	22 (22)	.00	.072	30	20.9*
22	10 (10)	9 (9)	8 (9)	7 (5)	7 (4)	8 (4)	7 (3)	7 (3)	6 (3)	2 (2)	.00	.72	44	20.8*
23	22 (18)	39 (18)	23 (18)	29 (19)	26 (20)	24 (20)	26 (20)	25 (19)	22 (19)	18 (18)	.16	.072	44	38.8*

Table 5. continued

Simulation expt., No.	Population estimates and actual po- pulation size (in parenthesis) for each trapping day (i) <sup>a</sup>										Birth rates <sup>c</sup>	Death rates <sup>c</sup>	Home range radius <sup>b</sup> (m)	Chi- square	
	1	2	3	4	5	6	7	8	9	10					
24	32 (30)	34 (31)	41 (32)	39 (34)	40 (35)	42 (37)	51 (40)	47 (42)	44 (44)	44 (45)	.50	.00	44	8.7	
25	24 (14)	22 (15)	26 (15)	27 (17)	31 (17)	28 (20)	27 (20)	27 (20)	25 (20)	25 (20)	.49	.072	54	42.2*	
26	21 (21)	27 (21)	21 (21)	21 (21)	22 (21)	23 (21)	23 (21)	22 (21)	21 (21)	21 (21)	.00	.00	54	2.2	
27	27 (19)	47 (19)	36 (18)	36 (18)	35 (17)	33 (16)	31 (17)	27 (15)	24 (15)	24 (11)	.15	.72	54	144.3*	
Chi- Square	184.1	352.4	108.1	87.3	105.3	83.4	103.3	75.4							63.7

<sup>a</sup> Estimates, using EM-2 are not obtainable on the last day of a trapping period; thus, estimates are not listed for  $i=10$ .

<sup>b</sup> Home range radii were computed according to the methods described by Burge and Jorgensen (1973).

<sup>c</sup> Birth and death rates were sometimes distributed over all ten trapping days or imposed all at once. Examine the sequence of the numbers in the actual population size on a specific day.

\* Significant difference at the .95 level.

changing with no change in size, the estimates must be considered from an entirely different position. Medians and means are far less logical than they were for stable populations.

Chi square analyses similar to those performed on the data generated from stable populations provide the basis for reconsideration of the criteria for best single estimates (Table 5). If one considers only the  $\chi^2$  values among the nine days, he must conclude that although there is a significant departure of the estimate and actual number in all cases, the smallest values are found again on days eight and/or nine.

Unlike  $\chi^2$  values among the trapping days on Table 4, there is no continual decrease among them on Table 5. These fluctuations are obviously a matter of the accumulated changes among the populations due to birth and death. If the frequencies of change among the 27 experiments are totaled to see where changes in the populations were actually occurring, there was still no explanation evident since they could not be correlated with  $\chi^2$  changes.

Generally, one must consider each estimate separately since they are keyed directly to the population size for the given day; but, if a single estimate is required, those for the eighth and/or ninth days of trapping are likely to be the most reliable.

#### V. DISCUSSION

Small mammal estimators are numerous and all are designed to estimate numbers and densities, but under the constraints of rather specific assumptions. Generally, the assumptions that are most binding are: (1) that population numbers and activity centers do not change during the sampling period; (2) that probability of capture does not change during the trapping period and is equal for all individuals; and (3) that the estimator can accommodate varying sizes of home ranges, from which data can be obtained in one trapping effort and the densities determined. Although these assumptions are not likely ever to be completely satisfied, Smith, *et al.* (1972) provided a rather complete strategy and model for dealing with them in the analyses.

This paper demonstrates the implementation of the Smith *et al.* (1972) model while at the same time, making some important adjustments. Perhaps the most important modification is the method used to partition trap avoidance, dispersal and death in the absence of a dense line of traps (Fig. 1). In long term sampling efforts the estimator should approximate  $N$  and  $(\hat{N} - N)^2$  should be as small as possible for best accuracy. But, if population parameters such as recruitment and mortality are unknown, as they usually are, the estimator must be robust enough



to accommodate the changes; and if possible, provide some indication of what is actually happening to the population during the trapping period. The estimator (*EM-2*) described and demonstrated in this paper, attempts to deal with these problems.

The field design seems quite adequate to provide the necessary data and performed precisely as Smith *et al.* (1972) predicted it would, except the dense-line tended to prevent dispersal rather than measuring it. This was possibly due to its placement. Few animals in all of the experiments were recorded as coming onto or leaving the grid, possibly because of the distance between the grid and the dense-line. Indications are that this distance can be reduced and provide even better data from which the parameters can be partitioned, along with a meaningful reduction in the field effort. The experiments reported here are essentially without dense-line data, since so few animals used it. Better estimates of  $N_i$  would have been obtained if the dense-line did provide data that would assist in the partitioning.

Efficiencies of this estimator (*EM-2*) are observed in Tables 4 and 5, where considerable departures are evident. This is particularly true when data were obtained from a population that deliberately failed to satisfy the assumptions stated earlier (Table 5). Perhaps the most important consideration at this point is whether or not the estimator tries to adjust to changes in the population; and in most cases, it does although not as rapidly as would be desired. Whether or not these departures are greater or less than what other methods provide must be analysed further, since *EM-2* might still provide the most accurate estimate. A comparative study is presently being conducted and the results will be available soon.

A most serious limitation of many estimators is the lack of meaningful methods for obtaining confidence limits on the estimate. The *EM-2* is no exception, although the method described is acceptable. Its basic problems are inevitable wide limits, in most cases too wide to be helpful unless there are rather large numbers of animals moving onto the grid. If the methods for estimating confidence are good, the results would suggest that the dense-line could be considerably closer to the grid, perhaps even the outer two lines of traps on the grid.

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#### OCENA LICZEBNOŚCI MAŁYCH SSAKÓW METODĄ POWTÓRNYCH ZŁOWIEŃ, ZE ZMIENNYMI DZIELONYMI

##### Streszczenie

Metoda oznaczania liczebności i zagęszczenia drobnych ssaków z podziałem estymatora została przedstawiona przez Smitha, Jorgensena i Tolley'a w 1972 roku. Choć ich model (*EM-1*) nie był zbyt praktyczny, bowiem wymagał danych uzyskiwanych na powierzchniach o dużej gęstości linii, to jednak stworzył podstawę do niniejszych modyfikacji i metod uzupełniających. Główna zmiana polega na podaniu estymatora (*EM-2*), który nie wymaga dużego zagęszczenia linii ani dużego zagęszczenia pułapek. Obecna metoda może być używana prawie do wszystkich rodzajów powierzchni odłownych, o ile stosuje się łowienie i wypuszczanie zwierząt.

Podana metoda pozwala także na ustalenie danych dla poszczególnych dni całego okresu odłowów a więc uchwycenie zmian w badanej populacji. Większość estymatorów cechuje się zbyt małą liczbą potrzebnych wskaźników, natomiast *EM-2* posiada wiele wskaźników przeliczeniowych i współczynników prawdopodobieństwa, które są pomocne przy obliczaniu parametrów populacyjnych.

Dla przykładu pokazano jak działa przyjęty estymator w odniesieniu do symulowanych populacji, w sytuacji kiedy liczebność była stała. Stanowiło to podstawę do oceny wyników innych badań. Ogólnie można powiedzieć, że ustalenia było najwierniejsze dla ostatnich dni odłowów, nawet w sytuacji kiedy liczebność populacji była zmienna.