

# MARK–RECAPTURE ESTIMATES OF POPULATION PARAMETERS FOR SELECTED SPECIES OF SMALL MAMMALS

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We used program CAPTURE to analyze 1,535 capture–recapture data sets from 33 species of small mammals for sources of variation in capture probabilities and to characterize species-specific responses to mark–recapture trapping. Program CAPTURE contains 8 models to account for all possible combinations of heterogeneity (h), behavioral response (b), and time (t) effects on capture probabilities. Model  $M_0$  (equal capture probabilities) was selected most often by CAPTURE as the most appropriate model for small sample sizes, reflecting the difficulty of detecting unequal probabilities of capture in small data sets. Heterogeneity in capture probabilities among individuals was evident in larger data sets for all species of small mammals examined. Strong behavioral responses were detected in several species. *Sylvilagus*, *Tamias amoenus*, *Glaucomys sabrinus*, *Perognathus longimembris*, and *Microtus ochrogaster* were trap shy, whereas *Tamias striatus*, *Tamias townsendii*, *Spermophilus richardsonii*, *Perognathus parvus*, *Reithrodontomys megalotis*, *Peromyscus maniculatus*, *Peromyscus truei*, *Sigmodon hispidus*, *Microtus californicus*, and *Microtus pennsylvanicus* were trap prone. Time effects were not apparent for most species except where they were accompanied with heterogeneity. Murid species had the highest estimated probabilities of capture, followed by heteromyids, sciurids, and leporids in decreasing order. Estimates of abundance from model  $M_h$  were significantly greater than those from models  $M_b$ ,  $M_0$ , and  $M_t$ , which likely reflects the negative bias of these latter estimators.

Key words: behavioral response, capture probabilities, capture–recapture studies, heterogeneity, program CAPTURE, small mammal abundance, time effects

Multiple mark–recapture models have been used widely to estimate abundance of small-mammal populations; however, small sample sizes or failure of assumptions often lead to biased estimates of capture probabilities and abundance. Small sample sizes may result from low animal densities, low probabilities of capture, or inadequate sampling designs (White et al. 1982). The assumption that capture probabilities are equal among individuals and different trap occasions was a fundamental assumption of some of the early estimators of animal abundance (Caughley 1977:134). Variation in capture probabilities can result from inherent heterogeneity among individuals, behavioral response after initial capture, and time effects (Otis et al. 1978). Probabilities of capture may differ among individuals (heterogeneity) depending on their sex, age, social status, activity

patterns, and on the location of traps in relation to centers of animal activity (Bailey 1969; Crowcroft and Jeffers 1961; Huber 1962; Melchior and Iwen 1965; Perry et al. 1977; Smith 1968; Summerlin and Wolfe 1973). Individuals of some species may be less likely to enter traps previously occupied by other species (Boonstra et al. 1982; Heske and Repp 1986) or by dominant conspecifics (Wuensch 1982). Conversely, individuals of several rodent species more readily enter traps occupied previously by conspecifics (Daly and Behrends 1984; Heske 1987; Montgomery 1979; Stoddart and Smith 1986), especially those of the opposite sex (Drickamer 1984; Mazdzer et al. 1976) or that they themselves had occupied (Daly and Behrends 1984). Removal of some individuals of a population also may increase capture probabilities of conspecifics (Verts and Carraway 1986). Stoddart and Smith (1986) also concluded that trap-borne odors introduce significant bias into livetrapping procedures. All of these potential influences on capture probabilities contribute to heterogeneity of capture probabilities among individuals.

On the other hand, behavioral response is a function of capture history and is categorized as trap prone (individuals

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have higher probabilities of recapture than of initial capture), trap shy (individuals have lower probabilities of recapture than of initial capture), or trap neutral (individuals have equal probabilities of recapture and initial capture). Mammalian populations usually have either mostly trap-prone (Edwards and Eberhardt 1967; Geis 1955; Tanaka 1956), trap-shy (Balph 1968; Tanaka 1956), or trap-neutral (Tanaka 1956) individuals after initial capture. Behavioral response may even be inherited instead of being a direct result of previous positive or negative encounters with traps (Crowcroft and Jeffers 1961). Lastly, time of trapping influences probabilities of capture, because weather, season, and time of day affect activity patterns of mammals (Doucet and Bider 1974; Drickamer 1987; Gauthier and Bider 1987; Getz 1961; Perry et al. 1977; Scheibe 1984).

Otis et al. (1978) developed program CAPTURE for estimating animal abundance for closed populations from multiple mark-recapture data, and the program was modified to include additional estimators (Rexstad and Burnham 1991). Program CAPTURE is based on models for closed populations in which capture probabilities vary due to time, behavioral response, and individual heterogeneity. CAPTURE incorporates the following 8 models and estimators:  $M_0$  = probability of capture is constant among individuals and over time (null model);  $M_h$  = probability of capture differs among individuals (heterogeneity—Burnham and Overton 1979; Chao 1988);  $M_b$  = probability of recapture differs from that of initial capture (behavioral effects—Zippin 1958);  $M_t$  = probability of capture differs with each trapping occasion (time effects—Chao 1989; Darroch 1958);  $M_{bh}$  = behavioral and heterogeneity effects (Otis et al. 1978; Pollock and Otto 1983);  $M_{th}$  = time and heterogeneity effects (Chao et al. 1992);  $M_{tb}$  = time and behavioral effects (Rexstad and Burnham 1991); and  $M_{tth}$  = time, behavioral, and heterogeneity effects (no estimator). CAPTURE program provides an estimate of the mean maximum distance moved between successive captures, a test for population closure, chi-square goodness-of-fit tests of data to models, ranking of models from the most to least appropriate, estimates of initial capture ( $\hat{p}$ ) and recapture ( $\hat{c}$ ) probabilities, and estimates of abundance with 95% confidence intervals. These features allow data to be analyzed for sources of variation in capture probabilities and permit objective selection of the appropriate model and estimator, assuming that the data are sufficient to test for differences in capture probabilities.

Because species differ in their activity patterns, inherent capture probabilities, and behavioral response to trapping methods and designs, a comparison of mark-recapture data from many taxonomic groups has been needed for some time. No capture-recapture study will provide unbiased estimates of population abundance unless the sampling design is specifically aimed at the particular species under study, and the behavior of the species must be understood before any attempts are made to compute statistically valid estimates of population size (Cormack 1968). Grid sizes, trap spacings, and the number of trapping occasions may be influential on a site- and species-specific basis. The purpose of this study was to characterize capture responses of selected species of small mammals to mark-recapture studies and to provide recommendations for

future such studies. We also provide data on distances of movement between successive captures that will be useful in determining the appropriate distance between trap stations.

## MATERIALS AND METHODS

Mark-recapture data sets were acquired from mammalogists who were willing to provide their data (see Appendix I). We identified potential data sets by reviewing scientific journals published between 1960 and 1990. Journals reviewed included *Acta Theriologica*, *American Midland Naturalist*, *Canadian Field-Naturalist*, *Canadian Journal of Zoology*, *Ecology*, *Journal of Mammalogy*, *Journal of Wildlife Management*, *Great Basin Naturalist*, *Ohio Journal of Science*, and *Northwest Science*. Emphasis was on North American taxa. Minimum requirements for usable data sets were no removal trapping,  $\geq 3$  trapping occasions,  $\geq 10$  individuals caught per study, trapping designs consisting of  $> 25$  traps, and mortality in traps  $< 10\%$  before the last trapping occasion. Forty-seven colleagues provided 1,535 usable data sets from 33 species (see Appendix I for a list of contributors). Insectivora species were not included because of high mortality in traps, which violated the assumption of population closure and resulted in minimum recaptures. The largest number of data sets was acquired for *Peromyscus maniculatus* ( $n = 283$ ), *Dipodomys merriami* ( $n = 188$ ), and *Sigmodon hispidus* ( $n = 177$ ), permitting more extensive analyses for these species. Small data sets with 10–19 trapped individuals generally resulted in selection of model  $M_0$  (Hammond 1990), so they were excluded from most of the analyses and results presented herein.

All raw data were formatted for CAPTURE, and animals that died in traps before the final trapping occasion were removed from data sets. In a few data sets, 1 or 2 trapping occasions were eliminated from either the beginning or end of a session to minimize time effects caused by unusually low or high numbers of captures related to inconsistent trapping procedures or sudden changes in weather that affected animal activity. All data sets were analyzed with program CAPTURE, and the following information was tabulated: probabilities from the 7 chi-square goodness-of-fit tests of models to the data, model-selection criteria, capture probability ( $\hat{p}$ ) from the models with estimators ( $M_0$ ,  $M_h$ ,  $M_b$ ,  $M_{bh}$ ,  $M_t$ ,  $M_{th}$ , and  $M_{tb}$ ), recapture probability ( $\hat{c}$ ) from model  $M_b$ , and mean maximum distance moved between successive captures. The assumption of population closure was not evaluated in this analysis, because “no truly suitable test for this assumption” is available (Otis et al. 1978:66) in CAPTURE, and “the test has poor power and is seldom capable of properly rejecting the null hypothesis of closure” (Rexstad and Burnham 1991:9).

*Sources of variation in capture probabilities.*—Model-selection criteria were compared from data sets with  $> 39$  animals captured and at least 6 trapping occasions to determine sources of variation in capture probabilities. Rankings of the models by CAPTURE were examined to detect violation of the assumption of equal probabilities of capture. Because the number of individual animals captured ( $M_{t+1}$ ) may influence selection of the most appropriate model (Menkens and Anderson 1988), data sets were divided arbitrarily into 3 sample sizes of  $M_{t+1} = 10$ –19, 20–39, and  $> 39$  based on the frequency distribution of sample sizes. Chi-square tests were used to detect differences in model selection within and among size classes. A model selected by CAPTURE to be the most appropriate for a data set does not always fit the data or provide estimates of population parameters (i.e.,  $M_{tth}$ ); therefore, selection criteria (range = 0.00–1.00) of all models were examined to choose a “best” model for the data. The best model provided estimates of population parameters, received the highest selection criterion  $> 0.75$ , and fit the data according to the chi-square

goodness-of-fit tests ( $P > 0.05$ ). Models  $M_{th}$  and  $M_{tb}$  were selected as best if selection criterion was  $>0.90$  and the coefficient of variation was  $<50\%$ . The percentage of times that each model was selected as best was calculated for each species, and chi-square tests were used to detect significant differences among genera within families and among species within genera ( $P < 0.01$ ).

The selection criteria of all the models in CAPTURE were used to identify sources of variation in capture probabilities. "Effect scores" (F. Ramsey, pers. comm.) were calculated from the model-selection criteria for heterogeneity (h), behavior (b), and time (t) effects by the following equations:

$$h = (M_h + M_{bh} + M_{th} + M_{tbh}) - (M_o + M_b + M_t + M_{tb}) \quad (1)$$

$$b = (M_b + M_{bh} + M_{tb} + M_{tbh}) - (M_o + M_h + M_t + M_{th}) \quad (2)$$

$$t = (M_t + M_{th} + M_{tb} + M_{tbh}) - (M_o + M_h + M_b + M_{bh}) \quad (3)$$

Effect scores potentially ranged from  $-3.91$  to  $+3.91$  if calculated from the most extreme set of selection criteria with 2 models sharing the top rank (e.g., 1.00, 1.00, 0.99, 0.98, 0.03, 0.02, 0.01, and 0.00). A positive score for h indicated that capture probabilities were heterogeneous; a negative score indicated that they were not. The same interpretation applies to b and t. Effect scores were calculated for each data set from each species, and a 2-tailed *t*-test was performed to determine whether the average scores were significantly greater than or less than 0.0.

**Capture probabilities and behavioral response.**—Average capture probabilities were calculated for each species from the best model for each data set. Analysis of variance and the protected least-significant difference ( $P < 0.05$ —Snedecor and Cochran 1980:232–237) were used to test for significant differences among taxa. To characterize the behavioral response for each species, we 1st calculated the ratio of probability of recapture to probability of 1st capture ( $\hat{c}_b/\hat{p}_b$ ) from model  $M_b$  for all data sets for which CAPTURE indicated a significant behavioral effect. This ratio also was used to characterize the response of a population as trap neutral if behavioral effect was not significant, trap prone if  $\hat{c}_b/\hat{p}_b > 1$ , or trap shy if  $\hat{c}_b/\hat{p}_b < 1$ . Chi-square tests were used to test for significant differences in behavioral response among species within genera, among species within families, and among genera within families.

Capture probabilities from the best model were regressed on the total number of individuals captured, trap spacing, and number of trapping occasions. STATGRAPHICS (STSC, Inc. 1988) was used to determine which of 4 regression models (exponential, linear, multiplicative, and reciprocal) resulted in the highest coefficient of determination ( $r^2$ ) for each relationship. Transformation of the raw data resulted in uniform residuals; however, nontransformed values are presented to ease understanding of curvilinear relationships.

**Animal movement.**—We used program CAPTURE to compute the mean maximum distance moved in meters for animals captured at least twice during each trapping session. When trap spacing differed among data sets for a species, analysis of variance was used to determine whether the trap spacing significantly influenced estimates of animal movement. The recommended trap spacing for a species was calculated as one-third average mean maximum distance moved, which resulted in the minimum of 4 traps per home range as recommended by White et al. (1982).

Differences between grid and assessment line data for *Perognathus longimembris*, *Chaetodipus formosus*, *Chaetodipus intermedius*, *Dipodomys merriami*, *Peromyscus maniculatus*, and *Peromyscus truei* were compared with chi-square tests to determine whether differences were significant between the 2 trapping designs. Only 1 species could be tested for selection of best model because of inadequate data for the

other species. Hammond (1990) found no significant chi-squared differences ( $P < 0.1$ ) between probabilities of capture for each of the 6 species; therefore, assessment line data were included in these analyses.

## RESULTS

**Selection of the best model (estimator).**—The model-selection criteria often followed patterns that frequently did not reflect actual sources of variation in capture probabilities. For example, when  $M_o$  was selected as the most appropriate model, the criteria for the other models followed a predictable order in magnitude, such that  $M_h$  was almost always 2nd, and  $M_{tbh}$  3rd. This was illustrated by the mean and *SD* of selection criteria from 102 data sets for *P. maniculatus*:  $M_o = 1.00$ ,  $M_h = 0.82 \pm 0.08$ ,  $M_{tbh} = 0.74 \pm 0.13$ ,  $M_{bh} = 0.65 \pm 0.12$ ,  $M_{th} = 0.48 \pm 0.14$ ,  $M_b = 0.32 \pm 0.15$ ,  $M_{tb} = 0.32 \pm 0.10$ , and  $M_t = 0.02 \pm 0.06$ . This pattern was not a function of size of the data set. Also when  $M_h$  was most appropriate,  $M_o$  and  $M_{tbh}$  were usually ranked next, followed by the other models incorporating heterogeneity (63 data sets;  $M_h = 1.00$ ,  $M_o = 0.78 \pm 0.14$ ,  $M_{tbh} = 0.72 \pm 0.16$ ,  $M_{bh} = 0.57 \pm 0.16$ ,  $M_{th} = 0.38 \pm 0.17$ ,  $M_b = 0.37 \pm 0.16$ ,  $M_{tb} = 0.34 \pm 0.13$ ,  $M_t = 0.00 \pm 0.01$ ). When model  $M_b$  was most appropriate, it usually was followed by models that incorporated behavioral effects then by  $M_o$  (27 data sets;  $M_b = 1.00$ ,  $M_{bh} = 0.70 \pm 0.20$ ,  $M_{tb} = 0.69 \pm 0.13$ ,  $M_{tbh} = 0.52 \pm 0.22$ ,  $M_{th} = 0.44 \pm 0.17$ ,  $M_o = 0.43 \pm 0.19$ ,  $M_h = 0.39 \pm 0.23$ ,  $M_t = 0.03 \pm 0.17$ ).  $M_t$  usually was followed by models that incorporated time effects then those incorporating behavioral effects (7 data sets;  $M_t = 1.00$ ,  $M_{th} = 0.75 \pm 0.07$ ,  $M_{tbh} = 0.43 \pm 0.25$ ,  $M_{tb} = 0.35 \pm 0.15$ ,  $M_b = 0.27 \pm 0.21$ ,  $M_o = 0.27 \pm 0.20$ ,  $M_h = 0.11 \pm 0.17$ ,  $M_{bh} = 0.03 \pm 0.05$ ).

Patterns of model selection varied significantly with size of data set ( $\chi^2 > 10.0$ ,  $P < 0.01$ ; Table 1). Model  $M_o$  was chosen most often when small numbers of individuals were captured ( $M_{t+1} = 10$ –19). However,  $M_o$  was selected significantly less as size of data set increased, whereas  $M_h$ ,  $M_b$ ,  $M_{bh}$ , and  $M_{tb}$  were selected more often (Table 1). Model  $M_h$  (32%) was selected more often than  $M_o$  for the larger data sets ( $M_{t+1} > 39$ ). Similar patterns were apparent within taxa (Table 1). Model  $M_h$  was selected more often than  $M_o$  for the largest data sets for all families and subfamilies except Sigmodontinae. Model  $M_b$  was chosen at least as often as  $M_o$  for the largest data sets for sciurids, *P. maniculatus*, and *S. hispidus*; models  $M_{bh}$  and  $M_{tbh}$  were selected more often than  $M_o$  for *P. maniculatus*. Consequently, most of the following results are taken from the larger ( $M_{t+1} > 19$ ) data sets.

When only larger data sets ( $M_{t+1} > 19$ ) were analyzed (Table 2), models  $M_o$  and  $M_h$  were selected most often (31% and 24%, respectively) as the most appropriate models. However,  $M_b$  and  $M_{tbh}$  were the most appropriate models for many species; models  $M_{bh}$ ,  $M_t$ ,  $M_{th}$ , and  $M_{tb}$  were selected relatively infrequently. Overall,  $M_h$  (heterogeneity) was selected  $>25\%$  of the time for *Sylvilagus floridanus*, *Spermophilus richardsonii*, *Glaucomys sabrinus*, *Perognathus parvus*, *Chaetodipus intermedius*, *Dipodomys merriami*, *Dipodomys ordii*, *Clethrionomys gapperi*, and *Microtus pennsylvanicus*, indicating heterogeneity among individuals in capture probabilities for

**TABLE 1.**—Percentage of time that each of the models was chosen by CAPTURE by 3 size classes of data sets for selected taxa of small mammals. Chi-square results are indicated for 2 comparisons: the distribution of each model across sample size classes (vertical) and the distribution of models within each size class (horizontal).

Taxa	Number of individuals trapped	Number of data sets	Most appropriate model (%)										$P^a$
			$M_0$	$M_h$	$M_b$	$M_{bh}$	$M_t$	$M_{th}$	$M_{tb}$	$M_{tth}$	$M_{tbh}$	$M_{tthb}$	
Leporidae	10–19	20	65	5	10	0	0	5	0	15			<sup>b</sup>
combined	20–39	23	52	22	0	9	0	0	0	17			
	>39	21	19	38	5	5	10	14	5	5			
Sciuridae	10–19	59	58	12	7	5	2	11	0	5			***
combined	20–39	56	32	23	14	7	5	5	2	11			***
	>39	50	10	20	20	12	4	6	0	28			***
Heteromyidae	10–19	98	66	8	2	4	0	7	2	10			**
combined,	20–39	91	45	23	4	5	2	9	3	8			***
except for	>39	82	22	35	9	7	5	5	7	10			***
<i>Dipodomys</i>	10–19	49	59	12	2	6	4	10	2	4			***
<i>merriami</i>	20–39	77	49	17	8	4	5	8	1	8			***
	>39	62	31	39	8	5	0	3	6	8			***
Muridae													
Sigmodontinae	10–19	90	62	4	3	1	4	8	0	17			***
combined,	20–39	68	37	26	12	6	3	4	1	10			***
except for	>39	26	35	12	19	0	4	4	15	12			
<i>Peromyscus</i>	10–19	108	64	1	6	4	1	8	2	14			***
<i>maniculatus</i>	20–39	99	26	9	30	4	4	5	4	17			***
	>39	76	9	26	20	12	1	4	7	21			**
<i>Sigmodon</i>	10–19	43	74	9	0	0	0	0	0	16			***
<i>hispidus</i>	20–39	83	41	16	10	11	2	5	2	13			***
	>39	51	16	43	16	6	4	6	2	8			***
Arvicolinae	10–19	63	68	6	0	2	3	14	3	3			***
combined	20–39	77	42	23	5	5	5	9	3	8			***
	>39	65	15	37	12	6	2	11	2	15			***
All taxa	10–19	528	64	7	4	3	2	8	1	11			***
combined	20–39	574	39	19	12	6	4	6	2	11			***
	>39	433	18	32	14	7	3	6	5	14			***
All		1,535	42	19	10	5	3	7	3	12			
Significance <sup>a</sup>			**	**	**	**				**			

<sup>a</sup> Asterisks indicate level of significance: \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

<sup>b</sup> Empty cells indicate too few data sets in 1 or more subclasses to do chi-square test.

these species. Model  $M_b$  (behavioral effects) was selected >25% of the time for *Tamias townsendii*, *Reithrodontomys megalotis*, and *P. maniculatus*, indicating behavioral responses to livetrapping by these species. Model  $M_{tth}$  was selected >25% of the time for *Sylvilagus nuttallii* and *T. townsendii*. Model  $M_h$  was selected most often for *S. floridanus*, *T. townsendii*, *S. richardsonii*, *P. parvus*, *C. intermedius*, and *M. pennsylvanicus*. Model  $M_b$  was selected at least as often as  $M_0$  for *T. townsendii*, *S. richardsonii*, *R. megalotis*, *P. maniculatus*, and *M. pennsylvanicus*; model  $M_{bh}$  more often for *T. townsendii*, *S. richardsonii*, and *P. parvus*; model  $M_t$  more often for *T. townsendii* and *P. parvus*; model  $M_{th}$  at least as often for *P. parvus* and *M. pennsylvanicus*; model  $M_{tb}$  more often for *P. parvus*; and model  $M_{tth}$  at least as often for *T. townsendii*, *S. richardsonii*, *P. parvus*, and *P. maniculatus*.

Selection of the “best model” for larger data sets ( $M_{t+1} > 19$ ) revealed that 0–31% of the data sets for each species fit a model without an estimator ( $M_{tth}$ ) in CAPTURE. However, model  $M_h$  was the best model more than twice as often for *S.*

**TABLE 2.**—Percentage of time that each CAPTURE model was chosen as the most appropriate model for selected species of small mammals. Data sets consist of at least 20 captured individuals.

Taxa	Number of data sets	Model selected (%)									
		$M_0$	$M_h$	$M_b$	$M_{bh}$	$M_t$	$M_{th}$	$M_{tb}$	$M_{tth}$	$M_{tbh}$	$M_{tthb}$
Leporidae											
<i>Sylvilagus floridanus</i>	31	32	39	3	10	6	3	3	3		
<i>S. nuttallii</i>	13	46	8	0	0	0	15	0	31		
Sciuridae											
<i>Tamias minimus</i>	12	25	17	0	17	17	17	0	8		
<i>T. townsendii</i>	26	4	15	38	8	8	0	0	27		
<i>Spermophilus richardsonii</i>	34	12	32	15	18	0	3	0	21		
<i>Glaucomys sabrinus</i>	18	44	33	6	0	0	11	0	6		
Heteromyidae											
<i>Perognathus longimembris</i>	28	57	11	7	11	0	0	4	11		
<i>P. parvus</i>	39	3	56	0	5	5	13	8	10		
<i>Chaetodipus formosus</i>	20	55	20	15	0	0	5	5	0		
<i>C. intermedius</i>	28	18	43	4	0	11	0	14	11		
<i>Dipodomys merriami</i>	139	41	27	8	4	3	6	4	8		
<i>D. microps</i>	22	55	9	9	5	5	14	0	5		
<i>D. ordii</i>	20	30	25	0	20	0	15	0	10		
Muridae											
Sigmodontinae											
<i>Reithrodontomys megalotis</i>	12	33	17	33	0	0	8	0	8		
<i>Peromyscus leucopus</i>	30	50	23	7	3	0	7	3	7		
<i>P. maniculatus</i>	175	19	17	26	7	3	5	5	19		
<i>P. truei</i>	41	32	12	12	7	7	2	10	17		
<i>Sigmodon hispidus</i>	129	33	24	12	9	3	5	2	12		
Arvicolinae											
<i>Clethrionomys gapperi</i>	37	35	32	3	3	0	11	0	16		
<i>C. rutilus</i>	28	39	18	7	7	11	11	4	4		
<i>Microtus ochrogaster</i>	24	54	13	13	8	4	0	0	8		
<i>M. pennsylvanicus</i>	36	11	42	17	8	3	11	3	6		
All	942	31	24	13	7	4	6	4	12		

*floridanus* than for *S. nuttallii*, and  $M_b$  was best 38% of the time for *T. townsendii* compared to never for *Tamias minimus*. *Perognathus* species differed significantly; more than half the time model  $M_0$  was selected as best for *P. longimembris* and  $M_h$  for *P. parvus*. Differences within *Peromyscus* and *Microtus* species also were significant. Model  $M_0$  was chosen much less often as best for *P. maniculatus* than for *Peromyscus leucopus* and *P. truei*. Model  $M_h$  was best 42% of the time for *M. pennsylvanicus* compared to 13% for *Microtus ochrogaster*. These results indicate considerable variability among genera and species within genera.

The effect scores for larger data sets revealed significant influences on capture probabilities, particularly the presence of strong heterogeneity and behavioral effects for some species (Table 3). Capture probabilities were significantly affected by heterogeneity for all species ( $t > 10.0$ ,  $P < 0.01$ ) and therefore most data sets. Behavioral response was significant for *T. townsendii*, *S. richardsonii*, *P. maniculatus*, and *P. truei*. Time effects were absent from most data sets because of a high failure rate ( $\bar{X} = 87\%$ , range = 44–100%) of the goodness-of-fit test of  $M_t$ , which usually caused  $M_t$  to receive a selection

**TABLE 3.**—Effects of heterogeneity (h), behavior (b), and time (t) on capture probabilities of selected species of small mammals.<sup>a</sup> Positive scores indicate selection of models associated with an effect; negative scores indicate rejection of an effect. Data sets consist of at least 20 captured individuals.

Taxa	n	Significance of effects					
		h	P <sup>b</sup>	b	P <sup>b</sup>	t	P <sup>b</sup>
Leporidae							
<i>Sylvilagus floridanus</i>	31	0.70	**	0.01		−1.00	**
<i>S. nuttalli</i>	13	0.88	**	−0.41		−0.38	
Sciuridae							
<i>Tamias minimus</i>	12	0.58	**	−0.35		−0.20	
<i>T. townsendii</i>	26	0.38	**	0.76	**	−0.59	**
<i>Spermophilus richardsonii</i>	34	0.96	**	0.46	**	−0.89	**
<i>Glaucomys sabrinus</i>	18	0.86	**	−0.19		−1.01	**
Heteromyidae							
<i>Perognathus longimembris</i>	28	0.80	**	0.13		−0.81	**
<i>P. parvus</i>	39	0.78	**	0.13		−0.48	**
<i>Chaetodipus formosus</i>	20	0.82	**	0.19		−1.03	**
<i>C. intermedius</i>	28	0.54	**	0.11		−0.58	
<i>Dipodomys merriami</i>	139	0.83	**	−0.07		−0.83	**
<i>D. microps</i>	22	0.79	**	−0.06		−0.81	**
<i>D. ordii</i>	20	1.01	**	−0.19		−0.87	**
Muridae							
Sigmodontinae							
<i>Reithrodontomys megalotis</i>	12	0.75	**	0.21		−0.70	
<i>Peromyscus leucopus</i>	30	0.81	**	0.18		−1.12	**
<i>P. maniculatus</i>	175	0.60	**	0.68	**	−0.64	**
<i>P. truei</i>	41	0.58	**	0.48	**	−0.53	**
<i>Sigmodon hispidus</i>	129	0.83	**	0.11		−0.86	**
Arvicolinae							
<i>Clethrionomys gapperi</i>	37	1.09	**	0.06		−0.97	**
<i>C. rutilus</i>	28	0.75	**	−0.08		−0.34	
<i>Microtus ochrogaster</i>	24	0.85	**	0.03		−0.85	**
<i>M. pennsylvanicus</i>	36	0.84	**	0.17		−0.67	**

<sup>a</sup> Effect scores were calculated from the model-selection criteria given by CAPTURE for each of the 8 models (details in text); values may range from −3.91 to +3.91.

<sup>b</sup> Values are effect scores and asterisks (\*\*) indicate level of significance ( $P < 0.01$ ).

criterion of 0.00, and because of the presence of strong heterogeneity and behavioral response.

**Capture probabilities and behavioral response.**—We found considerable variation in capture probabilities among families and genera. Leporids and sciurids had lower capture probabilities than heteromyids and murids (Table 4). *Sylvilagus* and *T. minimus* had the lowest capture probabilities (0.06–0.11), whereas *Dipodomys microps*, *P. leucopus*, and *Clethrionomys* had the highest capture probabilities (0.50–0.60). Capture probabilities varied significantly among genera in Sciuridae and both subfamilies of Muridae ( $\chi^2 > 6.0$ ,  $P < 0.05$ ). Capture probabilities of *S. richardsonii* were significantly greater than those of other sciurid genera; those of *Peromyscus* were high and exceeded those of *Sigmodon* and *Reithrodontomys*, and those of *Clethrionomys* were significantly greater than those of *Microtus*. Variation in capture probabilities was related to innate differences within a species, differences in locality, season of trapping, the model used to calculate ( $\hat{p}$ ), and field methodology.

**TABLE 4.**—Estimated probability of capture ( $\hat{p}$ ) computed by the best CAPTURE model for selected species of small mammals. Data sets consist of at least 20 captured individuals.

Taxa	$\hat{p}$			Comparison of genera within families <sup>a</sup>
	<i>n</i>	Mean	<i>SD</i>	
Leporidae				
<i>Sylvilagus floridanus</i>	27	0.06	0.03	
<i>S. nuttallii</i>	8	0.08	0.03	
Sciuridae				
<i>Tamias minimus</i>	10	0.11	0.11	A
<i>T. townsendii</i>	20	0.28	0.10	
<i>Spermophilus richardsonii</i>	21	0.32	0.14	B
<i>Glaucomys sabrinus</i>	14	0.18	0.14	A
Heteromyidae				
<i>Perognathus longimembris</i>	22	0.31	0.19	A
<i>P. parvus</i>	31	0.40	0.16	
<i>Chaetodipus formosus</i>	20	0.38	0.23	A
<i>C. intermedius</i>	25	0.37	0.13	
<i>Dipodomys merriami</i>	129	0.31	0.17	A
<i>D. microps</i>	19	0.55	0.14	
<i>D. ordii</i>	17	0.32	0.18	
Muridae				
Sigmodontinae				
<i>Reithrodontomys megalotis</i>	11	0.34	0.17	AB
<i>Peromyscus leucopus</i>	29	0.60	0.20	B
<i>P. maniculatus</i>	146	0.40	0.19	
<i>P. truei</i>	30	0.47	0.23	
<i>Sigmodon hispidus</i>	102	0.24	0.14	A
Arvicolinae				
<i>Clethrionomys gapperi</i>	33	0.50	0.13	A
<i>C. rutilus</i>	24	0.57	0.18	
<i>Microtus ochrogaster</i>	18	0.27	0.16	B
<i>M. pennsylvanicus</i>	32	0.28	0.17	

<sup>a</sup> Means of genera with the same letter within a family or subfamily were not significantly different ( $P > 0.05$ ). Differences within genera were not tested because data received for some species were the result of only 1 or 2 study designs.

Estimated probability of capture was negatively related ( $F > 11.5$ ,  $P < 0.01$ ) to number of trapping occasions for 6 species (Table 5), all of which were trap shy or neutral to initial capture (Tables 3 and 6). This relation was particularly strong ( $r > -0.70$ ) for *S. floridanus*, *T. minimus*, and *C. intermedius*. No significant correlations were found between capture probabilities and the number of individuals captured, the total number of captures, or trap spacing ( $F < 10.5$ ,  $P > 0.01$ ).

The ratio of recapture to capture probabilities for model  $M_b$  ( $\hat{c}_b/\hat{p}_b$ ) for larger data sets varied greatly among and within species because of extreme variability in behavioral response to livetrapping. Behavioral responses to livetrapping varied significantly among genera in all families ( $\chi^2 > 9.5$ ,  $P < 0.01$ ) and within *Tamias*, *Perognathus*, and *Peromyscus* species (Table 6). Two (*G. sabrinus* and *D. microps*) of the 3 species with the least variation in behavioral response were noticeably trap shy. *S. floridanus*, *S. nuttallii*, *T. minimus*, *P. longimembris*, *D. microps*, and *M. ochrogaster* tended to be trap shy also, although sample sizes were small for some of these species. *T. townsendii*, *S. richardsonii*, *P. parvus*, *R. megalotis*, *P. maniculatus*, *P. truei*, *S. hispidus*, and *M.*

**TABLE 5.**—Regression of estimated probability of capture ( $\hat{p}$ ) on number of occasions per trapping session for selected species of small mammals. The model yielding the highest coefficient of determination ( $r^2$ ) was chosen from 4 regression models.<sup>a</sup> Value given is  $r^2$  from relationships with a significant  $F$ -statistic ( $P < 0.01$ ).

Taxa	<i>n</i>	$r^2$	Regression equation
Leporidae			
<i>Sylvilagus nuttallii</i>	8	0.79** <sup>b</sup>	$y = 0.14x^{-0.31}$
Sciuridae			
<i>Tamias minimus</i>	10	0.59**	$y = 0.35 - 0.028x$
Heteromyidae			
<i>Perognathus parvus</i>	31	0.31***	$y = 0.69 - 0.058x$
<i>Chaetodipus intermedius</i>	25	0.64***	$y = 1.03x^{-0.84}$
<i>Dipodomys merriami</i>	129	0.29***	$y = 0.77x^{-0.67}$
Muridae			
Arvicolinae			
<i>Microtus pennsylvanicus</i>	32	0.21**	$y = \exp(-0.53 - 0.14x)$

<sup>a</sup> Models: exponential, linear, multiplicative, and reciprocal.

<sup>b</sup> Two asterisks (\*\*) indicate  $P < 0.01$ , and 3 asterisks (\*\*\*) indicate  $P < 0.001$ . Data sets consist of at least 20 captured individuals.

*pennsylvanicus* were trap prone, although a few data sets for some of these species indicated trap-shy responses. *P. parvus* was the only strongly trap-prone heteromyid (Table 6), whereas the other species in this family were either trap shy or neutral. There was considerable variability in behavioral responses among murid rodents.

**Animal movement.**—Mean maximum distance moved between successive captures varied greatly within and among species (Fig. 1). Sciurids moved greater distances than did murids, which, in turn, moved greater distances than did heteromyids (Figs. 1–3). Almost all mean maximum distances moved for sciurids were greater than the trap spacing used in studies of these species. *S. richardsonii* moved less than other sciurids, which may be partly a function of the smaller average trap spacing used in those studies, its fossorial behavior patterns, or both. *Perognathus* and *Dipodomys* species moved greater distances than did *Chaetodipus* (Fig. 2). Mammal movement varied significantly with trap spacing for 10 species ( $F > 10.5$ ,  $P < 0.01$ ), because spacing was often unique to each study. Small sample sizes were a problem in some of these analyses because trap spacings for some of the smallest number of data sets were associated with the highest or lowest mean maximum distance moved for a species. For example, only 2 of 22 *M. pennsylvanicus* trapping sessions occurred on a grid with 11.4-m trap spacing, and the average mean maximum distance moved of 4.7 m for this spacing was 17–29% of the mean maximum distance moved for the other data sets.

## DISCUSSION

Our analyses clearly indicated that many small-mammal species have characteristic responses to multiple mark-recapture trapping. The sources of variation in capture probabilities were identified by the most appropriate model selected by CAPTURE, our determination of the best model,

and the effect scores. Determination of behavioral response was impeded with some data sets because the test for differences between capture and recapture probabilities for model  $M_b$  was affected by low precision (i.e., small sample sizes). The proportions of data sets showing different categories of behavioral response provided the most reliable information. Only a few of the species showed a strong and consistent behavioral response to livetrapping. In contrast, virtually all species displayed heterogeneity in capture probabilities among individuals, and this was prominent throughout most data sets. This result emphasizes the importance of the estimators for models  $M_h$ ,  $M_{th}$ ,  $M_{bh}$ , and  $M_{tbh}$  for estimating abundance of small mammals. Model  $M_h$  has 2 estimators (Burnham and Overton 1979; Chao 1988), model  $M_{th}$  has 1 estimator (Chao et al. 1992), and model  $M_{bh}$  has 2 estimators (Otis et al. 1978; Pollock and Otto 1983) provided by program CAPTURE. Because there are many more parameters to estimate than minimum-sufficient statistics for these models, maximum-likelihood estimators for them did not exist for a period of time (Otis et al. 1978), and the above authors have derived estimators from other methods. More recently, Pledger (2000) derived a group of mixture models so that all the basic models of Otis et al. (1978) are placed in a maximum-likelihood framework. This allows one to run all 8 models, including  $M_{tbh}$ , in program MARK (White and Burnham 1999), which also provides Akaike information criterion model selection and model averaging (Burnham and Anderson 1998). In addition, Huggins (1991) developed an estimator to account for heterogeneity by observable covariates such as age, sex, weight, trapping history, or rainfall, but it is difficult to account for all sources of inherent heterogeneity. The estimators of Chao (1988, 1989) perform better than the other estimators when data are sparse and most individuals are captured only once or twice. Her estimators tend to be less biased and confidence interval coverage is usually closer to the nominal level (95%) than the jackknife estimators as shown by computer simulations (Chao 1988). For large sample sizes (>40 individuals captured more than twice), the jackknife estimators of Burnham and Overton (1979) and Pollock and Otto (1983) have minimum bias and good precision and are recommended with these data sets. The generalized removal estimator (Otis et al. 1978) has a negative bias, which can be large if capture probabilities are very heterogeneous (Pollock and Otto 1983). For large data sets, the jackknife estimators of Pollock and Otto (1983) or Burnham and Overton (1979) will have less negative bias. In fact, the expectation of the Pollock and Otto (1983) estimator is equivalent to the 1st-order jackknife estimator of Burnham and Overton (1979).

The effect of time on capture probabilities was rejected for most of the species of small mammals and data sets, although some of the data sets showed time effects due to extreme weather changes and particularly multiple trapping occasions in a 24-h period. Time effects on capture probabilities in addition to heterogeneity and behavior responses complicated abundance estimation, because model  $M_{tbh}$  does not have an estimator in program CAPTURE, and the statistical properties of the estimator for model  $M_{tb}$  have not been described

**TABLE 6.**—Proportion (%) of data sets showing behavioral response to mark–recapture trapping by selected species of small mammals.<sup>a</sup>

Taxa	n	Trap response (% of data sets)			$\chi^2$ value for differences <sup>c</sup>		
		Shy <sup>b</sup>	None <sup>c</sup>	Prone <sup>d</sup>	Among species within families	Among genera within families	Among species within genera
Leporidae							
<i>Sylvilagus floridanus</i>	30	13.3	80.0	6.7			0.45
<i>S. nuttallii</i>	6	16.7	83.3	0.0			
					44.64***	18.30**	
Sciuridae							
<i>Tamias minimus</i>	11	9.1	90.9	0.0			27.03***
<i>T. townsendii</i>	20	0.0	5.0	95.0			
<i>Spermophilus richardsonii</i>	9	11.1	33.3	55.6			
<i>Glaucomys sabrinus</i>	17	11.8	88.2	0.0			
					47.89***	15.94**	
Heteromyidae							
<i>Perognathus longimembris</i>	20	30.0	70.0	0.0			19.48***
<i>P. parvus</i>	33	0.0	54.5	45.5			
<i>Chaetodipus formosus</i>	19	15.8	68.4	15.8			0.31
<i>C. intermedius</i>	28	10.7	75.0	14.3			
<i>Dipodomys merriami</i>	123	12.2	79.7	8.1			2.85
<i>D. microps</i>	22	13.6	86.4	0.0			
<i>D. ordii</i>	17	5.9	82.4	11.8			
					61.16***	29.96***	
Muridae							
					27.45***	5.23	
Sigmodontinae							
<i>Reithrodontomys megalotis</i>	9	0.0	55.6	44.4			
<i>Peromyscus leucopus</i>	30	10.0	76.7	13.3			22.37***
<i>P. maniculatus</i>	172	2.9	42.4	54.7			
<i>P. truei</i>	36	11.1	52.8	36.1			
<i>Sigmodon hispidus</i>	73	8.2	58.9	32.9			
					13.35	3.07	
Arvicolinae							
<i>Clethrionomys gapperi</i>	36	2.8	75.0	22.2			6.21
<i>C. rutilus</i>	26	19.2	73.1	7.7			
<i>Microtus ochrogaster</i>	17	23.5	64.7	11.8			4.22
<i>M. pennsylvanicus</i>	34	8.8	55.9	35.3			

<sup>a</sup> Results are from model  $M_b$  with results of chi-square tests of behavioral response for different taxonomic groups included.

<sup>b</sup> CAPTURE test for behavioral response was significant ( $P < 0.05$ ), and  $\hat{c}_b/\hat{p}_b < 1.0$ .

<sup>c</sup> CAPTURE test for behavioral response was not significant ( $P \geq 0.05$ ).

<sup>d</sup> CAPTURE test for behavioral response was significant ( $P > 0.05$ ), and  $\hat{c}_b/\hat{p}_b > 1.0$ .

<sup>e</sup> Level of significance is indicated by 2 asterisks (\*\*),  $P < 0.01$ , or 3 asterisks (\*\*\*),  $P < 0.001$ . Data sets consist of  $>20$  captured individuals.

(Rexstad and Burnham 1991). However, Chao et al. (1992) developed a nonparametric estimator for model  $M_{th}$  that is recommended when capture probabilities are low and data are sparse; it is the only estimator for this model provided in program CAPTURE. We recommend study designs that attempt to minimize time effects on capture probabilities for the above reasons. This can be done by avoiding multiple capture occasions during a 24-h period, avoiding trapping during extreme weather conditions, and making sure effort is constant among trap occasions.

Models in program CAPTURE generally provide less biased estimates than the Lincoln–Petersen estimator, enumeration methods (Otis et al. 1978), and open-population models (Nichols 1986). Chi-square goodness-of-fit tests and model rankings can be used to identify sources of variation in capture probabilities, and CAPTURE can be used to determine the most-appropriate model for a given data set. CAPTURE also can be used to estimate the mean maximum distance moved by the animals, which is useful in estimating density (Wilson and Anderson 1985). Despite its utility, CAPTURE requires a large

amount of data for model selection. CAPTURE frequently failed to select the correct model for simulated data sets with  $<50$  individuals, resulting in biased estimates from the inappropriate model (Menkens and Anderson 1988; White et al. 1982). Menkens and Anderson (1988) suggested that an estimator be chosen subjectively, based on the CAPTURE results and on knowledge of the study population. Based on our results, we recommend that capture–recapture results should consist of  $>5$  trapping sessions and  $\geq 40$  captured individuals ( $M_{t+1}$ ) with  $\hat{p} > 0.2$  in order for the user to rely on the model-selection criteria provided by CAPTURE.

Specific weaknesses of the model-selection procedure in CAPTURE include the large data requirements for the chi-square goodness-of-fit tests. When one of the chi-square tests fails because of insufficient data, the resulting chi-square probability is set at 0.5. In our analyses, the goodness-of-fit test for  $M_i$  (test 6) failed much of the time, and  $M_i$  usually received a very low or high model-selection criterion in these cases. Because  $M_0$  usually was selected as the most appropriate model for small data sets, the a priori probabilities of selecting each of the models in

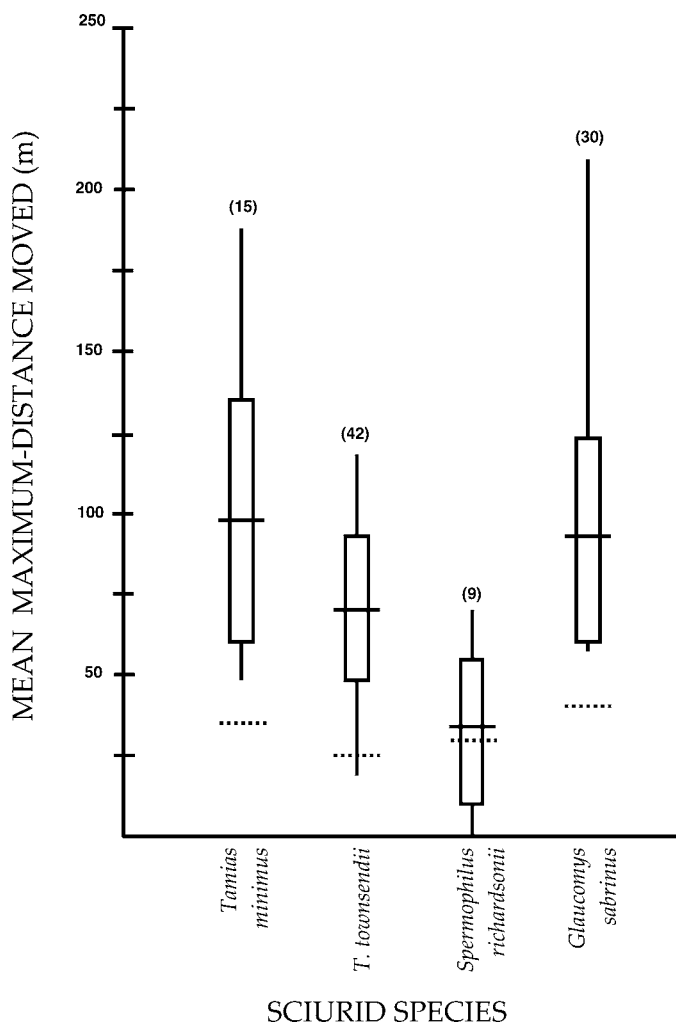


FIG. 1.—Mean, SD, and range of the mean maximum distance moved (m) between successive captures for sciurid species. Average trap spacing is indicated with a dotted line; sample size is in parentheses.

CAPTURE probably should be unequal in the discriminate-function analysis algorithm. Models  $M_h$ ,  $M_b$ , and  $M_{bh}$  are more realistic and were selected more frequently for larger data sets; they should be given higher a priori probabilities of selection in the CAPTURE algorithms. The user must be aware of the small sample limitations of the program and be able to recognize spurious results. When CAPTURE selects  $M_o$  as most appropriate for small data sets, the user could decide incorrectly that capture probabilities were equal, which is highly unlikely.

Small grids (<100 trap stations) rarely provide adequate numbers of traps to capture sufficient individuals in a population. They also have a greater edge effect than do larger grids, resulting in greater probability of bias when determining the effective trapping area of a grid for estimates of density. Traps are often set too far apart for many species so the commonly used spacing (15–20 m) needs to be reduced to place at least 4 traps in a home range (White et al. 1982). Use of pitfall traps instead of metal live traps may increase captures for some species or age classes within a species (Boonstra and Krebs 1978; Williams and Braun

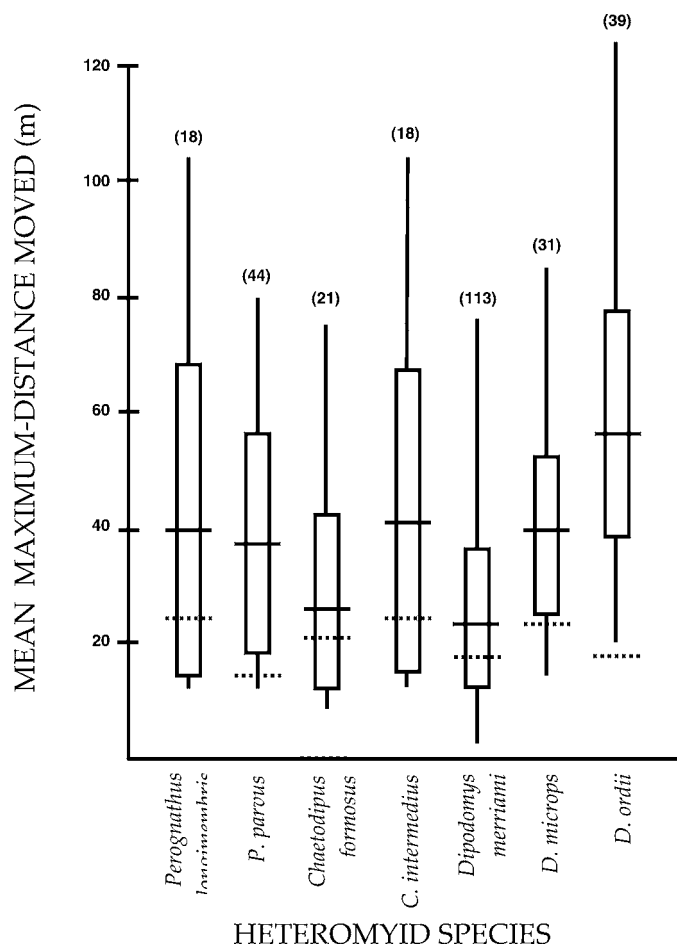


FIG. 2.—Mean, SD, and range of the mean maximum distance moved (m) between successive captures for heteromyid species. Average trap spacing is indicated with a dotted line; sample size is in parentheses.

1983), but these traps often result in considerable mortality, which creates biases in the model-selection and population estimators in program CAPTURE. High trap mortality should be avoided at all costs, because program CAPTURE will interpret mortalities as a trap-shy response and potentially select the inappropriate model and estimator for the data.

Use of program CAPTURE or MARK is recommended to estimate abundance and to detect sources of variation in capture probabilities. We recommend 5–10 trapping occasions except for species with low capture probabilities and higher annual survival such as *Sylvilagus* species, *T. minimus*, and *G. sabrinus* (Rosenberg et al. 1995). Designs for these species may require 15–25 trapping occasions (Rosenberg et al. 1995). CAPTURE can select reliable models from <10 occasions, if enough animals are caught and recaptured. This can be achieved with a large grid of at least 100–150 traps and by reducing trap spacing to  $\leq 10$ –15 m when animal movement is low.

Open population models (Jolly 1965; Seber 1965) also are available for estimating abundance when deaths, births, or movements in or out of an area of study are anticipated. Unfortunately, the estimators for these models require large



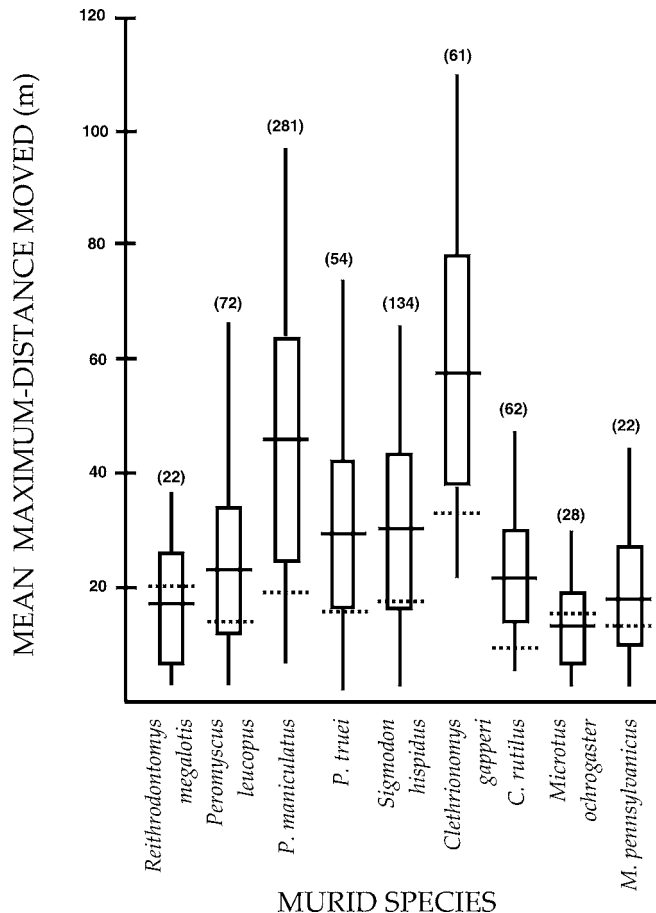


FIG. 3.—Mean, SD, and range of the mean maximum distance moved (m) between successive captures for murid species. Average trap spacing is indicated with a dotted line; sample size is in parentheses.

(>100 captures/occasion) data sets that are difficult to obtain in most mammal studies (Jolly 1965). In addition, they allow for only time effects on capture probabilities (model  $M_t$ ), not heterogeneity or behavioral responses (White et al. 1982). Consequently, abundance estimates from these models tend to be negatively biased (Nichols and Pollock 1983) and lack precision. Also, estimates from the Jolly–Seber model were highly variable and often unrealistic from one trap occasion to the next, and they rarely exceeded the total number of individuals captured (Hammond 1990). In contrast, this model has been used quite effectively for estimating survival rates with program MARK for many kinds of animals (Lebreton et al. 1992; Pollock et al. 1990).

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## APPENDIX I

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