

AN ABSTRACT OF THE THESIS OF

Ellen L. Hammond for the degree of Master of Science  
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for Selected Species of Small Mammals

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Abstract approved: \_\_\_\_\_

Robert G. Anthony

I used program CAPTURE to analyze 1,535 data sets for 33 North American species of small mammals for sources of variation in capture probabilities and to characterize species-specific responses to mark-recapture trapping. CAPTURE incorporates seven models to account for all possible combinations of heterogeneity (h), behavioral response (b), and time effects (t) on capture probabilities, in addition to the null model ( $M_0$ ) which requires equal capture-probabilities. The following information was tabulated for each data set: 1) results of the closure test; 2) probabilities of fit of the data to the models; 3) model-selection criteria; 4) abundance estimates, confidence intervals, and estimated probabilities of capture and recapture; and 5) mean maximum-distance moved.

Population closure was not rejected 70-100% of the time for 30 species when models  $M_0$  or  $M_h$  were chosen by CAPTURE. Differences within families were significant only for Heteromyidae. Frequency of

closure decreased significantly as length of trapping session increased for 4 of 5 species for which I performed the test.

Model  $M_0$  was selected most often by CAPTURE as the most appropriate model for most species, which merely reflected the inability of the program to detect unequal probabilities of capture from small data sets. However, heterogeneity was evident in Sylvilagus floridanus, Tamias townsendii, Spermophilus richardsonii, Glaucomys sabrinus, Peroznathus parvus, Chaetodipus intermedius, Dipodomys merriami, Dipodomys ordii, Reithrodontomys spp., Peromyscus maniculatus, Sigmodon hispidus, Clethrionomys spp., Microtus californicus, and M. pennsylvanicus. Strong behavioral responses (trap proneness or trap shyness) were detected in I. townsendii, S. richardsonii, R. megalotis, P. maniculatus, and M. pennsylvanicus. Time effects, particularly with heterogeneity, were apparent for Sylvilagus nuttallii, Tamias minimus, D. ordii, C. gapperi, M. californicus, and M. pennsylvanicus. Sylvilagus spp., Tamias amoenus, G. sabrinus, Peroznathus longimembris, and Microtus ochrogaster were trap shy. Tamias striatus, I. townsendii, S. richardsonii, P. parvus, R. megalotis, P. maniculatus, Peromyscus truei, S. hispidus, M. californicus, and M. pennsylvanicus were trap prone. Murid species had the highest estimated probabilities of capture, followed in decreasing order by heteromyids, sciurids, and leporids.

Estimates of abundance from model  $M_h$  were greatest and often significantly greater than those from, in decreasing order,  $M_{bh}$ ,  $M_b$ ,  $M_0$ , and  $M_t$ . Coefficients of variation of abundance estimates from models  $M_b$  and  $M_{bh}$  were usually twice as great as those from models  $M_0$ ,  $M_h$ , and  $M_t$ , and the coefficients of variation from  $M_{bh}$  were

significantly greater than those from  $M_t$  and  $M_0$ . Coefficient of variation is not an appropriate measure of the reliability of abundance estimates from CAPTURE models.

Abundance estimates from the Jolly-Seber model were almost always less than those from CAPTURE models, regardless of which CAPTURE model was the most appropriate, and they rarely exceeded the total number of animals captured during the trapping session. The negative biases of these estimates were so great that they more likely were due to unequal probabilities of capture rather than to emigration.

MARK-RECAPTURE ESTIMATES OF POPULATION PARAMETERS  
FOR SELECTED SPECIES OF SMALL MAMMALS

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

## INTRODUCTION

Mark-recapture studies of animal populations usually are based on invalid assumptions that lead to biased estimates of population parameters, such as actual animal abundance and capture probabilities. Most traditionally used models are modifications of the Petersen-Lincoln method (Petersen 1896, Lincoln 1930) for estimating abundance ( $N$ ). This method consists of capturing and marking a sample of animals ( $M$ ), releasing the sample, and noting the proportion of marked individuals ( $m$ ) in a subsequent sample ( $n$ ). (Notation is defined in Appendix A.) It is assumed that this proportion ( $m/n$ ) equals the proportion of marked individuals in the population ( $M/N$ ), so the abundance estimate ( $\hat{N}$ ) equals  $Mn/m$ . Extensions of this model and their applications are reviewed in several references (Cormack 1968, Caughley 1977, Tanner 1978, Begon 1979, Blower et al. 1981, Seber 1982).

More complex methods, including modifications of the Petersen-Lincoln model, have been developed for use on closed populations (no gain or loss of individuals during a specified period of time). Most closed-population models have critical underlying assumptions:

- 1) The probability that an individual will be captured ( $p$ ) equals the probability of being recaptured ( $c$ ).

- 2) All individuals have the same inherent probability of being captured ( $p_i = p$ ,  $i = 1, \dots, N$ ).
- 3) No animal is recruited into or lost from the population between the time of marking and of recapture.

Schnabel (1938) first proposed the multiple-mark-recapture method to increase sample sizes and the reliability of the Petersen-Lincoln estimate. If individuals are marked, released, and recaptured in a closed population  $t$  times, the number of marked individuals in the population before the  $j$ th sample,  $M_j$ , is always known. The situation then becomes identical to a parallel series of Petersen-Lincoln estimates (Cormack 1968). A similar method was developed by Schumacher and Eschmeyer (1943).

When individuals are born, die, emigrate, or immigrate during the experiment, animal abundance must be estimated with open-population models. Open models allow for time effects on capture probabilities by permitting changes in abundance between captures and in capture probabilities at each occasion within a trapping session. Jolly (1965) and Seber (1965) independently developed an open-population model based on the Petersen-Lincoln model. In this case,  $M_j$  must be estimated, because it cannot be known in an open population. Abundance estimates from this model usually are biased negatively when assumptions 1) and 2) are violated (Cormack 1972, Nichols and Pollock 1983); however, the bias is reduced when capture probabilities are high (Jett et al. 1986). Many researchers recommended the Jolly-Seber model for quantifying the dynamics of open populations (Cormack 1968, Wilbur and Landwehr 1974, Blower et al. 1981, Nichols and Pollock 1983).

Multiple-mark-recapture models are used widely in studies of small-mammal populations; however, small sample sizes or failure of the assumptions often bias  $\hat{N}$ . Small sample sizes may result from low animal densities, low probabilities of capture, or inadequate sampling designs (White et al. 1982). Sample sizes and composition (sex/age classes) also can be influenced by trap type (Morris 1968, Boonstra and Krebs 1978, Mihok et al. 1982, Williams and Braun 1983, Boonstra and Rodd 1984), number of occasions per trapping session (Gentry et al. 1968, Olsen 1975), timing of trapping occasions (O'Farrell 1974, Scheibe 1984), trap spacing, and grid size. Trap spacing of less than the customary 15 m will increase the probability that an individual encounters a trap (Smith et al. 1975, Guthery and Herbert 1983). In addition, White et al. (1982) and Guthery and Herbert (1983) suggested that grids often are too small to sample a population adequately.

The assumption that capture probabilities are equal is crucial to the reliability of mark-recapture models used to estimate animal abundance (Caughley 1977:134). Failure of this assumption leads to nonrandom sampling of individuals, which results in negatively biased  $\hat{N}$ 's. Variation in capture probabilities can result from inherent heterogeneity, behavioral response, and time (Otis et al. 1978). Probabilities of capture differ among individuals (heterogeneity) depending on their social status, sex, age, and on the location of traps in relation to centers of animal activity (Crowcroft and Jeffers 1961, Huber 1962, Melchior and Iwen 1965, Bailey 1968, Smith 1968, Bailey 1969, Summerlin and Wolfe 1973, Perry et al. 1977). Behavioral response is a function of capture history and is categorized as:

- 1) trap prone = individuals have higher probabilities of recapture than of initial capture,
- 2) trap shy = individuals have lower probabilities of recapture than of initial capture, or
- 3) trap neutral = individuals have equal probabilities of recapture and of initial capture.

Populations may have mostly trap-prone (Geis 1955, Tanaka 1956, Edwards and Eberhardt 1967), trap-shy (Tanaka 1956, Balph 1968), or trap-neutral individuals (Tanaka 1956). Behavioral response may even be inherited instead of being a direct result of previous positive or negative encounters with traps (Crowcroft and Jeffers 1961). Time of trapping influences probabilities of capture, because weather, season, and time of day affect activity patterns of animals (Getz 1961, Doucet and Bider 1974, Perry et al. 1977, Scheibe 1984, Drickamer 1987, Gauthier and Bider 1987). In addition, individuals of some species may be less likely to enter traps entered previously by other species (Boonstra et al. 1982, Heske and Repp 1986) or by dominant conspecifics (Wuensch 1982). Removal of some individuals may increase capture probabilities of conspecifics (Verts and Carraway 1986). Individuals of several rodent species more readily enter traps occupied previously by conspecifics (Montgomery 1979, Daly and Behrends 1984, Stoddart and Smith 1986, Heske 1987), especially those of the opposite sex (Mazdzer et al. 1976, Drickamer 1984) or that they themselves had occupied (Daly and Behrends 1984). Stoddart and Smith (1986:199) concluded that "trap-borne odours introduce significant bias into live-trapping

procedures. Most rodent population ecologists seem unaware of this and make little attempt to correct for it."

Estimators from closed-population models have been tested on data from populations of known size (Edwards and Eberhardt 1967, Mares et al. 1981). The Lincoln-Petersen, Schnabel, and Schumacher-Eschmeyer methods underestimated the true population size because of failure of the assumption of equal probability of capture (Edwards and Eberhardt 1967, Mares et al. 1981). Width of confidence intervals for all 3 estimators decreased with increasing length of trapping session, and after 8 trapping occasions, only the Petersen-Lincoln estimator had confidence intervals that included the true population size (Mares et al. 1981). Use of the frequency of capture method (Eberhardt 1969) avoids the problems of unequal capture probabilities; animal abundance is estimated from the capture frequencies (the number of animals caught  $j$  times). The number of animals never caught is estimated by fitting the capture frequencies to a zero-truncated geometric distribution (Eberhardt 1969) or by use of the jackknife method (Burnham and Overton 1979).

Otis et al. (1978) developed a computer program, CAPTURE, for estimating animal abundance in a closed population from multiple mark-recapture data. CAPTURE is based on models for populations in which capture probabilities vary (Moran 1951, Zippin 1956, Darroch 1958, and Burnham and Overton 1979). It incorporates the following 8 models:

- 1)  $M_0$  = probability of capture is constant among individuals and over time (null model),



- 2)  $M_h$  = probability of capture differs among individuals (heterogeneity),
- 3)  $M_b$  = probability of recapture differs from that of initial capture (behavioral effects),
- 4)  $M_t$  = probability of capture differs with each trapping occasion (time effects),
- 5)  $M_{bh}$  = behavioral and heterogeneity effects,
- 6)  $M_{th}$  = time and heterogeneity effects,
- 7)  $M_{tb}$  = time and behavioral effects, and
- 8)  $M_{tbh}$  = time, behavioral, and heterogeneity effects.

Currently, no estimators for the last 3 models are available, because the number of population parameters to be estimated is greater than the number of minimum sufficient statistics (Otis et al. 1978). The CAPTURE program provides: 1) an estimate of the mean maximum-distance moved by animals, 2) a test for population closure, 3) chi-square goodness-of-fit tests of the data to the models, 4) ranking of the models from the most to least appropriate, 5) estimates of probability of initial capture ( $\hat{p}$ ) and recapture ( $\hat{c}$ ), and 6) estimates of abundance with 95% confidence intervals (Appendix B). These features allow data to be analyzed for sources of variation in capture probabilities and permit objective selection of the appropriate model.

There is a need to analyze and compare mark-recapture data from many taxonomic groups, because species differ in their activity patterns, inherent capture probabilities, and behavioral response to trapping methods and study designs.

[No] capture-recapture study will give [unbiased] estimates unless the sampling technique is specifically aimed at the particular species under study: and, the behaviour of the species must be understood before any attempts are made to provide statistically valid estimates of the population parameters. (Cormack 1968:473)

Grid sizes, trap spacing, and the number of trapping occasions may be influential on a site- and species-specific basis. In the most extreme case, a design suitable for 1 species may be inadequate to reliably estimate abundance of coexisting species. If assumptions likely to be violated are known in advance, the study design can be adjusted to minimize expected biases.

The purpose of this study was to characterize responses of selected species of small mammals to multiple mark-recapture and to evaluate estimates of population parameters from widely varying study designs. I used the CAPTURE program to: 1) determine species-specific trends in the violation of assumptions of population closure and equal probabilities of capture, 2) identify the most appropriate closed-population model for a species, 3) characterize behavioral responses to trapping, 4) evaluate trapping designs, and 5) compare  $\hat{N}$ 's from closed and open (Jolly-Seber) population models. This exercise also allowed me to evaluate CAPTURE as a tool for analyzing mark-recapture data and to provide guidelines for future mark-recapture studies.

## METHODS

Mark-recapture data sets were acquired from ecologists who had already published their data or were willing to provide unpublished data. Potential data sets were identified by examining scientific journals published since 1960. Journals surveyed included Acta Theriologica, American Midland Naturalist, The Canadian Field-Naturalist, Canadian Journal of Zoology, Ecology, Journal of Mammalogy, The Journal of Wildlife Management, Great Basin Naturalist, Ohio Journal of Science, Pacific Science, and others. Emphasis was on North American taxa. Minimum requirements for usable data sets (trapping sessions) were: no removal trapping,  $\geq 3$  trapping occasions,  $\geq 1$  trapping occasion per day,  $\geq 10$  individuals caught, trapping designs consisting of  $\geq 25$  traps, and mortality in traps  $< 10\%$  before the last trapping occasion.

All raw data were formatted for CAPTURE, and animals that died in traps before the final trapping occasion were deleted from the data sets. Data from studies in which the environment or animals were manipulated were used for only pre- or post-treatment trapping sessions. Data from grids straddling disjunct habitats were divided into corresponding data sets. In some data sets, 1 or 2 trapping occasions were eliminated from either the beginning or end of a session to minimize time effects caused by unusual numbers of captures related to inconsistent trapping procedures or sudden changes in weather that affected animal activity. Data from multiple trapping occasions per 24 h usually resulted in systematic, cyclic patterns of

capture probabilities (e.g. 6 occasions in 2 or 3 days:  $\hat{p} = 0.65, 0.08, 0.60, 0.04, 0.68, 0.05$ ;  $\hat{p} = 0.71, 0.52, 0.18, 0.78, 0.43, 0.09$ , respectively). Such time effects are undesirable because they often lead to selection of models with no estimators ( $M_{th}$ ,  $M_{tb}$ ,  $M_{tbh}$ ), and they obscure evidence of other sources of variation in capture probabilities. Cyclic time-effects can be avoided easily by trapping only once per day or by combining captures from all daily trapping occasions. Therefore, data with cyclic time-effects were reformatted; depending on the form of the raw data, trapping occasions occurring at certain times were eliminated or all daily trapping occasions were combined. Data with non-cyclic changes in capture probabilities were not reformatted.

All data sets were analyzed with CAPTURE, and the following information was tabulated: 1) results of the closure test; 2) probabilities from the 7 chi-square goodness-of-fit tests of models to the data; 3) model-selection criteria; 4)  $\hat{N}$ , confidence interval, and  $\hat{p}$  from the models with estimators ( $M_0$ ,  $M_h$ ,  $M_b$ ,  $M_{bh}$ ,  $M_t$ ); 5)  $\hat{c}$  from  $M_b$ , and 6) mean maximum-distance moved. The assumption of population closure was evaluated only for those data sets for which models  $M_0$  or  $M_h$  were chosen as the most appropriate (Otis et al. 1978). Closure was not rejected when the  $P$ -value from the test for population closure was  $>0.05$ , however, Otis et al. (1978:66) cautioned that "no truly suitable tests for this assumption" are available. Chi-square tests were used to detect significant differences in closure among species within families, among genera within families, and among species within

genera. When at least 1 of the expected values was  $<5$ , a chi-square test incorporating the continuity correction factor was used.

The Mantel-Haenszel (1959) test was used to detect an association between results of the closure test and length of trapping session, trap spacing, or grid size. The Mantel-Haenszel test detects a linear association between 2 variables and is an extension of the chi-square test. The statistic is the excess number of a certain variable, summed over independent  $2 \times 2$  contingency tables. The total variance is the sum of the variance of the excess for each table. The total excess, when divided by the square root of the total variance, is the  $Z$ -statistic and it follows a normal distribution. In my analyses, 1 variable was the number of closed as opposed to open populations and the factor (other variable) was the number of occasions ( $t$ ) per trapping session (Table 1). Table 1A includes all the values used in the calculations. Table 1B illustrates the calculations for the excess number of closed populations when  $t = 3$ . The number of closed populations expected if closure were a random process when  $t = 3$  was calculated as a chi-square test:  $(\text{number of closed populations})(\text{number of trapping occasions with } t = 3)/(\text{total number of populations})$ . The 'excess' number of closed populations equaled the number observed minus the number expected. Then, all data from  $t = 3$  were ignored, and  $t = 4$  was compared with  $t > 4$  (Table 1C), and so on.

Rankings of the models by CAPTURE were examined to detect violation of the assumption of equal probabilities of capture. Because the number of animals captured ( $M_{t+1}$ ) may influence selection of the most appropriate model (Menkens and Anderson 1988), data sets were

Table 1. Demonstration of the Mantel-Haenszel test, used to determine a linear relationship between the number of occasions (t) per trapping session and the results of the test for population closure. Formulas for excess (E) and variance (V) are given.

A. ALL DATA IN A 2x6 TABLE

Population closure	t				Total number of data sets
	3	4	5	6	
Not rejected	$C_3$	$C_4$	$C_5$	$C_6$	$C_{3-6}$
Rejected	$O_3$	$O_4$	$O_5$	$O_6$	$O_{3-6}$
	$T_3$	$T_4$	$T_5$	$T_6$	$T$

B. EXCESS FOR t = 3

Population closure	t		Total number of data sets
	3	>3	
Not rejected	$C_3$	$C_{4-6}$	$C_{3-6}$
Rejected	$O_3$	$O_{4-6}$	$O_{3-6}$
	$T_3$	$T_{4-6}$	$T$

$$E_3 = C_3 - [C_{3-6}T_3/T]$$

$$V_3 = (C_{3-6}O_{3-6}T_3T_{4-6})/T^2(T-1)$$

C. EXCESS FOR t = 4

Population closure	t		Total number of data sets
	4	>4	
Not rejected	$C_4$	$C_{5-6}$	$C_{4-6}$
Rejected	$O_4$	$O_{5-6}$	$O_{4-6}$
	$T_4$	$T_{5-6}$	$T_{4-6}$

$$E_4 = C_4 - [C_{4-6}T_4/T_{4-6}]$$

$$V_4 = (C_{4-6}O_{4-6}T_4T_{5-6})/(T_{4-6}^2(T_{5-6}-1))$$

D. EXCESS FOR t = 5

Population closure	t		Total number of data sets
	5	6	
Not rejected	$C_5$	$O_6$	$C_{5-6}$
Rejected	$O_5$	$O_6$	$O_{5-6}$
	$T_5$	$T_6$	$T_{5-6}$

$$E_5 = C_5 - [C_{5-6}T_5/T_{5-6}]$$

$$V_5 = (C_{5-6}O_{5-6}T_5T_6)/(T_{5-6}^2(T_6-1))$$

E. TOTAL FOR t = 3-6

$$\text{Excess} = E = E_3 + E_4 + E_5$$

$$\text{Variance} = V = V_3 + V_4 + V_5$$

$$\text{Mantel-Haenszel test statistic} = Z = E/V^{1/2}$$

divided into 3 size classes of  $M_{t+1}$ : <19, 20-39, and >40. The chi-square test was used to detect differences in model selection within and among size classes. Because a model designated by CAPTURE to be the most appropriate for the data does not always fit the data or provide estimates of population parameters (e.g.  $M_{th}$ ,  $M_{tb}$ ,  $M_{tbh}$ ), the selection criteria of all models were examined to select 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 ( $P > 0.05$ ). The percentage of times that each model was selected as best was calculated for each species, and the chi-square test was 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 the sources of variation in capture probabilities. 'Effect scores' were calculated from the model-selection criteria for heterogeneity (H), behavior (B), and time (T) effects:

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

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

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

Effect scores could theoretically range from -3.91 to +3.91 (if calculated from the most extreme set of selection criteria with 2 models sharing the top rank: 1.00, 1.00, 0.99, 0.98, 0.03, 0.02, 0.01, and 0.00). A positive score for H suggested that capture probabilities were heterogeneous; a negative score suggested the opposite. Effect scores were calculated for each data set from each species, and a 1-

tailed  $t$ -test was performed to determine whether the scores were significantly greater than or less than 0.0. Model-selection criteria were compared from data sets with  $\geq 39$  animals captured and  $\geq 6$  trapping occasions to determine whether criteria reflected real sources of variation in capture probabilities or whether criteria followed predictable patterns as a result of the CAPTURE algorithm.

Average capture probabilities ( $\hat{p}$ 's) were calculated for each species by use of the estimate from the best model for each data set. Analysis of variance (ANOVA) ( $P < 0.01$ ) 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, I first calculated the ratio of probability of recapture to probability of first capture ( $\hat{c}_b/\hat{p}_b$ ) from model  $M_b$  for all data sets for which CAPTURE indicated a significant behavioral effect (Model  $M_0$  rejected for  $M_b$  [ $P < 0.05$ ]). 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  $\hat{c}_b/\hat{p}_b < 1$ . This classification helped to clarify the behavioral response of species with imprecise  $\hat{c}_b/\hat{p}_b$  ratios (high coefficients of variation). Chi-square tests were used to test for significant differences in behavioral response among species within families, among genera within families, and among species within genera.

The  $\hat{N}$ 's,  $\hat{p}$ 's, and coefficients of variation (CV's) of  $\hat{N}$  from the 5 models were compared. Percent relative-difference,  $[(\hat{N}_1 - \hat{N}_2)/\hat{N}_1]100$ , of the  $\hat{N}$ 's from all 5 models was calculated for all data sets for all



pair-wise comparisons. The Kruskal-Wallis ( $P < 0.01$ ) test and Dunn's method ( $P = 0.05$ ) for nonparametric analysis of variance and multiple comparison (Zar 1984:176-179, 199-201) were used to test for significant differences among CV's of  $\hat{N}$ 's calculated by the best model and among all  $\hat{N}$ 's,  $\hat{p}$ 's, and CV's of  $\hat{N}$ . The  $\hat{p}$ 's calculated by the best model and the CV's of  $\hat{N}$  from model  $M_{bh}$  ( $CV_{bh}$ ) were regressed on  $M_{t+1}$ , the total number of captures, trap spacing, and number of trapping occasions. CV's from Model  $M_{bh}$  were selected, because these values were greater than those from other models, thus providing the most conservative measure of precision.  $CV_{bh}$ 's also were regressed on  $\hat{p}$ 's. STATGRAPHICS (STSC, Inc. 1988) was used to determine which of 4 regression models (exponential, linear, multiplicative, and reciprocal) resulted in the highest correlation coefficient ( $r$ ) for each relationship. Transformation of the raw data resulted in uniform residuals; however, non-transformed values are presented in Appendices D-F to ease understanding of curvilinear relationships.

I used CAPTURE to compute the mean maximum-distance moved in meters (MMDM) for animals captured at least twice during each trapping session. When trap spacing differed among data sets for a species, ANOVA was used to determine whether the trap spacing significantly influenced estimates of animal movement. The recommended trap spacing for a species was calculated as 1/3 average-MMDM. One-half MMDM has been used as a crude estimate of the radius of the average home-range (Wilson and Anderson 1985), so 1/3 MMDM resulted in the minimum of 4 traps per home range recommended by White et al. (1982). Animal

density in animals/ha ( $\hat{D}$ ) was estimated by substituting 1/2 MMDM for the strip width around the grid (Wilson and Anderson 1985):

$$\hat{D} = \hat{N}/\hat{A} = \hat{N}_{\text{best model}} / (\text{Area enclosed by grid} + \text{border of } 1/2 \text{ MMDM}).$$

MMDM was regressed on  $\hat{D}$  to determine whether animal movement was correlated with density. MMDM was incorporated in  $\hat{D}$ , but this  $\hat{D}$  was considered less biased than one incorporating a border of 1/2 of the trap spacing.

To compare estimates of population size from the Jolly-Seber method and CAPTURE, I used only larger data sets that consisted of  $\geq 40$  captured individuals,  $\geq 7$  trapping occasions, and a grid size larger than 5 x 5 traps. These larger data sets were required to show consistent selection of 1 or 2 models throughout a major portion of the trapping session. Animals that died during the trapping sessions were excluded from the Jolly-Seber analyses (as they were from CAPTURE analyses). Thus, in the Jolly-Seber equation, the number of animals captured on each occasion equaled the number released ( $n_i$  and  $s_i$ , respectively, in Jolly's 1965 notation). Population size at each trapping occasion after the first was estimated by use of CAPTURE and the Jolly-Seber model. I used the computer program JOLLY (Pollock et al. 1990) to compute Jolly-Seber estimates and to perform chi-squared goodness-of-fit tests of the data to the model.

## RESULTS

Forty-seven biologists provided 1,535 appropriate data sets for 33 species (Table 2). Nomenclature corresponds to that in Carlton and Musser (1984) and Jones et al. (1986) and is presented in Appendix C. Other species were not included in the analysis, because too few data sets were received for them. Insectivora species were excluded because of high mortality in traps. The largest number of data sets was acquired for Peromyscus maniculatus (283), Dipodomys merriami (188), and Sigmodon hispidus (177), permitting some unique analyses for these species.

Trapping designs used to obtain most data I analyzed were fairly representative of designs commonly used for those species, except for some arvicolines. Sylvilagus floridanus was trapped 10-31 days (mean = 20), and Sylvilagus nuttallii was trapped for 3-31 days (mean = 7). Sciurids were trapped an average of 5-9 days per species, with ranges of 3-16 days, except for 3-5 day trapping sessions for Tamias striatus. Tamias amoenus, Tamias minimus, and Glaucomys sabrinus were trapped on grids with primarily 40 m between traps, whereas other sciurids were trapped on grids with 10-40 m between traps (mean = 12-25 m per species). Traps for heteromyids were generally set 3-10 times, usually during 3-4 days, and most trap spacing was 10-15 m, except traps were 20-23 m apart to obtain all data for Perognathus longimembris, Chaetodipus formosus, Dipodomys microps, and 16 data sets for D. merriami. Sigmodontines generally were trapped 3-10 days, although 7 trapping sessions each of Reithrodontomys fulvescens and S. hispidus

Table 2. Individuals who contributed data to this investigation<sup>a</sup>, with list of species and number of data sets.

Contributor	Affiliation	Species (Number of data sets)
Allred, D.	Brigham Young University; Provo, UT	<u>Perognathus longimembris</u> (18), <u>Chaetodipus formosus</u> (10), <u>Dipodomys merriami</u> (16), <u>D. microps</u> (31)
Anthony, R.	Oregon State University; Corvallis, OR	<u>Sylvilagus floridanus</u> (34), <u>Perognathus parvus</u> (5), <u>Dipodomys merriami</u> (2), <u>Peromyscus leucopus</u> (4), <u>P. maniculatus</u> (10), <u>Microtus pennsylvanicus</u> (6)
Boula, K.	US Forest Service; Troutdale, OR	<u>Tamias minimus</u> (2), <u>Perognathus parvus</u> (3), <u>Peromyscus maniculatus</u> (9)
Caldwell, L.	Battelle Laboratories; Hanford, WA	<u>Perognathus parvus</u> (9)
Chappell, M.	University of California, Riverside, CA	<u>Tamias amoenus</u> (14), <u>I. minimus</u> (11)
Doyle, A.	US Forest Service; Juneau, AK	<u>Tamias townsendii</u> (10)
Dueser, R.	University of Virginia; Charlottesville, VA	<u>Peromyscus leucopus</u> (66), <u>P. maniculatus</u> (44)
Fuller, W.	University of Alberta; Edmonton, Alberta, Canada	<u>Peromyscus maniculatus</u> (45), <u>Clethrionomys gapperi</u> (23)
Gambs, R.	California Poly. State Univ.; San Luis Obispo, CA	<u>Chaetodipus californicus</u> (13), <u>Reithrodontomys megalotis</u> (14)
Garland, T.	University of Washington; Seattle, WA	<u>Chaetodipus formosus</u> (14), <u>Dipodomys merriami</u> (11)
Getz, L.	University of Illinois at Urbana-Champaign, IL	<u>Microtus ochrogaster</u> (7)
Grant, W.	Texas A & M University; College Station, TX	<u>Reithrodontomys fulvescens</u> (7), <u>Sigmodon hispidus</u> (5)
Guthery, F.	Texas A & I University; Kingsville, TX	<u>Reithrodontomys fulvescens</u> (2), <u>Sigmodon hispidus</u> (19)
Heske, E.	University of Arizona; Tucson, AZ	<u>Microtus californicus</u> (17)
Jett, D.	University of Georgia; Athens, GA	<u>Microtus pennsylvanicus</u> (9)
Kerley, D.	Eastern Oregon State College; LaGrande, OR	<u>Perognathus parvus</u> (22), <u>Dipodomys ordii</u> (35), <u>Peromyscus maniculatus</u> (50)
Kingsbury, P.	Canadian Forestry Service; Sault Ste. Marie, Ontario	<u>Clethrionomys gapperi</u> (1)
Langley, A.	Georgia Dept. of Natural Resources; Atlanta, GA	<u>Sigmodon hispidus</u> (27)
Layne, J.	Archbold Biological Station; Lake Placid, FL	<u>Peromyscus gossypinus</u> (11), <u>Sigmodon hispidus</u> (22)
Lefebvre, L.	US Fish & Wildlife Service; Gainesville, FL	<u>Sigmodon hispidus</u> (43)
Llewellyn, J.	Boston University; Boston, MA	<u>Peromyscus truei</u> (1)
McClenaghan, L.	San Diego State University; San Diego, CA	<u>Dipodomys agilis</u> (17), <u>D. merriami</u> (2)
McLean, R.	Div. of Vector-Borne Viral Diseases; Ft. Collins, CO	<u>Tamias minimus</u> (1), <u>Spermophilus richardsonii</u> (9), <u>Peromyscus maniculatus</u> (9)
Meserve, P.	Northern Illinois University; DeKalb, IL	<u>Peromyscus maniculatus</u> (3), <u>Reithrodontomys megalotis</u> (7)
Mihok, S.	Atomic Energy of Canada Limited; Pinawa, Manitoba	<u>Peromyscus maniculatus</u> (20), <u>Clethrionomys gapperi</u> (19)
Nichols, J.	Patuxent Wildlife Research Center; Laurel, MD	<u>Sigmodon hispidus</u> (2), <u>Microtus pennsylvanicus</u> (8)
Nydegger, N.	US Bureau of Land Management; Boise, ID	<u>Perognathus parvus</u> (2)
O'Farrell, M.	private consultant; Santa Ynez, CA	<u>Perognathus amplus</u> (11), <u>P. longimembris</u> (13), <u>P. parvus</u> (1), <u>Chaetodipus formosus</u> (7), <u>C. intermedius</u> (29), <u>C. penicillatus</u> (8), <u>Dipodomys merriami</u> (79), <u>D. microps</u> (2)
Otis, D.	Colorado State University; Fort Collins, CO	<u>Sylvilagus floridanus</u> (1), <u>Tamias minimus</u> (1), <u>Spermophilus richardsonii</u> (34), <u>Perognathus parvus</u> (1), <u>Peromyscus maniculatus</u> (3), <u>Microtus ochrogaster</u> (1), <u>M. pennsylvanicus</u> (4)

Table 2. (Continued).

Contributor	Affiliation	Species (Number of data sets)
Parmenter, R.	Utah State University; Logan, UT	<u>Peromyscus maniculatus</u> (11)
Raphael, M.	US Forest Service; Laramie, WY	<u>Tamias townsendii</u> (5), <u>Peromyscus maniculatus</u> (24), <u>P. truei</u> (7)
Ribble, D.	University of California, Berkeley, CA	<u>Perognathus flavus</u> (7), <u>Dipodomys ordii</u> (1), <u>Reithrodontomys megalotis</u> (1), <u>Peromyscus californicus</u> (9), <u>P. maniculatus</u> (12), <u>P. truei</u> (38)
Robinson, W.	Northern Michigan University; Marquette, MI	<u>Microtus pennsylvanicus</u> (9)
Rosenberg, D.	Oregon State University; Corvallis, OR	<u>Tamias townsendii</u> (16), <u>Glaucomys sabrinus</u> (26), <u>Peromyscus maniculatus</u> (8)
Scheibe, J.	Southeast Missouri State Univ.; Cape Girardeau, MO	<u>Peromyscus truei</u> (16)
Schreiber, K.	US Fish & Wildlife Service; Kearneysville, WV	<u>Tamias striatus</u> (4)
Slade, N.	University of Kansas; Lawrence, KS	<u>Sigmodon hispidus</u> (8), <u>Microtus ochrogaster</u> (20)
Smith, A.	Arizona State University; Tempe, AZ	<u>Peromyscus maniculatus</u> (14), <u>Clethrionomys gapperi</u> (18)
Smith, N.	University of Arizona; Tucson, AZ	<u>Chaetodipus intermedius</u> (4), <u>Dipodomys merriami</u> (42)
Snyder, D.P.	University of Massachusetts; Amherst, MA	<u>Tamias striatus</u> (15)
Verts, B.J.	Oregon State University; Corvallis, OR	<u>Sylvilagus nuttallii</u> (29), <u>Perognathus parvus</u> (2)
West, S.	University of Washington; Seattle, WA	<u>Clethrionomys rutilus</u> (11)
Whitford, W.	New Mexico State University; Las Cruces, NM	<u>Chaetodipus penicillatus</u> (6), <u>Dipodomys merriami</u> (36), <u>D. ordii</u> (3), <u>Peromyscus leucopus</u> (2), <u>P. maniculatus</u> (10), <u>Sigmodon hispidus</u> (1)
Whitney, P.	BEAK Consultants; Portland, OR	<u>Clethrionomys rutilus</u> (52)
Wilkins, K.	Baylor University; Waco, TX	<u>Sigmodon hispidus</u> (50)
Witt, J.	US Bureau of Land Management; Roseburg, OR	<u>Tamias townsendii</u> (1), <u>Glaucomys sabrinus</u> (14)
Wolff, J.	Villanova University; Villanova, PA	<u>Peromyscus maniculatus</u> (9)

<sup>a</sup>The following people contributed data that could not be used for various reasons: R. Dolbeer, K. Geluso, J. Goertz, G. Haas, D. Innes, D. R. Johnson, D. W. Johnson, S. Malecha, and M. Price.

were analyzed as 22 daily occasions. Trap spacing averaged 10-20 m per species (minima = 7-15 m and maxima = 15-25 m, except 50 m was used to obtain 14 data sets for P. maniculatus). Trapping designs were less uniform among arvicolines. Arvicolines usually were trapped for 3-7 days; some trapping sessions consisting of morning/evening trapping. Trap spacing averaged 10-15 m per species (minima = 5-10 m and maxima = 10-15 m), except for a range of 20-50 m for Clethrionomys gapperi and the 2-m spacing used to capture all Microtus californicus. And, M. californicus was trapped several times per night.

Data for several species indicated strong time effects related to multiple trapping occasions within a 24-h period. When traps were examined mornings and evenings, Peromyscus leucopus and P. maniculatus were rarely caught in traps left open during the day, and those captured during the day usually had already been captured the previous night. Data from such trapping sessions always resulted in selection of model  $M_t$ ,  $M_{th}$ ,  $M_{tb}$ , or  $M_{tbh}$  as the most appropriate. Therefore, data from all daily trapping sessions usually were combined.

Perognathus amplus, Chaetodipus intermedius, D. merriami, M. californicus, and Microtus ochrogaster often had cyclic capture probabilities when traps were examined several times during the day or night, and data for these species were reformatted when the cyclic patterns resulted in selection of models  $M_t$ ,  $M_{th}$ ,  $M_{tb}$ , or  $M_{tbh}$ . Capture probabilities of Dipodomys agilis were not strongly affected by multiple trapping occasions per night. Data sets were usually too small for time effects to result in selection of models without estimators for data from morning-evening trapping sessions of I.

amoenus, I. minimus, P. longimembris, C. formosus, Chaetodipus penicillatus, D. merriami, S. hispidus, Clethrionomys rutilus, M. ochrogaster, and Microtus pennsylvanicus. Capture probabilities from approximately one-half of the data sets of C. gapperi were not strongly affected by morning and evening trapping, so models incorporating time effects were not selected in most instances. Daily trapping occasions for the other half were combined, because too few animals were caught during the day.

Some ecologists did not use a basic rectangular grid with even spacing between traps. The following designs were used instead for some studies: approximate grids (S. floridanus), parallel lines (some Heteromyidae), assessment lines (some Heteromyidae and Peromyscus truei), grids with traps at alternate stations (P. longimembris, D. merriami, D. microps, and M. californicus), grids on which alternate stations were sampled on each occasion (Perognathus parvus, Dipodomys ordii, and P. maniculatus), or several transects that covered a roughly rectangular area (S. hispidus). These data were useful only for analysis of model selection and capture probabilities.

#### Population closure

Population closure was not rejected 70-100% of the time for all but 3 species when models  $M_0$  or  $M_h$  were chosen by CAPTURE (Table 3). Differences among taxa were significant only for Heteromyidae, in which closure was not rejected for 67-86% of data sets for Perognathus spp., 78-96% for Dipodomys spp., and 90-100% for Chaetodipus spp. ( $P < 0.01$ ). As a group, Perognathus spp. had the lowest frequency of

Table 3. Results of the test for population closure from data sets for which models  $M_0$  or  $M_h$  were selected as the most appropriate model by CAPTURE for selected species of small mammals. The results of chi-square tests of significance at different taxonomic levels are given.

Species	Number of data sets		Closure not rejected <sup>a</sup> (%)	Chi-square value for differences		
	Total	# with $M_0$ or $M_h$ selected		Among species within families	Among genera within families	Among species within genera
Leporidae						
<u>Sylvilagus floridanus</u>	35	26	80.8			0.05 <sup>b</sup>
<u>S. nuttallii</u>	29	17	88.2			
Sciuridae				14.06	8.82	
<u>Tamias amoenus</u>	14	9	100.0			2.92
<u>T. minimus</u>	15	8	75.0			
<u>T. striatus</u>	19	11	81.8			
<u>T. townsendii</u>	42	15	73.3			
<u>Spermophilus richardsonii</u>	43	22	100.0			
<u>Glaucomys sabrinus</u>	30	21	100.0			
Heteromyidae				26.17***	13.35**	
<u>Perognathus amplus</u>	11	6	66.7			2.80
<u>P. flavus</u>	7	5	80.0			
<u>P. longimembris</u>	31	22	86.4			
<u>P. parvus</u>	45	27	66.7			
<u>Chaetodipus californicus</u>	13	9	100.0			1.16
<u>C. formosus</u>	28	20	95.0			
<u>C. intermedius</u>	33	20	90.0			
<u>C. penicillatus</u>	14	12	91.7			
<u>Dipodomys agilis</u>	17	11	81.8			8.78
<u>D. merriami</u>	188	129	93.8			
<u>D. microps</u>	33	23	95.6			
<u>D. ordii</u>	39	27	77.8			
Muridae				12.14		
Sigmodontinae				4.46	0.15	
<u>Reithrodontomys fulvescens</u>	9	7	71.4			0.26 <sup>b</sup>
<u>R. megalotis</u>	22	12	91.7			
<u>Peromyscus californicus</u>	9	6	83.3			2.78
<u>P. gossypinus</u>	11	10	100.0			
<u>P. leucopus</u>	72	49	91.8			
<u>P. maniculatus</u>	283	132	84.8			
<u>P. truei</u>	61	31	90.3			
<u>Sigmodon hispidus</u>	177	113	86.7			
Arvicolinae				7.13	0.06	
<u>Clethrionomys gapperi</u>	61	46	84.8			0.13
<u>C. rutilus</u>	63	40	87.5			
<u>Microtus californicus</u>	17	8	100.0			6.56
<u>M. ochrogaster</u>	28	18	94.4			
<u>M. pennsylvanicus</u>	36	19	68.4			
Total	1,535	931				

<sup>a</sup>Test for population closure resulted in  $p > 0.05$  (Otis et al. 1978).

<sup>b</sup>Continuity correction factor was used to correct for expected values  $< 5$  in the chi-square test.

\*\*Significant at  $p = 0.01$ .

\*\*\*Significant at  $p = 0.001$ .



population closure of all taxa. This cannot be attributed solely to the use of assessment lines for this genus, because assessment lines often were used for Chaetodipus spp., which had significantly higher probabilities of population closure.

Peroznathus amplus, P. parvus, and M. pennsylvanicus had lower frequencies of population closure than most species. One-third of the P. amplus populations were considered open, probably because sample sizes were small and 3 of the 6 data sets were based on trapping strategies of parallel lines, with 53 m between lines. The probability of closure for 2 of these 3 populations was  $<0.00$ ; traps probably were too far apart to sample animal movement adequately. Twelve of 27 P. parvus trapping sessions were  $>4$  days, and longer trapping sessions were related to increased probability of rejecting closure for this species.

Spermophilus richardsonii, G. sabrinus, Chaetodipus californicus, Peromyscus gossypinus, and M. californicus populations were considered open 100% of the time, based on results of the closure test. These results for S. richardsonii and P. gossypinus were likely related to trapping sessions of  $<5$  occasions. Except for 3 trapping sessions, G. sabrinus were studied on large grids covering 12-19 ha that reduced the boundary-to-grid ratio and minimized the influence of movements onto or off of the grid. The 25-m trap spacings on grids used to capture C. californicus were considerably larger than the mean maximum-distance moved (4-19 m) and did not adequately sample animal movement. M. californicus was caught on grids with a 2-m trap spacing, which restricted animal movement.

The effect of trapping design on population closure was examined only for P. parvus, D. merriami, P. maniculatus, P. leucopus, and S. hispidus. Frequency of closure was significantly and inversely related to the number of occasions ( $t$ ) per trapping session for P. parvus, P. leucopus, P. maniculatus, and S. hispidus ( $P < 0.01$ ) (Table 4). When  $t > 5$ , >50% of the P. parvus and P. maniculatus populations were open, but this phenomenon occurred at  $t > 7$  for P. leucopus and  $t > 8$  for S. hispidus. There was no trend in the number of closed populations with increasing  $t$  for D. merriami. Population closure did not have a strong linear association with trap spacing or grid size for D. merriami, P. maniculatus, and S. hispidus ( $P < 0.05$ ). However, the proportion of closed populations was greater when the trap spacing was  $\geq 15$  m rather than  $\leq 10$  m for D. merriami ( $\chi^2 = 2.09$ ,  $P = 0.15$ ,  $df = 1$ ). Finally, probability of rejecting population closure was not significantly related to the total number of animals captured ( $\chi^2 = 0.068$ ,  $P = 0.97$ ;  $\chi^2 = 1.83$ ,  $P = 0.17$ ; and  $\chi^2 = 3.32$ ,  $P = 0.19$ ; for D. merriami, P. maniculatus, and S. hispidus, respectively).

Population closure probably was not rejected often enough. The null hypothesis consisted of population closure, so sufficient data were needed to reject closure. The closure test was performed mostly on data sets consisting of  $< 5$  occasions, because CAPTURE tended to select models  $M_0$  or  $M_h$  for short trapping sessions. Short trapping sessions allowed animals less time to move onto and off of the grid, and the test for closure was less powerful when occasions were few.

Table 4. Linear association between the number of occasions (t) per trapping session and the results of the test for population closure for selected species of small mammals.

Species	Values used for Mantel-Haentzel test <sup>a</sup>						Z value	
<u>Perognathus</u> <u>parvus</u>	t	3	4	5	6	9,10	2.81**	
	Closed(%) <sup>b</sup>	100	86	57	33	0		
	n	1	14	7	5	2		
	Excess	0.3	2.8	1.1	0.4			
	Variance	0.2	1.5	0.8	0.2			
<u>Dipodomys</u> <u>merriami</u>	t	3	4	5-15			1.25	
	Closed(%) <sup>b</sup>	96	77	98				
	n	51	22	56				
	Excess	1.2	-3.3					
	Variance	1.8	1.1					
<u>Peromyscus</u> <u>leucopus</u>	t	3	4	7	8,9		3.39**	
	Closed(%) <sup>b</sup>	97	88	100	0			
	n	38	8	1	2			
	Excess	2.1	1.2	0.7				
	Variance	0.6	0.5	0.2				
<u>Peromyscus</u> <u>maniculatus</u>	t	3	4	5	6	8-10	10.59**	
	Closed(%) <sup>b</sup>	99	87	67	0	33		
	n	74	30	16	6	6		
	Excess	10.2	20.2	3.6	-1.0			
	Variance	4.2	3.2	1.8	0.4			
<u>Sigmodon</u> <u>hispidus</u>	t	3	4	5	6	8	12-22	3.92***
	Closed(%) <sup>b</sup>	100	91	92	100	79	0	
	n	19	23	36	2	29	4	
	Excess	2.5	1.7	3.6	0.6	2.8		
	Variance	1.8	2.4	2.7	0.4	0.8		

<sup>a</sup>The Mantel-Haentzel method provided: the difference (excess) between the actual number of closed populations and the number expected according to a contingency table, the variance of the estimate of excess, and the Z-test statistic.

<sup>b</sup>Test for population closure resulted in  $p > 0.05$  (Otis et al. 1978).

\*\*Significant at  $p = 0.01$ .

\*\*\*Significant at  $p = 0.001$ .

## Model selection

Model  $M_0$  was selected most often by CAPTURE as the most appropriate model for 23 species (Table 5). Models  $M_h$ ,  $M_b$ ,  $M_{tbh}$ , and  $M_{bh}$  were the most appropriate models for many species; models  $M_{bh}$ ,  $M_t$ ,  $M_{th}$ , and  $M_{tb}$  were selected infrequently. Overall,  $M_h$  (heterogeneity) was selected  $\geq 25\%$  of the time for S. floridanus, S. richardsonii, G. sabrinus, P. amplus, Perognathus flavus, P. parvus, C. intermedius, R. fulvescens, P. gossypinus, C. gapperi, M. californicus, and M. pennsylvanicus. Model  $M_b$  (behavioral effects) was selected  $>15\%$  of the time for Tamias townsendii, P. amplus, Reithrodontomys megalotis, P. gossypinus, P. maniculatus, and M. pennsylvanicus. Model  $M_{tbh}$  was selected  $>15\%$  of the time for S. nuttallii, I. striatus, I. townsendii, S. richardsonii, P. maniculatus, P. truei, and M. californicus.

When only larger ( $>39$  individuals captured) data sets were considered, other models were selected more often than  $M_0$  for 18 species. Although  $M_0$  was chosen at least as often overall, model  $M_h$  was selected more than  $M_0$  for S. floridanus, S. richardsonii, D. merriami, D. ordii, R. megalotis, P. maniculatus, S. hispidus, and Clethrionomys spp., and model  $M_b$  was selected more than  $M_0$  for S. richardsonii, P. amplus, R. megalotis, and P. maniculatus.

Patterns of model selection varied significantly with size of data set ( $P < 0.01$ ) (Tables 6 and 7). Models  $M_0$  or  $M_h$  were chosen most often for small data sets, overall (Table 6). However,  $M_0$  was selected significantly less often as size of data set increased, whereas  $M_h$ ,  $M_b$ ,  $M_{bh}$ , and  $M_{tb}$  were selected significantly more often for large data sets than for small ones. Model  $M_0$  was chosen 64% of the time for small

Table 5. Percentage of times that each CAPTURE model was chosen as the most appropriate model for selected species of small mammals.

Species	Number of data sets	Model selected (%)							
		M <sub>0</sub>	M <sub>h</sub>	M <sub>b</sub>	M <sub>bh</sub>	M <sub>t</sub>	M <sub>th</sub>	M <sub>tb</sub>	M <sub>tbh</sub>
Leporidae									
<u>Sylvilagus floridanus</u>	35	37	37+	3	9	6	3	3	3
<u>S. nuttallii</u>	29	55	3	7	0	0	10+	0	24
Sciuridae									
<u>Tamias amoenus</u>	14	64	0	7	7	0	7	7	7
<u>T. minimus</u>	15	33	20	0	13	13+	13+	0	7
<u>T. striatus</u>	19	58	0	5	0	5	11	0	21+
<u>T. townsendii</u>	42	17	19+	29+	5	7	7	0	17+
<u>Spermophilus richardsonii</u>	43	26	26+	14+	16+	0	2	0	16+
<u>Glaucomys sabrinus</u>	30	43	27	7	3	0	10	0	10
Heteromyidae									
<u>Perognathus amplus</u>	11	27	27	18+	18+	0	0	0	9+
<u>P. flavus</u>	7 <sup>a</sup>	43	29	14	0	0	14	0	0
<u>P. longimembris</u>	31	61	10	7	10	0	0	3	10
<u>P. parvus</u>	45	9	51+	0	4+	4	11	9	11+
<u>Chaetodipus californicus</u>	13 <sup>a</sup>	69	0	8	0	0	8	0	15
<u>C. formosus</u>	28	57	14	11	0	0	4	4	11
<u>C. intermedius</u>	33	24	36+	3	0	9	3	12+	12
<u>C. penicillatus</u>	14 <sup>a</sup>	86	0	0	0	0	14	0	0
<u>Dipodomys agilis</u>	17 <sup>a</sup>	59	6	6	0	0	12	6	12
<u>D. merriami</u>	188	46	23+	6	5	3	7	3	7
<u>D. microps</u>	33	61	9	6	6	3	9	0	6
<u>D. ordii</u>	39	51	18+	0	15+	0	8+	0	8
Muridae									
Sigmodontinae									
<u>Reithrodontomys fulvescens</u>	9 <sup>a</sup>	11	67	11	0	0	0	0	11
<u>R. megalotis</u>	22	46	9+	18+	0	5	9+	0	14
<u>Peromyscus californicus</u>	9	78	11	0	0	0	0	0	11
<u>P. gossypinus</u>	11 <sup>a</sup>	82	9	0	0	0	0	0	9
<u>P. leucopus</u>	72	57	11	4	3	4	7	1+	13
<u>P. maniculatus</u>	283	36	11+	18+	6+	2	6	4	17+
<u>P. truei</u>	61	43	8	10	5	5	5	7	18
<u>Sigmodon hispidus</u>	177	42	22+	9	7	2	4	2	12
Arvicolinae									
<u>Clethrionomys gapperi</u>	61	51	25+	2	2	0	12+	0	10+
<u>C. rutilus</u>	63	54	10+	3	5	8	13	5	3
<u>Microtus californicus</u>	17	6	41+	0	0	0	18+	6	29+
<u>M. ochrogaster</u>	28	54	11	11	7	4	4	0	11
<u>M. pennsylvanicus</u>	36	11	42+	17+	8+	3	11+	3	6
Overall	1,535	42	19	10	5	3	7	3	12

\*Models chosen more often than M<sub>0</sub> for data sets with >39 individuals trapped.<sup>a</sup>No data sets with >39 individuals trapped.

Table 6. Percentage of times that each of the models was chosen by CAPTURE, by three size classes of data sets for 33 species of small mammals. Chi-square results are indicated for two comparisons: the distribution of each model across data size classes (vertical) and the distribution of models within each size class (horizontal).

Number of individual animals trapped	Number of data sets	Most appropriate model (%)								
		M <sub>0</sub>	M <sub>h</sub>	M <sub>b</sub>	M <sub>bh</sub>	M <sub>t</sub>	M <sub>th</sub>	M <sub>tb</sub>	M <sub>tbh</sub>	
<20	528	64	7	4	3	2	8	1	11	***
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	
		***	***	***	**			**		

\*\*Significant at  $\underline{p} = 0.01$ .

\*\*\*Significant at  $\underline{p} = 0.001$ .

Table 7. Percentage of times that each of the models was chosen by CAPTURE, by three size classes of data sets for selected taxa of small mammals. Chi-square results are indicated for two comparisons: the distribution of each model across data size classes (vertical) and the distribution of models within each size class (horizontal).

Taxon	Number of individual animals trapped	Number of data sets	Most appropriate model (%)								
			M <sub>0</sub>	M <sub>h</sub>	M <sub>b</sub>	M <sub>bh</sub>	M <sub>t</sub>	M <sub>th</sub>	M <sub>tb</sub>	M <sub>tbh</sub>	
LEPORIDAE	<20	20	65	5	10	0	0	5	0	15	- <sup>a</sup>
Combined	20-39	23	52	22	0	9	0	0	0	17	-
	>39	21	19	38	5	5	10	14	5	5	-
			-	-	-	-	-	-	-	-	
SCIURIDAE	<20	57	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	<20	98	66	8	2	4	0	7	2	10	***
Combined, except for	20-39	91	45	23	4	5	2	9	3	8	***
the following species	>39	82	22	35	9	7	5	5	7	10	***
			***	***	-		-		-		
<u>Dipodomys merriami</u>	<20	49	59	12	2	6	4	10	2	4	***
	20-39	77	49	17	8	4	5	8	1	8	***
	>39	62	31	39	8	5	0	3	6	8	***
			***		-	-	-	-	-	-	
MURIDAE:											
Sigmodontinae	<20	90	62	4	3	1	4	8	0	17	***
Combined, except for	20-39	68	37	26	12	6	3	4	1	10	***
the following species	>39	26	35	12	19	0	4	4	15	12	-
			-	-	-	-	-	-	-	-	
<u>Peromyscus maniculatus</u>	<20	108	64	1	6	4	1	8	2	14	***
	20-39	99	26	9	30	4	4	5	4	17	***
	>39	76	9	26	20	12	1	4	7	21	***
			***	***	***		-		-		
<u>Sigmodon hispidus</u>	<20	43	74	9	0	0	0	0	0	16	***
	20-39	83	41	16	10	11	2	5	2	13	***
	>39	51	16	43	16	6	4	6	2	8	***
			***	***	-	-	-	-	-		
Arvicolinae	<20	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	***
			***	***	-	-	-		-		

<sup>a</sup>Too few data sets in one or more subclasses to do chi-square test.

\*\*Significant at  $P = 0.01$ .

\*\*\*Significant at  $P = 0.001$ .

data sets ( $M_{t+1} < 20$ ) but only 18% of the time for large data sets ( $M_{t+1} > 39$ ). Model  $M_h$  (32%) was chosen more often than  $M_0$  for large data sets. Similar patterns were apparent within taxa (Table 7). Model  $M_h$  was selected more often than  $M_0$  for large data sets for all families or subfamilies except Sigmodontinae. Sigmodontinae had the fewest number of large data sets when P. maniculatus and S. hispidus were analyzed separately, but when they were included, Sigmodontinae followed the same trend as other taxonomic groups. Model  $M_b$  was chosen at least as often as  $M_0$  for large data sets for sciurids, P. maniculatus, and S. hispidus, and Models  $M_{bh}$  and  $M_{tbh}$  were chosen more often than  $M_0$  for P. maniculatus.

Selection of the best model (model with an estimator that fit the data [ $P > 0.05$ ] and received the greatest selection criterion  $>0.75$ ) revealed that 8-47% of the data sets for each species did not fit a model with an estimator ( $P < 0.05$ ) (Table 8). Most of these populations had such strong effects of time combined with heterogeneity or behavioral response that none of the models with an estimator received a selection criterion  $>0.75$  and fit the data. Percentages for the best models (based on my criteria) vary from those for most appropriate models (Table 5), because the most appropriate model did not always fit the data. For these data sets, a different model, or none at all, was selected as best. For instance, model  $M_{bh}$  was selected 83 times as most appropriate but fit the data only 25% of those times ( $P > 0.05$ ). The other models selected as best instead of  $M_{bh}$  were:  $M_0$  (8 times),  $M_h$  (3),  $M_b$  (23), and no model (28).



Table 8. Percentage of times that each of the CAPTURE models was chosen as the best model<sup>a</sup> for selected species of small mammals.

Species	Number of data sets	Best Model (%)						Chi-square value for differences <sup>b</sup>	
		M <sub>0</sub>	M <sub>h</sub>	M <sub>b</sub>	M <sub>bh</sub>	M <sub>t</sub>	No estimator	Among genera within families	Among species within genera
Leporidae									
<u>Sylvilagus floridanus</u>	35	34	37	9	0	6	14		8.14
<u>S. nuttallii</u>	29	48	10	7	3	3	28		
Sciuridae								19.94	
<u>Tamias amoenus</u>	14	50	14	7	0	7	21		24.48
<u>T. minimus</u>	15	40	13	0	0	20	26		
<u>T. striatus</u>	19	58	5	10	0	10	15		
<u>T. townsendii</u>	42	12	21	31	2	9	23		
<u>Spermophilus richardsonii</u>	43	23	34	14	7	0	20		
<u>Glaucomys sabrinus</u>	30	37	23	13	0	0	26		
Heteromyidae								15.12	
<u>Perognathus amplus</u>	11	36	9	9	0	0	46		41.20***
<u>P. flavus</u>	7 <sup>c</sup>	57	0	14	0	14	14		
<u>P. longimembris</u>	31	58	6	13	0	0	23		
<u>P. parvus</u>	45	9	47	4	4	4	31		
<u>Chaetodipus californicus</u>	13 <sup>c</sup>	62	8	15	0	8	8		too few
<u>C. formosus</u>	28	61	14	11	0	0	14		
<u>C. intermedius</u>	33	27	36	12	0	9	15		
<u>C. penicillatus</u>	14 <sup>c</sup>	86	0	0	0	0	14		
<u>Dipodomys agilis</u>	17 <sup>c</sup>	65	0	6	6	0	24		15.03
<u>D. merriami</u>	188	42	26	7	2	6	16		
<u>D. microps</u>	33	54	15	6	0	6	18		
<u>D. ordii</u>	39	51	20	5	3	0	20		
Muridae								51.37***	
Sigmodontinae								13.38	
<u>Reithrodontomys fulvescens</u>	9 <sup>c</sup>	22	22	11	0	0	44		too few
<u>R. megalotis</u>	22	46	9	18	0	9	18		
<u>Peromyscus californicus</u>	9	33	22	22	0	0	22		36.39
<u>P. gossypinus</u>	11 <sup>c</sup>	82	9	0	0	0	9		
<u>P. leucopus</u>	72	61	12	8	0	7	11		
<u>P. maniculatus</u>	283	36	16	21	4	3	19		
<u>P. truei</u>	61	44	10	15	0	5	26		
<u>Sigmodon hispidus</u>	177	41	24	12	1	3	18		
Arvicolinae								20.48***	
<u>Clethrionomys gapperi</u>	61	44	26	3	2	0	25		11.34
<u>C. rutilus</u>	63	48	10	5	0	8	30		
<u>Microtus californicus</u>	17	6	41	0	6	0	47		30.00***
<u>M. ochrogaster</u>	28	46	7	14	0	4	29		
<u>M. pennsylvanicus</u>	36	8	39	17	11	6	19		
Overall	1,535	41	20	12	2	4	20		

<sup>a</sup>The "best model" is the model with an estimator that had the highest selection criterion >0.75 and fit the data with  $p > 0.05$  according to chi-square tests for goodness-of-fit.

<sup>b</sup>Data sets were too small to calculate chi-square statistics at family and subfamily levels.

<sup>c</sup>No data sets with >39 individuals trapped.

\*\*\*Significant at  $p = 0.001$ .

Muridae and Arvicolinae were the only family or subfamily in which selection of the best model differed significantly among genera ( $P < 0.01$ ). Within those genera, selection varied significantly only among Microtus species ( $P < 0.01$ ). Selection of best model did not vary significantly among sciurid genera and species, partly because too few data sets were available for some Tamias spp. Differences were not significant among heteromyid genera; however, model  $M_h$  was selected predominantly for P. parvus. The 11 data sets for P. amplus were too few to provide reliable trends in model selection. Six of the data sets consisted of multiple trapping occasions per night, which resulted in cyclic time-effects in the data. These effects, when combined with heterogeneity and behavioral effects, caused only 54% of the data sets to fit a model with an estimator.

The effect scores (calculated from model-selection criteria) revealed influences on capture probabilities, particularly the presence of strong heterogeneity and behavioral effects (Table 9). Capture probabilities were significantly heterogeneous for all species except P. amplus ( $P < 0.01$ ). Behavioral response was significant for I. townsendii, S. richardsonii, and P. maniculatus. Time effects alone were significantly absent from most data sets because of 1) a high failure rate ( $\bar{x} = 90\%$ , range = 24-100%) of the goodness-of-fit test of  $M_t$ , which usually caused  $M_t$  to receive a selection criterion of 0.00, 2) the presence of strong heterogeneity and behavioral response, and 3) my deliberate minimization of cyclic time effects.

Table 9. Strength of the effects of heterogeneity (H), behavior (B), and time (T) on capture probabilities of selected species of small mammals. Values are results of one-tailed *t*-tests on 'effect scores'<sup>a</sup>. Positive scores reflect selection of models associated with a particular effect; negative scores indicate rejection of models.

Species	Number of data sets	Significance of effects		
		H	B	T
Leporidae				
<u>Sylvilagus floridanus</u>	35	0.70**	0.01	-1.06**
<u>S. nuttallii</u>	29	0.84**	-0.03	-0.72
Sciuridae				
<u>Tamias amoenus</u>	14	0.78**	-0.03	-0.91**
<u>T. minimus</u>	15	0.68**	-0.38	-0.36
<u>T. striatus</u>	19	0.80**	0.10	-0.73**
<u>T. townsendii</u>	42	0.51**	0.55**	-0.62**
<u>Spermophilus richardsonii</u>	43	0.95**	0.42**	-0.94**
<u>Glaucomys sabrinus</u>	30	0.82**	0.05	-1.05**
Heteromyidae				
<u>Perognathus amplus</u>	11	0.52	0.43	-0.77
<u>P. flavus</u>	7	0.82**	-0.18	-0.67
<u>P. longimembris</u>	31	0.80**	0.08	-0.86**
<u>P. parvus</u>	45	0.79**	0.10	-0.53**
<u>Chaetodipus californicus</u>	13	0.97**	-0.09	-0.87**
<u>C. formosus</u>	28	0.90**	0.08	-0.99**
<u>C. intermedius</u>	33	0.61**	0.00	-0.55
<u>C. penicillatus</u>	14	0.99**	-0.40**	-1.08**
<u>Dipodomys agilis</u>	17	0.96**	-0.03	-0.68**
<u>D. merriami</u>	188	0.84**	-0.13	-0.82**
<u>D. microps</u>	33	0.88**	-0.10	-0.91**
<u>D. ordii</u>	39	1.00**	-0.10	-1.08**
Muridae				
Sigmodontinae				
<u>Reithrodontomys fulvescens</u>	9	0.68**	0.55	-1.15**
<u>R. megalotis</u>	22	0.83**	-0.22	-0.54
<u>Peromyscus californicus</u>	9	0.90**	0.04	-0.92**
<u>P. gossypinus</u>	11	1.07**	-0.06	-1.23**
<u>P. leucopus</u>	72	0.89**	-0.01	-0.85**
<u>P. maniculatus</u>	283	0.74**	0.41**	-0.74**
<u>P. truei</u>	61	0.72**	0.25	-0.62**
<u>Sigmodon hispidus</u>	177	0.88**	0.05	-0.92**
Arvicolinae				
<u>Clethrionomys gapperi</u>	61	1.06**	-0.08	-0.94**
<u>C. rutilus</u>	63	0.78**	-0.25	-0.39
<u>Microtus californicus</u>	17	1.18**	0.05	-0.42
<u>M. ochrogaster</u>	28	0.89**	0.01	-0.86**
<u>M. pennsylvanicus</u>	36	0.84**	0.17	-0.67**

<sup>a</sup>Effect scores were calculated from the model selection criteria given by CAPTURE to each of the eight models (details in text); they can range from 3.91 to -3.91.

\*\*Significant at  $p = 0.01$ .

### Capture probabilities and behavioral response

Leporids and sciurids were caught less often than the heteromyids and murids (Table 10). Sylvilagus spp., I. amoenus, I. minimus, and R. fulvescens had the lowest capture probabilities (average  $\hat{p} = 0.06 - 0.21$  per species), whereas C. californicus, D. agilis, D. microps, P. gossypinus, P. leucopus, and Clethrionomys spp. had the highest ( $\hat{p} = 0.50 - 0.63$ ). The  $\hat{p}$ 's varied significantly among genera only in Sciuridae and both subfamilies of Muridae ( $P < 0.05$ ) (Table 10). The  $\hat{p}$ 's of S. richardsonii were significantly greater than those of other sciurid genera; those of Peromyscus spp. were high and greatly exceeded those of Sigmodon spp. and Reithrodontomys spp., and those of Clethrionomys spp. were significantly greater than those of Microtus spp. The  $\hat{p}$ 's within most genera varied greatly, with coefficients of variation of 23-152%. Variation was related to innate differences within a species, small sample sizes, differences in locality, methodology (especially the number of trapping occasions), and season of trapping, and, possibly, the model used to calculate  $\hat{p}$ . I did not determine significant differences within genera, because data received for some species were the result of only 1 or 2 study designs.

The ratio of recapture to capture probabilities for model  $M_b$  ( $\hat{c}_b/\hat{p}_b$ ) varied greatly among and within species (Table 11) because of extreme variability in behavioral responses and small sample sizes in many cases. An average failure rate of 13% (range = 0-45%) per species for the test of  $M_0$  and  $M_b$  indicated that data often were insufficient for  $M_b$  to provide estimates of population parameters. The coefficient of variation for S. floridanus, I. amoenus, C. formosus, R. megalotis,

Table 10. Estimated probability of capture ( $\hat{p}$ ) computed by the best CAPTURE model for selected species of small mammals.

Species	Number of data sets	$\hat{p}$		Comparison of means <sup>a</sup> Genera within families
		$\bar{x}$	SD	
Leporidae				
<u>Sylvilagus floridanus</u>	30	0.06	0.03	
<u>S. nuttallii</u>	21	0.21	0.22	
Sciuridae				
<u>Tamias amoenus</u>	11	0.14	0.09	A
<u>T. minimus</u>	11	0.14	0.14	
<u>T. striatus</u>	16	0.39	0.21	
<u>T. townsendii</u>	32	0.26	0.10	
<u>Spermophilus richardsonii</u>	24	0.35	0.17	B
<u>Glaucomys sabrinus</u>	22	0.25	0.22	A
Heteromyidae				
<u>Perognathus amplus</u>	6	0.37	0.22	A
<u>P. flavus</u>	6	0.43	0.17	
<u>P. longimembris</u>	24	0.29	0.18	
<u>P. parvus</u>	31	0.42	0.17	
<u>Chaetodipus californicus</u>	12	0.57	0.14	A
<u>C. formosus</u>	24	0.39	0.20	
<u>C. intermedius</u>	28	0.37	0.13	
<u>C. penicillatus</u>	12	0.27	0.14	
<u>Dipodomys agilis</u>	13	0.60	0.15	A
<u>D. merriami</u>	157	0.34	0.18	
<u>D. microps</u>	27	0.58	0.14	
<u>D. ordii</u>	31	0.35	0.16	
Muridae				
Sigmodontinae				
<u>Reithrodontomys fulvescens</u>	5	0.21	0.32	A
<u>R. megalotis</u>	18	0.30	0.16	
<u>Peromyscus californicus</u>	7	0.48	0.19	
<u>P. gossypinus</u>	10	0.60	0.14	
<u>P. leucopus</u>	64	0.63	0.20	B
<u>P. maniculatus</u>	229	0.49	0.22	
<u>P. truei</u>	45	0.46	0.22	
<u>Sigmodon hispidus</u>	140	0.26	0.14	
Arvicolinae				
<u>Clethrionomys gapperi</u>	46	0.50	0.17	B
<u>C. rutilus</u>	44	0.62	0.15	
<u>Microtus californicus</u>	9	0.44	0.14	
<u>M. ochrogaster</u>	20	0.27	0.16	
<u>M. pennsylvanicus</u>	29	0.29	0.17	A

<sup>a</sup>Means of genera with the same letter within a family or subfamily were not significantly different ( $P > 0.05$ ).

Table 11. Estimated probability of capture ( $\hat{p}_b$ ) and ratio of estimates of probability of recapture to capture ( $\hat{c}_b/\hat{p}_b$ ) for selected species of small mammals<sup>a</sup>.

Species	Number of data sets	$\hat{p}_b$		$\hat{c}_b/\hat{p}_b$		
		$\bar{x}$	SD	$\bar{x}$	SD	Range
<b>Leporidae</b>						
<u>Sylvilagus floridanus</u> <sup>b</sup>	4	0.12	0.03	0.33	0.18	(0.19- 0.59)
<u>S. nuttallii</u>	5	0.63	0.14	0.16	0.05	(0.10- 0.22)
<b>Sciuridae</b>						
<u>Tamias amoenus</u> <sup>b</sup>	3	0.41	0.12	0.37	0.07	(0.30- 0.44)
<u>T. minimus</u>	1	0.42		0.33		(0.33- 0.33)
<u>T. striatus</u>	5	0.41	0.21	2.12	1.54	(0.57- 4.68)
<u>T. townsendii</u>	24	0.24	0.09	2.87	1.36	(1.26- 6.65)
<u>Spermophilus richardsonii</u>	7	0.34	0.29	1.93	1.16	(0.08- 3.24)
<u>Glaucomys sabrinus</u>	6	0.55	0.32	0.40	0.20	(0.20- 0.67)
<b>Heteromyidae</b>						
<u>Perognathus amplus</u>	2	0.35	0.48	5.98	7.81	(0.46-11.50)
<u>P. flavus</u>	1	0.35		2.52		
<u>P. longimembris</u>	6	0.59	0.10	0.34	0.12	(0.20- 0.48)
<u>P. parvus</u>	16	0.23	0.16	3.29	2.80	(1.43-12.00)
<u>Chaetodipus californicus</u>	2	0.78	0.01	0.46	0.26	(0.27- 0.64)
<u>C. formosus</u> <sup>b</sup>	4	0.46	0.26	1.09	0.95	(0.48- 2.50)
<u>C. intermedius</u>	7	0.41	0.15	1.27	1.08	(0.18- 3.29)
<u>C. penicillatus</u>	0					
<u>Dipodomys agilis</u>	3	0.83	0.07	0.50	0.17	(0.31- 0.61)
<u>D. merriami</u>	30	0.47	0.23	1.07	0.93	(0.18- 3.28)
<u>D. microps</u>	5	0.71	0.04	0.52	0.10	(0.38- 0.63)
<u>D. ordii</u>	6	0.28	0.20	2.65	1.69	(0.56- 5.27)
<b>Muridae</b>						
<b>Sigmodontinae</b>						
<u>Reithrodontomys fulvescens</u>	1	0.79		0.31		
<u>R. megalotis</u> <sup>b</sup>	3	0.43	0.06	2.04	0.35	(1.67- 2.37)
<u>Peromyscus californicus</u>	2	0.60	0.34	1.08	0.74	(0.56- 1.61)
<u>P. gossypinus</u>	0					
<u>P. leucopus</u>	13	0.53	0.25	1.50	0.88	(0.23- 3.12)
<u>P. maniculatus</u>	119	0.35	0.20	2.39	1.50	(0.19- 8.40)
<u>P. truei</u>	18	0.56	0.20	1.52	0.79	(0.52- 3.30)
<u>Sigmodon hispidus</u>	32	0.29	0.16	2.21	1.54	(0.20- 8.21)
<b>Arvicolinae</b>						
<u>Clethrionomys gapperi</u>	10	0.48	0.21	1.55	0.52	(0.67- 2.31)
<u>C. rutilus</u>	10	0.68	0.23	1.18	0.97	(0.39- 3.50)
<u>Microtus californicus</u>	8	0.40	0.18	1.39	0.52	(0.36- 2.14)
<u>M. ochrogaster</u> <sup>b</sup>	6	0.44	0.21	0.71	0.50	(0.19- 1.67)
<u>M. pennsylvanicus</u>	15	0.34	0.20	1.78	1.31	(0.38- 5.87)

<sup>a</sup>Estimates were computed with Model  $M_b$  for data sets which showed behavioral effects according to the chi-square goodness-of-fit tests for Model  $M_b$  and for which  $M_b$  produced estimates of population parameters. Some of the CAPTURE results received for S. richardsonii and S. hispidus did not include estimates of parameters from  $M_b$ .

<sup>b</sup>Values were recalculated without outliers when the coefficient of variation was >0.90.

and M. ochrogaster exceeded 0.90 because of 1-2 outliers that were 2-26 times as great as the next higher value for each species. (These outliers were eliminated from the results presented in Table 11.) Some S. floridanus populations were so trap prone that the average  $\hat{c}_b/\hat{p}_b$  ratio equaled  $2.76 \pm 5.20$ ; however, the ratio averaged 0.33 when 2 outliers were removed. The 7 species represented by the greatest sample sizes had coefficients of variation from 47 to 87%. Three (S. nuttallii, D. microps, and D. agilis) of the 4 species with the least variation in behavioral response were noticeably trap shy. S. floridanus, S. nuttallii, I. amoenus, G. sabrinus, P. longimembris, D. agilis, D. microps, and M. ochrogaster tended to be trap shy although sample sizes were small for several of these species. I. townsendii, P. parvus, and R. megalotis had only trap-prone behavioral responses (all  $\hat{c}_b/\hat{p}_b$  ratios  $> 1.0$ ). I. striatus, S. richardsonii, D. ordii, P. leucopus, P. maniculatus, P. truei, S. hispidus, C. gapperi, M. californicus and M. pennsylvanicus also were trap prone, although some of the  $\hat{c}_b/\hat{p}_b$  ratios for these species ranged well below 1.0, indicating a few trap-shy populations.

The classification of data sets by behavioral response of species generally supported the previous results from analysis of  $\hat{c}_b/\hat{p}_b$  ratios and more clearly characterized the responses of taxa (Table 12). Responses varied significantly among genera in all families and subfamilies except Sigmodontinae ( $P < 0.01$ ). Responses among species varied significantly within the Tamias, Perognathus, and Peromyscus genera. P. parvus was the only strongly trap-prone heteromyid (Tables 11 and 12);  $\hat{c}_b/\hat{p}_b$  was never  $< 1.4$ . I. striatus, I. townsendii, S.

Table 12. Behavioral response to mark-recapture trapping by selected species of small mammals<sup>a</sup>.

Species	Number of sets	Trap response(%)			Chi-square value for differences		
		Shy <sup>b</sup>	None <sup>c</sup>	Prone <sup>d</sup>	Among species within families	Among genera within families	Among species within genera
<hr/>							
Leporidae							
<u>Sylvilagus floridanus</u>	34	11.8	82.4	5.9			3.49
<u>S. nuttallii</u>	16	31.2	68.8	0.0			
Sciuridae					54.18***	18.24**	
<u>Tamias amoenus</u>	11	27.3	63.6	9.1			34.85***
<u>T. minimus</u>	12	8.3	91.7	0.0			
<u>T. striatus</u>	18	5.6	72.2	22.2			
<u>T. townsendii</u>	34	0.0	29.4	70.6			
<u>Spermophilus richardsonii</u>	12	16.7	41.7	41.7			
<u>Glaucomys sabrinus</u>	29	20.7	79.3	0.0			
Heteromyidae					71.46***	21.9***	
<u>Perognathus amplus</u>	8	12.5	75.0	12.5			22.79***
<u>P. flavus</u>	5	0.0	80.0	20.0			
<u>P. longimembris</u>	22	27.3	72.7	0.0			
<u>P. parvus</u>	38	0.0	57.9	42.1			
<u>Chaetodipus californicus</u>	11	18.2	81.8	0.0			5.31
<u>C. formosus</u>	24	12.5	75.0	12.5			
<u>C. intermedius</u>	33	9.1	78.8	12.1			
<u>C. penicillatus</u>	11	0.0	100.0	0.0			
<u>Dipodomys agilis</u>	17	17.6	82.4	0.0			10.79
<u>D. merriami</u>	166	12.0	81.9	6.0			
<u>D. microps</u>	33	15.2	84.8	0.0			
<u>D. ordii</u>	32	3.1	81.2	15.6			
Muridae					79.93***	27.61***	
Sigmodontinae					38.44***	1.27	
<u>Reithrodontomys fulvescens</u>	2	50.0	50.0	0.0			6.74
<u>R. megalotis</u>	12	0.0	66.7	33.3			
<u>Peromyscus californicus</u>	9	11.1	77.8	11.1			29.02***
<u>P. gossypinus</u>	11	0.0	100.0	0.0			
<u>P. leucopus</u>	67	7.5	80.6	11.9			
<u>P. maniculatus</u>	275	4.7	56.7	38.6			
<u>P. truei</u>	51	9.8	64.7	25.5			
<u>Sigmodon hispidus</u>	98	7.1	67.4	25.5			
Arvicolinae					30.82***	15.80***	
<u>Clethrionomys gapperi</u>	60	3.3	83.3	13.3			5.05
<u>C. rutilus</u>	60	11.7	83.3	5.0			
<u>Microtus californicus</u>	17	5.9	52.9	41.2			7.54
<u>M. ochrogaster</u>	21	23.8	66.7	9.5			
<u>M. pennsylvanicus</u>	34	8.8	55.9	35.3			

<sup>a</sup>Results are from data sets for which Model M<sub>b</sub> produced estimates of population parameters. The results of chi-square tests of behavioral response at different taxonomic levels are included. Some of the CAPTURE results received for S. richardsonii and S. hispidus did not include estimates of parameters from M<sub>b</sub>.

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

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

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

\*\*Significant at  $P = 0.01$ .

\*\*\*Significant at  $P = 0.001$ .



richardsonii, P. parvus, R. megalotis, P. maniculatus, M. californicus, and M. pennsylvanicus were clearly trap prone, whereas P. leucopus, P. truei, and S. hispidus had that tendency. S. nuttallii, I. amoenus, G. sabrinus, and P. longimembris were clearly trap shy, whereas C. californicus, D. agilis, and D. microps were trap shy when a behavioral response was present. C. penicillatus and P. gossypinus showed no significant behavioral response to trapping, but this may be because no large data sets were available for these species; CAPTURE infrequently detected behavioral effects in small data sets (Tables 6 and 7).

Results from these analyses were similar to those from the effect scores (Table 9) except when the scores did not indicate strong behavioral responses. Model-selection criteria more strongly reflected heterogeneity in capture probabilities than behavioral response for G. sabrinus, S. hispidus, and Microtus spp.

#### Animal movement

Mean maximum-distance moved (MMDM) varied greatly within and among species (Fig. 1). Sciurids moved greater distances than murids, which, in turn, moved more than heteromyids. Almost all MMDM's of sciurids were greater than the trap spacing used in those studies. I. striatus and S. richardsonii moved less than other sciurids, but this may be partly a function of the smaller average trap spacing used in studies on those species. Perognathus and Dipodomys spp. moved greater distances than did Chaetodipus spp. Average trap-spacings in studies of C. californicus and C. intermedius were much greater than actual

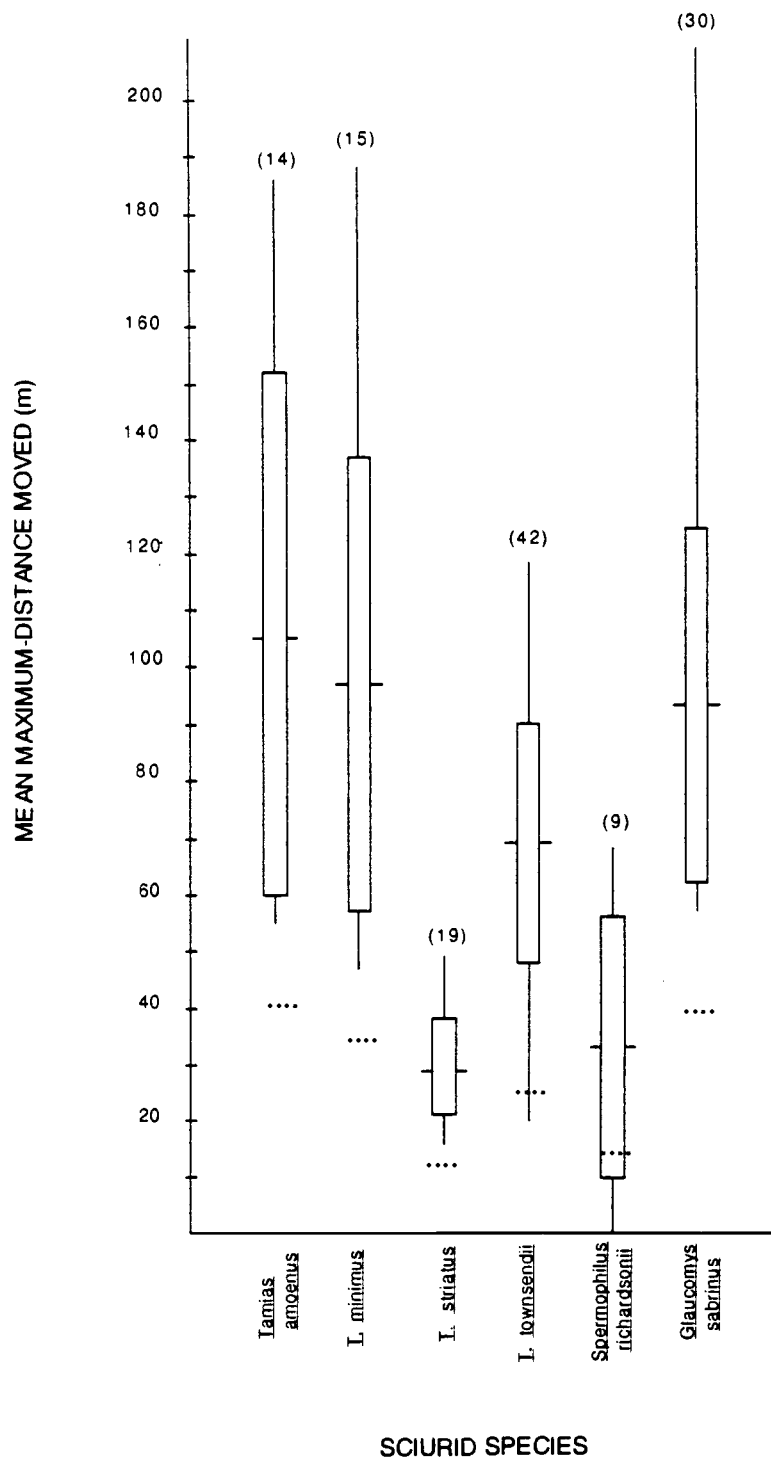


Fig. 1a. Mean, standard deviation, and range of the mean maximum-distance in meters (MMDM) moved by animals, computed by CAPTURE for each sciurid species. Average trap-spacing is indicated with a dotted line; sample size is in parentheses.

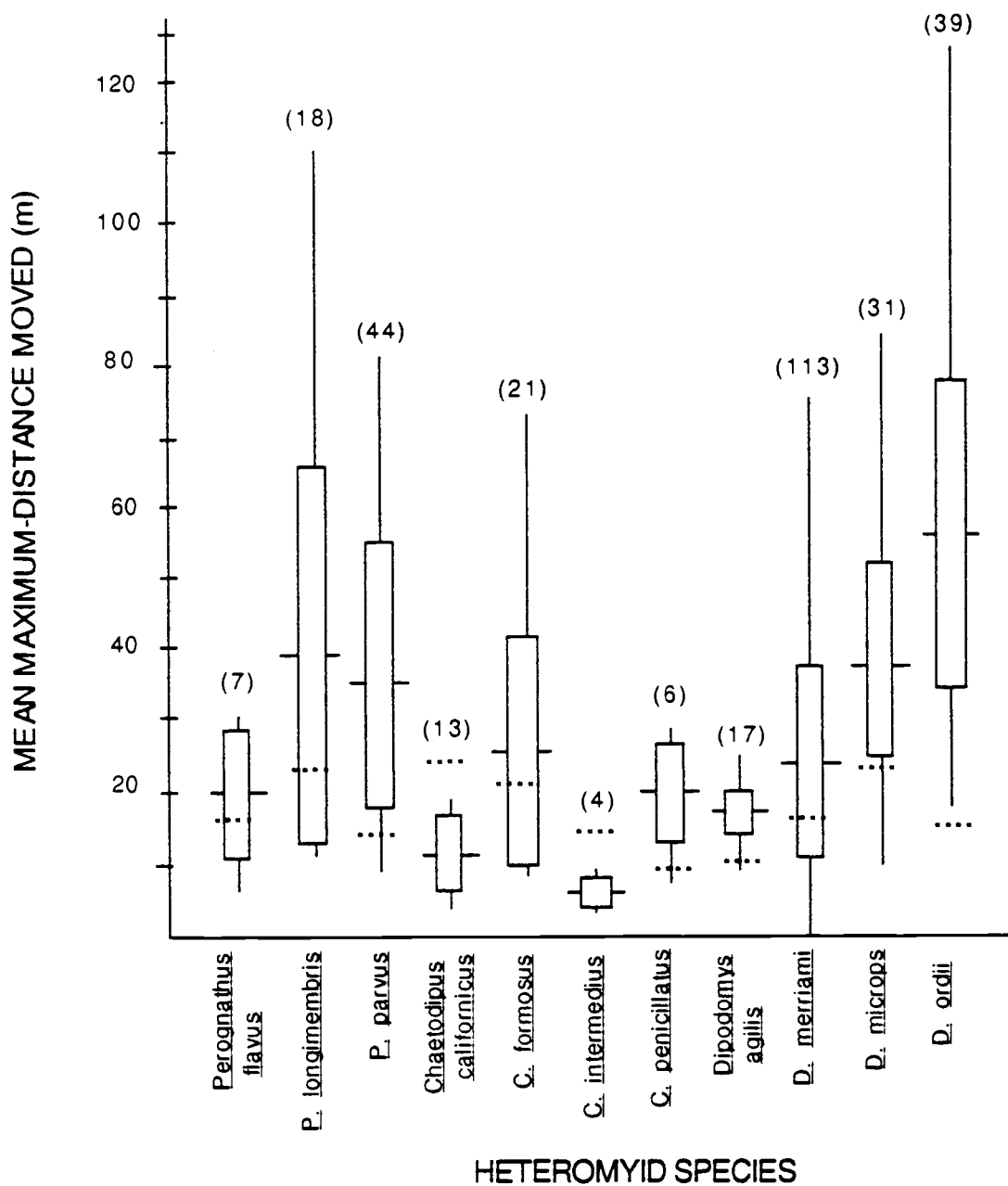


Fig. 1b. Mean, standard deviation, and range of the mean maximum-distance moved in meters (MMDM) by animals, computed by CAPTURE for each heteromyid species. Average trap-spacing is indicated with a dotted line; sample size is in parentheses.

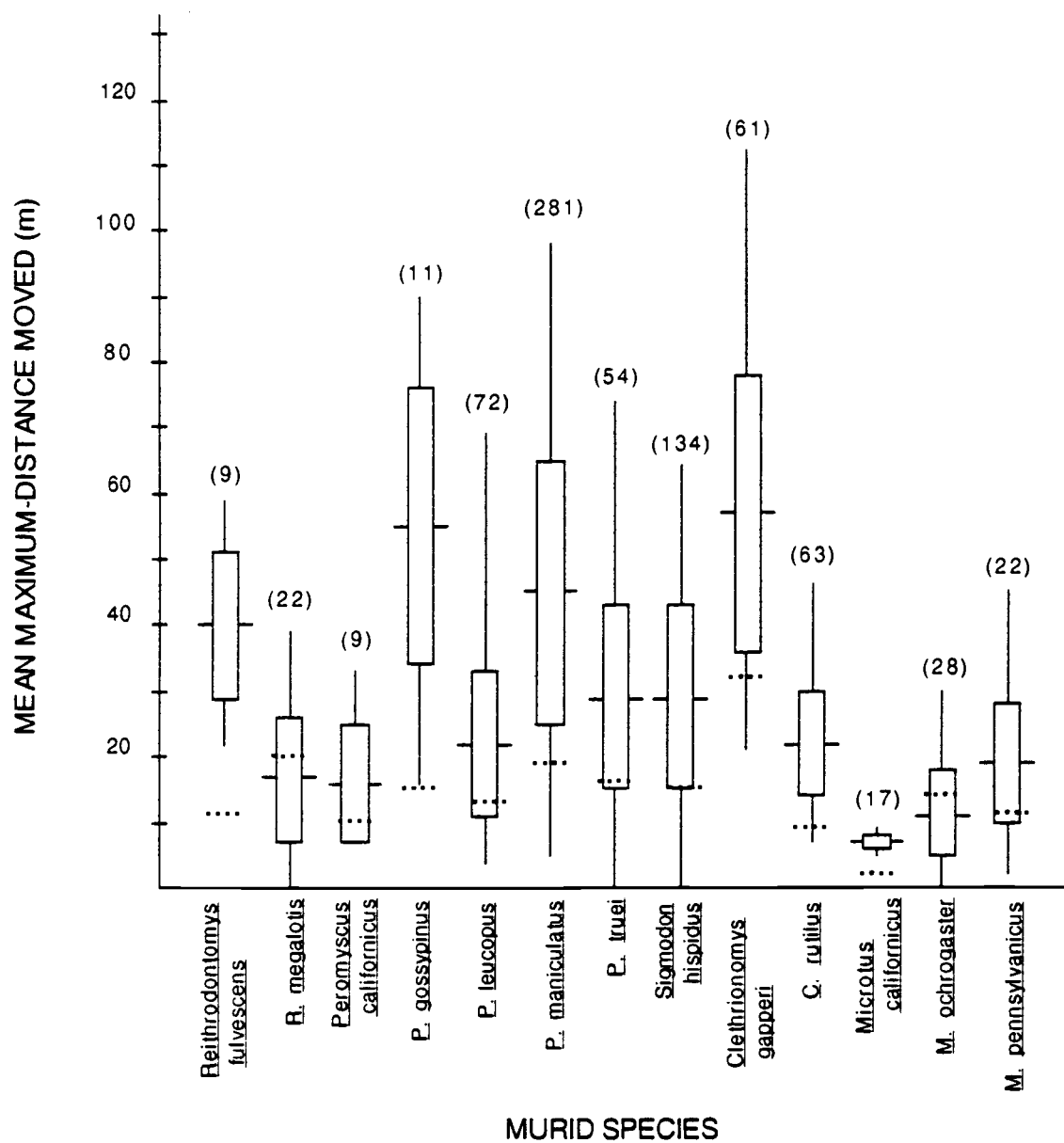


Fig. 1c. Mean, standard deviation, and range of the mean maximum-distance moved in meters (MMDM) by animals, computed by CAPTURE for each murid species. Average trap-spacing is indicated with a dotted line; sample size is in parentheses.

animal movement. Sigmodontines tended to move greater distances than did arvicolines, although this too may have been a function of trap spacing.

Animal movement varied significantly with trap spacing for 10 species ( $P < 0.01$ ), but spacing was often unique to different studies. Other characteristics of studies such as animal habitat and length of trapping session probably influenced results. Small sample sizes were a problem in many of these analyses, and trap spacings represented by the smallest number of data sets were associated with the highest or lowest MMDM for a species. For example, only 2 of 22 M. pennsylvanicus trapping sessions occurred on a grid with a 11.4-m trap spacing; the average MMDM of 4.7 m for this spacing was 17-29% of the MMDM for the other 3 spacings. Only data for D. merriami ( $F = 11.31$ ,  $P < 0.0001$ ,  $df = 112$ ) clearly indicated the positive relationship between MMDM and trap spacing.

Mean maximum-distance moved and estimate of density ( $\hat{D}$ ) were related inversely for 12 species (Table 13, Appendix D), although their correlation was often too low for these relationships to have much predictive value ( $P < 0.01$ ;  $0.28 < r < 0.81$ ). The relationships can be useful, however, for future studies of I. townsendii, P. parvus, D. agilis, C. rutilus, and M. pennsylvanicus because of high correlations ( $r > 0.70$ ). If abundance can be grossly estimated from sightings of animals or active vole-runways (Batzli 1969, Pearson 1971, Carroll and Getz 1976), then movements can be predicted from approximate densities and the trap spacing selected accordingly.

Table 13. Regression of mean maximum-distance moved in meters (MMDM) on estimates of density in animals/ha (D) for selected species of small mammals (for which at least 10 data sets were analyzed). The model yielding the highest correlation coefficient (r) was chosen from 4 regression models<sup>a</sup> incorporated into STATGRAPHICS. Value given is r from relationships with a significant F-ratio ( $P < 0.01$ )<sup>b</sup>.

Species	Number of data sets	Regression of MMDM on $\hat{D}$	
		r	Regression equation
Sciuridae			
<u>Tamias amoenus</u>	11		
<u>T. minimus</u>	11		
<u>T. striatus</u>	16		
<u>T. townsendii</u>	32	-0.71***	$y = \exp(4.52 - 0.05x)$
<u>Glaucomys sabrinus</u>	22		
Heteromyidae			
<u>Perognathus longimembris</u>	16		
<u>P. parvus</u>	30	-0.73***	$y = \exp(3.91 - 0.02x)$
<u>Chaetodipus californicus</u>	12		
<u>C. formosus</u>	18	-0.63**	$y = 43.38x^{-0.33}$
<u>Dipodomys agilis</u>	13	-0.74**	$1/y = 0.01 + 0.002x$
<u>D. merriami</u>	91	-0.59***	$y = 31.55x - 0.16$
<u>D. microps</u>	26		
<u>D. ordii</u>	31	-0.68***	$1/y = 0.02 + 0.0005x$
Muridae			
Sigmodontinae			
<u>Reithrodontomys megalotis</u>	18		
<u>Peromyscus gossypinus</u>	10		
<u>P. leucopus</u>	64	-0.49***	$y = 75.36x^{-0.48}$
<u>P. maniculatus</u>	228	-0.28***	
<u>P. truei</u>	39	-0.63***	$y = 41.36x - 0.61$
<u>Sigmodon hispidus</u>	106	-0.57***	$y = 37.38x - 0.19$
Arvicolinae			
<u>Clethrionomys gapperi</u>	46		
<u>C. rutilus</u>	44	-0.76***	$y = 120.86x^{-0.53}$
<u>Microtus californicus</u>	9		
<u>M. ochrogaster</u>	20		
<u>M. pennsylvanicus</u>	17	-0.81***	$y = \exp(3.34 - 0.005x)$

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

<sup>b</sup>Graphs of significant relationships with  $r > 0.70$  are in Appendix D.

\*\*Significant at  $P = 0.01$ .

\*\*\*Significant at  $P = 0.001$ .

# Evaluating CAPTURE results: model selection and parameter estimates

The model-selection criteria often followed predictable patterns that resulted from the CAPTURE algorithm and did not reflect actual sources of variation in capture probabilities. When  $M_0$  was selected as the most appropriate model, the criteria for the other models followed a predictable order in magnitude with small variation. This was illustrated by the mean and standard deviation of criteria from 102 trapping sessions for P. maniculatus:  $M_0 = 1.00$ ,  $M_h = 0.82 \pm 0.08$ ,  $M_{tbh} = 0.74 \pm 0.13$ ,  $M_{bh} = 0.65 \pm 0.12$ ,  $M_{th} = 0.48 \pm 0.14$ ,  $M_b = 0.32 \pm 0.15$ ,  $M_{tb} = 0.32 \pm 0.10$ , and  $M_t = 0.02 \pm 0.06$ . When model  $M_0$  was chosen as the most appropriate model by CAPTURE, other models received predictable criteria and rankings such that  $M_h$  was almost always second,  $M_{tbh}$  third, etc.

This pattern was not a function of size of the data set. When only larger data sets ( $M_{t+1} > 39$  and  $t > 5$ ) were analyzed for all species combined, the means from the 16 data sets for which  $M_0$  was most appropriate were similar to those listed for all data sets, although standard deviations were sometimes greater. Patterns of model selection were also evident in the larger data sets when other models were selected as most appropriate. When  $M_h$  was most appropriate,  $M_0$  and  $M_{tbh}$  were usually ranked next, followed by the other models incorporating heterogeneity (63 data sets;  $M_h = 1.00$ ,  $M_0 = 0.78 \pm 0.14$ ,  $M_{tbh} = 0.72 \pm 0.16$ ,  $M_{bh} = 0.57 \pm 0.16$ ,  $M_{th} = 0.38 \pm 0.17$ ,  $M_b = 0.37 \pm 0.16$ ,  $M_{tb} = 0.34 \pm 0.13$ ,  $M_t = 0.00 \pm 0.01$ ). However, when model  $M_b$  was most appropriate, it usually was followed by models incorporating behavioral effects and then by  $M_0$  (28 data sets;  $M_b = 1.00$ ,  $M_{bh} = 0.71$

$\pm 0.20$ ,  $M_{tb} = 0.69 \pm 0.13$ ,  $M_{tbh} = 0.53 \pm 0.22$ ,  $M_{th} = 0.45 \pm 0.17$ ,  $M_0 = 0.44 \pm 0.21$ ,  $M_h = 0.39 \pm 0.25$ ,  $M_t = 0.03 \pm 0.17$ ); and  $M_t$  was usually followed by models incorporating time effects followed by those incorporating behavioral effects (7 data sets;  $M_t = 1.00$ ,  $M_{th} = 0.75 \pm 0.07$ ,  $M_{tbh} = 0.43 \pm 0.25$ ,  $M_{tb} = 0.35 \pm 0.15$ ,  $M_b = 0.27 \pm 0.21$ ,  $M_0 = 0.27 \pm 0.20$ ,  $M_h = 0.11 \pm 0.17$ ,  $M_{bh} = 0.03 \pm 0.05$ ). When  $M_{bh}$  was most appropriate,  $M_b$  or  $M_h$  occasionally received a criterion  $>0.75$  (21 data sets;  $M_{bh} = 1.00$ ,  $M_{tbh} = 0.80 \pm 0.14$ ,  $M_h = 0.69 \pm 0.20$ ,  $M_b = 0.69 \pm 0.16$ ,  $M_0 = 0.66 \pm 0.13$ ,  $M_{th} = 0.46 \pm 0.19$ ,  $M_{tb} = 0.45 \pm 0.12$ ,  $M_t = 0.00$ ). When  $M_{th}$  was selected, a model with an estimator rarely received a criterion  $>0.75$  (15 data sets;  $M_{th} = 1.00$ ,  $M_{tbh} = 0.64 \pm 0.20$ ,  $M_t = 0.47 \pm 0.30$ ,  $M_{tb} = 0.35 \pm 0.30$ ,  $M_0 = 0.33 \pm 0.23$ ,  $M_h = 0.29 \pm 0.30$ ,  $M_b = 0.27 \pm 0.28$ ,  $M_{bh} = 0.18 \pm 0.20$ ). Model  $M_b$  often received a criterion  $>0.75$  when  $M_{tb}$  was most appropriate (7 data sets;  $M_{tb} = 1.00$ ,  $M_{tbh} = 0.79 \pm 0.11$ ,  $M_b = 0.69 \pm 0.34$ ,  $M_{th} = 0.65 \pm 0.25$ ,  $M_0 = 0.45 \pm 0.27$ ,  $M_h = 0.36 \pm 0.27$ ,  $M_{bh} = 0.22 \pm 0.18$ ,  $M_t = 0.12 \pm 0.21$ ). Model  $M_{tbh}$  usually was followed by  $M_h$  and  $M_0$  (39 data sets;  $M_{tbh} = 1.00$ ,  $M_h = 0.75 \pm 0.21$ ,  $M_0 = 0.72 \pm 0.16$ ,  $M_{bh} = 0.61 \pm 0.27$ ,  $M_{th} = 0.52 \pm 0.18$ ,  $M_{tb} = 0.48 \pm 0.15$ ,  $M_b = 0.40 \pm 0.20$ ,  $M_t = 0.04 \pm 0.16$ ).

Abundance estimates ( $\hat{N}$ 's) from the 5 models followed consistent trends in magnitude (Table 14). Lowest  $\hat{N}$ 's were obtained from model  $M_t$ , followed in increasing order by  $M_0$ ,  $M_b$ ,  $M_{bh}$ , and  $M_h$ .  $\hat{N}$ 's from  $M_0$ ,  $M_b$ , and  $M_{bh}$  differed by  $<10\%$  from each other. Those from models  $M_t$  and  $M_0$  were similar and differed by an average of  $<4\%$ .  $\hat{N}$ 's differed most between those from  $M_t$  or  $M_0$  and  $M_h$ ;  $M_0$  and  $M_h$  were the 2 most commonly selected models for most data sets.  $\hat{N}$ 's from models  $M_0$  and  $M_t$



Table 14. Comparison of estimates of animal abundance ( $\bar{N}$ ) provided by CAPTURE models for 1535 data sets from selected species of small mammals. Values (%) are the mean and standard deviation (sample sizes in parentheses<sup>a</sup>) of the percent difference of estimates from models, relative to the estimate from the model listed vertically<sup>b</sup>.

CAPTURE models	CAPTURE models				
	$M_o$	$M_h$	$M_b$	$M_{bh}$	$M_t$
$M_o$	0	-20.0 $\pm$ 27.3 (1466)	- 8.6 $\pm$ 38.1 (1272)	- 9.2 $\pm$ 40.2 (1318)	2.6 $\pm$ 7.2 (1446)
$M_h$	12.2 $\pm$ 24.0 (1466)	0	8.8 $\pm$ 29.4 (1274)	8.4 $\pm$ 30.9 (1332)	14.6 $\pm$ 22.8 (1446)
$M_b$	0.2 $\pm$ 31.4 (1272)	-18.0 $\pm$ 32.0 (1274)	0	- 0.2 $\pm$ 10.2 (1268)	3.0 $\pm$ 27.4 (1272)
$M_{bh}$	- 0.5 $\pm$ 35.1 (1318)	-18.3 $\pm$ 33.9 (1332)	- 1.0 $\pm$ 14.7 (1268)	0	2.6 $\pm$ 30.6 (1316)
$M_t$	- 3.9 $\pm$ 19.2 (1446)	-24.1 $\pm$ 33.1 (1446)	-11.3 $\pm$ 39.4 (1272)	-12.0 $\pm$ 41.4 (1316)	0

<sup>a</sup>The number of comparisons are all <1,535, because models did not always produce estimates of population parameters.

<sup>b</sup> $(\bar{N}_{\text{vert}} - \bar{N}_{\text{hori}})/\bar{N}_{\text{vert}} * 100$ .

probably were negatively biased, because these models require that capture probabilities be constant among individuals.

Estimates from models  $M_b$  and  $M_{bh}$  differing an average of  $\geq 1\%$ , because both are "removal models" and model  $M_{bh}$  is the general case of model  $M_b$ . The most specific model, and the one first tested, is essentially  $M_b$ ; it is usually not rejected unless heterogeneity is extreme (White et al. 1982:69).

The  $\hat{N}$ 's differed significantly among CAPTURE models ( $P < 0.001$ ).  $\hat{N}$ 's from model  $M_h$  were significantly greater than  $\hat{N}$ 's from models  $M_b$ ,  $M_o$ , and  $M_t$  for D. merriami ( $\chi^2 = 16.06$ ,  $df = 900$ ) and S. hispidus ( $\chi^2 = 21.54$ ,  $df = 657$ ), but not for P. maniculatus ( $P = 0.02$ ,  $\chi^2 = 10.96$ ,  $df = 1,399$ ). The order of the models by magnitude of  $\hat{N}$  was the same as that in Table 14 ( $\hat{N}_h > \hat{N}_b$  or  $\hat{N}_{bh} > \hat{N}_o > \hat{N}_t$ ).

Capture probabilities ( $\hat{p}$ 's) differed significantly among models for all 3 species, but models were not ranked consistently by magnitude of  $\hat{p}$  ( $P < 0.0002$ ). In 2 comparisons,  $\hat{p}$ 's from model  $M_h$  were significantly less than  $\hat{p}$ 's from the other models, and those  $\hat{p}$ 's did not differ significantly from each other. In the third comparison, the  $\hat{p}$ 's from models  $M_b$ ,  $M_{bh}$ , and  $M_h$  were significantly less than those from  $M_o$  and  $M_t$ . The  $\hat{p}$ 's increased with total number of different individuals trapped or total number of captures, and these relationships were significant for 4 and 2 species, respectively ( $P < 0.01$ ), but, correlations were  $< 0.59$ . The relationship between  $\hat{p}$  and  $t$  was stronger (Table 15, Appendix E), because as  $t$  increased, more animals with low  $\hat{p}$ 's were captured, reducing the overall  $\hat{p}$  of the population during the trapping session (Cormack 1972).

Table 15. Relationships between estimated probability of capture ( $\hat{p}$ ), number of occasions ( $t$ ) per trapping session, and coefficient of variation of abundance estimates from model  $M_{bh}$  ( $CV_{bh}$ ) for selected species of small mammals. The model yielding the highest correlation coefficient ( $r$ ) was chosen from 4 regression models<sup>a</sup> incorporated into STATGRAPHICS. Value given is  $r$  from relationships with a significant  $F$ -ratio ( $P < 0.01$ )<sup>b</sup>.

Species	Number of data sets <sup>c</sup>	r	
		$\hat{p}$ regressed on t	CV <sub>bh</sub> regressed on: t $\hat{p}$
Leporidae			
<u>Sylvilagus floridanus</u>	30- 35		-0.60***
<u>S. nuttallii</u>	13- 21	-0.65**	
Sciuridae			
<u>Tamias amoenus</u>	9- 12		
<u>T. minimus</u>	10- 13		
<u>T. striatus</u>	15- 18		
<u>T. townsendii</u>	29- 37		-0.62***
<u>Spermophilus richardsonii</u>	7- 24		
<u>Glaucomys sabrinus</u>	20- 28	-0.75***	-0.71***
Heteromyidae			
<u>Perognathus amplus</u>	too few		
<u>P. flavus</u>	too few		
<u>P. longimembris</u>	21- 24		-0.86***
<u>P. parvus</u>	29- 40	-0.49**	-0.75***
<u>Chaetodipus californicus</u>	10- 12		
<u>C. formosus</u>	18- 25	-0.53**	-0.68***
<u>C. intermedius</u>	28- 33	-0.81***	
<u>C. penicillatus</u>	9- 12		
<u>Dipodomys agilis</u>	13- 17		-0.76**
<u>D. merriami</u>	91-171	-0.58***	-0.51***
<u>D. microps</u>	27- 33		-0.52**
<u>D. ordii</u>	27- 34		-0.60**
MURIDAE:			
Sigmodontinae			
<u>Reithrodontomys fulvescens</u>	too few		
<u>R. megalotis</u>	13- 18		-0.77**
<u>Peromyscus californicus</u>	7- 9		
<u>P. gossypinus</u>	10- 11		
<u>P. leucopus</u>	61- 68	-0.44***	-0.71***
<u>P. maniculatus</u>	227-276	-0.53***	0.17**      -0.74***
<u>P. truei</u>	39- 53		-0.88***
<u>Sigmodon hispidus</u>	90-140	-0.52***	-0.36***      -0.59***
Arvicolinae			
<u>Clethrionomys gapperi</u>	46- 60		-0.36**      -0.71***
<u>C. rutilus</u>	43- 60		-0.78***
<u>Microtus californicus</u>	9- 17	-0.88**	
<u>M. ochrogaster</u>	16- 21	-0.57**	-0.71**
<u>M. pennsylvanicus</u>	28- 35		-0.77***

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

<sup>b</sup>Appendix E contains graphs of significant relationships between  $\hat{p}$  and  $t$  with  $r > 0.70$ ; Appendix F contains graphs for all significant relationships between  $CV_{bh}$  and  $\hat{p}$  ( $P < 0.01$ ).

<sup>c</sup>Number of data sets differed among comparisons.

\*\*Significant at  $P = 0.01$ .

\*\*\*Significant at  $P = 0.001$ .

Coefficients of variation (CV's) of abundance estimates ( $\hat{N}$ 's) varied considerably and differed significantly among models for D. merriami, P. maniculatus, and S. hispidus ( $P < 0.001$ ) (Fig. 2). CV's of  $\hat{N}_b$  and  $\hat{N}_{bh}$  ( $CV_{bh}$ ) were twice as great as those of  $\hat{N}_h$ ,  $\hat{N}_o$ , and  $\hat{N}_t$  for all 3 species, and  $CV_{bh}$  was always significantly greater than CV's of  $\hat{N}_t$  and  $\hat{N}_o$ . Seventy-five percent of CV's from  $\hat{N}_h$ ,  $\hat{N}_o$ , and  $\hat{N}_t$  were  $< 0.20$ . When only the CV's of  $\hat{N}$ 's from the best model were analyzed, their values covered a smaller range for each model than when all CV's were compared, and differences were still significant ( $P < 0.001$ ) ( $\chi^2 = 18.62$ , 157 data sets;  $\chi^2 = 45.08$ , 229 data sets; and  $\chi^2 = 13.99$ , 140 data sets; for D. merriami, P. maniculatus, and S. hispidus, respectively). However, multiple-comparison tests were inconclusive because models  $M_b$ ,  $M_t$ , and  $M_{bh}$  provided few estimates (e.g. 14, 12, and 4, respectively, for D. merriami). Because  $CV_{bh}$  usually covered the broadest range of values and had the greatest median, it appeared to give the most conservative estimate of the precision of a data set. Therefore, I used  $CV_{bh}$  to examine the effects of trapping design on the relative precision of a data set.

The relationship between  $CV_{bh}$  and  $\hat{p}$  was the strongest of all relationships tested.  $CV_{bh}$  decreased significantly yet was poorly correlated ( $r < 0.71$ ) with total number of captures (9 species), number of different individuals captured (3 species), or length of trapping session (3 species), but was significantly related to  $\hat{p}$  at  $P < 0.01$  for 20 of the 33 comparisons and for another 6 species at the 0.05 level (Table 15, Appendix F).  $CV_{bh}$  decreased curvilinearly as  $\hat{p}$  increased for all comparisons, with most  $r$ -values ranging from -0.59 to

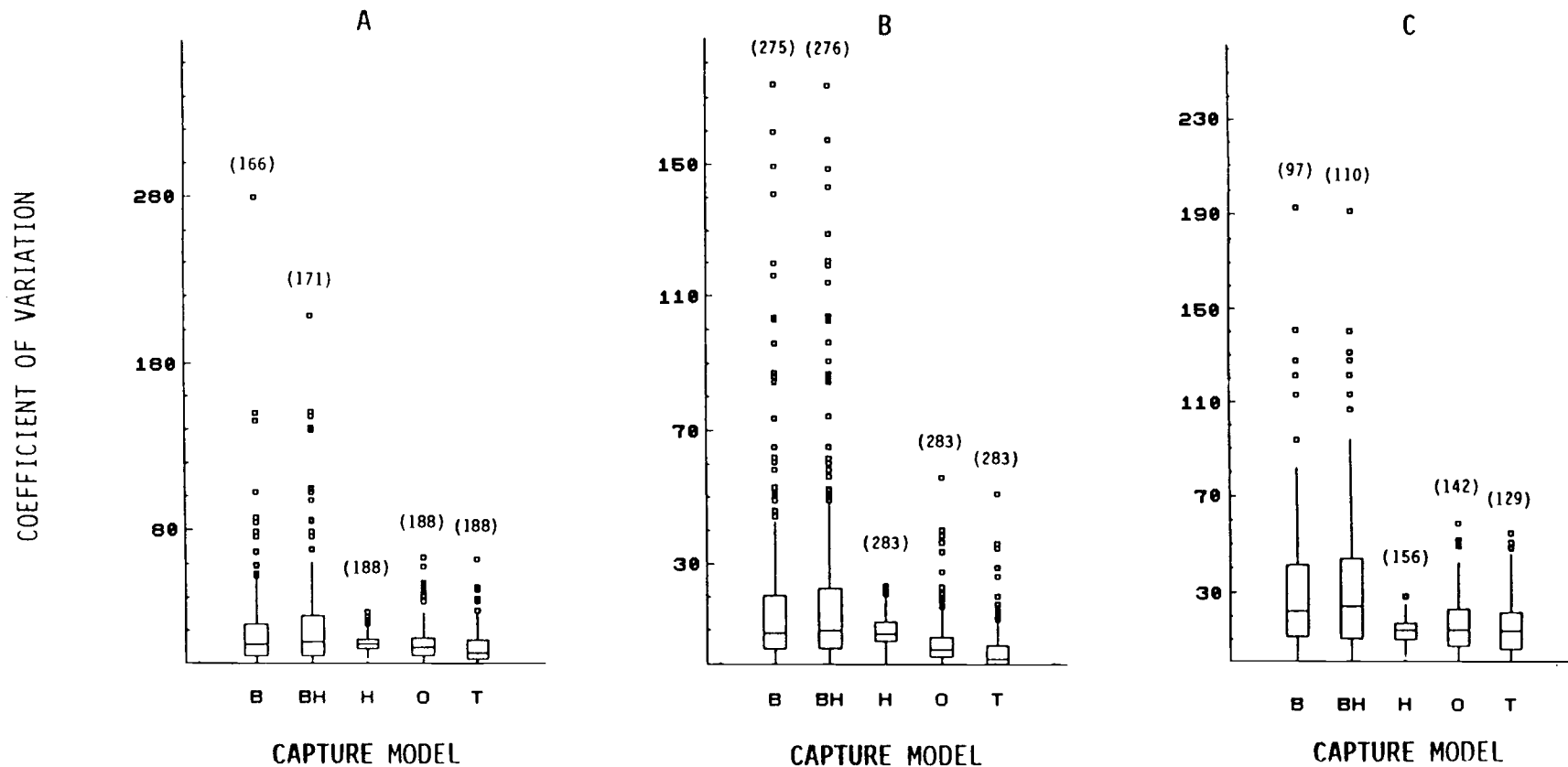


Fig. 2. Median and range of coefficients of variation from all abundance estimates from each of the 5 CAPTURE models for A) *Dipodomys merriami*, B) *Peromyscus maniculatus*, and C) *Sigmodon hispidus*. The large box covers the middle 50% of the values, and the central line is at the median. The lines extend to minimum and maximum values, but values beyond 1.5 times the interquartile range (distance between top and bottom ends of the box) are marked by dots. Sample sizes are in parentheses.

-0.81. Thus  $\hat{p}$  should be maximized to obtain the most precise  $\hat{N}$ . The  $\hat{p}$  at which  $CV_{bh} < 20\%$  ('minimal'  $\hat{p}$ ) varied among taxa. Lowest minimal  $\hat{p}$ 's (0.04 and 0.09) were calculated for S. floridanus and G. sabrinus, respectively. Most species required a minimum  $\hat{p}$  of 0.20-0.35. The minimum  $\hat{p}$  was greater than the average  $\hat{p}$ , for I. minimus (minimum = 0.17, average = 0.14), P. longimembris (0.36, 0.29), R. megalotis (0.37, 0.30), and S. hispidus (0.33, 0.26); therefore, most  $\hat{N}$ 's from  $M_b$  and  $M_{bh}$  for these species have unacceptably large CV's. Minimum  $\hat{p}$ 's were within 10% of the average, respectively, for I. striatus (0.36, 0.39), S. richardsonii (0.33, 0.35), C. formosus (0.36, 0.39), and D. ordii (0.33, 0.35). Minimum  $\hat{p}$ 's were lower than average  $\hat{p}$  for the remainder of the species, suggesting that acceptable precision was achieved >50% of the time when using Models  $M_b$  or  $M_{bh}$ , and almost 100% of the time when using other models, although abundance estimates could still have been biased. Minimum  $\hat{p}$ 's were much less than their average  $\hat{p}$  for some species: G. sabrinus (0.09, 0.25), P. parvus (0.23, 0.42), D. agilis (0.41, 0.60), D. merriami (0.22, 0.34), D. microps (0.31, 0.58), P. leucopus (0.23, 0.63), P. maniculatus (0.31, 0.49), C. gapperi (0.30, 0.50), C. rutilus (0.43, 0.62), and M. pennsylvanicus (0.14, 0.29).

Estimates of animal abundance: Jolly-Seber and CAPTURE models

Abundance estimates from CAPTURE and from the Jolly-Seber model ( $\hat{N}_{JS}$ ) (Model A in Pollock et al. 1990) were compared for 16 data sets (Figs. 3-18). The Jolly-Seber model fit the data for all but 2 data sets ( $P \geq 0.04$ ) (Figs. 6 and 15).  $\hat{N}_{JS}$ 's were negatively biased when

compared to  $\hat{N}$ 's from CAPTURE for all but the 2 smallest data sets, for which  $\hat{N}_{JS}$ 's approximated  $\hat{N}$ 's from models  $M_0$  and  $M_t$  (Figs. 3 and 4).  $\hat{N}$ 's from CAPTURE usually were  $\geq M_{t+1}$  during the trapping session, whereas only 9 estimates from the Jolly-Seber model exceeded  $M_{t+1}$  (Figs. 3, 5, 7, 12, and 13). For most comparisons,  $M_{t+1}$  was 10-50% greater than the average  $\hat{N}_{JS}$  during the trapping session, providing further evidence for the strong negative bias of  $\hat{N}_{JS}$ ; animals likely were not emigrating in such great numbers over the course of 7-11 day trapping sessions.

Estimates from each model fluctuated less during trapping sessions with greater  $M_{t+1}$ , especially when  $M_{t+1} > 60$ . Low probabilities of capture ( $\hat{p} = 0.15$ ) were probably responsible for the erratic I. amoenus estimates (Fig. 12). Abundance estimates from CAPTURE models were more stable than those from the Jolly-Seber model for several trapping sessions (Figs. 6, 11-13, 15, 17, and 18); however, some estimates for model  $M_h$  were erratic (Figs. 7, 12, 14, and 16).  $\hat{N}_{JS}$ 's often fluctuated between trapping occasions (Figs. 6, 12, 13, and 18), because estimates were strongly affected by small numbers of recaptures in a sample. Estimates from the Jolly-Seber model of the number of marked animals in the population occasionally were twice as great as the actual number marked and released before that time (e.g. 128 and 57, respectively, for  $t = 8$ , Fig. 12).

Estimates from the Jolly-Seber model were almost identical to those from model  $M_t$  (the CAPTURE model for which assumptions most closely matched those of the Jolly-Seber model) when  $\hat{p}$ 's were high (Fig. 4), but estimates from both models, particularly Jolly-Seber,

were erratic when  $\hat{p}$ 's were low (Fig. 6). Unlike CAPTURE, the Jolly-Seber model did not provide an  $\hat{N}$  for the last trapping occasion, and the estimates near the end of the trapping session were often erratic because of small numbers of recaptures.

Survival and capture probabilities are assumed constant in a restricted version of the Jolly-Seber model (Model D in Pollock et al. 1990). This model fit 12 data sets and fit them better than Model A, according to chi-square goodness-of-fit tests in program JOLLY ( $P > 0.05$ ). Abundance estimates varied little during trapping sessions and were usually more negatively biased than those from Model A. I did not use these estimates in my analysis, because the assumptions of Model D most closely approximated those of  $M_0$  and were unrealistic for this study.



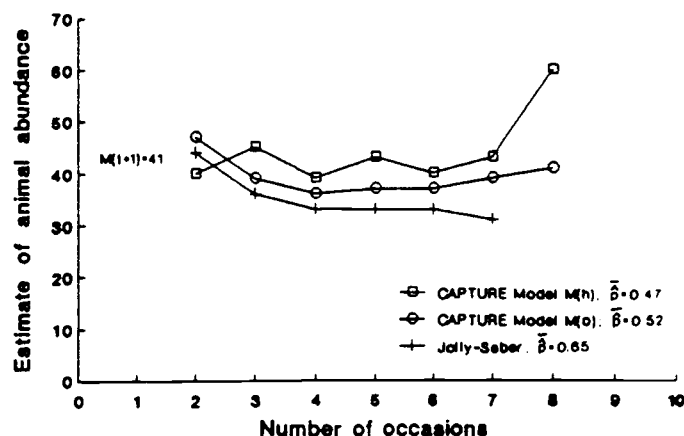


Figure 3. Estimates of abundance ( $\hat{N}$ ) of *Peromyscus maniculatus* from CAPTURE models  $M_h$  and  $M_0$ , and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_h$  and  $M_0$  were equally appropriate throughout the session (except  $M_{tbh}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

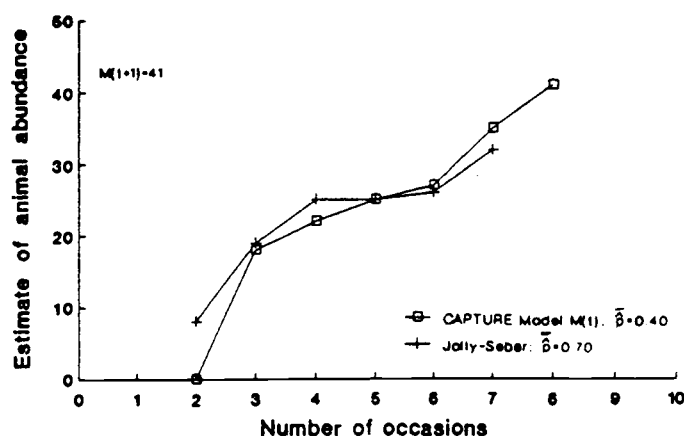


Figure 4. Estimates of abundance ( $\hat{N}$ ) of *Perognathus parvus* from CAPTURE model  $M_t$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session. Model  $M_t$  was most appropriate at the end of the session ( $M_{tbh}$  was selected for  $j = 2-6$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

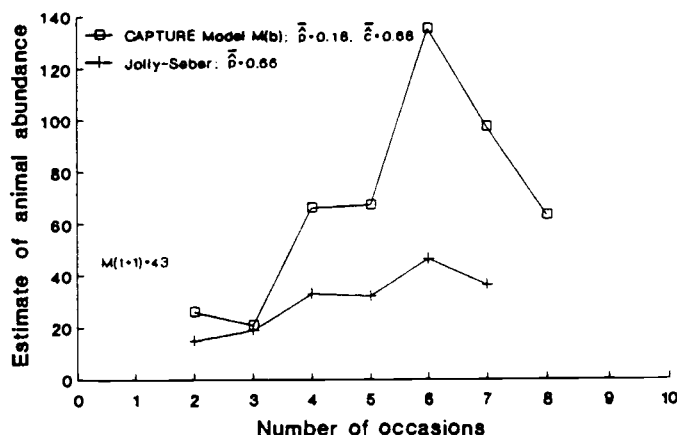


Figure 5. Estimates of abundance ( $\hat{N}$ ) of Peromyscus maniculatus from CAPTURE model  $M_b$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_b$  was most appropriate throughout the session (except  $M_{tbh}$  and  $M_0$  were selected for  $j = 2$  and 3, respectively).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

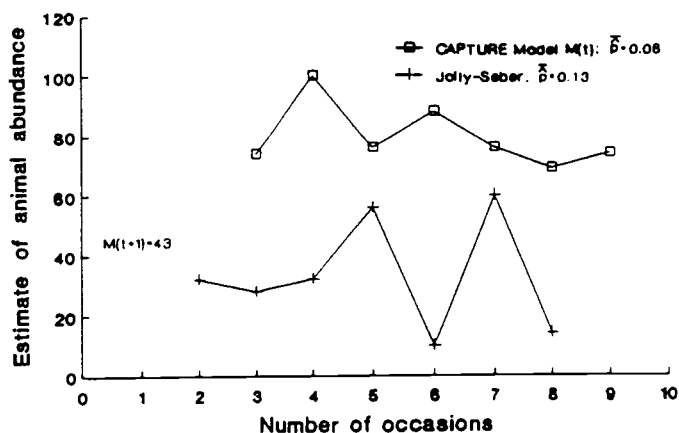


Figure 6. Estimates of abundance ( $\hat{N}$ ) of Tamias minimus from CAPTURE model  $M_t$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_t$  was most appropriate at the end of the session ( $M_0$  was selected for  $j = 2-5$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

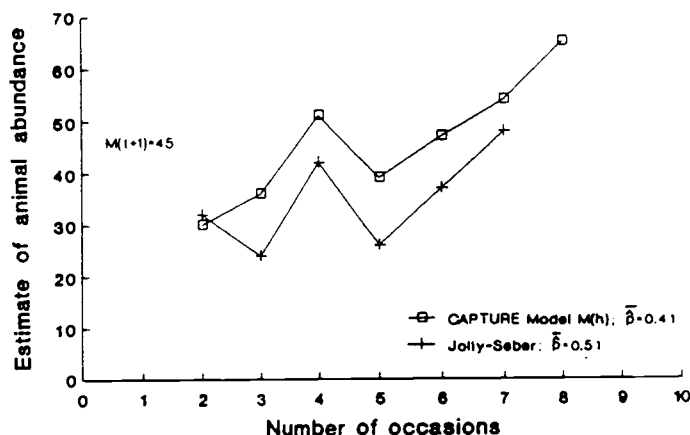


Figure 7. Estimates of abundance ( $\hat{N}$ ) of *Peromyscus maniculatus* from CAPTURE model  $M_h$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_h$  was most appropriate throughout the session (except  $M_{tbh}$  and  $M_0$  were selected for  $j = 2$  and 3, respectively).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

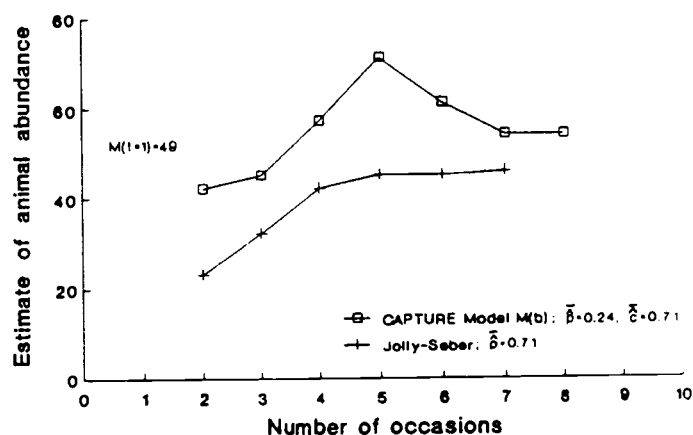


Figure 8. Estimates of abundance ( $\hat{N}$ ) of *Tamias townsendii* from CAPTURE model  $M_b$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_b$  was most appropriate throughout the session (except  $M_{tbh}$  and  $M_0$  were selected for  $j = 2$  and 3, respectively).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

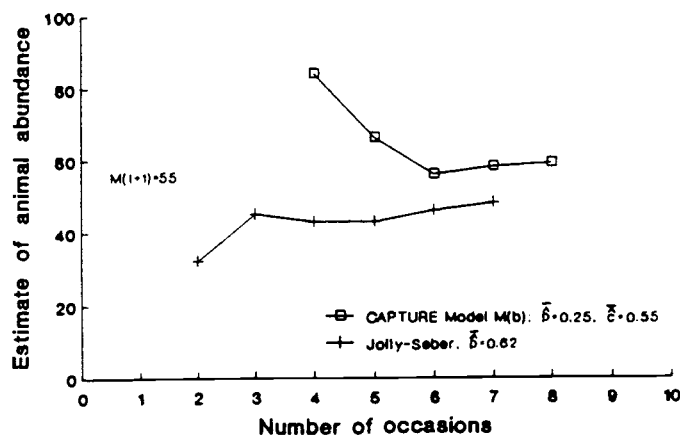


Figure 9. Estimates of abundance ( $\hat{N}$ ) of Tamias townsendii from CAPTURE model  $M_b$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_b$  was most appropriate throughout the session (except  $M_{tbh}$  and  $M_0$  were selected for  $j = 2$  and  $3$ , respectively).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

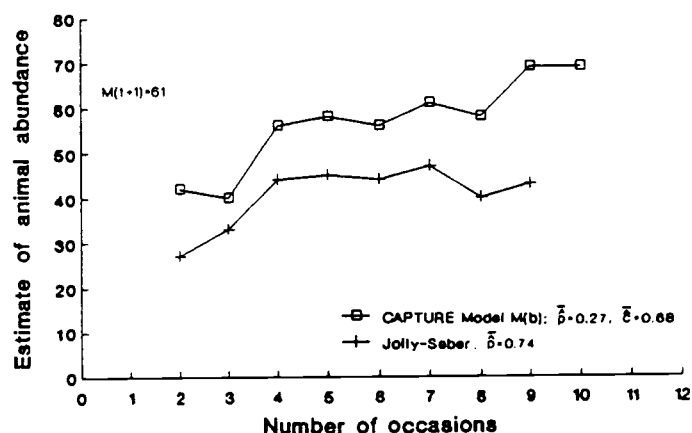


Figure 10. Estimates of abundance ( $\hat{N}$ ) of Tamias townsendii from CAPTURE model  $M_b$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_b$  was most appropriate throughout the session (except  $M_{tbh}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

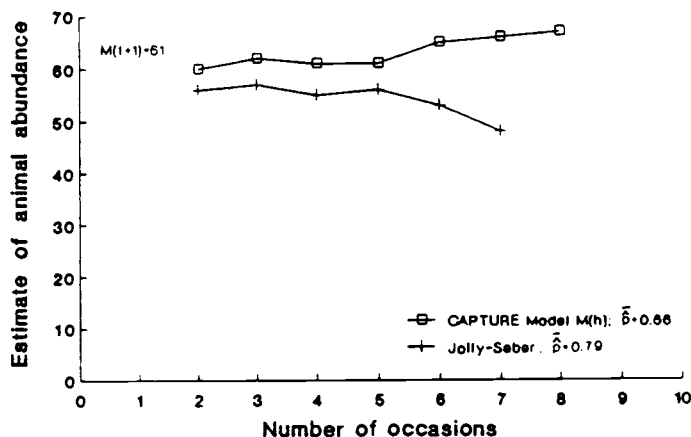


Figure 11. Estimates of abundance ( $\hat{N}$ ) of Peromyscus maniculatus from CAPTURE model  $M_h$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_h$  was most appropriate throughout the session (except  $M_{tbh}$  and  $M_0$  were selected for  $j = 2$  and 3, respectively).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

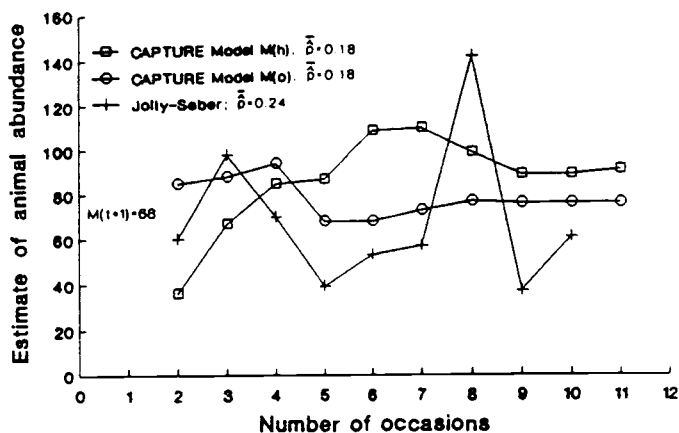


Figure 12. Estimates of abundance ( $\hat{N}$ ) of Tamias amoenus from CAPTURE models  $M_h$  and  $M_0$ , and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_h$  and  $M_0$  were equally appropriate throughout the session.  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

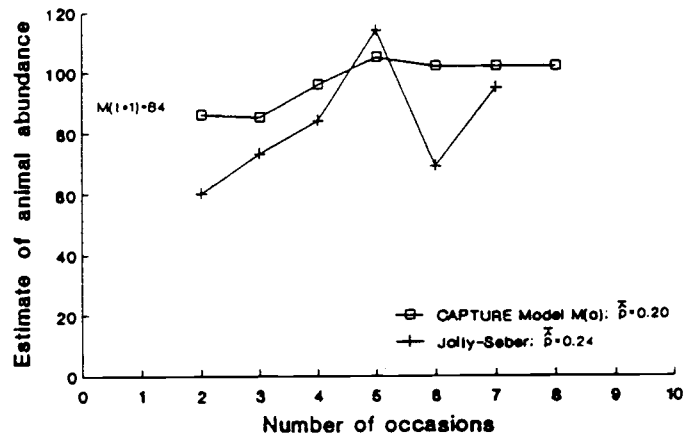


Figure 13. Estimates of abundance ( $\hat{N}$ ) of *Microtus pennsylvanicus* from CAPTURE model  $M_0$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_0$  was most appropriate throughout the session (except  $M_{tbh}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

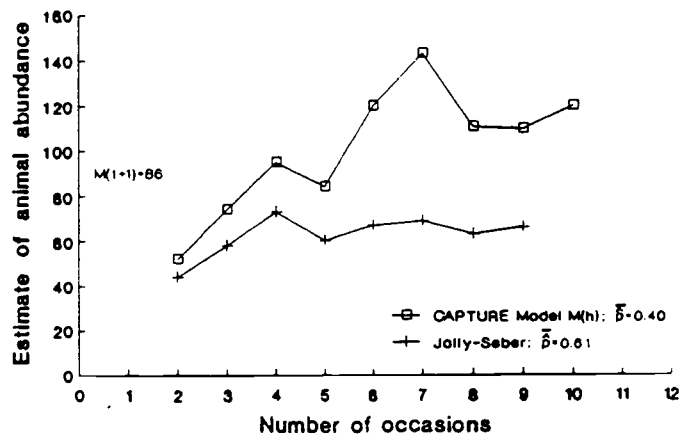


Figure 14. Estimates of abundance ( $\hat{N}$ ) of *Tamias townsendii* from CAPTURE model  $M_h$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_h$  was most appropriate throughout the session (except  $M_{tbh}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

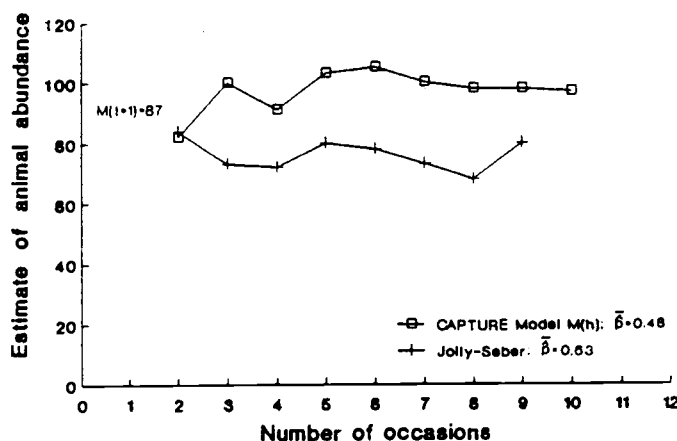


Figure 15. Estimates of abundance ( $\hat{N}$ ) of *Tamias townsendii* from CAPTURE model  $M_h$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_h$  was most appropriate throughout the session (except  $M_{t+1}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

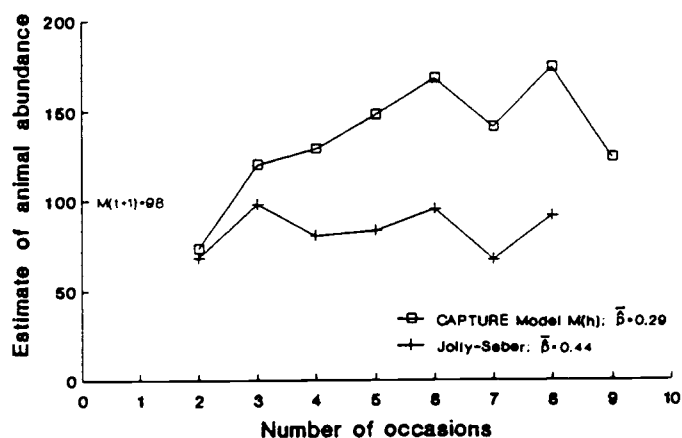


Figure 16. Estimates of abundance ( $\hat{N}$ ) of *Microtus californicus* from CAPTURE model  $M_h$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_h$  was most appropriate throughout the session (except  $M_{t+1}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

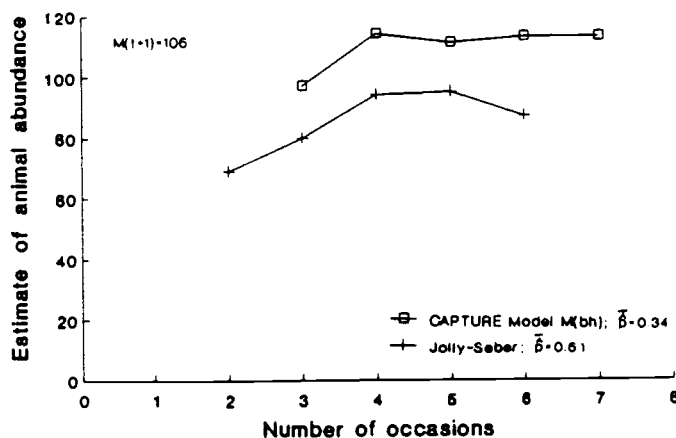


Figure 17. Estimates of abundance ( $\hat{N}$ ) of *Microtus pennsylvanicus* from CAPTURE model  $M_{bh}$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_{bh}$  was most appropriate throughout the session (except  $M_{t+bh}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.

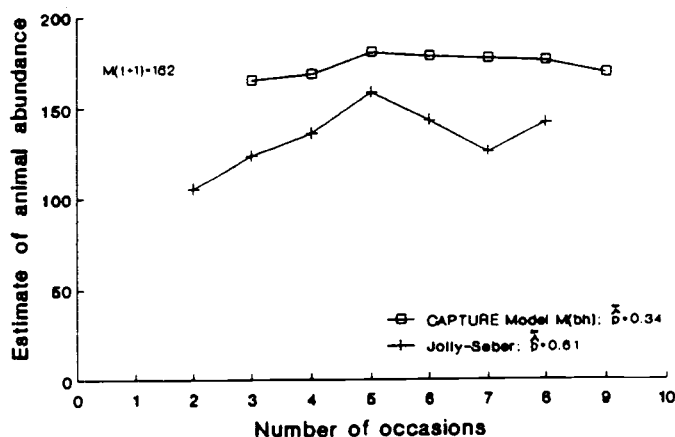


Figure 18. Estimates of abundance ( $\hat{N}$ ) of *Microtus pennsylvanicus* from CAPTURE model  $M_{bh}$  and the Jolly-Seber model, calculated for each occasion ( $j$ ) within a trapping session.  $M_{bh}$  was most appropriate throughout the session (except  $M_{t+bh}$  was selected for  $j = 2$ ).  $M_{t+1}$  = total number of individuals captured;  $\hat{p}$  = capture probability.



## DISCUSSION

My analyses clearly indicated that many small-mammal species have characteristic responses to multiple mark-recapture trapping. Although data for approximately 1/2 the species were received primarily from only 1 source each, I believe this precluded only inferences of species-specific capture probabilities. Other responses were less strongly related to individual experimental designs.

The underlying sources of variation in capture probabilities were best characterized by the identity of the most appropriate model selected by CAPTURE, my determination of the best model, and the significance of the effect scores. Determination of behavioral response was impeded, because the ratio of capture to recapture probabilities ( $\hat{c}_b/\hat{p}_b$ ) was affected by small sample sizes and had extremely large coefficients of variation. The proportions of data sets in different categories of response provided the most reliable information on behavioral response to mark-recapture procedures. The quantitative comparisons of capture probabilities and behavioral responses should be useful when planning future studies of these species.

The literature is largely devoid of information on capture probabilities of animals, and attempts to describe trap response and capture probabilities are imprecise. In this investigation I often inferred responses based on published data (e.g. number of captures and number of marked animals), qualitative statements such as "hard to catch," and mathematical expressions such as "trap success," "trapping

efficiency" (Whitney 1976), "recapture efficiency" (Cameron and Kincaid 1982), and "trappability" (Smith and Vrieze 1979). These terms are difficult to interchange, quantify, or even to define. Interpretation in terms of probabilities of capture and recapture is difficult, so results from different studies are not directly comparable. Trap success, defined as the number of animals caught per 100 trap nights, is one of the least useful terms, even as an index of abundance. Low trap success means either that there were few animals or that there were many but they had low probabilities of capture or recapture.

#### Taxonomic trends and recommendations for future studies

Family Leporidae.--Heterogeneity strongly affected capture probabilities of Sylvilagus spp., and was noted for S. floridanus (Geis 1955, Huber 1962, Edwards and Eberhardt 1967, Bailey 1969, this study). Heterogeneity was attributed mostly to the greater probabilities of capture of juveniles compared to adults and females compared to males. Bailey (1969) reported that the additional heterogeneity among individuals caused population estimates from models requiring equal capture probabilities to underestimate  $N$ , even when separate  $\hat{N}$ 's were calculated for each sex-and-age class. Geis (1955) noted strong heterogeneity in his study animals not consistently related to their age or sex; most of the animals had low probabilities of capture and only a few had high probabilities. Heterogeneity in S. nuttallii was correlated with genotype (Skalski 1977), and capture probabilities of S. floridanus were affected by weather conditions (Huber 1962). S. floridanus appeared to be trap prone (Geis 1955, Huber 1962, Edwards

and Eberhardt 1967)); however, only 6% of the data sets I analyzed were from trap-prone populations. My results reflect those presented in the literature concerning heterogeneity. Model  $M_h$  was selected frequently for data sets from S. floridanus, and  $M_{th}$  was selected for large data sets from S. nuttallii. S. floridanus had a low probability of capture (Geis 1955, Edwards and Eberhardt 1967, this study); average probabilities of capture were calculated at 0.08 (Geis 1955), and 0.06 and 0.13 (Edwards and Eberhardt 1967) and were similar to my calculation of 0.06 (Table 10).

Because S. floridanus has such low probabilities of capture and recapture, it is imperative to maximize the number of animals captured and the total number of captures and recaptures to obtain valid results from mark-recapture models. This could be achieved by increasing the size of the grid and by placing traps in heavily used, mowed corridors at a density of 10 traps/ha (Huber 1962). Trapping sessions should continue until time effects notably influence capture probabilities or until abundance estimates stabilize. However, when a S. nuttallii is trapped for >10 consecutive days, capture probability likely will become <0.01 (this study) and survival will approach zero (B.J. Verts, pers. comm.).

Family Sciuridae.--Heterogeneity in capture probabilities was frequently reported for sciurid species. Chappell (1978) noted that I. amoenus was more frequently caught than I. minimus, although my analysis of his data indicated both species had similar, low probabilities of capture and recapture. Females had higher

probabilities of capture than did males (Chappell 1978), and heterogeneity affected capture probabilities of these species. However, capture probabilities of I. amoenus also were affected by behavioral response, and those of I. minimus also were affected by time of trapping (Table 5). All except 3 data sets that I analyzed for I. minimus and I. amoenus were from Chappell's (1978) study, so species-specific responses to trapping cannot be attributed to differences in study design. Mares et al. (1981) reported that a population of I. striatus of known size showed strong heterogeneity in capture probabilities and no evidence of a behavioral response; however, my results indicated trap proneness, and model  $M_b$  was selected frequently for this species. I. townsendii was caught easily, and females were caught more easily than males (Sullivan et al. 1983). My results showed strong heterogeneity, high  $\hat{p}$ , and extreme trap proneness for this species; models  $M_h$  and  $M_b$  were selected often. S. richardsonii exhibited extreme heterogeneity (Matschke et al. 1982, 1983, this study) and was strongly trap prone (this study). Both  $M_h$  and  $M_b$  were selected frequently for this species. The average probability of capture of S. richardsonii (Table 12) was almost identical with the value of 0.35 calculated by Matschke et al. (1982), none of whose data I used. G. sabrinus was extremely trap shy and had heterogeneous capture probabilities (this study).

Trap spacing of 30 m is suitable for I. amoenus, I. minimus, and G. sabrinus. Spacing >30 m usually resulted in  $\hat{p} < 0.2$  for I. minimus. Movement of I. townsendii was strongly correlated with animal density, and this relationship may be used to calculate optimal trap spacing.

Ten-meter spacing may be most appropriate for I. striatus and S. richardsonii.

Family Heteromyidae.--Heteromyids tended to have heterogeneous capture probabilities (Daly and Behrends 1984) and be trap shy (Allred and Beck 1963). P. longimembris was one of the most trap-shy species in my analysis; however, because of their small body size, the animals may enter traps frequently without triggering them (B.J. Verts, pers. comm.). Only P. parvus (Hedlund and Rogers 1980), D. agilis (M'Closkey 1972), and D. merriami (Chew and Chew 1970) were trap prone; my results agreed with those for P. parvus but not D. agilis, and only 6% of the data sets for D. merriami that I analyzed indicated trap proneness. Time of trapping affected capture probabilities, perhaps because heteromyid activity was strongly influenced by the amount of moonlight and by endogenous rhythms (Milstead 1961, O'Farrell 1974, Kaufman and Kaufman 1982, Price et al. 1984).

Chapman and Packard (1974) reported that "pocket mice" in general were difficult to capture and mark. Perognathus merriami (now P. flavus [Wilson 1973]) was "difficult to recapture" (Chapman and Packard 1974:286), but my  $l$  value indicated trap-proneness for that population, so behavioral response varies in this species. Data presented by Daly and Behrends (1984) appear to indicate trap shyness of Perognathus fallax, but, an average  $\hat{p}$  of 0.64 was calculated for P. fallax by use of the Jolly-Seber method (McClenaghan 1983), and my values for Perognathus spp. were moderate (0.29-0.42).

Model  $M_h$  was suitable for P. parvus, whereas  $M_b$  was appropriate for P. longimembris. Results for P. flavus and P. amplus were

inconclusive. The most suitable model for Chaetodipus was probably  $M_h$ , because this genus lacked a consistent behavioral response. Despite behavioral responses in Dipodomys,  $M_h$  was selected more often, especially for large data sets.

Traps spacing should be 5-15 m for Perognathus spp. and Dipodomys, and 5-10 m for Chaetodipus. Dependable  $\hat{N}$ 's of P. parvus probably can be obtained in trapping sessions of 6-8 days (to maintain population closure) because of high probabilities of capture ( $\hat{p}$  averaged 0.42) for this species. Capture probabilities of trap-shy P. longimembris and D. agilis should be greater to obtain reliable estimates. This can be achieved for P. longimembris by redesigning traps to make them easier for these small animals to trigger the trap. Optimal trap spacing can be chosen for P. parvus and D. agilis depending on the population density.

Heteromyids often are studied by examining traps several times per night. The problems in analyzing such data are well illustrated by D. agilis, which has a "generally high proportion of recaptures" (M'Closkey 1972:663) except during summer months. My analysis indicated trap shyness, even though the species had a high probability of capture (Tables 10 and 12). I suspect that my results actually were related to the sampling design used to obtain data for this species, because traps were examined 2-3 times per night for 2 nights. However, species and sexes of heteromyids are not equally active throughout the night (O'Farrell 1974). An animal active during different portions of the night has noticeably different probabilities of capture during a short trapping session. If sexes are active for

different lengths of time, this can cause heterogenous responses within a species. If an animal is caught while active and has longer periods of inactivity when it does not enter set traps, it appears to be trap shy. However, if the setting of traps were coordinated with activity patterns of the animals, "trap shy" individuals might actually be trap neutral or trap prone. Trap shyness of heteromyids for which I analyzed data may be attributable to this phenomenon. I removed most time effects by combining trapping occasions, but enough occasions may have occurred during periods of low activity that the animals seemed "trap shy." A session consisting of 2 nights with only 2-3 occasions per night was too short for CAPTURE to detect changes in capture probabilities as a result of time. Thus, model  $M_t$  was not selected and the effect of time on capture probabilities was overlooked. When traps are set and examined several times during the night to capture species active at different times, then time effects can be expected. Many of my data for heteromyids consisted of multiple trapping occasions per night, and capture probabilities varied as a result.

Heteromyids are more active during the darkest phases of the moon or when clouds are present (Milstead 1961). Poor planning in the timing of trapping occasions can result in either time effects or low probabilities of capture, both undesirable. The best method is to combine all nightly captures into 1 occasion and increase the number of nights in the study to 5-10 when the sky is darkest. This would maximize the number of animals captured and the number of recaptures.

Family Muridae; Subfamily Sigmodontinae.--Reithrodontomys spp. had heterogeneous capture probabilities in previous studies related to the scent in traps or presence of dominant species (Cameron 1977b, Cameron and Kincaid 1982, Heske and Repp 1986) and because of their attraction to conspecific odors in traps (Heske and Repp 1986). R. megalotis data also indicated inherent heterogeneity, and M'Closkey (1972) believed that some adults were never caught. Cameron (1977b) reported that R. fulvescens had a high probability of capture, but my estimate of  $\hat{p}$  was moderately low ( $0.21 \pm 0.32$ ). Probabilities of recapture for R. fulvescens were not sex-specific (Cameron 1977b); however more males than females were caught initially, probably because of differential movement between the sexes (Cameron 1977a). Data presented in Chew and Chew (1970:8) seemed to indicate that R. megalotis was difficult to recapture, but my analyses indicated possible trap proneness. R. fulvescens was reported to be difficult to recapture (Packard 1968), and my single estimate ( $\hat{c}_b/\hat{p}_b = 0.31$ ) supported this contention. Model  $M_b$  or  $M_h$  was most appropriate for the Reithrodontomys populations in my analyses.

Temporary-removal trapping may provide useful abundance estimates for Reithrodontomys when the presence of dominant species is affecting capture probabilities of subordinates (Cameron 1977b). Trap spacing for R. megalotis should be reduced to approximately 5-10 m, less than one-half of the average spacing used in this analysis.

Peromyscus gossypinus had high probabilities of capture (Shadowen 1963, this study) influenced by heterogeneity (this study). However, low probabilities were reported during a snap-trapping study; only 48%



of the individuals caught in 27 days were trapped in the first 5 days and only 59% in the first 9 days (Gentry et al. 1968). These results may have been related to avoidance of snap traps or to low probabilities of capture in that population. The sex ratio after 27 days was 1:1, but twice as many males as females had been removed by the fifth day (Gentry et al. 1968). More males usually were caught than females in live-trapping studies (Pournelle 1952, McCarley 1959, Terman and Sassaman 1967, Bigler and Jenkins 1975, Smith and Vriese 1979). Sex ratios were equal at birth (Pournelle 1952) or favored males (Bigler and Jenkins 1975). Thus, males may have greater capture probabilities than do females.

In previous studies, *P. leucopus* had high probabilities of capture influenced by heterogeneity and had little or no behavioral response (Getz 1961, Myton 1974). My results agreed. Sex ratios varied, but more males than females tended to be caught (Terman and Sassaman 1967, Myton 1974, Barry and Franq 1980). Individuals more likely entered traps previously occupied by conspecifics (Mazdzer et al. 1976), particularly if they were of the opposite sex, regardless of the time of year (Drickamer 1984). However Barry and Franq (1980) found no evidence for odor-induced entry into traps. Animal activity was greatest during the first half of the night (Drickamer 1987), varied nightly (Marten 1973), increased on nights after the animals were trapped (Sheppe 1967), decreased as morning temperature increased (Ruffer 1961), and was not affected by moon phase (Ruffer 1961).

Investigators generally acknowledged trap proneness and high probabilities of capture and recapture of *P. maniculatus* (e.g. Klein

1960, Metzgar 1979). Trap proneness was attributed to the greater probability of encountering a trap because of greater movement during nights after first trapping (Sheppe 1967); however, Peromyscus often visited stations without being trapped (Sheppe 1967). My results indicated that it is one of the more mobile small-mammal species. Time effects were apparent seasonally (Metzgar 1979) and nightly (Drickamer 1987, Gauthier and Bider 1987). Reasons for heterogeneity included sex-specific attraction to scented traps (Wuensch 1982, Drickamer 1984), however, sexes may not have had significantly different capture frequencies (Drickamer 1987). Unequal sex ratios in trapped samples of P. maniculatus may result from unequal sex ratios in the population (Terman and Sassaman 1967) and not to differential probabilities of capture. My results for P. maniculatus indicated high abundance and probabilities of capture, trap proneness, and heterogeneity; and,  $M_b$  usually was the most appropriate model.

Capture probabilities of P. truei were heterogeneous, and model  $M_b$  also was selected for this species. Sexes had time-specific activity patterns (Scheibe 1984), so time effects could also strongly influence capture probabilities of this species.

Trap spacing should be 5-10 m for P. californicus, P. leucopus, and P. truei, and 15 m for P. gossypinus and P. maniculatus, although animal movement is affected significantly by spacing and, to some extent, by animal density (Stickel 1960, Brant 1962, this study). However, Shadowen (1963:104) increased his trap spacing from 15 m to 23 m when trapping Ochrotomys (= Peromyscus) nuttallii and P. gossypinus "because of the distance traveled by the small mammals."

Trapping sessions of P. gossypinus should be >5 days to sample adequately the female population. Trapping sessions of P. leucopus can be <8 days to maximize the probability of population closure, because the capture probability of this species is so great ( $\hat{p} = 0.63 \pm 0.20$ ).

Sigmodon hispidus had low, strongly heterogeneous capture probabilities and was trap prone in my analyses. These characteristics possibly resulted in a high number of individuals never being caught (Wiegert and Mayenschein 1966, Guthery 1980). Lefebvre et al. (1982) and Guthery and Herbert (1983) reported low  $\hat{p}$ 's (0.12-0.16), and Hall (1974) trapped relatively few animals during the first 2 days of his trapping session. Most data from Lefebvre et al. (1982) and Guthery (1980) were included in my study; however, their analyses probably differed somewhat from mine. S. hispidus has a strong social organization, in which dominant, heavier animals have higher probabilities of capture and are trapped before subordinates (Summerlin and Wolfe 1973, Hall 1974, Joule and Cameron 1974). S. hispidus had a higher probability of capture in temporary-removal studies (Joule and Cameron 1974), probably because subordinate individuals had more opportunities to enter traps as dominant individuals were removed. The recapture rate varied seasonally (Cameron 1977a, Guthery and Herbert 1983), and females had higher probabilities of recapture than did males (Cameron 1977b). Guthery (1980:284) stated that "trapping, marking, and releasing do not affect probability of capture of this species" until later analysis with CAPTURE revealed trap proneness in the same population (Guthery and Herbert 1983). Layne (1974) also reported trap proneness. Because of time effects, 18% of the trapping sessions I

analyzed did not yield a selection criterion  $>0.75$  for a model with an estimator that fit the data; Guthery and Herbert (1983) noted similar problems with their data. Time effects also were apparent in Lefebvre et al.'s (1982) study, and activity levels were not related to photoperiod, but to local environmental factors (Kilduff and Dube 1979). Joule and Cameron (1974) suggested that a 15-m trap spacing was suitable for temporary-removal trapping, but Guthery and Herbert (1983) believed that 15.2 m was too great and that trapping sessions of 4-5 days were too short. Wiegert and Mayenschein (1966) found localized populations of S. hispidus not sampled because of clumped distributions of animals and excessively large distances between traps.

Because S. hispidus has low, heterogenous capture probabilities, trap spacing should be 10 m to increase trap density, rather than the customary 15 m. After 12 days, population closure most likely will be violated, but if trapping sessions must be  $>12$  days to capture most individuals, a closed-population model should still be used to account for heterogeneity.

Family Muridae; Subfamily Arvicolinae.--Drickamer (1987) reported that C. gapperi only was captured at night, but the daily activity of this species varies with snow cover (Kucera and Fuller 1978). Forty-five of 63 C. rutilus and 23 of 61 C. gapperi data sets I analyzed consisted of morning and evening trapping occasions, and model  $M_{th}$  was selected often. Merritt and Merritt (1978) reported that Jolly-Seber estimates were similar to the trap-revealed census of a population of C. gapperi. Most animals probably were captured because of trap

proneness and high probabilities of capture (Morris 1955). My results agreed; C. gapperi was slightly trap prone, and average  $\hat{p} = 0.62$  and 0.50 for C. gapperi and C. rutilus, respectively. C. rutilus was trap neutral (Tanaka 1956). Whitney (1976) assumed that C. rutilus he studied had unequal probabilities of capture and so used enumeration (Krebs 1966) instead of mark-recapture estimators to estimate population size. Population sizes of Clethrionomys were best estimated with model  $M_h$  in my analyses. Optimal trap spacing may be 5-10 m for C. rutilus and 20 m for C. gapperi.

Microtus californicus was trap prone (Fisler 1961, Krebs 1966) and had heterogeneous capture probabilities (Krebs 1966), which may have been related to odors in traps (Heske 1987). My analyses confirmed strong heterogeneity and trap proneness; however, model  $M_h$  was more suitable than  $M_b$  for this species. Trap spacing should be 5-7 m; traps spaced 12 m apart in a trapping line mostly caught the animals with the largest home ranges (Fisler 1961).

Microtus ochrogaster possibly was trap prone (Gaines and Rose 1976); however only 10% of the data sets that I analyzed were characterized as such. Males and females usually had equal probabilities of capture (Yang et al. 1970, Gaines and Rose 1976), and adults had greater capture probabilities than did juveniles (Yang et al. 1970). This species had an inconsistent behavioral response (this study), and my results were too inconclusive to provide guidelines for future studies. However, the number of animals captured and the total number of captures need to be greater to counteract low probabilities of capture and probable trap shyness.

Microtus pennsylvanicus often was trap prone (Getz 1961, Van Vleck 1968) and sometimes trap shy (Kucera and Fuller 1978). My results indicated mostly trap proneness, with some trap shyness. Trapping success corresponded to weather conditions (Getz 1961, Marten 1973, Gauthier and Bider 1987). Animals were active day and night with a peak during the day (Ambrose 1973), and morning-evening trapping did not appear to affect capture probabilities (Getz 1961). Capture probabilities were low (Van Vleck 1969, Olsen 1975, this study), particularly when population density was low (Van Vleck 1968). However, capture probabilities from the Jolly-Seber model equalled 0.70 - 1.00 (Nichols 1986), and Jett et al. (1986) computed  $\hat{p}$ 's of 0.51-0.93 with use of CAPTURE. Snap trapping indicated a 1:1 sex ratio, although significantly more females than males were captured in live traps (Van Vleck 1968); Jett et al. (1986) reported no difference in capture probabilities among sex-and-age classes. Heterogeneity in capture probabilities was attributed to avoidance of traps previously entered by other species and an even greater avoidance of previously unoccupied traps (Boonstra et al. 1982).

Dependable  $\hat{N}$ 's of M. pennsylvanicus probably can be calculated by model  $M_h$  (Jett et al. 1986, Jett and Nichols 1987), but  $M_b$  or  $M_{bh}$  may also be appropriate. Care should be taken to maximize the number of animals captured and total captures by increasing the numbers of traps, extending trapping sessions for at least 5-10 days, and reducing the trap spacing to 5-10 m. Spacing of 14 m results in only 2 traps per home range (Van Vleck 1969). However, animal movement is influenced by trap spacing and by animal density (Hayne 1950, this study).

## CAPTURE program

Models in CAPTURE often are more realistic and provide less biased estimates than previous methods such as Petersen-Lincoln, enumeration methods, and open-population models. The models in CAPTURE are for closed populations, and closure was not rejected in 67-100% (depending on the species) of the trapping sessions I analyzed. Four useful formats are available for input data-sets, and the user can request general or specific analyses. Results of the 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 trapping session. However, the selection of this model must be evaluated by the user based on the information provided by CAPTURE and by familiarity with the study. CAPTURE also can be used to estimate the mean maximum-distance moved by the animals, which can be used to estimate density (Wilson and Anderson 1985).

Despite its utility, CAPTURE requires a large amount of data and can be used inappropriately with small data sets. CAPTURE frequently failed to select the correct model for simulated data sets with <50 individuals, resulting in biased estimates from the inappropriate model (White et al. 1982, Menkens and Anderson 1988). Menkens and Anderson (1988) suggested that a CAPTURE model be chosen subjectively, based on the CAPTURE results and on knowledge of the study population. I believe that data should consist of >5 trapping sessions and  $\geq 40$  captured individuals ( $M_{t+1}$ ) with  $\hat{p} > 0.2$  before the user can be confident in the model rankings provided by CAPTURE.

Specific weaknesses of the model-selection procedure 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 my analysis, the goodness-of-fit test for  $M_t$  failed most of the time, and  $M_t$  usually received a selection criterion of 0.00. But, the chi-square probability of 0.5 may have caused other models incorporating time to be selected more frequently than was realistic. Also, the rankings did not always appear to correspond to the results of the chi-square tests. The model-selection criteria often were artifacts of the CAPTURE algorithm and did not necessarily reflect sources of variation in the study population. Because  $M_0$  usually was selected as the most appropriate model only for small data sets, the a priori probabilities of selecting each of the models in CAPTURE probably should be made unequal in the discriminate-function analysis. Models  $M_h$ ,  $M_b$ , and  $M_{bh}$  are more realistic and selected more frequently for larger data sets; they should be given higher a priori probabilities of selection in the CAPTURE algorithms. However, because different models are more appropriate for different species, I do not know what criterion to use to determine the a priori probabilities.

Models  $M_{th}$ ,  $M_{tb}$ , and  $M_{tbh}$  provide no estimates of abundance. But, selection of these models can be minimized by examining traps once per day, not trapping in inclement weather, or combining data for each 24-hr period when traps are examined more than once per day to reduce animal mortality.



The ratio of  $\hat{c}_b/\hat{p}_b$  could be considered as an additional parameter for calculating  $\hat{N}$  from model  $M_{tb}$ , which has no estimator at this time. Although model  $M_{tb}$  was selected least often by CAPTURE overall, it was selected often for several species, including C. intermedius and some murids. However, the coefficients of variation indicate that this ratio is clearly too variable for most species to provide a consistent estimate of  $\hat{c}$  from  $\hat{p}$ . If  $\hat{c}_b/\hat{p}_b$  ratios were consistent,  $\hat{c}_b$  could be estimated from  $\hat{p}_b$ , and the number of parameters to be estimated would not be greater than the number of minimum sufficient statistics.

The user must be aware of the limitations of the program and be able to recognize spurious results. When CAPTURE selects  $M_0$  as most appropriate for small data sets, the user could decide erroneously that capture probabilities were equal, when they were not. Model  $M_0$  is negatively biased and provides unrealistically narrow confidence intervals for its  $\hat{N}$ 's. The closure test incorporated in CAPTURE is not powerful, and results should be compared with knowledge of the study animals. Results of the chi-square goodness-of-fit tests should be used to evaluate the fit of the most appropriate model; however, the tests, especially for models  $M_t$  and  $M_{bh}$ , require large amounts of data. Estimated variances of the  $\hat{N}$ 's from models  $M_0$  and  $M_t$  are misleadingly small and result in unreliable confidence intervals. The coefficient of variation of  $\hat{N}$  varies significantly and predictably depending on which CAPTURE model is used; therefore, it should be used only to compare precision of  $\hat{N}$ 's from the same model.  $\hat{N}$ 's from model  $M_h$  often were significantly greater than those from other models, so spatial or

temporal comparisons of population abundance may be invalid if  $\hat{N}$ 's from  $M_h$  are compared with those from other models.

I recommend that output from future versions of CAPTURE include warnings to guard against its inappropriate use. Specifically, the closure test should be labeled as appropriate only for larger data sets for which models  $M_0$  or  $M_h$  are chosen as most appropriate. The user should be warned to examine the chi-square tests to determine whether the most appropriate model fits the data. If model  $M_0$  is chosen as most appropriate, the user should be reminded to decide whether the data set was large enough to obtain reliable results from the model-selection procedure. Confidence intervals of abundance estimates should be labeled with their true coverage according to simulation results, e.g. coverage of  $M_h$  is  $< 90\%$  rather than  $95\%$ . And, the user should be informed that abundance estimates from model  $M_h$  are significantly greater than those from other models.

#### Mark-recapture studies in general

Mark-recapture studies are improving because a growing number of ecologists recognize that models traditionally used for estimating abundance are negatively biased when capture probabilities vary. Recent methodologies are making greater use of longer trapping sessions to increase the number of animals captured and the total number of recaptures. Grids also seem to be larger, with smaller trap spacing. Investigators are providing conclusive evidence of behavioral responses and heterogeneity in capture probabilities. CAPTURE is being used to determine the presence of variation in capture

probabilities and to obtain estimates from models that more effectively use all of the information available in patterns of capture frequencies. Although CAPTURE requires population closure, Matschke et al. (1982) believed that accounting for heterogeneity was more important than having complete closure in order to obtain reliable estimates of abundance.

However, mark-recapture studies are still plagued by inadequate trapping designs, and results are not easy to compare among studies. Too many ecologists still rely on 2 trapping occasions to minimize effort and to estimate population abundance with the Petersen-Lincoln estimator. This estimator is biased negatively when capture probabilities vary (Edwards and Eberhardt 1967, Bohlin and Sundstrom 1977, Mares et al. 1981). Even 3 trapping occasions do not provide sufficient information to determine whether capture probabilities are equal (Otis et al. 1978). Small grids 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 still set too far apart; for many species the commonly used spacing needs to be halved to place at least 4 traps in a home range. Setting traps at alternate stations on consecutive occasions may reduce trap proneness, but the trapping design varies on each occasion and animals no longer have equal probabilities of capture in any one trap. Consequently, this approach is highly discouraged for estimating abundance. 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 1983). Setting more than 1 trap/station will probably also increase capture probabilities, especially if animal density is high. Enumeration methods (Krebs 1966) may provide useful information only for the same species during the course of a single study (Nichols 1986). However, such indices are strongly biased negatively (Jolly and Dickson 1983, Nichols and Pollock 1983), especially when animals have low probabilities of capture (Hilborn et al. 1976), and low abundance and low probabilities of capture are often not distinguishable.

Use of open-population models (Jolly 1965, Seber 1965) is discouraged for small-mammal studies, because these models usually allow only time effects and equal probabilities of capture on each trapping occasion. Abundance estimates from the Jolly-Seber model often barely exceed the minimum number of animals known alive from the trapping census and are biased by strong heterogeneity and behavioral responses, low probabilities of capture, and the proportion of recaptures in a sample. Use of the model requires extremely large samples for reliable estimates of abundance; such sample sizes are difficult to obtain for small-mammal populations.

Lefebvre et al. (1982) compared estimates of abundance of S. hispidus from Jolly-Seber and CAPTURE models. The estimates agreed in overall trends from month to month, but less so from day to day during the monthly trapping sessions when Jolly-Seber estimates barely exceeded the minimum known number of animals alive. Lefebvre et al. (1982) attributed the poor performance of the Jolly-Seber estimator to strong heterogeneity in capture probabilities. Cameron (1977b)

reported that Jolly-Seber estimates were at times too great because the model was sensitive to small numbers of recaptures. Pollock (1982) and Pollock et al. (1990) suggest that  $\hat{N}$ 's be obtained from CAPTURE for trapping sessions and that probabilities of survival between trapping sessions be calculated with the Jolly-Seber model. The high percentage of data sets I analyzed for which closure was not rejected indicates that adequate closure often can be maintained during the course of a trapping session. However, transient animals may be a noticeable component of the population being trapped (Shadowen 1963), and in such cases, trapping sessions could be kept short, especially if capture probabilities are high.

One of my major recommendations is for ecologists to plan a study to either estimate animal abundance or movements, not both. Techniques such as assessment lines or transects are not appropriate for estimating abundance, except to calculate the strip around the grid for estimating effective trapping area. To obtain reliable estimates of abundance, trap spacing must be small enough to sample most of the population in a relatively short time before population closure is violated. To estimate animal movement, however, traps must be far enough apart that they do not interfere significantly with natural movements of animals. Trapping sessions long enough to provide sufficient captures for movement data (Mares et al. 1980), particularly for species with low capture probabilities, are too long to insure the likelihood of population closure.

Use of CAPTURE is highly recommended to estimate abundance and to detect sources of variation in capture probabilities for large data

sets. However, the minimum of 8-10 occasions per trapping session recommended by Otis et al. (1978) may often lead to lack of closure in some small-mammal populations. I recommend 5-8 trapping occasions except for species with low capture probabilities and higher survival such as S. floridanus, S. nuttallii, I. minimus, I. amoenus, and G. sabrinus. Designs for these species may require 15-25 trapping occasions (days), although trapping should end when results indicate strong time effects. The ecologist must balance the need to maintain population closure with the need to maximize number of captures and recaptures. 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 12x12 traps and by reducing trap spacing to  $\leq 10$  m when animals movement is low. A grid arrangement adequate at one time and place may sample too few animals at another, because animal density and movement varies temporally and spatially (Stickel 1960). Size and configuration of grids may need to be adjusted with observed changes in animal density.

My results clearly indicate that capture probabilities vary among individuals and that taxa can be characterized by capture probabilities. When species with different probabilities of capture coexist in the study area, the trapping scheme must be designed to capture sufficient individuals of the species with the lower abundance or capture probabilities. This may be accomplished by temporary-removal trapping of the dominant species, increasing the numbers of traps, or increasing the number of trapping occasions. Time effects must be avoided, because models incorporating time often are biased

negatively or have no estimators. If circumstances seem to require use of open-population models, the species-specific trends I outlined will provide information concerning probabilities of capture and the sources most likely to affect those probabilities. Use of this information will permit design of the study in advance to reduce the bias of open-population models.

Many of my analyses are incomplete and require further investigation. Analyses of heteromyid data, in particular, relied on small sample sizes. The analyses should be repeated with larger sample sizes consisting of data from grids, not from assessment lines. The effect of the number of trapping occasions on population closure needs to be examined with larger sample sizes for more species. A more reliable test for population closure is needed to test that critical assumption of closed-population models. The effect of one species on the behavior of another as it relates to trapping would greatly improve interpretation of mark-recapture results. And, it would be useful to derive estimators for models incorporating time effects because of the prevalence of those effects in mark-recapture data.

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## APPENDICES

## Appendix A. Definitions of notation used in the text.

Notation	Definition
$\hat{c}_b$	estimated probability of recapture, computed by model $M_b$ .
CV	coefficient of variation.
CV <sub>bh</sub>	coefficient of variation of abundance estimate from model $M_{bh}$ .
M	total number of marked animals in the population.
$M_b$	model in which capture probabilities vary because of behavioral response.
$M_{bh}$	model in which capture probabilities vary because of behavioral response and by individual animal.
$M_h$	model in which capture probabilities vary by individual animal.
$M_j$	number of marked animals in the population before the $j$ th occasion, $j=1, \dots, t$ .
$M_o$	model in which capture probabilities are constant.
$M_t$	model in which capture probabilities vary by time.
$M_{tb}$	model in which capture probabilities vary by time and because of behavioral differences.
$M_{th}$	model in which capture probabilities vary by time and individual animals.
$M_{tbh}$	model in which capture probabilities vary by time and because of behavioral response and individual differences.
$M_{th}$	model in which capture probabilities vary by time and because of individual differences.
$M_{t+1}$	number of marked animals in the population after the $j$ th occasion, $j=1, \dots, t$ .
MMDM	mean maximum-distance moved, computed by program CAPTURE.
N	actual number of animals in the population (population parameter).
$\hat{N}$	estimated number of animals in the population.
$\hat{p}$	estimated probability of capture.
$\hat{p}_b$	estimated probability of capture, computed by model $M_b$ .
r	correlation coefficient.
t	number of trapping occasions per session.

## Appendix B. Examples of CAPTURE output.

Animal by animal summary of capture data.

DATA=8X12 GRID @25M T=7; AM/PM CAPTURES

Animal ID	Num. Cap.	Maximum Dist.	Average Dist.	Standard Error
0001	3	4.2	2.1	2.12
0004	1	0.0	0.0	0.00
0007	3	1.0	1.0	0.00
0010	4	1.4	0.8	0.42
0013	2	0.0	0.0	0.00
0016	3	2.2	2.1	0.12
0019	4	3.6	2.7	0.46
0022	4	4.1	2.4	0.20
0025	1	0.0	0.0	0.00

Animal ID	Num. Cap.	Maximum Dist.	Average Dist.	Standard Error
0002	2	0.0	0.0	0.00
0005	4	3.0	3.0	0.00
0008	3	2.2	1.6	0.62
0011	5	3.2	1.0	0.75
0014	1	0.0	0.0	0.00
0017	2	9.9	9.9	0.00
0020	5	4.1	1.4	0.97
0023	4	3.2	2.2	0.51

Animal ID	Num. Cap.	Maximum Dist.	Average Dist.	Standard Error
0003	4	3.0	1.0	0.58
0006	2	2.0	2.0	0.00
0009	4	2.2	0.8	0.42
0012	4	1.4	1.1	0.14
0015	2	2.2	2.2	0.00
0018	4	3.2	1.1	0.65
0021	1	0.0	0.0	0.00
0024	5	3.6	2.1	0.38

Note that average distance only refers to distance between successive captures while maximum distance refers to the greatest distance between any two capture points. Also distance is in units of trap intervals, i.e., if the inter-trap distance is 5 meters and the max. distance is 1.4, then the max. distance in meters is 1.4\*5 or 7 meters.

## Summary by frequency of capture of maximum distance between capture points.

Number Captures	Sample Size	Mean of Max Dist.	Standard Error
2	5	2.83	1.831
3	4	2.43	0.671
4	9	2.79	0.310
5	3	3.63	0.278
6	0	0.00	0.000
7	0	0.00	0.000
Total	21	2.85	1.004

## Appendix B. Continued.

Closure procedure.

DATA=8X12 GRID @25M T=7; AM/PM CAPTURES

Overall test results --  
 z-value 2.173  
 Probability of a smaller value 0.98511

Model selection procedure.

DATA = 8X12 GRID @25M T=7; AM/PM CAPTURES

Occasion	j=	1	2	3	4	5	6	7
Animals caught	n(j)=	15	2	16	1	17	2	24
Total caught	M(j)=	0	15	15	18	18	21	21 25
Newly caught	u(j)=	15	0	3	0	3	0	4
Frequencies	f(j)=	4	5	4	9	3	0	0

## 1. Test for heterogeneity of trapping probabilities in population.

Null hypothesis of model M(o) vs. alternate hypothesis of model M(h)

Chi-square value = 3.981 degrees of freedom = 2 Probability of larger value = 0.13664

## 2. Test for behavioral response after initial capture.

Null hypothesis of model M(o) vs. alternate hypothesis of model M(b)

Chi-square value = 2.222 degrees of freedom = 1 Probability of larger value = 0.13606

## 3. Test for time specific variation in trapping probabilities.

Null hypothesis of model M(o) vs. alternate hypothesis of model M(t)

Chi-square value = 377.449 degrees of freedom = 6 Probability of larger value = 0.00000

## 4. Goodness of fit test of model M(h)

Null hypothesis of model M(h) vs. alternate hypothesis of not model M(h)

Chi-square value = 82.062 degrees of freedom = 6 Probability of larger value = 0.00000

## Appendix B. Continued.

Model selection procedure, continued.

DATA=8x12 GRID @25M T=7; AM/PM CAPTURES

## 5. Goodness of fit test of model M(b)

Null hypothesis of model M(b) vs. alternate hypothesis of not model M(b)

Chi-square value = 83.189 degrees of freedom = 8 Probability of larger value = 0.00000

## 5a. Contribution of test of homogeneity of first capture probability across time

Chi-square value = 16.382 degrees of freedom = 3 Probability of larger value = 0.00095

## 5b. Contribution of test of homogeneity of recapture probabilities across time

Chi-square value = 66.807 degrees of freedom = 5 Probability of larger value = 0.00000

## 6. Goodness of fit test of model M(t)

Null hypothesis of model M(t) vs. alternate hypothesis of not model M(t)

Expected values too small. Test not performed.

## 7. Test for behavioral response in presence of heterogeneity.

Null hypothesis of model M(h) vs. alternate hypothesis of model M(bh)

Chi-square value = 8.852 degrees of freedom = 2 Probability of larger value = 0.01196

Model selection criteria. Model selected has maximum value.

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	0.15	0.00	0.32	0.09	1.00	0.90	0.64	0.39

Appropriate model probably is M(t)

Suggested estimator is Darroch.

## Appendix B. Continued.

---

Model M(o): population estimation with constant probability of capture.

DATA=8X12 GRID @25M T=7; AM/PM CAPTURES

Number of trapping occasions was 7  
Number of animals captured,  $M(t+1)$ , was 25  
Total number of captures,  $n$ ., was 77

Estimated probability of capture,  $p\text{-hat}$  = 0.4400

Population estimate is 25 with standard error 0.6974

Approximate 95 percent confidence interval 23 to 27

## Appendix B. Continued.

---

 Model M(h): population estimation with variable probability of capture by animal.

DATA=8X12 GRID @25M T=7; AM/PM CAPTURES

Number of trapping occasions was 7  
 Number of animals captured,  $M(t+1)$ , was 25  
 Total number of captures,  $n$ ., was 77

Frequencies of capture,  $f(i)$ 

i= 1 2 3 4 5 6 7  
 $f(i)$ = 4 5 4 9 3 0 0

## Computed jackknife coefficients

	N(1)	N(2)	N(3)	N(4)	N(5)
1	1.857	2.571	3.143	3.571	3.857
2	1.000	0.405	-0.452	-1.310	-1.976
3	1.000	1.000	1.305	1.833	2.357
4	1.000	1.000	1.000	0.904	0.749
5	1.000	1.000	1.000	1.000	1.013

## The results of the jackknife computations

i	N(i)	SE(i)	.95 Conf. Limits		Test of $N(i+1)$ vs. $N(i)$
0	25				Chi-square (1 d.f.)
1	28.4	2.52	23.5	33.4	0.004
2	28.3	3.87	20.7	35.9	0.110
3	27.5	5.64	16.5	38.6	0.304
4	26.2	7.56	11.4	41.0	0.534
5	24.8	9.20	6.7	42.8	0.000

Average  $p$ -hat = 0.4231

Interpolated population estimate is 26 with standard error 0.7858

Approximate 95 percent confidence interval 24 to 28

Histogram of  $f(i)$ 

Frequency	4	5	4	9	3	0	0
9				*			
8				*			
7				*			
6				*			
5		*		*			
4	*	*	*	*			
3	*	*	*	*	*		
2	*	*	*	*	*		
1	*	*	*	*	*		



## Appendix B. Continued.

---

Model M(b): population estimation with constant probability removal estimator.

DATA=8X12 GRID @25M T=7; AM/PM CAPTURES

Occasion	j=	1	2	3	4	5	6	7
Total caught	M(j)=	0	15	15	18	18	21	25
Newly caught	u(j)=	15	0	3	0	3	0	4

Estimated probability of capture,  $p\text{-hat}$  = 0.341335

Estimated probability of recapture,  $c\text{-hat}$  = 0.481481

Population estimate is 26 with standard error 1.7522

Approximate 95 percent confidence intervals 22 to 30

Histogram of u(j)

Frequency	15	0	3	0	3	0	4
-----------	----	---	---	---	---	---	---

---

Each \* equals 2 points

16	*						
14	*						
12	*						
10	*						
8	*						
6	*						
4	*	*		*		*	
2	*	*		*		*	

---

## Appendix B. Continued.

---

 Model M(bh): population estimation with variable probability removal estimator.

DATA=8x12 GRID @25M T=7; AM/PM CAPTURES

Occasion	j=	1	2	3	4	5	6	7
Total caught	M(j)=	0	15	15	18	18	21	21
Newly caught	u(j)=	15	0	3	0	3	0	4

k	N-hat	SE(N)	Chi-sq.	Prob.	Estimated p-bar(j), j=1,..., 7						
1	25.89	1.752193	16.383	0.0009	0.3413	0.3413	0.3413	0.3413	0.3413	0.3413	0.3413
2	Failure criterion = -14 no estimates for this step.										
3	Failure criterion = -4 no estimates for this step.										
4	Failure criterion = -9 no estimates for this step.										
5	Failure criterion = -2 no estimates for this step.										

Population estimate is 26 with standard error 1.7522

Approximate 95 percent confidence interval 22 to 30

Histogram of u(j)

Frequency	15	0	3	0	3	0	4
-----------	----	---	---	---	---	---	---

-----  
Each \* equals 2 points

16	*						
14	*						
12	*						
10	*						
8	*						
6	*						
4	*	*		*		*	
2	*	*		*		*	

## Appendix B. Continued.

---

M(t): population estimation with time specific changes in probability of capture.

DATA=8X12 GRID @25M T=7; AM/PM CAPTURES

Occasion	j=	1	2	3	4	5	6	7
Animals caught	n(j)=	15	2	16	1	17	2	24

Total animals captured 25

p-hat(j)= 0.60 0.08 0.64 0.04 0.68 0.08 0.96

Population estimate is 25 with standard error 0.0147

Approximate 95 percent confidence interval 24 to 26

Histogram of n(j)

Frequency	15	2	16	1	17	2	24
-----------	----	---	----	---	----	---	----

-----  
Each \* equals 3 points

24							*
21							*
18					*		*
15	*		*		*		*
12	*		*		*		*
9	*		*		*		*
6	*		*		*		*
3	*	*	*		*	*	*

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s u c c e s s f u l   e x e c u t i o n  

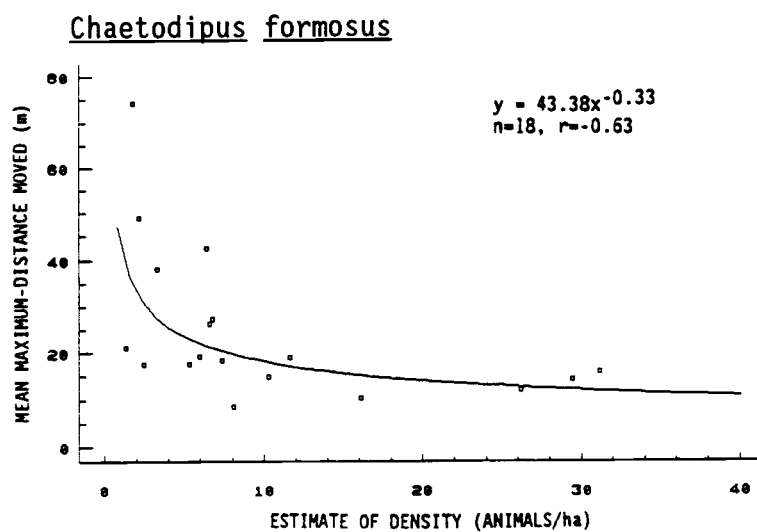
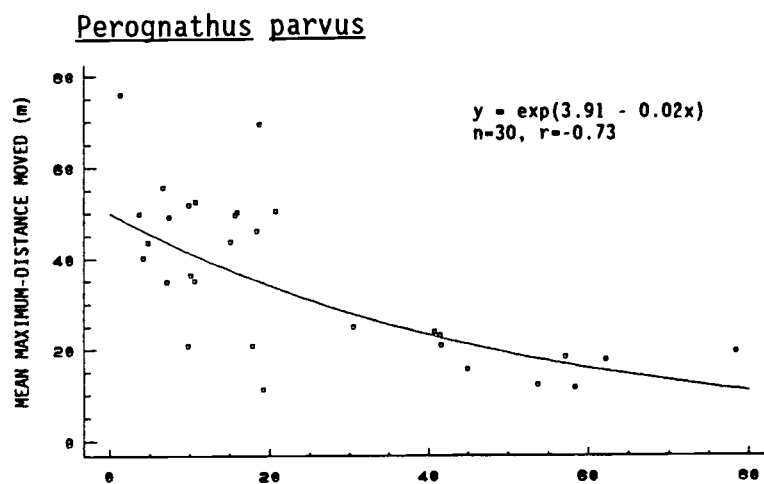
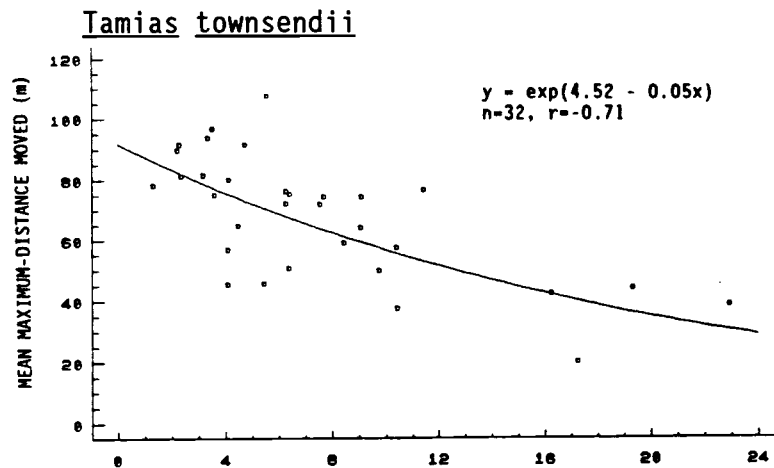
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Appendix C. Scientific and common names of the small-mammal species for which I analyzed data.

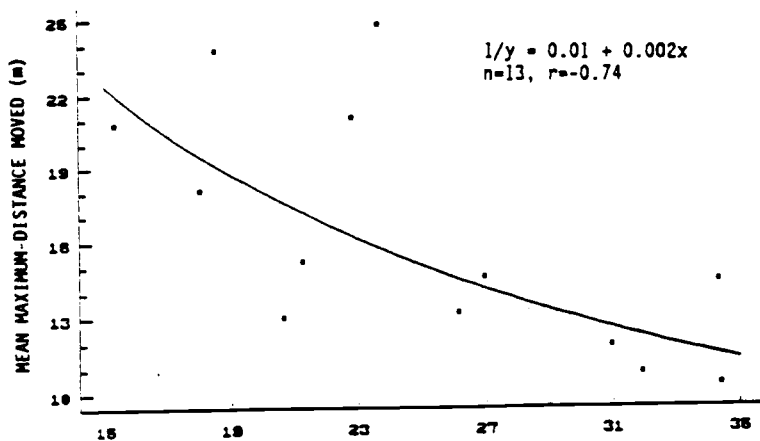
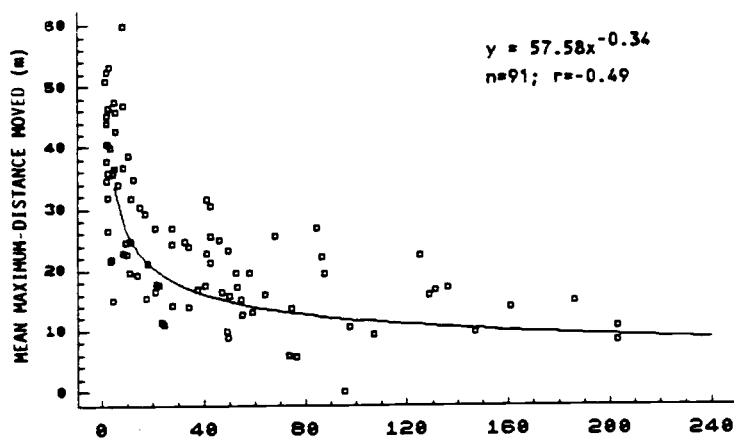
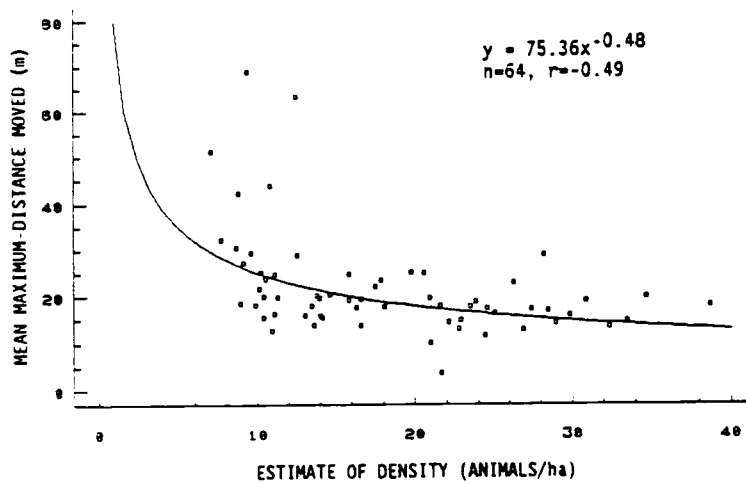
Scientific name	Common name
Order LAGOMORPHA	
Family LEPORIDAE	
<u>Sylvilagus floridanus</u>	Eastern Cottontail
<u>Sylvilagus nuttallii</u>	Nuttall's or Mountain Cottontail
Order RODENTIA	
Family SCIURIDAE	
<u>Tamias amoenus</u>	Yellow-pine Chipmunk
<u>Tamias minimus</u>	Least Chipmunk
<u>Tamias striatus</u>	Eastern Chipmunk
<u>Tamias townsendii</u>	Townsend's Chipmunk
<u>Spermophilus richardsonii</u>	Richardson's Ground Squirrel
<u>Glaucomys sabrinus</u>	Northern Flying Squirrel
Family HETEROMYIDAE	
<u>Peroznathus amplus</u>	Arizona Pocket Mouse
<u>Peroznathus flavus</u>	Silky Pocket Mouse
<u>Peroznathus longimembris</u>	Little Pocket Mouse
<u>Peroznathus parvus</u>	Great Basin Pocket Mouse
<u>Chaetodipus californicus</u>	California Pocket Mouse
<u>Chaetodipus formosus</u>	Long-tailed Pocket Mouse
<u>Chaetodipus intermedius</u>	Rock Pocket Mouse
<u>Chaetodipus penicillatus</u>	Desert Pocket Mouse
<u>Dipodomys agilis</u>	Agile Kangaroo Rat
<u>Dipodomys merriami</u>	Merriam's Kangaroo Rat
<u>Dipodomys microps</u>	Chisel-toothed Kangaroo Rat
<u>Dipodomys ordii</u>	Ord's Kangaroo Rat
Family MURIDAE	
Subfamily SIGMODONTINAE	
<u>Reithrodontomys fulvescens</u>	Fulvous Harvest Mouse
<u>Reithrodontomys megalotis</u>	Western Harvest Mouse
<u>Peromyscus californicus</u>	California Mouse
<u>Peromyscus gossypinus</u>	Cotton Mouse
<u>Peromyscus leucopus</u>	White-footed Mouse
<u>Peromyscus maniculatus</u>	Deer Mouse
<u>Peromyscus truei</u>	Piñon Mouse
<u>Sigmodon hispidus</u>	Hispid Cotton Rat
Subfamily ARVICOLINAE	
<u>Clethrionomys gapperi</u>	Southern Red-backed Vole
<u>Clethrionomys rutilus</u>	Northern Red-backed Vole
<u>Microtus californicus</u>	California Vole
<u>Microtus ochrogaster</u>	Prairie Vole
<u>Microtus pennsylvanicus</u>	Meadow Vole

Appendix D. Mean maximum-distance moved (MMDM) regressed on estimate of density ( $\hat{D}$ ).

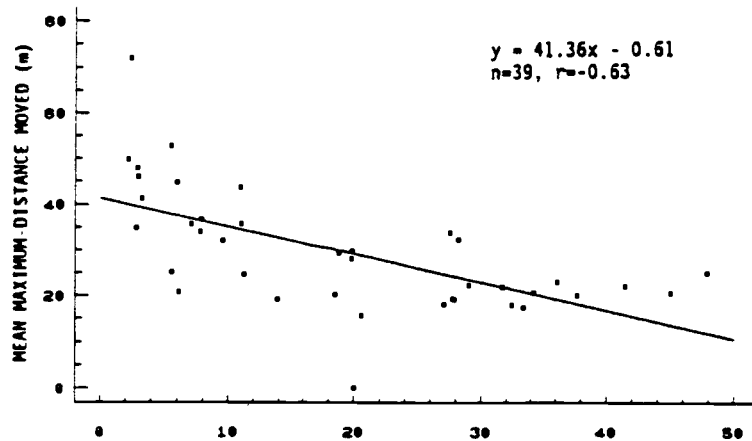
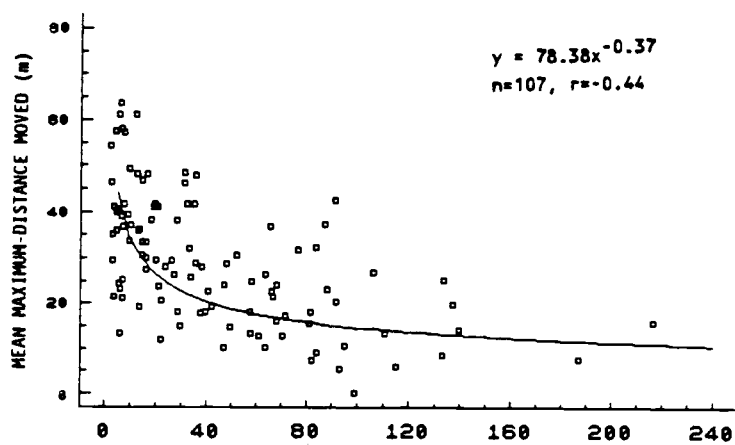
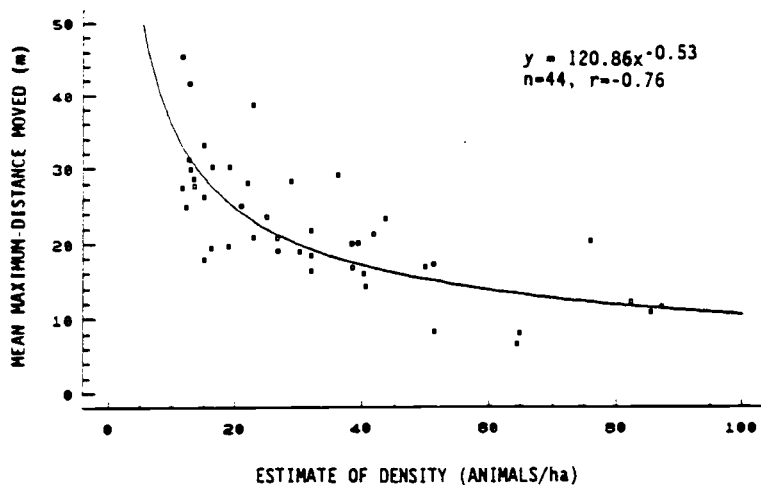
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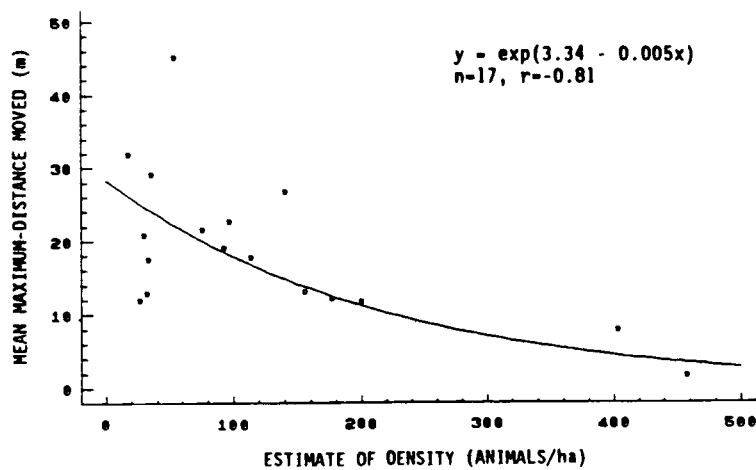
## Appendix D. Continued.

Dipodomys agilisDipodomys merriamiPeromyscus leucopus

## Appendix D. Continued.

Peromyscus trueiSigmodon hispidusClethrionomys rutilus

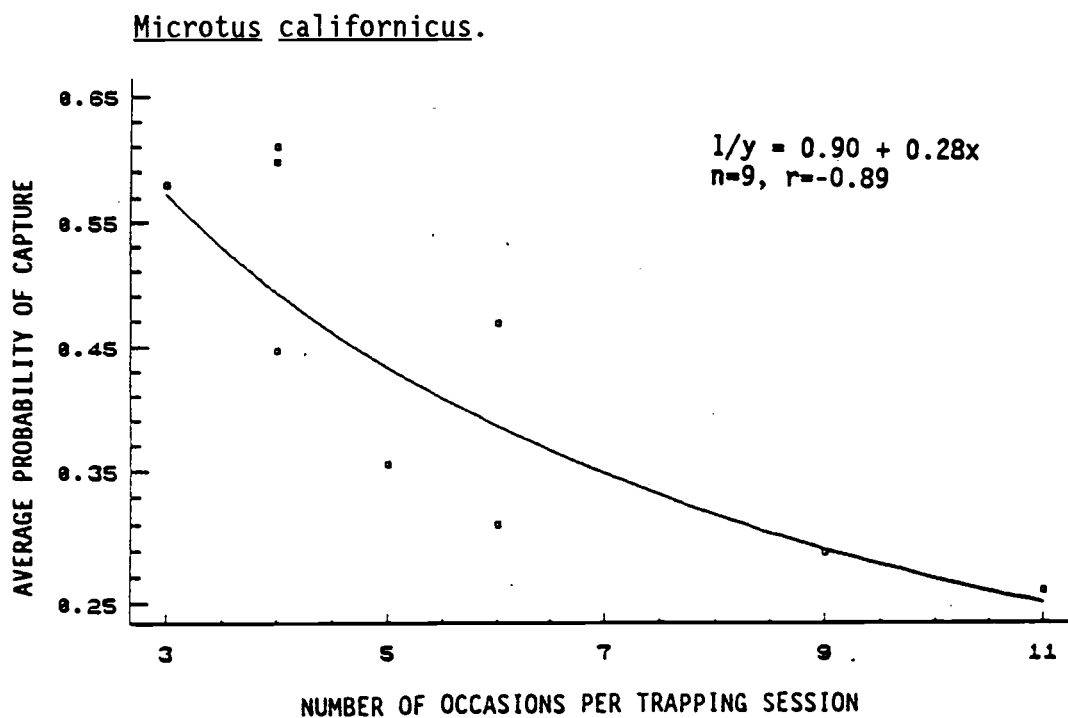
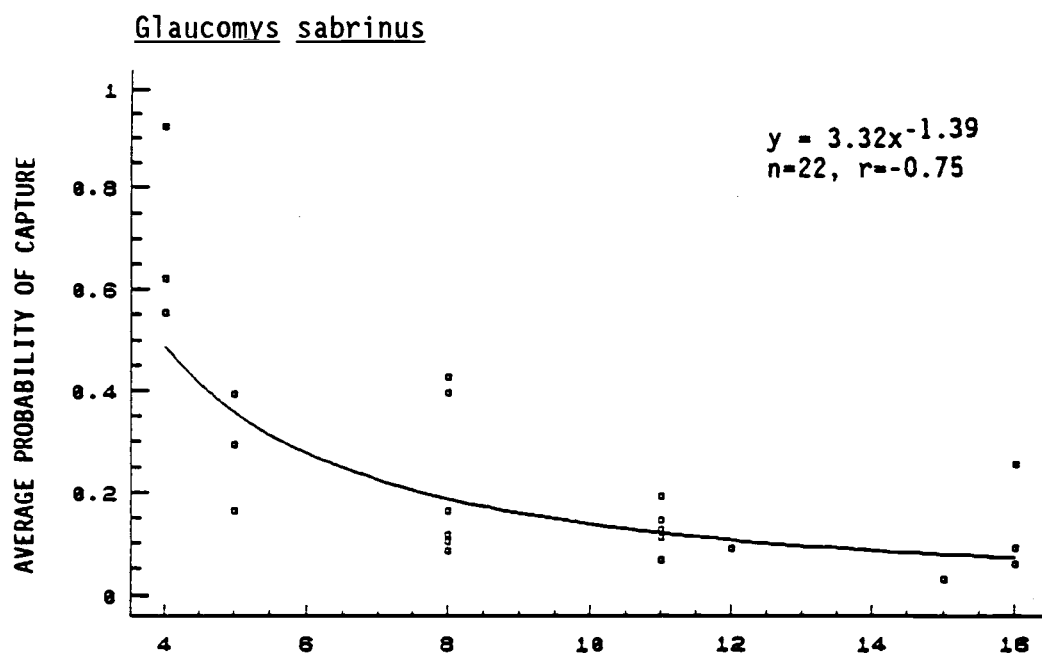
## Appendix D. Continued.

Microtus pennsylvanicus



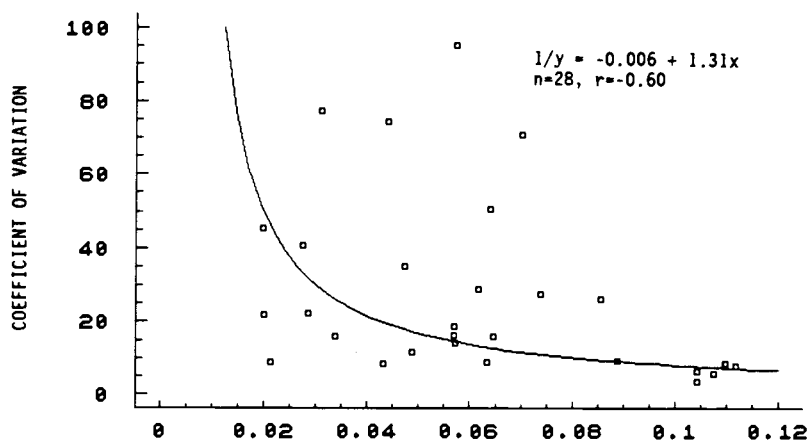
Appendix E. Estimated probability of capture ( $\hat{p}$ ) regressed on the number of occasions ( $t$ ) per trapping session.

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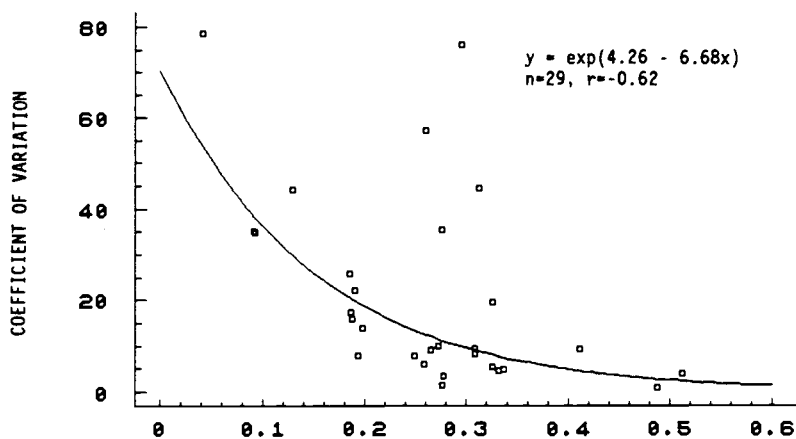


Appendix F. Coefficient of variation of abundance estimates from model  $M_{bh}$  ( $CV_{bh}$ ) regressed on estimated probability of capture ( $\hat{p}$ ).

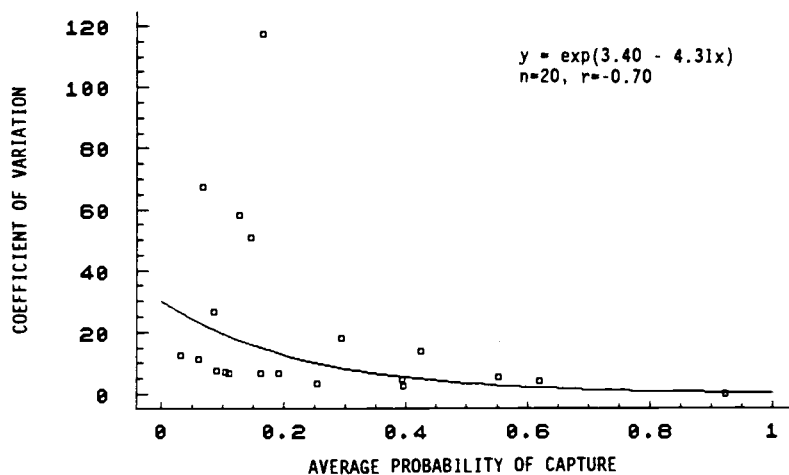
Sylvilagus floridanus (2 outliers removed:  $CV_{bh} = 177$  &  $286\%$ )



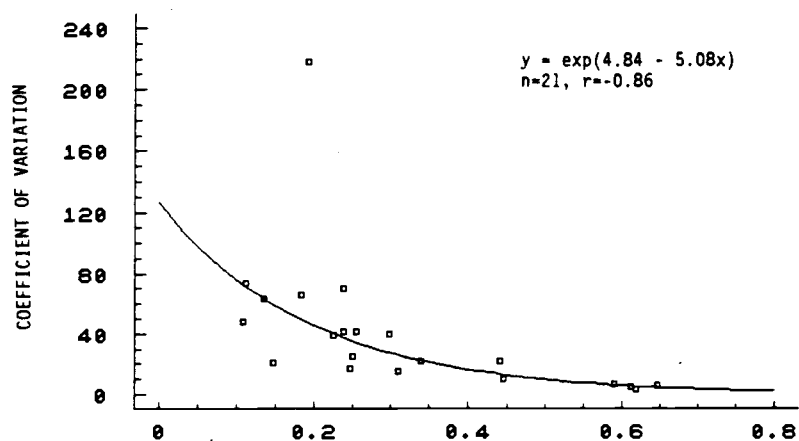
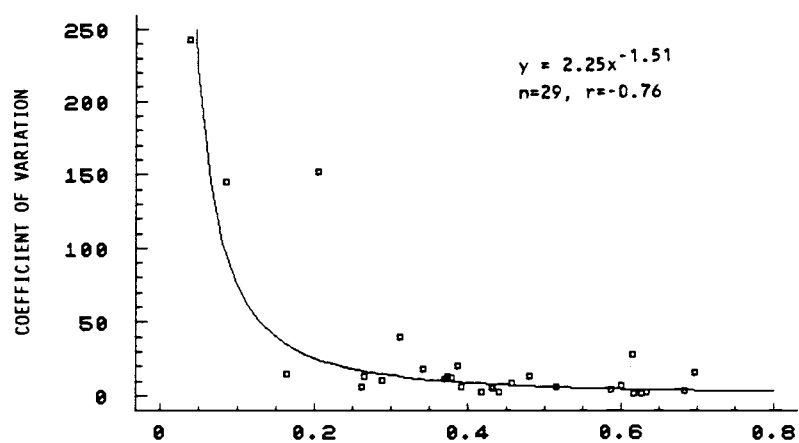
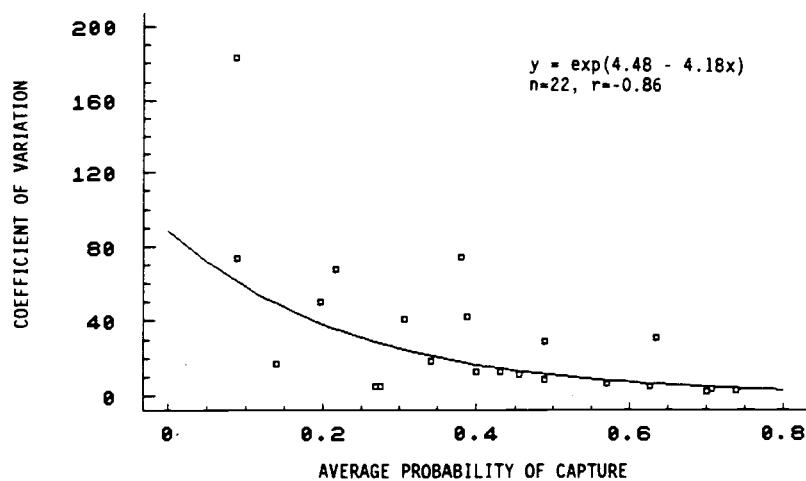
Tamias townsendii



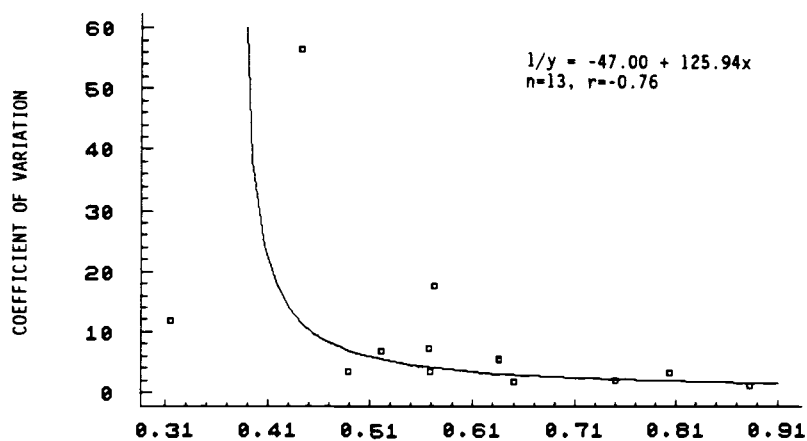
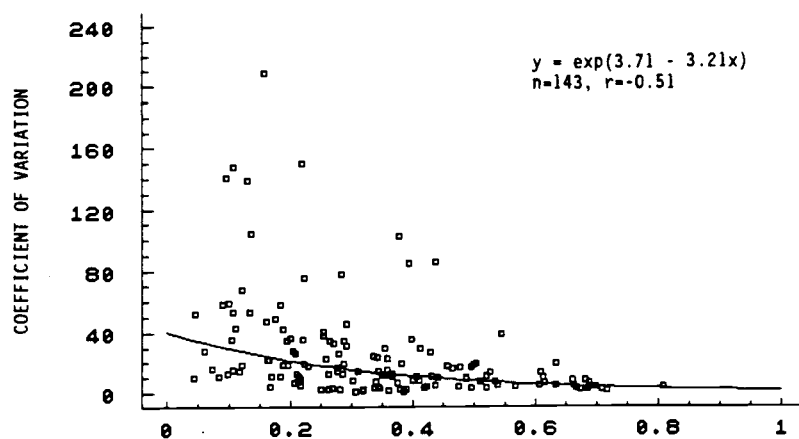
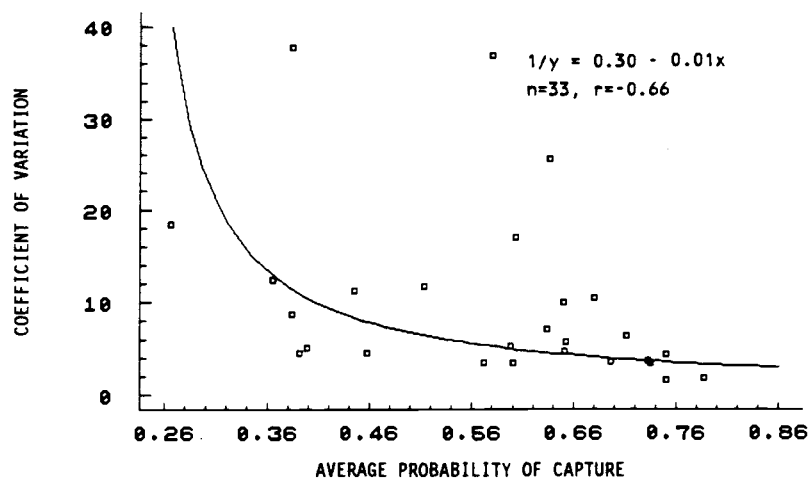
Glaucomys sabrinus



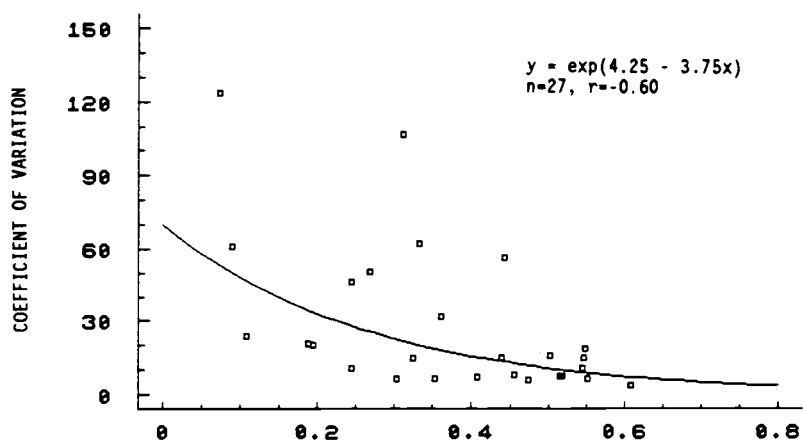
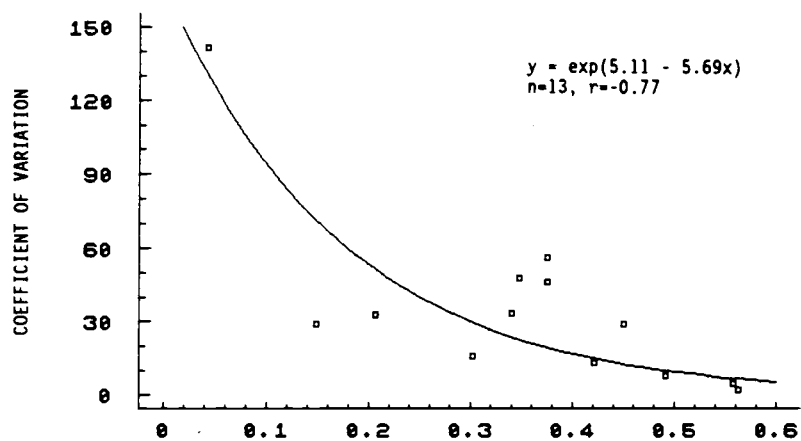
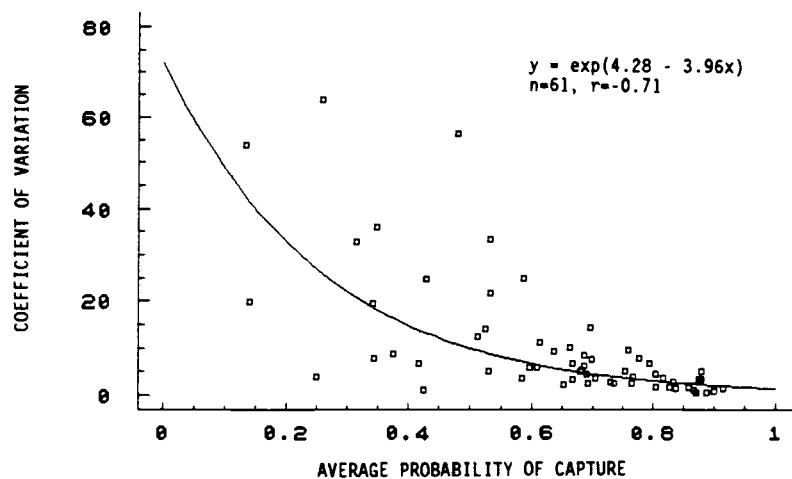
## Appendix F. Continued.

Perognathus longimembrisPerognathus parvusChaetodipus formosus

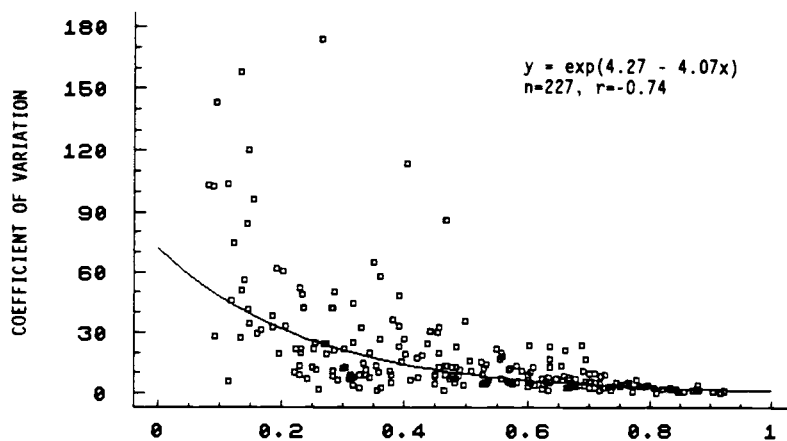
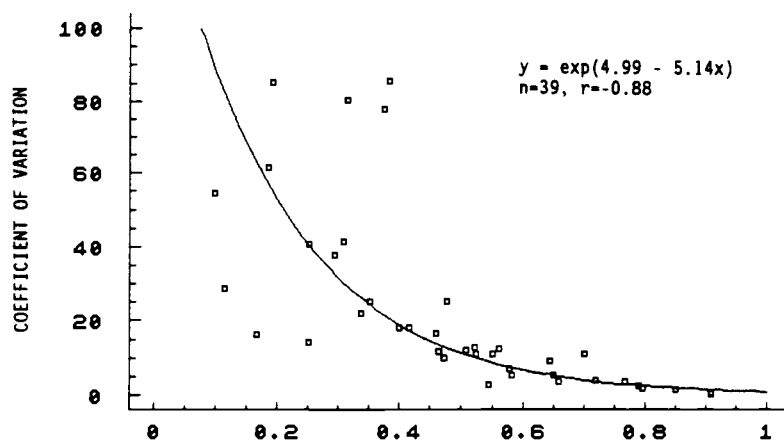
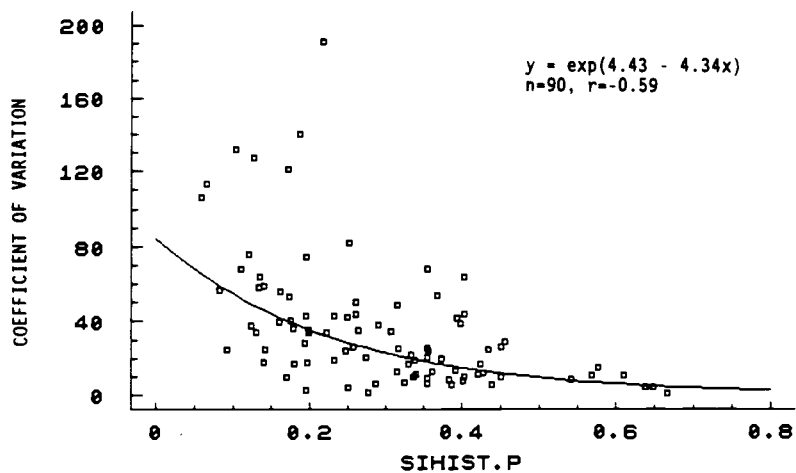
## Appendix F. Continued.

Dipodomys agilisDipodomys merriamiDipodomys microps

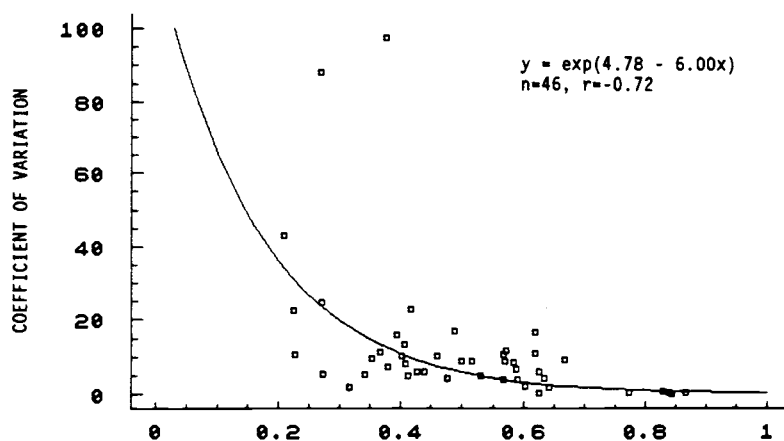
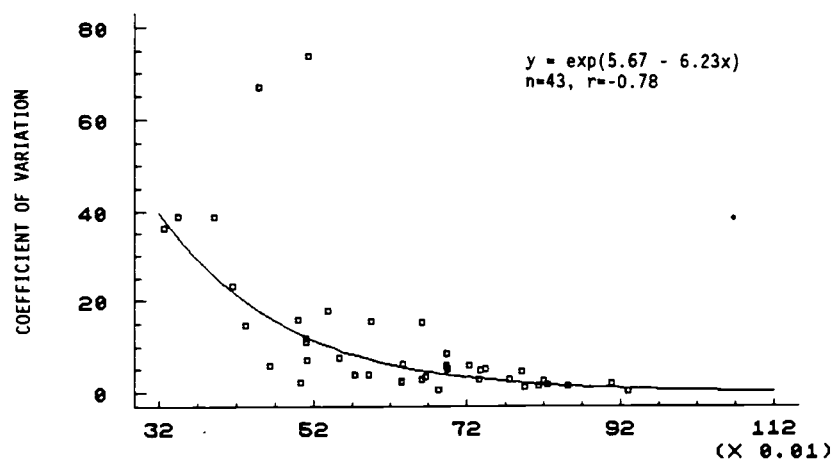
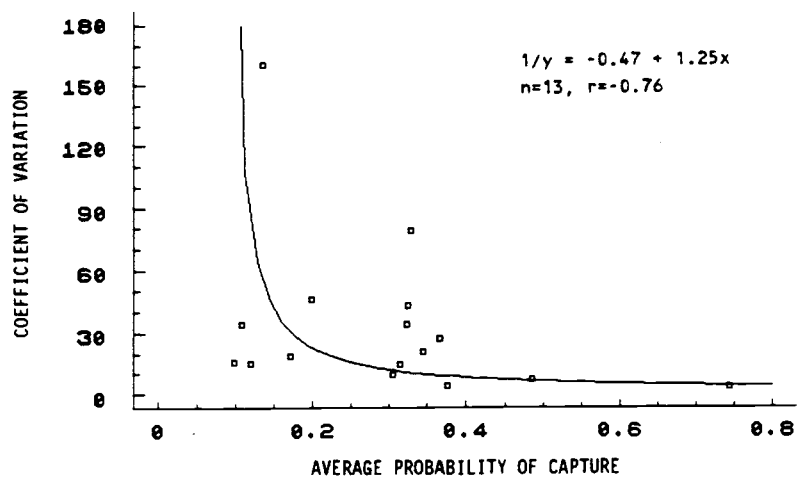
## Appendix F. Continued.

Dipodomys ordiiReithrodontomys megalotisPeromyscus leucopus

## Appendix F. Continued.

Peromyscus maniculatusPeromyscus trueiSigmodon hispidus

## Appendix F. Continued.

Clethrionomys gapperiClethrionomys rutilusMicrotus ochrogaster

## Appendix F. Continued.

