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UTILIZING FIELD AND COMPUTER TECHNIQUES
ON KNOWN POPULATIONS

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Stanley J. Zarnoch
Major professor

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AN EVALUATION OF MARK-RECAPTURE ESTIMATORS UTILIZING FIELD AND COMPUTER TECHNIQUES ON KNOWN POPULATIONS

By

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ABSTRACT

AN EVALUATION OF MARK-RECAPTURE ESTIMATORS UTILIZING FIELD AND COMPUTER TECHNIQUES ON KNOWN POPULATIONS

By

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Since many different mark-recapture estimators are available to the biologist, it is desirable to evaluate their performance. Field evaluation of the estimators was possible because four mark-recapture experiments were performed on *Microtus pennsylvanicus* populations of known size. Of the nine estimators evaluated, the nonparametric frequency of capture method is recommended for estimating the size of trap-happy mice populations. Besides demonstrating a low sample bias and variance, it has the advantage of not being affected by population stratification.

In addition, a computer simulation model for mark-recapture experiments in a closed population was validated for future use. The model incorporates home range movements, spatial patterns, and a learning process (trap-happy or trap-shy), and yields typical mark-recapture data. It should prove to be a useful tool for providing insights into decision-making alternatives in mark-recapture experiments.

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INTRODUCTION

Mark-recapture techniques have a long history and a wide array of designs and analyses. Since the 1950's, the literature on estimation methods has increased tremendously. Fortunately, the book by Seber (1973) and the review by Cormack (1968) provide comprehensive summaries. Dr. Seber also plans to publish a review of recent developments in the very near future (Eberhardt et al. 1979).

Generally, a mark-recapture experiment consists of placing live-traps in a regular grid pattern over the habitat to be studied. The experiment consists of two or more trapping periods, each a random sample of the individuals in the population. In each sample, the previously marked individuals are recorded, unmarked individuals are marked, and all are returned to the population. The next sample is taken after an adequate time has been allowed for the marked and unmarked individuals to randomly mix (Zarnoch and Burkhart 1980). The aim of the experiment would be to investigate one or more of these properties (Caughley 1977):

1. movement
2. growth rate
3. age-specific fecundity rates
4. age-specific mortality rates
5. size of the population
6. rate of birth and immigration combined

7. rate of death and emigration combined
8. rate of harvesting
9. rate of increase

An estimate of population size has traditionally been the main objective. In addition to research problems, a wide variety of environmental assessment studies and biological inventory programs require the estimation of animal abundance. These needs have been further emphasized by the requirement for the preparation of Environmental Impact Statements imposed by the National Environmental Protection Act in 1970 (Otis et al. 1978). Mark-recapture methods have been used extensively to estimate fish, insect, and small mammal populations. They have recently found wider application in big game censusing (Rice and Harder 1977).

Since many different estimators are available to the biologist, it is desirable to evaluate their performance. The validity of an estimate and its 95% confidence limits depends at least upon the condition that all the assumptions underlying the mathematical model from which the estimator is obtained are upheld (Roff 1973a). The only measure of accuracy generally available is the standard error estimated from the data. Field evaluation of the estimators is possible if mark-recapture experiments are performed in areas where the true sizes of the population are known. However, this information is rarely available.

Five mark-recapture studies on known populations were found in the literature.

(1) Edwards and Eberhardt (1967) reported the results of a live-trapping study in Ohio on a penned population of 135 wild cottontails (Sylvilagus floridanus). The estimators they examined were the Schnabel, Schumacher-Eschmeyer, two frequency of capture methods (based on the poisson and geometric distributions), and linear regression.

(2) Cook et al. (1967) released 1093 individuals of the North American moth Hyalophora promethea in Trinidad where they do not naturally occur. The method of estimation adopted was that of Fisher and Ford, which is well suited to a census where there are rather few returns and where the estimate sought is the total population of images during the season.

(3) Smith (1968) used two sampling methods to determine the number of mice of two species, Mus musculus and Peromyscus polionotus, in an abandoned field in Florida. He first live-trapped using the mark-release technique and later captured the mice by digging out their burrows (evidence suggests that the later technique revealed the exact structure of the population). Animal abundance was estimated using the Lincoln and Hayne (Schumacher-Eschmeyer) methods.

(4) Carothers (1973) conducted a mark-recapture experiment on the taxicab population of Edinburgh, Scotland.

The population is a real one (though not involving animals) and had a known size of 420. Estimators used include the Lincoln (Chapman's modification), Schnabel, Schumacher-Eschmeyer, Marten, Tanaka, geometric frequency of capture, and Jolly-Seber.

(5) Rice and Harder (1977) conducted a helicopter-assisted mark-recapture study on a white-tailed deer (*Odocoileus virginianus*) population in northern Ohio. Part of their study area was a 122 ha Test Area with a known deer population of 155. They used the Lincoln Index to estimate deer density.

The need for additional controlled studies where the population size is known has been stressed by Otis et al. (1978), Begon (1979), and Zarnoch (1979).

The objectives of this study are threefold:

(1) To conduct mark-recapture experiments on closed populations (no recruitment or losses) of known size.

(2) To evaluate nine mark-recapture estimators (these include two modifications of the Lincoln and one of the Schnabel).

(3) To calculate additional needed parameters and validate for future use the simulation model for mark-recapture experiments in a closed population developed by Zarnoch (1976).

STUDY AREA

The study was conducted in a mouse-proof, predator-free enclosure at the MSU Wildlife Research Area in Okemos, Michigan. The enclosure was built in a ½ acre (0.2 ha) overgrown clearing. The clearing sloped about -5 degrees to the north towards the Red Cedar River. The vegetation was predominantly brome grass (Bromus spp.), Queen Anne's lace (Daucus Carota), and white sweet clover (Melilotus alba) (Gleason and Cronquist 1963). During the study, the sweet clover extended over most of the enclosure and was 4-5 ft (1.2-1.5 m) tall.

The square enclosure covered 0.27 acres (0.11 ha); each side was 109 ft (33.2 m) long. The fence was constructed by using 36-inch-wide sheets of 24-gauge steel supported by 2x4's. The walls of the fence extended 22-24 inches above the ground. The bottom six inches of the steel sheets were bent along their length at a 90-degree angle to form a perpendicular shelf. This shelf was buried in the soil 6-8 inches deep so that the shelf projected towards the inside, thus preventing the voles from digging out (Price 1967). A 20-inch border was mowed inside the fence and a 6.5-ft border outside, to aid in detecting digging or disturbances and in keeping voles and mice away from the fence (Schwartz and Schwartz 1959). Both borders were mowed before each of the four experiments began.

To prevent mammalian predators from entering the study area, two strands of electric wire surrounded the enclosure. One strand ran along the top of the fence; the other six inches below. To exclude avian predators, the top of the enclosure was completely covered with Conwed plastic netting. The netting was black, weighed 2.75 pounds/ 1000 square feet, and had a strand count of 1.5 x 1.2 strands per inch. At the edges of the enclosure, the netting was attached directly to the top of the fence. In the center, it was supported by 2x2's and 17-gauge wire at an average height of approximately 6.5 ft.

Construction of the enclosure began in May 1979. The steel fence was completed on June 27, 1979; movement of small mammals into or out of the study area was restricted. The top was covered with plastic netting on July 6, 1979, completing the enclosure.

Throughout the study, an attempt was made to keep the study area as natural and undisturbed as possible. There were a few exceptions. In mid-May, straw was spread over a few areas in the southwest corner where the vegetation was slightly sparser than in the rest of the enclosure. The straw added ground structure and cover. To facilitate trapping and to provide a measure of location, a 10 x 10 permanent grid of red flags was established inside the enclosure. Each flag was designated by a letter and a number corresponding to its row and column (Figure 1). Flags were spaced 10 ft (3.0 m) apart; the outermost rows and columns were approximately 9.5 ft (2.9 m) from the fence. Another addition was water stations. Getz (1963) and other authors have noted that the meadow vole appears to have a high moisture requirement. To ensure adequate moisture, 16 Little Giant water containers were placed throughout the study area (Figure 1). Each container consisted of an open water-ring and a jar with a one-gallon water reserve. The average home range of Microtus pennsylvanicus in southern Michigan has been reported as .10-.50 acres for males and .04-.28 acres for females (Blair 1940, Hayne 1950, and Getz 1961). Therefore, by having 16 water stations throughout the study area, the size and shape of the home ranges should not be affected.

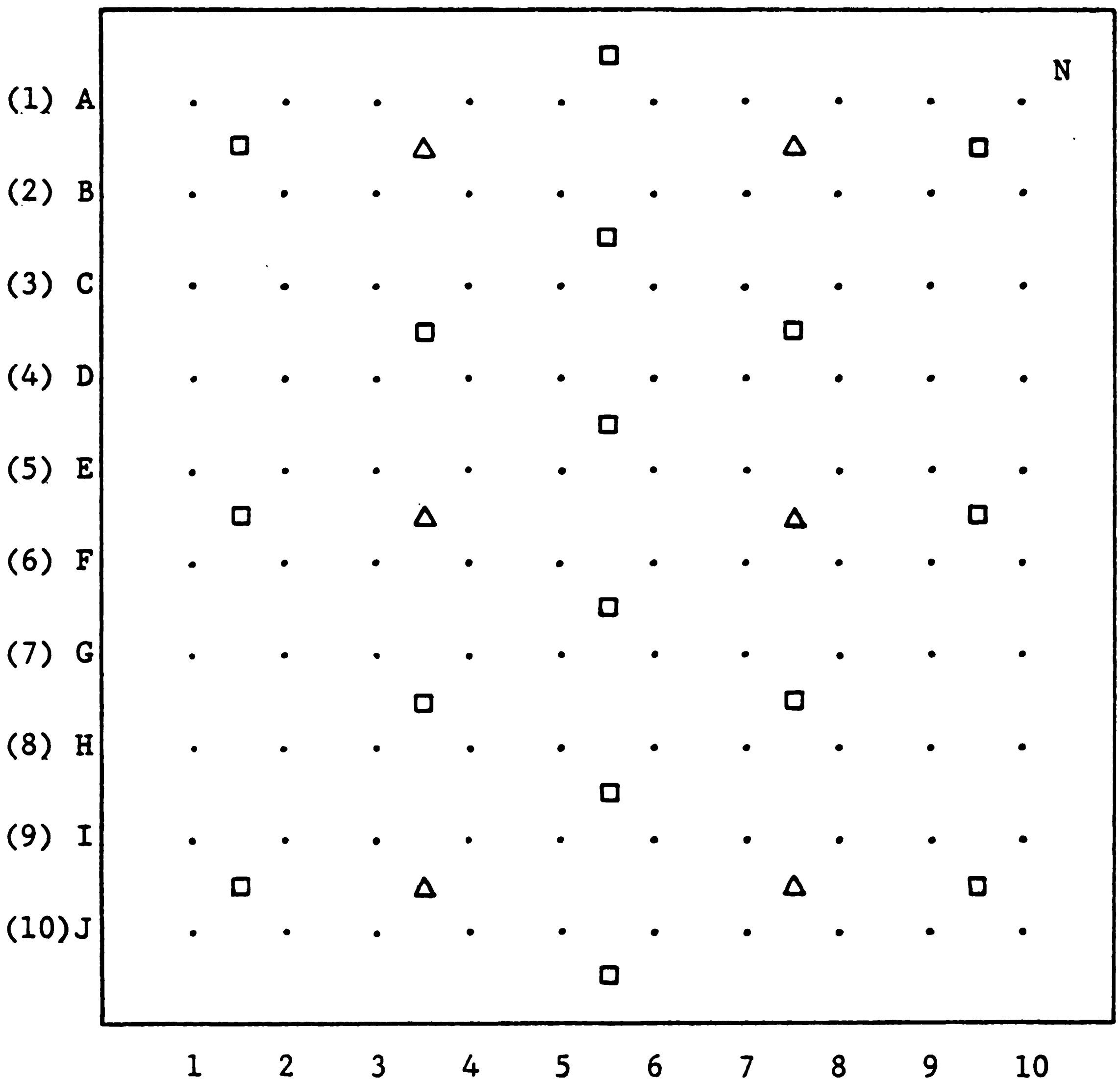
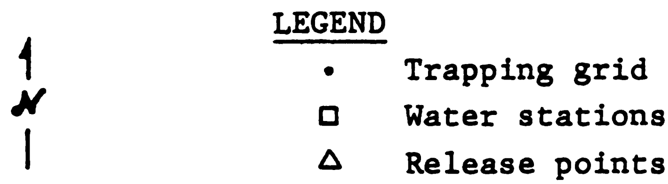


Figure 1. Location of the trapping grid, water stations, and release points.



METHODS

Mark-Recapture Estimators

The nine mark-recapture estimators of population size that are evaluated in this study are presented below.

Lincoln Index estimators

The Lincoln Index is a two-sample mark-recapture estimator. The second sample is usually taken by trapping the individuals, but this is not always necessary. Any method for this second sample may be used, provided it is a random sample of the population. Let

n_1 = number of individuals in sample 1 that were initally taken from the population, marked, and released,

n_2 = number of individuals in sample 2,

m_2 = number of marked individuals in sample 2, and

N = number of individuals in the total population.

Assuming that the ratio of marked to the total number of individuals is constant over the two samples, then the Lincoln Index estimator is (Lincoln 1930)

$$\hat{N} = \frac{n_1 n_2}{m_2} .$$

A modification of the estimator N is given by Chapman (1951) as

$$\hat{N}' = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1.$$

An alternative estimator was developed by Bailey (1951, 1952) by using a binomial approximation to the conditional hypergeometric distribution of m_2. The modification developed under this model is

$$\hat{N}* = \frac{n_1(n_2 + 1)}{(m_2 + 1)} \quad .$$

Because the Lincoln estimator is traditionally for a two-sample experiment, a modification was formulated for a multiple sample mark-recapture experiment. This consisted of considering sample 1 as all trapping periods before the last and sample 2 as the last trapping period.

Schnabel estimators

The Schnabel is an S-sample mark-recapture estimator. For each of the S samples, the total sample size and number of previously marked individuals are recorded, all unmarked individuals are marked, and the entire sample is returned to the population. Let

n_j = number of individuals in the j^{th} sample,

m_j = number of marked individuals in the j^{th} sample,

$M_j = \sum_{j'=1}^{j-1} (n_{j'} - m_{j'})$ = number of marked individuals in the population just before the j^{th} sample is taken,

S = number of samples taken, and

N = number of individuals in the total population.

Then assuming $\frac{M_j}{N}$ is small and m_j follows the poisson distribution, the Schnabel estimator for N is (Schnabel 1938)

$$\hat{N} = \frac{\sum_{j=1}^{s} n_j M_j}{\sum_{j=1}^{s} m_j} .$$

The Schnabel estimator defined above was modified by Chapman (1952). Chapman's modification is

$$\hat{N}' = \frac{\sum_{j=1}^{s} (n_j M_j)}{\sum_{j=1}^{s} m_j + 1} .$$

Schumacher-Eschmeyer estimator

The Schumacher-Eschmeyer estimator employs the same estimation techniques as the Schnabel estimators; that is, the same sampling scheme, variables, and data are needed (Schumacher and Eschmeyer 1943). Schumacher and Eschmeyer, however, utilized a regression method weighted by the sample sizes, n_j (Seber 1973). The Schumacher-Eschmeyer estimator is

$$\hat{N} = \frac{\sum_{j=1}^{s} (n_j M_j^2)}{\sum_{j=1}^{s} (m_j M_j)} .$$

Tanaka estimator

For the situation when the probability of capture for marked animals appears to differ from the probability for unmarked, Tanaka (1951, 1952) has proposed a linear regression model which yields the estimator

$$\hat{N} = \text{antilog} \ \hat{\theta}$$

where

$\hat{\theta} = \bar{x} + \bar{y}/\hat{\gamma}$,

$x_j = \log M_j$,

$y_j = m_j/n_j$,

$Y_j = -\log y_j$, and

$$\hat{\gamma} = -\frac{\Sigma(Y_j - \bar{Y})(x_j - \bar{x})}{\Sigma(x_j - \bar{x})^2} .$$

Variables not defined are the same as in the Schnabel.

Geometric estimator

The frequency of capture approach has been utilized in estimating population size from a multiple-sample mark-recapture experiment. It uses the frequency of capture of individuals over all samples.

The geometric estimator (Eberhardt et al. 1963, Edwards and Eberhardt 1967, Nixon et al. 1967, and Eberhardt 1969) is based on the assumption that the frequency of capture follows a geometric distribution truncated at the zero class. Let

ℓ = number of times an individual is caught $\ell=1,2,3,\ldots,$

f_ℓ = number of individuals caught ℓ times,

S = number of samples taken, and

N = total population size.

The geometric estimator is then defined as

$$\hat{N} = \frac{\left(\sum_{\ell=1}^{\infty} f_\ell\right)\left(\sum_{\ell=1}^{\infty} \ell f_\ell - 1\right)}{\left(\sum_{\ell=1}^{\infty} \ell f_\ell - \sum_{\ell=1}^{\infty} f_\ell\right)}$$

where it is obvious that all terms subscripted with $\ell>S$ are equal to zero and can be ignored.

Nonparametric estimator

Overton (1969) presented a nonparametric estimator based on the frequency of capture. Each animal has probability p_i, $0<p_i\leq 1$, of capture on a given occassion, where p_i is constant over all S occassions, but may vary among animals. Using the variables defined for the geometric estimator, the nonparametric is

$$\hat{N} = \sum_{\ell=1}^{S} \frac{f_\ell}{\theta_\ell}$$

where

$$\theta_\ell = 1 - (1 - \frac{\ell}{S})^S$$

The Mark-Recapture Simulation Model

The majority of methods available for estimating population parameters by mark-recapture sampling require the assumption that, in any particular sample, the mean probability of capture of the previously marked individuals is equal to that of the unmarked individuals (though this probability may vary from one sample to another) (Carothers 1971). In most practical situations, this assumption carries the further implication that in any particular sample, all individuals in the population under study have an equal probablity of capture, and that this probability is independent of the individual's history of capture (Cormack 1966). There is, however, considerable evidence that this assumption is not, in general, valid for animal populations (Young et al. 1952, Getz 1961, Huber 1962, Edwards and Eberhardt 1967, Nixon et al. 1967, Bailey 1969, and Tanaka 1970).

Failure of equal probability of capture has been classified by Cormack (1966) as due to either or both of the following:

(a) The probability that a particular individual is caught in any sample is a property of the individual, this "catchability" having some distribution over the population.

(b) The probability that an individual is caught in any sample depends upon its previous history of capture.

A third cause is given by Eberhardt (1969):

(c) The probability of capture may depend upon the relative opportunity of capture (the geography of trap locations and home ranges).

The simulation model developed by Zarnoch (1976) mimics mark-recapture experiments in a closed population when the assumption of equal probability of capture is violated due to causes (b) and (c) above. The model incorporates home range movements, spatial patterns, and a learning process ("trap-happy" or "trap-shy"), and yields typical mark-recapture data. The model will be validated in this study for future use in evaluating mark-recapture estimators and experiments.

Biological Components

The brief description of the model given here is summarized from the more detailed account by Zarnoch (1976). The three major components of the model are home range movements, spatial pattern of the population, and behavioral response to capture of the animals.

The home range (utilization distribution) of an individual is modeled by a bivariate normal probability density function (Koeppl et al. 1975, Van Winkle 1975). The general form of the bivariate normal probability density function is restricted to the case where $\rho = 0$, yielding as the utilization distribution

$$f(x,y) = (\tfrac{1}{2}\pi\sigma_x\sigma_y) \exp\left(-\tfrac{1}{2}\left[\left(\frac{x-\mu_x}{\sigma_x}\right)^2 + \left(\frac{y-\mu_y}{\sigma_y}\right)^2\right]\right)$$

where

x = x coordinate location of the animal,

y = y coordinate location of the animal,

(μ_x, μ_y) = center of activity,

σ_x = standard deviation of the distance from the center of activity to the x coordinate location,

σ_y = standard deviation of the distance from the center of activity to the y coordinate location, and

ρ = correlation coefficient between x and y.

In the model, interest is centered on the effect of animal spatial patterns on catchability in a mark-recapture experiment. The model is capable of generating uniformly, contagiously, or randomly distributed populations. Since the animals are not sessile, but move according to their specific utilization distributions, the spatial pattern of the population is represented by the pattern of the animals' centers of activity.

As previously explained, it is now recognized that most species of animals exhibit some departure from equal probability of capture. The process whereby an animal becomes trap-happy or trap-shy may be considered learning; trap-happiness corresponds to an animal learning to be trapped while trap-shyness is learning to avoid being trapped. The learning model used is the fixed-point form of the linear operator model of Bush and Mosteller (1955).

Let

$P_{i,j}$ = probability that individual i will be captured on trapping period j, and

α = a learning process parameter ($0 \leq \alpha \leq 1$).

Then trap-happiness was modeled by the function

$$p_{i,j+1} = \begin{cases} \alpha p_{i,j} + 1 - \alpha & \text{if animal } i \text{ is captured in trapping period } j \\ p_{i,j} & \text{if animal } i \text{ is not captured in trapping period } j. \end{cases}$$

Capturing an animal increases its probability of capture during subsequent trapping periods. However, not capturing the individual on a trapping period will not affect the probability of capture on the next trial. This assumption was imposed for simplicity and is probably reasonable in many situations if the time between trappings is short. Note that as α decreases, the intensity of learning increases.

The reverse situation is the case of trap-shyness in which capture presents a punishing experience to the animal and leads to the individual learning to avoid traps. Utilizing the same definitions of $p_{i,j}$ and α as above, the trap-shy model is

$$p_{i,j+1} = \begin{cases} \alpha p_{i,j} & \text{if animal } i \text{ is captured in trapping period } j \\ p_{i,j} & \text{if animal } i \text{ is not captured in trapping period } j. \end{cases}$$

The probability that a trap-shy animal will be caught approaches zero as the number of times captured approaches infinity; that is, the animal will learn to avoid traps. Not capturing an individual on one trial does not affect the probability of capture on the next. This seems reasonable if the time period between trappings is short. Again, note that as α decreases, the intensity of learning increases.

The Trapping Process

The trapping process incorporates the effect of home range, spatial pattern, learning behavior, and trap competition on the estimators. Assuming that the population is closed (subjected to neither births, deaths, nor migration), let

N = the number of individuals in the population, and

S = number of trapping periods.

The model consists of a population of N individuals whose centers of activities have either a random, regular, or contagious spatial pattern on a computer grid. It is also possible to locate animals in the fixed pattern, which consists of specifying the x-y coordinate locations of the individuals' centers of activity. It is not required that all animals in the population should have the same spatial pattern.

The distribution of the traps over the grid follows the same procedure as outlined above for the animals. Although several options exist, the most typical pattern in mark-recapture experiments is the regular spatial pattern.

During trapping period j, (j=1,2,...,S), each individual is moved to a location determined by its utilization distribution by selecting a variate $(x_{i,j}, y_{i,j})$ from the bivariate normal probability density function. One can also specify a uniform utilization distribution which allows individuals to move at random over the study grid.

The trapping mechanism consists of trap locations, trap radii, and trap areas such that an individual is considered trapped if it falls within the trap area of an unoccupied trap. The determination of the trap radius for an individual is based upon its probability of capture. As the probability of capture increases (decreases) during the trapping experiment, its trap radius increases (decreases) according to a mathematical algorithm which ensures this specific probability of capture given all traps (single-capture traps are being used) are unoccupied. As traps become occupied during a given trapping period, the probability of capture of nontrapped individuals diminishes. This represents the effect of trap competition.

The trap radius $r_{i,j}$ for individual i during trapping period j is the same for all traps, indicating that each trap has equal "capturing ability." However, traps may vary in their probability of capturing the individual because of their location with respect to the animal's utilization distribution. In the model, it is assumed that all traps have an equal capturing ability for all individuals at the beginning of the trapping experiment. This implies that $r_{i,1} = r_{i',1} = r$ for i, i = 1, 2,...,N, which is reasonable since this is prior to the animals being exposed to trapping and learning behavior. The average initial probability of capture $\bar{p}$, is defined as the average probability of capture of the animals in the population prior to trapping period 1.

Since we are keeping $r_{i,1} = r$ a constant for $i = 1,2,\ldots,N$, each $p_{i,1}$ is evaluated numerically. Thus, there will be a distribution for $p_{i,1}$ since the probabilities $p_{i,1}$ are dependent on the utilization distribution. This heterogeneity of capture probabilities is a reflection of the trap locations within an animal's home range. It should be realized that this does not reflect inherent behavior since any two animals with identical geographical location of traps in their home ranges will have the same initial probability of capture. After each trapping period, an animal's probability of capture, $p_{i,j}$, is modified according to the appropriate learning theory model defined previously. Consequently, its trap radius is modified in the next trapping period to reflect this change in probability of capture. Theoretically, the trap radius is determined as that radius such that the proportion of the volume under the utilization distribution over the area outlined by circular disks of the specified radius around each trap (compensating for intersecting disks) is equal to the specified probability of capture.

The trapping mechanism represents a single-capture device, indicating that only one individual can be captured in any one trap during trapping period j. To avoid biases, the movements of the individuals during any trapping period are ordered by random selection. Thus, generally no animal will always be the last to be moved and subjected to many traps that have already been filled. Also, if an individual moves into the trap area of a "closed" trap, it maintains this location but is not considered trapped. If the individual is within the trap radii of two traps, it is considered captured by the closest trap. It is realized that in a trapping experiment some traps may be accidently sprung or animals may escape. Here it is assumed that these situations cannot occur.

The model also has a trapping option that allows traps to be activated or deactivated over the course of the experiment. For example, this would allow the investigator the capability of having certain traps open only during every other trapping period.

Collection of Data

After the enclosure was completed, it was necessary to remove all the animals inside. On July 10, 1979, 100 snap-traps baited with a mixture of rolled oats and peanut butter were set inside the enclosure, one by each flag. The traps were checked at least once daily for 10 days. Studies by Stickel and by Pelikan and Zejda indicate that virtually complete removal of small mammals can be achieved within three days by intensive snap-trapping (Yang et al. 1970). Two mole traps were set on mole runways during this 10-day period as well as later, when necessary, during the trapping experiments.

Approximately 40 snap-traps were set around the outside of the enclosure fence in the mowed border strip. They were checked and maintained daily from July 11, 1979 until October 6, 1979 (the end of the last trapping experiment). The purpose of these snap traps was to catch marked voles escaping from the enclosure as well as animals attempting to enter.

After all resident animals had been removed from the enclosure, four mark-recapture experiments were conducted on introduced known populations of meadow voles (*Microtus pennsylvanicus*). The number, sex, and source of the meadow voles used for each experiment is given below:

(I) 40 voles (18 males and 22 females). They were live-trapped near the study area (11 in Leather traps and 29 in Longworth traps) and held for 18 days or less before being released (the majority were held 3 days or less).

(II) 31 voles (16 males and 15 females). They were obtained from the lab colony at Pennsylvania State University (Dr. John Shenk, Dept. of Agronomy). The colony, originating at Michigan State University, has approximately a 16-year history of captivity.

(III) 40 voles (20 males and 20 females). They were live-trapped near the study area (in Longworth traps) and held in lab for 28-31 days before being released.

(IV) 40 voles (25 males and 15 females). They were born and raised in the lab by pregnant females captured near the study area. All the voles were 33-50 days old when released.

Ideally, assuming an equal sex ratio in a natural population (Getz 1960), 20 males and 20 females would have been used in each experiment. The actual number of each sex used, however, depended upon availability. Only a total of 31 meadow voles were available for experiment II, instead of 40.

Prior to being released into the enclosure, each animal was weighed, tagged, and toe-clipped. All animals were tagged on the left rear leg with a size 4 Monel leg band from the National Band and Tag Company. The numbering system used in toe-clipping required at most two clips, one toe per foot (Taber and Cowan 1969). The leg bands provided an easy method of individual identification; the toe clips provided permanent identification if any of the leg bands were lost.

Krebs et al. (1969) separated Microtus age groups by weight into juveniles (<22 g), subadults (22-33 g), and adults (>33 g). However, he noted that few juveniles are caught in live-traps and that many animals reach stable asympotes of weight at small adult body size. In experiments I-IV of this study, only seven, three, five, and seven voles, respectively, weighed less than 22 g. The smallest overall weighed 16.0 g; all but four under 22 g were females. Because young females begin breeding at about 25 days of age and males at 45 days (Burt 1957), almost all the meadow voles used in this study would probably be considered sexually mature. Although an effort was made to only use animals weighing more than 22 g (to lower variability), the inclusion of some juveniles in the population is a natural phenomenon.

Four mark-recapture experiments were performed, each lasting 19 days. The inclusive dates were:

(I) July 21 - August 8, 1979

(II) August 8 - August 26, 1979

(III) August 26 - September 13, 1979

(IV) September 13 - October 6, 1979
(snap-trapped five extra days at the end).

One day 1 of each experiment, three gallons of oats were scattered throughout the enclosure to ensure an adequate food supply. Then an approximately equal number of Microtus were released at each of the six points shown in Figure 1. A 4-day interval was allowed for the introduced population to adjust to its new surroundings. This was based on an arbitrary decision which recognized that some time for adjustment was desirable, but that the longer trapping was delayed the higher the probability of mortality.

On the evening of day 5, 100 Longworth traps were set inside the enclosure, one by each flag. The Longworth is an aluminum trap made of two sections, a tunnel and a nest box. The latter contains both nesting material and food (cotton and oats) and therefore not only attracts the small mammal, but also ensures that it is warm, dry, and fed after capture. The attracted animal enters the tunnel, but, by stepping on a sensitive treadle at the nest-box end, closes and locks the tunnel entrance behind it (Begon 1979). Longworths are one of the most extensively used live-traps in small mammal mark-recapture studies (Morris 1968, Grant 1970). Each trap was covered by a 1x10x12-inch board to shield it from sunshine and rain. Trap spacing was 10 ft (3 m) apart. Tanaka (1966) has recommended a trap spacing of 5 m (15 ft) for ordinary or outbreaking densities of voles; the formula of Otis et al. (1978) based on home range implies a spacing of 5 m (15 ft) or less.

The live-traps were checked each morning at 7-8 a.m. for 10 days (days 6-15). Captured animals were identified, recorded by trap coordinates, and released. All the traps were closed during the morning check to prevent captures and, hence, mortality during the day due to the heat; they were reset at approximately 7 p.m. each evening.

On day 15, the tenth day of live-trapping, all animals captured were removed from the enclosure. Each live-trap was replaced by a snap-trap (100 total) baited with a mixture of peanut butter and rolled oats. The snap-traps were checked at least once daily through day 19 (4 days).

A summarized schedule for each experiment is:

Day 1 *Microtus* released

Day 5 Live-traps set

Day 6 Live-traps checked for the first time

Day 15 Live-trapping ends; snap traps set

Day 19 Snap-trapping ends.

During each trapping experiment, any "unmarked" animals that were caught were removed from the enclosure. This included animals of other species as well as marked animals from earlier experiments.

Snap-trapping at the end of each experiment was necessary to verify that members of the introduced population were still alive and inside the enclosure. All removed members of the experimental population were weighed and positively identified by toe-clip and leg band.

Data Analysis

Mark-recapture estimators

In the four mark-recapture experiments, each animal was considered "marked" after its first capture. Using a program developed on the CDC 750, Model 175, computer at Michigan State University, estimates of population size were computed after trapping periods two through ten of each experiment using the available field data and the nine mark-recapture estimators discussed previously.

Since the size of the known population varied between experiments, the percent bias in the population estimates was examined instead of the actual bias. The percent bias is defined as

$$B = 100(E - K)/K$$

where

m_1 = number of animals introduced at the start of the experiment,

m_2 = number of animals known to be alive,

E = the mark-recapture population estimate, and

$$K = \begin{cases} m_1 & \text{if } E > m_1 \\ m_2 & \text{if } E < m_2 \\ E & \text{elsewhere.} \end{cases}$$

The average percent bias was computed for each estimator for each of the trapping periods 5-10.

Yang et al. (1970) found that both sexes of *Microtus ochrogaster* were equally susceptible to live-traps. In the present study, the frequency of capture for males and females was compared for each mark-recapture experiment with a goodness of fit test adjusted for small sample size (Gill 1978).

If males and females do not show the same response to live-trapping, part of the bias in the mark-recapture estimates may be due to sex. In an attempt to improve the population estimates, the mark-recapture field data from each experiment was analyzed separately for males and for females. An estimate of population size for trapping periods two through ten was computed for each sex using the nine mark-recapture estimators given previously. Total population size was approximated by adding the male and female population estimates for each trapping period together.

The four mark-recapture experiments were "replicates," except for time and the specific experimental animals used. Because the source and trapping background of the voles in the four different experiments varied slightly, the Kolmogorov-Smirnov 2-sample test (MSU Computer Laboratory 1978) was used to determine whether the frequencies of capture follow the same distribution. If all four populations follow the same distribution, then the results of all four mark-recapture experiments can be compared and are expected to be very similar. A small probability level indicates that there is some difference in the distribution of the two mark-recapture experiments being tested (MSU Computer Laboratory 1978).

The mark-recapture simulation model

In order to validate the simulation model, various parameters had to be estimated from the field data. Before utilizing the simulation model, the learning theory option (trap-happy, trap-shy, or no learning), the spatial pattern of the animals, and estimates for the variance of x, the variance of y, the correlation coefficient (ρ), the parameter in the learning theory model (α), and the initial probability of capture ($p_{i,1}$) need to be determined.

Spatial Pattern

Because there was no prior reason for believing that the animals were not distributed in a random spatial pattern, the test due to Hopkins and Skellam (Pielou 1969) was used to check for randomness. Each animal was placed at its center of activity, the average x and y coordinates of its points of capture. For each test, 30 points corresponding to trap locations were choosen from a random number table (Snedecor and Cochran 1967). The spatial pattern of the animals that was chosen for the simulation model was based on the results of this test.

Home Range Parameters

All the animals within each population were assumed to have the same bivariate normal home range parameters. An estimate of the pooled variance of x and variance of y were calculated by using the x and y coordinates of all the capture points of all animals. The parameter ρ, the correlation coefficient between x and y, determines the narrowness of the elipse containing the major portion of the observations. In the model, the general form of the bivariate normal probability density function is restricted to the case where ρ is equal to zero. The validity of this restriction can be examined by testing the estimated correlation coefficient (r) for each animal. However, several sample correlations (for individual animals) may possibly be drawn from a common ρ. If this is true, the r's may be combined into an estimate of ρ which is more reliable than that afforded by any of the separate r's. To test the hypothesis that several r's are from the same ρ, and to combine them into a pooled estimate of ρ, the procedures of Snedecor and Cochran (1967) are followed, using the bias correction for averaging large numbers of correlations. The pooled rho with a 95% confidence interval was estimated for each experiment regardless of the results of the pooling test. Only animals live-trapped four or more times could be included in the calculations.

Learning Behavior

If the catching and handling affect the catchability of marked individuals after their first capture, then the sampling will not be random within the marked population. Testing the assumption of equal catchability in the marked population verifies whether the animals are either trap-happy or trap-shy. Leslie's technique based on the frequency of recapture of individuals (Seber 1973) was applied with the first two trapping samples consituting the marked population (animals not removed at the end of the experiment were not included). The simulation model option for either no learning, trap-happiness, or trap-shyness is based on the test results.

Learning Parameters

Estimates of two parameters, α (the learning process) and $p_{i,1}$ (the initial probability of capture) are still needed (if the no learning option is selected then $\hat{\alpha} = 1.0$). To obtain the estimates, the methods developed by Bush and Mosteller (1955) for free-recall verbal learning experiments were adopted. Their experiments were conducted as follows. A list of N monsyllabic words is read aloud to a subject. The subject is then instructed to write down all the words that he can recall. The experimenter gives him no indication of how well he has performed. Then the order of the words is randomized, and the procedure is repeated. The experiment is continued in this way for many trials until the proportion of words recalled nearly reaches an asymptote. When redefining the model of Bush and Mosteller (1955) for my study, a word becomes a meadow vole, recall of a word is the capture of an animal, and each listing by the subject of the words he can recall is a trapping period.

Three basic assumptions made in analyzing the data are:

(1) All animals have the same initial probability of capture, $p_{i,1}$, and that all animals have the same learning parameters (i.e., we have a group of N "identical" subjects).

(2) Non-capture of an animal does not changes its probability of being captured during the next trapping period.

(3) All the animals can be caught (trap-happy) or none of the animals can be caught (trap-shy) during a trapping period. That is, the proportion of animals caught (or not caught) approaches an asymptote of unity.

The initial probability of capture, $p_{i,1}$, is estimated from that portion of the data which is independent of α, the learning parameters. The data for each animal from trapping period one up through the trapping period in which each animal is first captured is used to estimate $p_{i,1}$. A unique unbiased estimate, $\bar{p}$, of $p_{i,1}$ when N is fixed and Z is the only observed statistic, is given by

$$\bar{p} = \frac{N - 1}{Z - 1}$$

where

N = the number of different animals captured during the trapping experiment, and

Z = the sum over all animals of the number of trapping periods preceded by a zero frequency of capture. (If an animal is not caught until trapping period 4, then it has 4 trapping periods preceded by a zero frequency of capture. Unless the investigator has definite knowledge of uncaptured animals present in the population, then

$$Z = \sum_{i=1}^{N} f_i$$

where f is the trapping period in which the animal was first captured.)

Thus, $\bar{p}$ will tend to decrease as the number of animals captured increases, until every animal in the population has been captured at least once.

The mean total number, $\bar{T}$, of non-captures may be used to estimate α as

$$\hat{\alpha} = 1 - \frac{-\ln \bar{p}}{\bar{T}} .$$

If

N_i = the number of known animals in the population on day i, and

$$C_j = \begin{cases} \text{the number of times an animal j has been captured (if the population is trap-happy)} \\ \text{or} \\ \text{the number of times animal j has not been captured (if the population is trap shy,} \end{cases}$$

then for a given day i

$$\bar{T} = \left[i\,(N_i) - \sum_{j=1}^{N_i} C_j \right] / N_i .$$

For days 6-10 of each mark-recapture experiment, two estimates of α and $p_{i,1}$ were computed from two sets of data. First, only the field data available from trapping periods one through the day when the parameters were estimated was utilized; these will be referred to as the incomplete estimates. These estimates are calculated from the amount of information normally available to a biologist conducting a mark-recapture study. The second set of data also included animals known to be present but not captured during the live-trapping. The only animals from the introduced population not included were those never captured during the live-trapping and not removed during the snap-trapping phase. These estimates will be referred to as the complete estimates. The complete estimates may be an improvement over the incomplete estimates because they are based on the entire population, not just the marked animals.

Model Validation

After the model's parameters were estimated from the field data, the validity of the model was checked by simulating mark-recapture experiments. If the model is valid, the population estimates calculated from the simulated mark-recapture data should closely approximate the population estimates calculated from the original field data.

Two simulations were run for each mark-recapture experiment. The first used the incomplete estimates of α and $p_{i,1}$ (based only on the field trapping data); the second, the complete estimates (based on all known data). Because each simulation costs 10-13 dollars, replications were not made initially. In all the simulations, 100 traps were arranged in a 10 x 10 regular spatial pattern. The number of animals placed on the computer grid for each simulation was approximately the average of the introduced population size and the minimum number of animals known to be present in the corresponding field experiment. The bias in the model's estimate was found by subtracting the original estimate from the simulation value.

After the initial exploratory simulations, each experiment was replicated ten times with the incomplete estimates of α and $p_{i,1}$ from day 10. The incomplete estimates were chosen because they typify most mark-recapture studies; the estimates from day 10 were thought to be the best because they were based on the most information. The population size in the simulations was the minimum number of animals known to be present on day 10, a verified true population size. The animals were placed in a random spatial pattern. The bias in the model's estimate was calculated by subtracting the original field estimate from the average of the ten simulation values.

When attempting to validate the model, the best test should result from the utilization of all possible information available, even information not normally available to the investigator during a mark-recapture study. In addition to using the complete estimates of α and $p_{i,1}$, the animals were placed in a fixed pattern on the computer grid. All animals known to be present on trapping day 10 were placed on the 10 x 10 computer grid at their center of activity. Because of the high cost of simulations, ten replications were generated for experiment III only. Experiment III was chosen because the true population size was closely known and because all the animals had a very similar capture and lab history prior to being released into the enclosure. Again, the bias in the simulation estimates was calculated by subtracting the original field estimate from the average simulation value.

RESULTS

In the initial trap-out period prior to experiment I, one *Microtus* and one mole (*Scalopus aquaticus*) were removed from the enclosure. Moles continued to be a problem during the study, especially when they dug near or under the fence, because mice, shrews, and other animals often use the tunnels more than the moles do (Schwartz and Schwartz 1959). Three more moles were later removed, one during experiment I and two during III. During the study, the snap traps in the mowed border outside the fence captured ten deermice (*Peromyscus maniculatus*), six meadow voles, one eastern chipmunk (*Tamias striatus*), and a variety of birds. None of the *Microtus* were marked animals from the experimental populations. Inside the enclosure, a deermouse and two shorttail shrews (*Blarina brevicauda*) were captured during the removal period of experiment III; five shorttail shrews were captured during experiment IV. Throughout the entire study, no unmarked *Microtus* (animals not marked and introduced during the mark-recapture experiments) were trapped inside the enclosure.

Part of the field data (tag number, sex, and capture dates) for experiments I-IV is given in the Appendix. Animals not captured on trap day 10 or during the snap-trapping period were not removed from the enclosure at the end of the experiment; they are not known to be alive or inside the enclosure past their last date of capture. This includes one animal (1023) from experiment I, one (1049) from II, two (1110, 1123) from III, and four (1137, 1141, 1146, 1173) from IV. One animal from III (1095) was found dead in the enclosure on day 19 of that experiment. One animal introduced in experiment IV was found dead prior to the start of live-trapping; therefore the introduced population of IV is considered to be 39. No other mortality was known to have occurred during the initial adjustment or the live-trapping phase of any experiment.

Based on their points of capture during the study, the voles seem to have established their home ranges by the start of the live-trapping. There are no examples of a dramatic shift in an animal's capture locations. In all four experiments, the animals showed a positive average weight gain from the time of introduction to the time of removal. This indicates there was sufficient food available to sustain the Microtus population. The average weight gain was 4.12, 4.04, 4.08, and 1.97 grams in experiments I-IV respectively. Throughout the study, very few closed Longworth traps were empty when checked (average of 1.3 traps/day).

During experiments I and II, the weather was mostly cloudy and humid with rain falling several days in both I and II. During experiments III and IV, the weather was sunny and warm. The temperature throughout the study was fairly uniform, reaching between 65 and 85 degrees most afternoons. The coolest daytime temperatures occurred during experiment II.

Mark-Recapture Estimators

The mark-recapture estimates are plotted for trapping periods two through ten (Figures 2-5). Because all three Lincoln estimators gave similar values, only Chapman's modification is shown and is simply called the Lincoln. For the same reason, only Chapman's modification of the Schnabel is shown and is just referred to as the Schnabel. The Tanaka estimate is never shown for day 2 because it is undefined.

The shaded area in Figures 2-5 is the "known" number of animals present in the enclosure (true population size). The number of animals released at the start of the experiment forms the upper boundary. The verified number of animals present (by capture or a later trapping) forms the lower boundary.

In experiment II, 26 voles out of the population of 31 were captured the first day; all had been captured at least once by day 4. Although these animals were not truly tame (Hediger 1954), they seem to have lost most of their inhibitions towards humans and traps during their history of captivity. On several occassions, some of these voles were caught only a few minutes after the traps were opened. They were also much less aggressive than the other vole populations when handled. For these reasons, experiment II has been

Legend for figures 2-5

M = Number of animals marked

L = Lincoln

S = Schnabel

SE = Schumacher-Eschmeyer

T = Tanaka

G = Geometric

N = Nonparametric

Known number of animals
(see text)

Figure 2. Experiment I. Mark-recapture estimates of of population size.

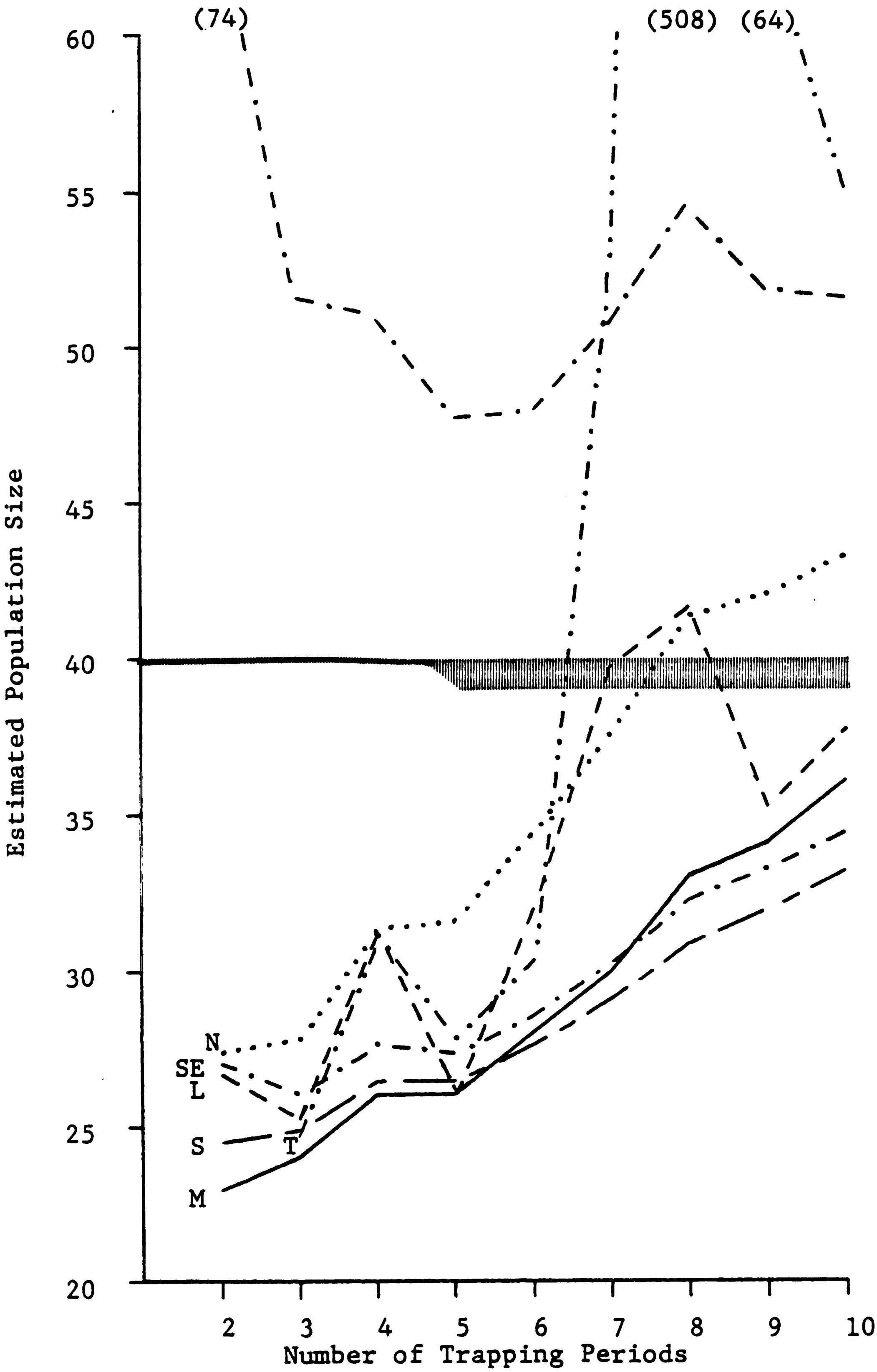

(74)
(508)
(64)
60
55
50
45
40
35
30
25
20
Estimated Population Size
N
SE
L
S
T
M
2
3
4
5
6
7
8
9
10
Number of Trapping Periods

Figure 2.

Figure 3. Experiment II. Mark-recapture estimates of population size.

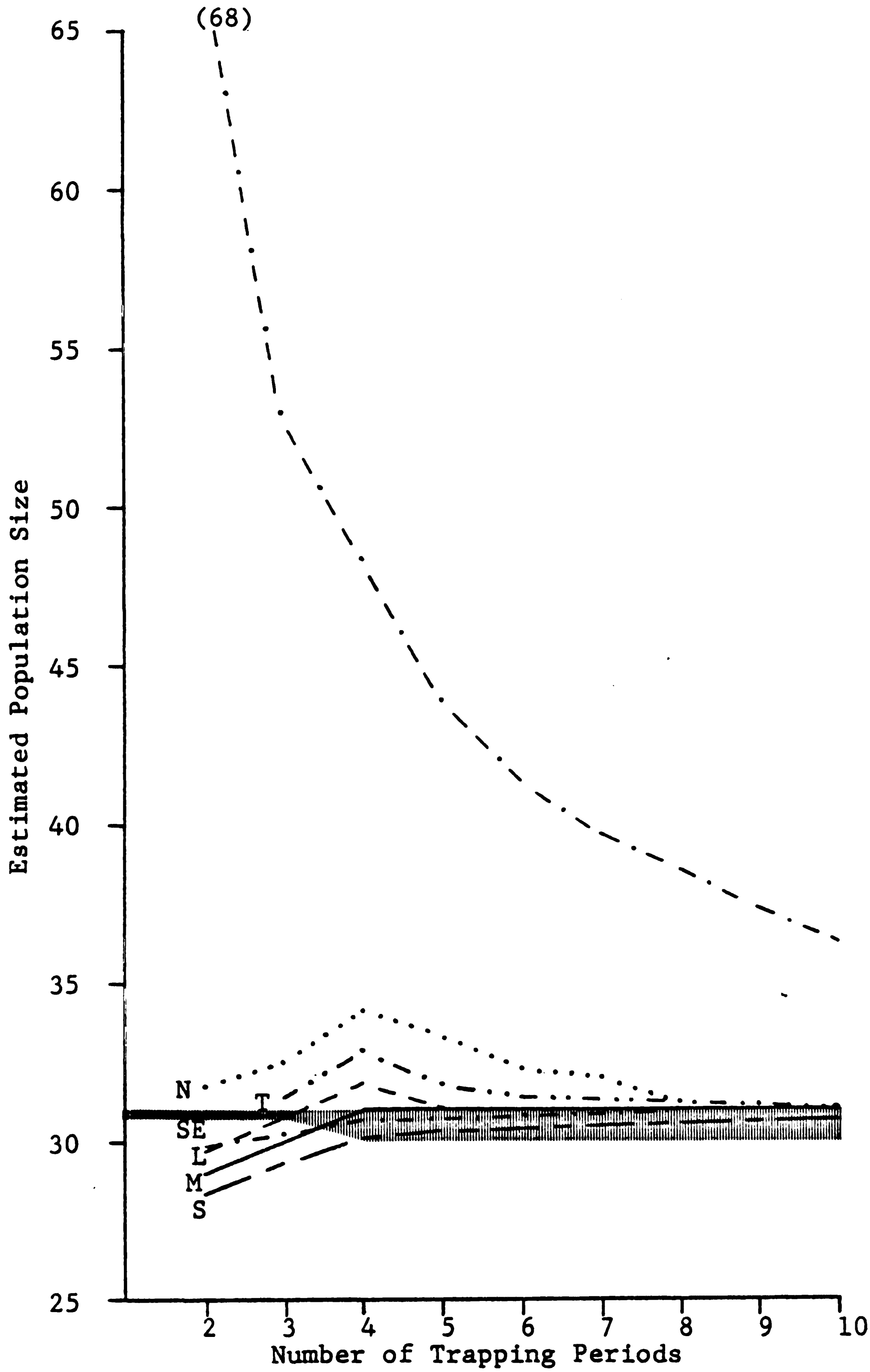
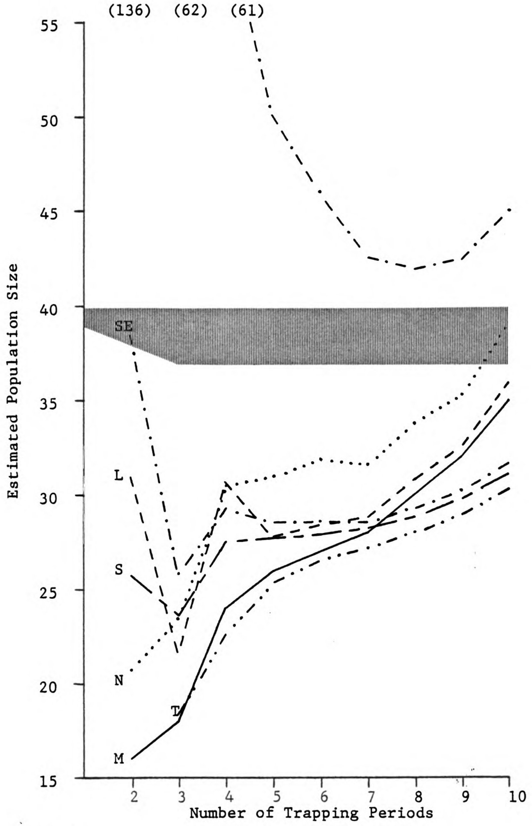

(68)
65
60
55
50
45
40
35
30
25
Estimated Population Size
N
T
SE
L
M
S
2
3
4
5
6
7
8
9
10
Number of Trapping Periods

Figure 3.

Figure 4. Experiment III. Mark-recapture estimates of population size.



(136)
(62)
(61)
55
50
45
40
35
30
25
20
15
Estimated Population Size
SE
L
S
N
T
M
2
3
4
5
6
7
8
9
10
Number of Trapping Periods

Figure 4.

Figure 5. Experiment IV. Mark-recapture estimates of population size.

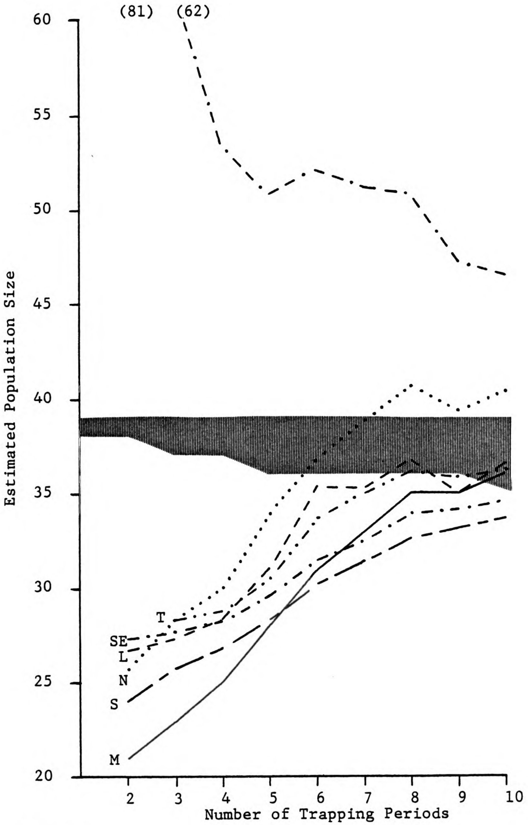

(81)
(62)
60
55
50
45
40
35
30
25
20
Estimated Population Size
T
SE
L
N
S
M
2
3
4
5
6
7
8
9
10
Number of Trapping Periods

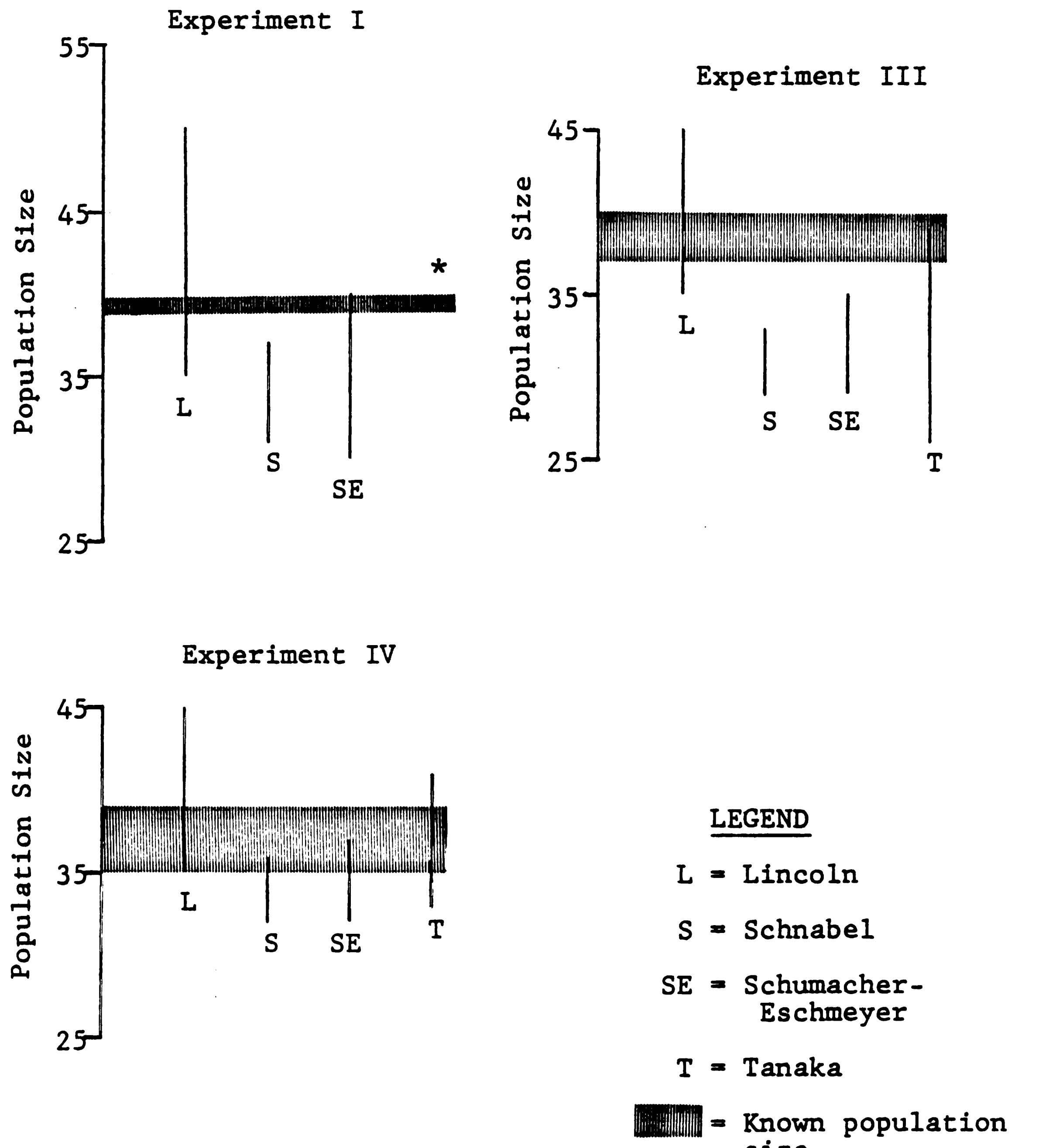
Figure 5.

excluded from the rest of the analysis except where it is used for illustrative purposes.

For experiments I, III, and IV, 95% confidence limits on the day 10 population estimates are shown for the Lincoln (Adams 1951), Schnabel, Schumacher-Eschmeyer, and Tanaka (Seber 1973) (Figure 6). Accurate methods for calculating the confidence intervals for the geometric and nonparametric frequency of capture estimators were not available. The average percent bias of the population mark-recapture estimators for experiments I, III, and IV is shown in Table 1.

To test for a difference in frequency of capture between males and females in each mark-recapture experiment, 2x4 contingency tables were constructed. In all three cases (I, III, and IV) there was no significant difference between sexes in the frequency of capture ($P>.30$). Experiment II also showed no significant difference ($P\approx.20$).

Although males and females showed the same response to live-trapping, the field data from each experiment was analyzed separately for males and females in an attempt to improve the population estimates by stratifying. The combined population sizes, approximated by adding the male and female population estimates together, are compared to the original field estimates in Table 2. Note that for the nonparametric frequency of capture estimator, the combined population estimates and the original field estimates are always exactly the same. In experiment II, none of the differences were



* The confidence interval for the Tanaka is not shown because of computational difficulties. The Tanaka estimate is 55.

Figure 6. 95% confidence intervals for the day 10 population estimates.

Table 1. The average percent bias in experiments I, III, and IV.

Trap Day	Lincoln	Schnabel	Schumacher-Eschmeyer	Tanaka	Geo-metric	Nonpara-metric
5	-23.99	-26.14	-23.57	-25.22	24.96	-13.82
6	-14.37	-23.23	-20.76	-18.95	22.78	-8.48
7	-8.11	-20.72	-18.25	-2.82*	21.47	-6.04
8	-4.27	-17.29	-14.60	441.91	24.01	-0.36
9	-8.10	-15.17	-12.75	12.66*	18.94	0.53
10	-2.06	-11.48	-9.04	6.52*	20.28	3.90

*The average of large positive and negative biases.

Table 2. The differences between the combined population estimates (males and females estimated separately and added together) and the original field population estimates.

		Trapping Periods								
		2	3	4	5	6	7	8	9	10
I	Lincoln**							3*		
III										
IV				8+						
I	Schnabel	4-								
III		6-								
IV		4-								
I	Schumacher-Eschmeyer									
III		---	13+	3+						
IV				3+						
I	Tanaka	---	---	---			23*	530+	28-	31*
III		---	---	5+						
IV		---	5+	589-	38-	29-	11*	8-	5*	4*
I	Geometric									
III		---	40-	9-						
IV				5-	3-	4-				
I	Nonparametric***									
III										
IV										

** All differences of less than 3 are omitted for all estimators

*** All values are exactly the same

LEGEND

+ Combined estimate is closer to the true value

- Combined estimate is farther from the true value

* The two estimates are approximately equidistant from the true value (on opposite sides)

--- Estimator is undefined

greater than 2.5; none of the differences after day 4 were greater than 1.0.

The Kolmogorov-Smirnov 2-sample test was employed to determine whether the frequencies of capture for experiments I, III, and IV follow the same distribution (are the populations "the same"). This test is sensitive to any type of difference in the two distributions - median, dispersion, skewness, etc. (MSU Computer Laboratory 1978). The following results were obtained by using an SPSS file (Nie et al. 1975) on the CDC 750 computer:

Populations compared	2-tailed probability
I and III	.2194
I and IV	.1893
III and IV	.9969

Only frequencies of capture for animals removed from the enclosure were entered into the tests. Since 95% confidence intervals are common in the literature and research (rejecting only if the 2-tailed probability $<.05$), it seems reasonable to conclude that all three populations have the same distribution. Thus, the results of these three mark-recapture experiments can be compared and are expected to be quite similar.

The Mark-Recapture Simulation Model

Parameter estimation

In order to use the simulation model, the spatial pattern of the population must be determined. The Hopkins and Skellam method tested the randomness of the distribution of the animals throughout the enclosure, based on their centers of activity. The results from experiments I, III, and IV all showed the animals to be distributed in a random spatial pattern ($P \geq .65$).

All of the animals in each population were assumed to have the same bivariate normal home range parameters. Estimates of the pooled variances of x and y are:

Experiment	Variance of x	Variance of y
I	1.224	2.034
III	1.482	2.565
IV	1.660	2.018

This seems to indicate more of a circular than an elliptical home range. In the model, the general form of the bivariate normal probability density function is restricted to the case where ρ, the correlation coefficient between x and y, is equal to zero. The hypothesis that several sample correlations are possibly drawn from a common ρ was tested for each experiment (Table 3). Regardless of the results of the pooling test, a pooled rho was estimated and its 95% confidence interval calculated (Table 3). Emphasis falls on two facts (Snedecor and Cochran 1967):

(1) In small samples the estimate, $\bar{r}$, is not very reliable.

(2) The limits are not equally spaced on either side of $\bar{r}$, a consequence of its skewed distribution.

Table 3. Significance of the test to pool the correlation coefficients of several animals, and an estimate of the common rho ($\bar{r}$) with a 95% confidence interval.

Experiment	Test for pooling		The common pooled rho	
	Degrees of freedom	Significance level of the test	Estimate ($\bar{r}$)	95% confidence interval
I	12	.197	.022	-.296,.335
III	16	.044	-.310	-.526,-.058
IV	17	.001	-.085	-.323,.162

In experiment I, the animal correlation coefficients can definitely be pooled and the common rho is equal to zero ($P>.05$). In experiment III, the correlation coefficients can be pooled at the .044 level. Zero is not included in the 95% confidence interval, but is in the 99% confidence interval (-.578, .024). Experiment IV should not be pooled, but if it was the common rho is equal to zero ($P>.05$). Taking into account the small sample sizes, the assumption in the simulation model that $\rho = 0$ seems justifiable for simplicity.

If trapping and handling affect the catchability of marked individuals after their first capture, then the sampling will not be random within the marked population implying a trap-happy or trap-shy situation. Seber's test for equal catchability among the marked animals was applied to the data from experiments I, III, and IV. Only animals that were removed at the end of the experiments were included. The results were highly significant in all three cases ($P\leq.001$ in I, $P<.01$ in III, and $P<.001$ in IV). Based on field observations and the estimates of γ in the Tanaka estimator (it is a measure of the degree of trap-happiness (Seber 1973)), the trap-happy option, rather than the trap-shy option, was selected for the learning theory model in all three experiments.

Estimates of the two parameters, α (the learning process) and $p_{i,1}$ (the initial probability of capture) were obtained from the methods developed by Bush and Mosteller (1955). The estimates were computed two ways: first from the field data on captured animals only (incomplete estimates); second from all animals known to be present in the enclosure (complete estimates). Tables 4-7 give the estimates of α and $p_{i,1}$ ($\hat{\alpha}$ and $\bar{p}$) at trapping periods 6-10 of experiments I-IV. Although the estimates may vary from day to day, the true values of α and $p_{i,1}$ remain constant throughout the experiment. In experiment II, the incomplete and complete estimates of $p_{i,1}$ are both .79 for trapping periods 6-10, because all the animals in the population had been caught at least once by day 4. The two estimates of α in experiment II are the same on each trap day because all animals are known; the values increase each trap day, however, because the mean number of recaptures increases while $\bar{p}$ stays constant ($\hat{\alpha} = 1 - \frac{-\ln \bar{p}}{\bar{T}}$ where $\bar{T}$ is the mean total number of non-recaptures). In experiments I, III, and IV, $\bar{p}$ based on the complete data remains almost constant. When based on the incomplete data, $\bar{p}$ starts out high, gets lower each day as more unmarked animals are captured, and will eventually be constant when all animals have been marked. The $\bar{p}$ based on the complete data fluctuates slightly because some animals have not yet been caught by trapping day 10.

In experiments I, III, and IV, the incomplete estimates of α tend to remain fairly constant, although experiment IV shows a small steady increase. The complete estimates

Table 4. Experiment I. Estimates of the initial probability of capture ($\bar{p}$) and the learning process ($\hat{\alpha}$).

Trap Day	Incomplete Estimates		Complete Estimates	
	$\bar{p}$	$\hat{\alpha}$	$\bar{p}$	$\hat{\alpha}$
6	.54	.831	.22	.652
7	.45	.826	.22	.709
8	.36	.815	.22	.746
9	.34	.824	.22	.770
10	.30	.822	.22	.786

Table 5. Experiment II. Estimates of the initial probability of capture ($\bar{p}$) and the learning process ($\hat{\alpha}$).

Trap Day	Incomplete Estimates		Complete Estimates	
	$\bar{p}$	$\hat{\alpha}$	$\bar{p}$	$\hat{\alpha}$
6	.79	.888	.79	.888
7	.79	.906	.79	.906
8	.79	.922	.79	.922
9	.79	.928	.79	.928
10	.79	.931	.79	.931

Table 6. Experiment III. Estimates of the initial probability of capture ($\bar{p}$) and the learning process ($\hat{\alpha}$).

Trap Day	Incomplete Estimates		Complete Estimates	
	$\bar{p}$	$\hat{\alpha}$	$\bar{p}$	$\hat{\alpha}$
6	.39	.746	.19	.623
7	.37	.760	.18	.654
8	.33	.759	.18	.682
9	.29	.754	.18	.701
10	.25	.752	.19	.726

Table 7. Experiment IV. Estimates of the initial probability of capture ($\bar{p}$) and the learning process ($\hat{\alpha}$).

Trap Day	Incomplete Estimates		Complete Estimates	
	$\bar{p}$	$\hat{\alpha}$	$\bar{p}$	$\hat{\alpha}$
6	.39	.737	.24	.650
7	.36	.759	.24	.694
8	.32	.765	.25	.732
9	.32	.782	.24	.746
10	.30	.789	.24	.763

start out low and increase with each trap day because the mean number of non-recaptures increases while $\bar{p}$ remains constant. With the exception of trap days 9 and 10 in experiment IV, the highest value of $\hat{\alpha}$ based on complete data (trap day 10) is always lower than any of the estimates of α for days 6-10 based on incomplete data.

Model Validation

Having now obtained all of the necessary information, two simulations for ten trapping periods were generated for each experiment (I, III, and IV). In all six simulations, 100 traps were activated for each trapping period, all animals in the population had the same bivariate normal distribution, the animals were distributed in a random spatial pattern, the trap-happy learning theory model was selected, and ρ was set equal to zero. For the simulations with the incomplete data (IN), $\bar{p}$ is the average of the day 6-10 estimates; the $\hat{\alpha}$ from day 10 was chosen. For the simulations with the complete data (C), $\bar{p}$ from day 10 was chosen; the $\hat{\alpha}$ is the average of the day 6-10 estimates. The values of $\bar{p}$, $\hat{\alpha}$, N (the population size), the variance of x, and the variance of y are given in Table 8. The bias in the estimates from the simulation data was calculated by subtracting the original field estimate (as for the Lincoln on day 7) from the simulation value. The bias was calculated on trap days 2-10 of each experiment for the Lincoln, Schnabel,

Table 8. The model simulation values of $\bar{p}$, $\hat{\alpha}$, N, the variance of x, and the variance of y.

Experiment	Data	$\bar{p}$	$\hat{\alpha}$	N	Var(x)	Var(y)
I	IN	.30	.82	40	1.224	2.034
I	C	.22	.79	40	1.224	2.034
III	IN	.25	.75	39	1.482	2.565
III	C	.18	.73	39	1.482	2.565
IV	IN	.30	.77	38	1.660	2.018
IV	C	.24	.76	38	1.660	2.018

<u>LEGEND</u>

$\bar{p}$ = Estimate of the initial probability of capture

$\hat{\alpha}$ = Estimate of the learning theory parameter

N = The population size

IN = Based on incomplete data

C = Based on complete data

Schumacher-Eschmeyer, geometric, and nonparametric estimators (Table 9-11). The Tanaka was not included because the field estimates were often highly variable. The average bias for trapping periods 5-10 is also given in the tables (9-11).

The average bias of the Schnabel and Schumacher-Eschmeyer is lower when the complete estimates are used. However, the geometric and nonparametric show a slightly larger bias, while the values for the Lincoln are approximately the same. All of the estimates, though, were based on one simulation. Ten replicate simulations were then generated for each experiment (I, III, and IV) using only the data pertinent to a typical mark-recapture experiment. All of the information entered was the same as in the previous simulations except for $\bar{p}$, $\hat{\alpha}$, and N. The $\bar{p}$ and $\hat{\alpha}$ were the incomplete estimates from day 10 (Tables 4, 6, and 7). The number of animals (N) was the minimum number known to be present in the enclosure during trapping periods 5-10 (5-9 for experiment III). These values are:

Experiment	$\bar{p}$	$\hat{\alpha}$	N
I	.30	.82	.39
III	.25	.75	.37
IV	.30	.79	.36

The values of $\bar{p}$, $\hat{\alpha}$, and N are very similar in all three experiments. Both $\bar{p}$ and $\hat{\alpha}$ are in the moderate range; neither is extremely high or extremely low.

Table 9. Experiment I. Bias in the simulation mark-recapture estimates.

Trap Day	Lincoln		Schnabel		Schumacher-Eschmeyer		Geometric		Nonparametric	
	IN	C	IN	C	IN	C	IN	C	IN	C
2	4.9	-1.6	2.5	-2.2	9.0	-1.0	46.4	2.4	-4.3	-4.0
3	11.8	6.3	9.1	2.5	12.8	4.1	41.4	14.9	3.6	2.4
4	-2.5	1.0	3.8	2.8	3.1	3.3	6.0	6.1	-0.5	2.2
5	12.0	3.8	6.2	3.1	6.1	3.1	12.3	1.1	5.1	1.9
6	6.9	-1.3	6.9	2.2	7.0	1.9	12.8	-2.9	7.0	-1.3
7	-2.7	-6.6	6.1	1.7	5.9	1.2	6.8	-6.0	4.4	-2.3
8	-3.0	-7.9	5.1	0.3	4.5	-0.6	0.9	-10.7	1.6	-5.2
9	5.7	-2.3	5.1	-0.4	4.7	-1.2	3.7	-9.7	2.6	-6.2
10	1.3	-4.7	4.3	-1.4	3.8	-2.2	0.2	-11.0	-0.6	-8.6
$\bar{x}$ of 5-10	3.4	-3.2	5.6	0.9	5.3	0.4	6.1	-6.5	3.4	-3.6

LEGEND

IN Based on incomplete data
C Based on complete data

Table 10. Experiment III. Bias in the simulation mark-recapture estimates.

Trap Day	Lincoln		Schnabel		Schumacher-Eschmeyer		Geometric		Nonparametric	
	IN	C	IN	C	IN	C	IN	C	IN	C
2	10.0	-6.0	7.3	-4.1	27.5	-11.5	120.0	-51.0	0.3	0.6
3	3.7	6.1	3.8	1.6	1.9	2.9	6.0	5.8	2.8	2.1
4	-1.7	-5.9	0.8	-2.5	-0.4	-3.1	-4.2	-12.5	-0.2	-2.8
5	-0.6	2.4	-0.2	-1.0	-0.4	-0.7	-2.4	-1.7	0.0	0.2
6	3.9	2.3	1.5	0.2	1.3	0.5	2.9	1.0	2.6	1.6
7	2.8	0.2	1.9	0.2	1.9	0.5	2.8	-0.8	2.1	0.0
8	1.8	-1.8	1.8	-0.3	1.8	-0.2	1.7	-3.2	0.3	-3.2
9	2.2	0.5	1.8	-0.3	1.7	-0.3	2.1	-0.8	1.0	-0.8
10	-2.0	-2.5	1.0	-0.8	0.9	-0.9	-2.6	-3.5	-4.1	-3.6
$\bar{x}$ of 5-10	1.4	0.2	1.3	-0.3	1.2	-0.2	0.8	-1.5	0.3	-1.0

<u>LEGEND</u>

IN Based on incomplete data
C Based on complete data

Table 11. Experiment IV. Bias in the simulation mark-recapture estimates.

Trap Day	Lincoln		Schnabel		Schumacher-Eschmeyer		Geometric		Nonparametric	
	IN	C	IN	C	IN	C	IN	C	IN	C
2	-13.8	-1.4	-12.8	-3.0	-14.5	0.6	-50.1	26.7	-12.0	-4.0
3	2.0	7.7	-6.8	4.8	-6.5	7.7	-10.2	23.4	-3.5	2.3
4	-2.0	-0.1	-4.7	2.6	-3.8	2.4	-6.5	4.9	-2.2	1.2
5	3.1	3.3	-1.9	2.9	-0.3	2.9	2.7	6.3	0.8	1.1
6	-3.0	-3.7	-1.7	1.2	-0.8	0.6	-2.9	-3.2	-1.4	-3.0
7	-2.3	-2.9	-1.9	0.3	-1.3	-0.5	-4.2	-5.8	-2.8	-4.7
8	-3.2	-1.9	-2.2	-0.2	-1.8	-0.9	-5.6	-5.2	-4.4	-4.4
9	1.0	1.0	-1.6	-0.5	-1.1	-1.0	-1.3	-3.9	-3.1	-4.0
10	-1.6	-2.6	-1.6	-0.9	-1.3	-1.4	-2.6	-4.8	-3.0	-5.7
$\bar{x}$ of 5-10	-1.0	-1.1	-1.8	0.5	-1.1	0.0	-2.3	-2.8	-2.3	-3.4

LEGEND

IN Based on incomplete data
C Based on complete data

For simplicity, only one mark-recapture estimator, the nonparametric, was selected to evaluate the model. The nonparametric estimator was chosen because of its low bias and mean square error (MSE, which incorporates the sample bias and variance) in model simulations with trap-happy populations (Zarnoch 1979, Zarnoch and Burkhart 1980). Zarnoch (1976) tested the same five estimators shown in Tables 9-11 with computer simulations and concluded that, in most situations, the sample bias, variance, and mean square error properties of the nonparametric estimator were at least as good as the next competitor and often better. In simulations with a trap-happy population where $\bar{p} = .30$ and $\hat{\alpha} = .90$ (close to the $\bar{p} = .25$-$.30$ and $\hat{\alpha} = .75$-$.82$ in this study), the nonparametric estimator clearly had the lowest bias, variance, and mean square error. The nonparametric field estimates in this study also showed the lowest average percent bias (Table 1).

In Figures 7-9, the field nonparametric estimates and the average simulation nonparametric estimates with 95% confidence intervals are plotted for trapping periods 2-10. The confidence intervals were calculated by multiplying the standard error of the bias by 2.262 ($t_{9,.025}$).

In another attempt to validate the model, ten replicate simulations of experiment III were generated utilizing all possible information available. In addition to using the complete estimates of α and $p_{i,1}$ from day 10 ($\bar{p} = .19$ and

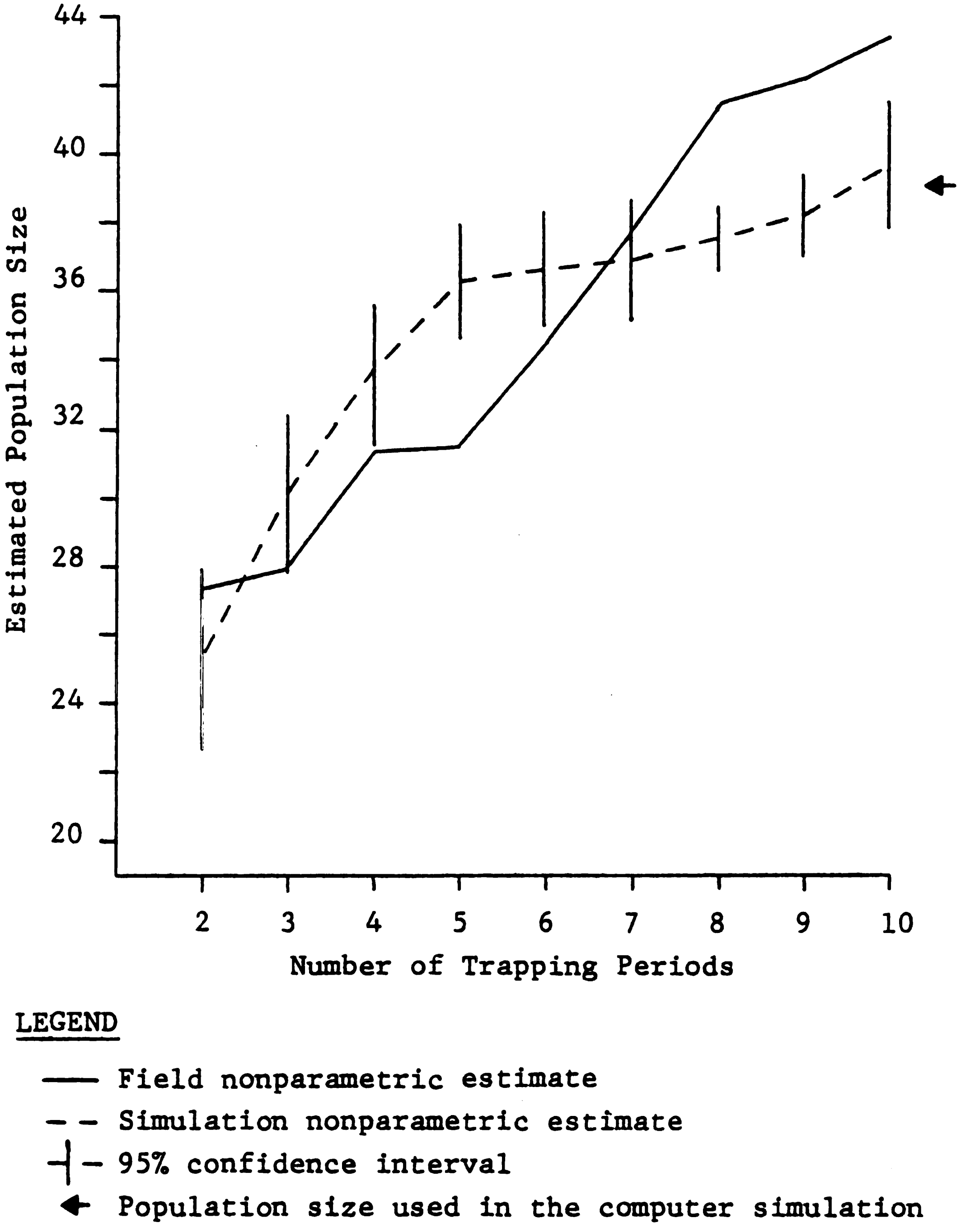
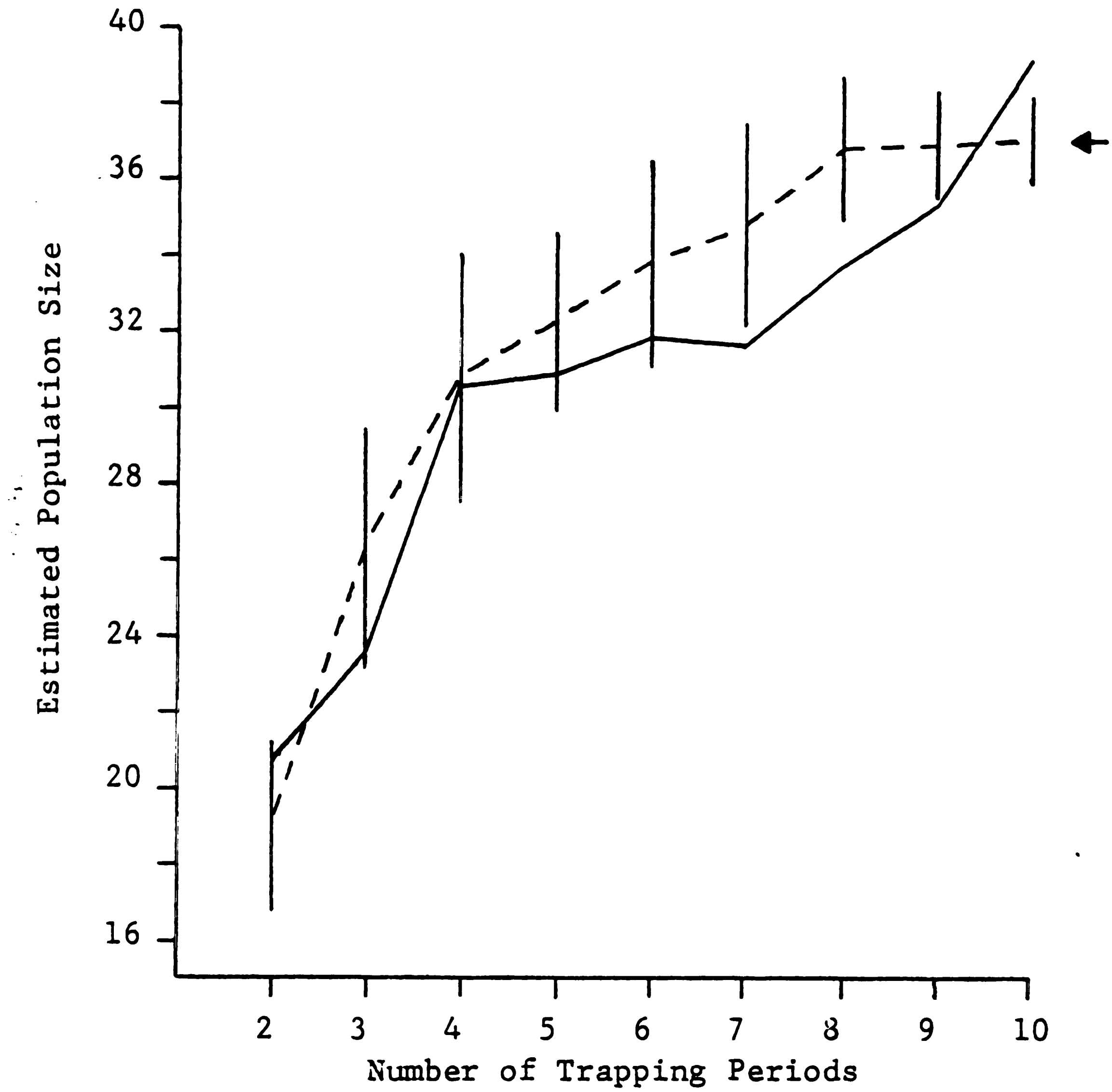


Figure 7. Experiment I (random spatial pattern). Field and simulation nonparametric estimates.



LEGEND

—— Field nonparametric estimate

– – Simulation nonparametric estimate

–|– 95% confidence interval

← Population size used in the computer simulation

Figure 8. Experiment III (random spatial pattern). Field and simulation nonparametric estimates.

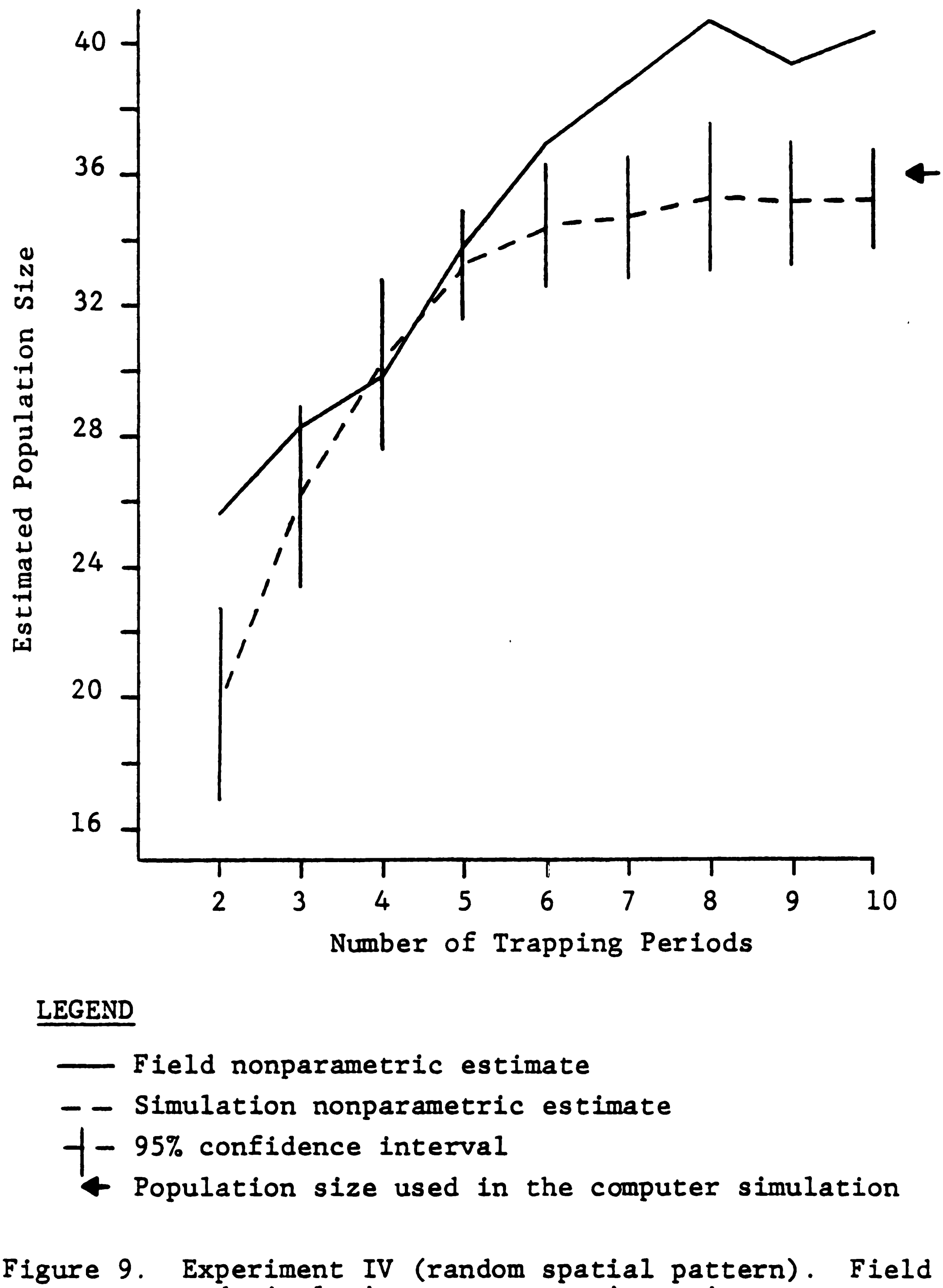
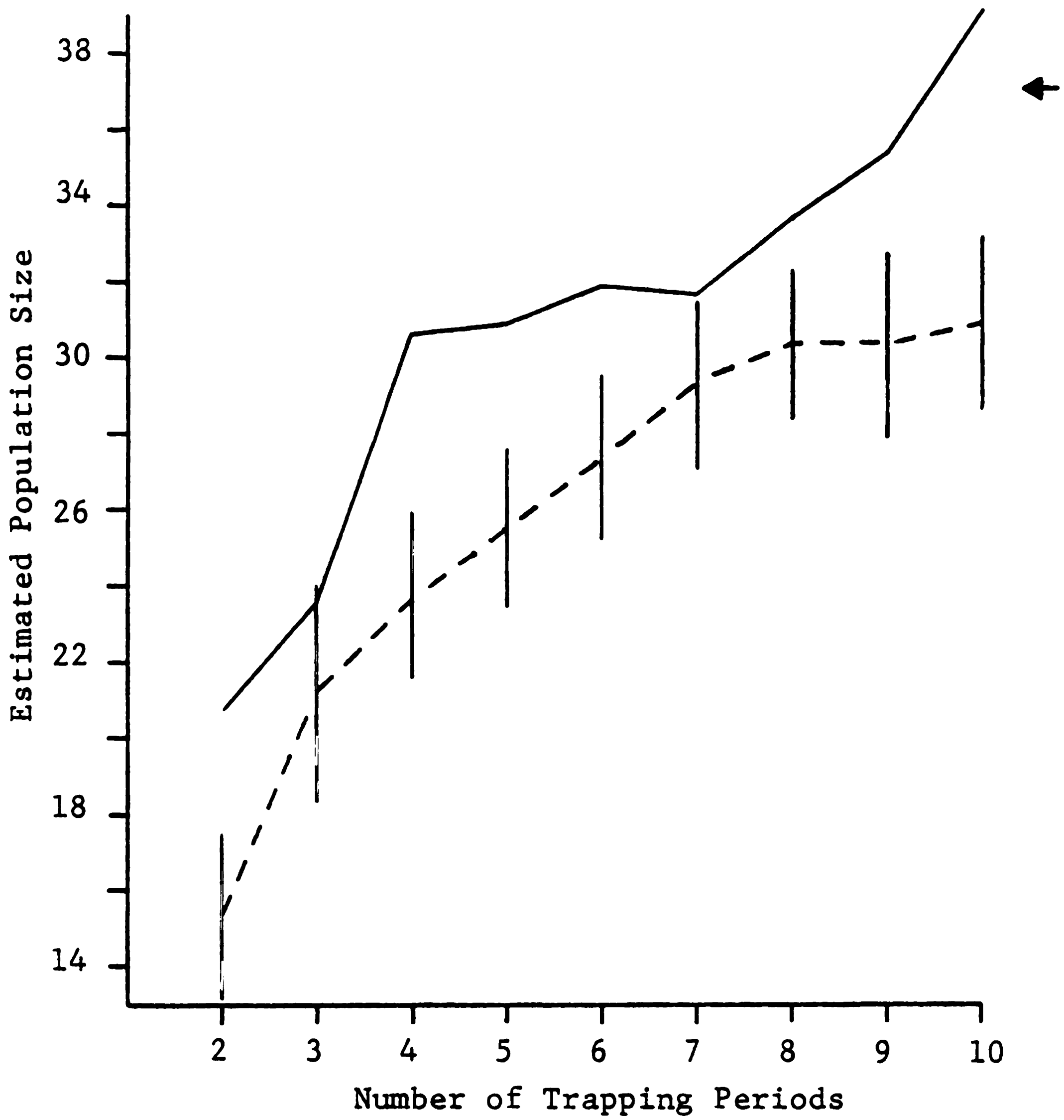


Figure 9. Experiment IV (random spatial pattern). Field and simulation nonparametric estimates.

$\hat{\alpha}$ = .73), the animals were placed in a fixed pattern corresponding to their centers of activity. Otherwise, the model specifications were the same as in the previous ten simulations for experiment III. The field nonparametric estimates and the average simulation nonparametric estimates are plotted in Figure 10 for trapping periods 2-10. Again, the confidence intervals were calculated by multiplying the standard error of the bias by 2.262.



LEGEND

—— Field nonparametric estimate

– – Simulation nonparametric estimate

┤– 95% confidence interval

◀ Population size used in the computer simulation

Figure 10. Experiment III (fixed spatial pattern). Field and simulation nonparametric estimates.

DISCUSSION

The mark-recapture experiments were conducted in the enclosure under field conditions as natural as possible. A population size of 40 animals is a density of 148 per acre. Christian (1971) estimated a density of *Microtus pennsylvanicus* in his study of 116-200 per acre; Hamilton (1937) estimated peak densities of *M. pennsylvanicus* at 160-230 per acre. So although the population density in this study is fairly high, it is certainly not unreasonable. The true population size was known exactly or within at most three animals throughout each experiment (except for four animals on day 10 of experiment IV). The 10 ft. trap spacing is closer than the spacing in many mark-recapture studies, but some animals in the population were still never captured during the ten days of live-trapping. The Kolmogorov-Smirnov 2-sample test showed that there was no significance difference between the frequency of capture distributions for experiments I, III, and IV. The *Microtus* in experiment IV were an unbiased, untrapped sample because they were born and raised in the lab. Therefore, the live-trapping of the animals released in experiments I and III seems to have produced an unbiased sample of the population. Although the animals had all been trapped once, they shared a common experience of one capture.

To procure Microtus for future studies, live-trapping, perhaps with a different type of trap than is to be used in the study, is an acceptable and easy method.

Mark-Recapture Estimators

(The discussion of results includes only experiments I, III, and IV of this study.)

The Lincoln estimator generally gave a negative bias, although most of the estimates from day 6-7 on had a bias of less than 10%. This corresponds very well to the fact that N' (Chapman's modification) is unbiased when $n_1 + n_2 \geq N$ (Seber 1973). Using other known populations, Carothers (1973) found an average bias of 15-30%, Rice and Harder (1977) calculated an average of five surveys that gave a result very close to the true value, and Smith (1968) reported that the Lincoln values were high for male mice and low for female mice. For reasonable accuracy, several authors have suggested that at least 50% of the population must be marked (Strandgaard 1967 and Roff 1973a). This corresponds to about trapping day 4 in my experiments. Seber (1973) concluded that of all methods in his book the Lincoln appears to be the most useful, provided that the assumptions underlying the method are satisfied and there are sufficient recaptures in the second sample. However, Cormack (1968) summarized by saying that although the Lincoln provided a simple and intuitively reasonable estimate of population size, there is a universal lack of faith in the assumptions.

The Schnabel is a multiple sample maximum likelihood estimator (Caughley 1977). The Schumacher-Eschmeyer is just a modified version of the Schnabel based on regression. It may often be more accurate (robust) when unequal probabilities of capture cause violation of the assumptions (Caughley 1977, Otis et al. 1978, and Overton 1969). In this study, the Schnabel and Schumacher-Eschmeyer gave very similar estimates after trap day 2, with the Schumacher-Eschmeyer always being slightly higher. On every trap day in all three experiments, both estimates had a large negative bias; after approximately day 7 they gave estimates below the number of marked animals in the population. Carothers (1973) and Edwards and Eberhardt (1967) both reported a large negative bias in the Schnabel and Schumacher-Eschmeyer when compared to known populations. Smith (1968) found that the Schumacher-Eschmeyer (Hayne) underestimated his true population of mice. Negative bias in the Schnabel has also been shown to occur in populations with heterogeneity of catchability by, among others, Seber (1970) and Zarnoch and Burkhart (1980). A Schnabel-type study on a closed population is affected more by failure of assumptions than a Lincoln-type study with a single release of animals (Cormack 1968).

The Tanaka estimator is based on departures from the underlying assumption that marked and unmarked animals have the same probability of capture (Seber 1973 and Eberhardt 1978). The overall results in this study were highly variable.

In experiment I, the Tanaka jumped from a large negative bias on days 4-6 to a large positive bias on days 7-10 (to 580 animals on day 8). In experiment III, the Tanaka consistently gave estimates below the number of marked animals in the population. In experiment IV, the estimates were close to the true population after day 5. Carothers (1973) concluded that the Tanaka estimates for his known population, though reasonable, generally have a considerable larger standard error and appear no less biased than "equal catchability" estimates. Few other examples are available in the literature. The Tanaka has the disadvantage of being undefined for day 2 or any other day when $n_i = 0$, $m_i = 0$, the variance of $x = 0$, or the variance of $Y = 0$.

The frequency of capture methods attempt to correct for violation of the assumption of equal probabilities of capture (Eberhardt 1978). The geometric maximum likelihood estimator gave very large positive biases in all experiments; even in experiment II where all animals in the population were marked by day 4. For known populations, Edwards and Eberhardt (1967) achieved useful estimates while Carothers (1973) concluded that the geometric is positively biased in populations with equal catchability and that the bias decreases as the variance of the distribution of probabilities of capture increases. Using computer simulations, Roff (1973b) and Zarnoch (1976) showed the geometric significantly overestimated population size; Romesburg and Marshall (1979) found the geometric unbiased, but that the approximate confidence intervals for N were inaccurate.

The nonparametric frequency of capture method has recieved little exposure in the literature. With a nonparametric approach, one does not need to assume how capture probabilities are distributed over the population. They are appealing because they are robust to specific assumptions regarding the experiment (Otis et al. 1978). In this study, the nonparametric gave good estimates of the true population after day 5-7. In general, the nonparametric went from a large negative bias at the beginning of the experiment to a slight positive bias at the end. Zarnoch (1976) tested five estimators (Lincoln, Schnabel, Schumacher-Eschmeyer, geometric, and nonparametric) by computer simulation. This led to acceptance of the nonparametric as the "best" of the five estimators when the population possesses heterogeneity of capture probabilities. In most situations, its sample bias, variance, and mean square error properties were at least as good as the next competitor and often better. The nonparametric also fared well when compared to the geometric, Schnabel, and Schumacher-Eschmeyer in other simulations (Zarnoch 1979, and Zarnoch and Burkhart 1980).

Confidence intervals (95%) for four of the estimators were presented in Figure 6. However, the positive correlation between the estimates of population size and their estimated standard errors is such that the variance is an insensitive measure of accuracy of the estimate (Manly 1971 and Roff 1973a). Underestimates will appear more accurate than they really are; confidence limits cannot therefore be placed on the estimates (Roff 1973b). Roff (1973a) suggests that an estimate be considered reliable if its coefficient of variation is less than 0.05 (which it is on almost every day of each experiment in this study) and the confidence limits taken to be $\hat{N} \pm 0.1\hat{N}$. Robson and Regier (1964) suggest that a 10% level of accuracy be the minimum acceptable for management work.

Considering a 10% level of accuracy as the minimum acceptable, the average percent bias in experiments I, III, and IV is examined for the six estimators (Table 1). The Schnabel, Schumacher-Eschmeyer, and geometric estimates are clearly unacceptable. The bias in the Tanaka is below 10% on two days, but this was achieved by averaging large positive and negative biases. The Lincoln has a negative bias of less than 10% on days 7-10; the nonparametric has a bias of less than 10% on days 6-10.

There is a good deal of evidence that sex and age influence catchability, so independent estimates for such categories should realistically be made whenever possible (Eberhardt 1969). Although males and females in this study did not differ significantly (P>.30) in their frequency of capture, the total population size was estimated by combining the separate estimates of the male and female populations. The combined estimates should be expected to be very close to the original field estimates (Table 2). The Tanaka shows a large discrepancy throughout all ten trapping periods, perhaps due to a large variability with small sample sizes. The combined estimates for the geometric give a slightly larger bias during the early trapping days. The estimates for the Lincoln, Schnabel, and Schumacher-Eschmeyer show a difference of less than 3.0 after day 4. The combined population estimates and the original field population estimates for the nonparametric are always exactly the same. This is because when the sexes are estimated separately, θ_ℓ is the same for the males and the females for each value of ℓ. Therefore, for each value of ℓ, $\frac{f_\ell}{\theta_\ell}$(males) + $\frac{f_\ell}{\theta_\ell}$ (females) = $\frac{f_\ell}{\theta_\ell}$ (males and females). And since the nonparametric estimate is the sum of the $\frac{f_\ell}{\theta_\ell}$ values, the overall combined estimate of population size is the same as the original field estimate. This is true even if the population is stratified.

Summary

Of the estimators evaluated, the nonparametric is recommended for estimating the size of trap-happy mice populations. Besides demonstrating a low sample bias and variance, it has the advantage of not being affected by population stratification.

The Mark-Recapture Simulation Model

In each of the three mark-recapture experiments (I, III, and IV), the animals were shown to be trap-happy and distributed in a random manner. The purpose of these tests was simply the selection of a learning theory model and a spatial pattern for the computer simulations. The variance of x and y were calculated and rho in the bivariate normal utilization distribution was assumed to be zero. A generalization could be made in the model to remove this restriction, giving the individuals the ability to possess different orientations of their major and minor axes. However, there seems to be little reason for removing this restriction (Table 3). The utility of removing it may also be of little value in practical simulations (Zarnoch 1976).

In previous studies, simulations with the mark-recapture model have been performed by choosing known parametric values for $p_{i,1}$ (the initial probability of capture) and α (the learning process). The problem existed of developing estimators of these parameters from field data. One method of estimation was adopted from the work of Bush and Mosteller (1955). They also provided a pair of equations for obtaining the simultaneous maximum likelihood estimates of α and $p_{i,1}$; these may be utilized in future work. In the method selected for this study, the field estimate of $p_{i,1}$ ($\bar{p}$ based on incomplete data) is always an upper bound. The value will tend to decrease each day as more unmarked animals are caught until every individual in the population has been caught at least once. The field estimates of α($\hat{\alpha}$ based on incomplete data) tend to remain fairly constant. However, when $\bar{p}$ reaches its minimum value, $\hat{\alpha}$ will necessarily increase because the mean number of non-recapture increases. Computer simulations with the incomplete and complete estimates had a similar average bias (days 5-10) for all five estimators (Table 9-11). Perhaps the lower values of both $\bar{p}$ and $\hat{\alpha}$ from the complete data on day 10 tend to cancel each other out (the animals have a lower initial probability of capture but an increased intensity of learning). More simulations are needed to verify this suggestion.

To validate the model developed by Zarnoch (1976), each experiment (I, III, and IV) was simulated ten times with the incomplete estimates. If the model is valid, the simulated data should provide approximately the same estimates as the field data when the true population is used in the simulations. It doesn't matter if both estimates are biased as long as they are not significantly different. Based on experience with both real and simulated data, Otis et al. (1978) gave some crude guidelines for estimation and testing techniques. Although in general the probabilities must be larger for smaller populations, they recommend that in no instance should N be less than 25 or average capture probabilities less than 0.10 when trapping small mammals for only a few occassions (say $\leq$10 trapping periods). The field data from this study meets those requirements.

The simulation nonparametric estimates based on a random spatial pattern tended to level off about day 7 at the entered population size. Thus, the average simulation values fall below the field estimates at the end of experiments I and IV. Otherwise, the two estimates of population size are in close agreement. The entered population, however, is the minimum number of animals known to be present in the enclosure. In experiment IV, for example, if the maximum field population size (39 instead of 36) was entered, the simulation estimates for days 6-10 would probably be much closer to the field estimates. It is also important to remember that the population estimates at each trapping period within any one mark-recapture experiment are correlated. If the 10% level of accuracy suggested by Roff (1973a) and Robson and Regier (1964) is again used instead of the 95% confidence limits, only two simulation estimates in experiment I (days 5 and 8), two in experiment III (days 3 and 7), and five in experiment IV (Days 2, 7, 8, 9, and 10) are unacceptable. All of the simulation estimates except day 2 in experiment IV are within 15% of the field estimate ("true value").

When the animals were placed in a fixed spatial pattern, the model simulations consistently gave negatively biased results. This is probably because the centers of activity used to place the animals were determined by averaging the trap coordinates of capture locations. As a result, the centers of activity of many animals were close to trap locations. Therefore, the animals were captured more often than expected providing an underestimation of the field estimates. The fixed spatial pattern may work well if a better method is used to calculate the center of activity.

Summary

The methods used to estimate $p_{i,1}$ and α seem acceptable, although future work may provide improvements. With these estimates, the mark-recapture simulation model of Zarnoch (1976) mimicked the field situations very closely. It should prove to be a useful tool for providing insights into decision-making alternatives in mark-recapture experiments. The magnitude of the bias could be evaluated, estimators compared, and an optimum number of trapping periods determined. It could also explore the need for periodic trap relocation when the variation in the probability of capturing animals is largely a function of trap location (Eberhardt 1969, Overton 1969, and Begon 1979). The model may prove to be valuable in the correction of field estimates by linear regression. This technique would yield improved estimates of the population size in mark-recapture experiments.

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LITERATURE CITED

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APPENDIX

EXPERIMENT I

Tag #	Sex	Trapping Period										Snap-Trapped
		1	2	3	4	5	6	7	8	9	10	
1006	M								X	X	X	
1007	M		X						X	X	X	
1008	F	X	X				X			X	X	
1009	F	X	X	X						X		X
1010	M		X									X
1011	M		X						X	X	X	
1012	F	X		X	X		X					X
1013	M	X	X	X	X						X	
1014	F	X		X					X	X	X	
1015	F	X										X
1016	M	X	X		X	X				X	X	
1017	F	X	X			X		X	X	X	X	
1018	F											X
1019	F	X	X	X	X		X	X	X	X	X	
1020	F							X			X	
1021	M	X		X	X	X	X		X	X	X	
1022	F	X	X									X*
1023	M				X							
1024	M								X			X
1025	M											X*
1026	F						X				X	
1027	F	X										X
1028	F											X
1029	F	X		X			X			X	X	
1030	F	X		X								X
1031	M		X	X			X			X	X	
1032	F				X							X
1033	F	X	X				X	X				X
1034	F										X	
1035	M	X	X	X	X		X	X	X	X	X	
1036	M			X								X
1037	F										X	
1039	M		X									X
1040	M											X
1041	M						X					X*
1042	F	X	X			X						X*
1043	F									X	X	
1044	F	X										X
1045	M								X	X	X	
1047	M							X			X	

X Captured
* Live-trapped during Experiment II

EXPERIMENT II

Tag #	Sex	Trapping Period										Snap-Trapped
		1	2	3	4	5	6	7	8	9	10	
1048	F	X	X		X	X	X	X	X	X	X	
1049	F	X	X	X								
1050	M	X	X	X	X	X		X		X	X	
1051	F	X		X			X	X		X	X	
1052	F		X				X		X		X	
1053	M	X								X	X	
1054	M	X	X		X		X	X	X	X	X	
1055	M	X		X	X	X	X			X		X
1056	F	X	X	X	X	X	X	X		X	X	
1057	F	X	X	X	X	X		X	X	X	X	
1058	F	X	X	X	X	X	X	X	X	X	X	
1059	F	X	X	X	X	X	X	X	X	X	X	
1060	M	X	X		X		X			X	X	
1061	M	X	X		X	X			X	X		X
1062	M	X	X	X		X			X		X	
1063	M	X					X	X			X	
1064	M				X		X			X	X	
1065	M		X			X		X	X		X	
1066	M		X	X		X				X	X	
1067	M	X	X	X				X	X	X	X	
1068	M			X		X				X	X	
1069	M	X	X	X	X						X	
1070	F	X	X					X	X	X	X	
1071	F	X	X			X	X	X		X	X	
1072	M	X	X		X	X	X	X	X	X	X	
1073	F	X	X	X	X	X	X	X	X	X	X	
1074	F	X	X	X	X	X	X	X	X	X	X	
1075	F	X	X	X		X	X	X	X	X		X
1076	M	X	X	X	X		X	X		X	X	
1077	F	X	X		X	X	X					X
1078	F	X		X						X	X	

X Captured

EXPERIMENT III

Tag #	Sex	Trapping Period										Snap-Trapped
		1	2	3	4	5	6	7	8	9	10	
1081	F					X	X					X*
1082	F			X		X	X		X	X	X	
1083	M								X	X	X	
1084	F	X			X				X			X
1085	M						X	X	X	X	X	
1086	M											X
1087	M											X
1088	F	X			X	X	X	X	X	X	X	
1091	M	X			X			X	X	X	X	
1092	F	X			X	X	X	X	X	X	X	
1093	M		X	X	X				X	X	X	
1094	F	X								X	X	
1095	M											
1096	M		X		X			X		X		X
1097	M				X	X		X	X	X	X	
1098	F									X	X	
1099	M	X	X	X	X	X	X	X	X	X	X	
1100	M										X	
1101	F	X			X		X	X	X	X		X
1103	F				X	X			X	X	X	
1104	F										X	
1105	M	X	X	X		X	X	X	X	X	X	
1106	M										X	
1107	M	X		X		X			X	X	X	
1108	F											X
1109	M							X	X	X	X	
1110	F		X									
1111	M	X						X	X	X	X	
1112	F									X		X
1113	M											X
1116	F			X		X			X	X	X	
1117	M								X	X	X	
1118	F		X	X			X				X	
1120	F					X		X	X		X	
1121	M		X			X	X	X	X	X	X	
1122	F				X			X		X	X	
1123	M	X										
1124	F				X	X		X	X	X	X	
1125	F				X	X	X	X	X	X	X	
1126	F				X							X

X Captured
* Live-trapped during experiment IV

EXPERIMENT IV

Tag #	Sex	Trapping Period										Snap-Trapped
		1	2	3	4	5	6	7	8	9	10	
1137	M		X									
1138	M	X	X			X			X	X	X	
1139	M	X	X				X					X
1140	F		X	X	X	X	X	X	X	X	X	
1141	M								X	X		
1142	F	X	X			X			X	X	X	
1143	F	X			X					X	X	
1144	M					X	X	X	X	X	X	
1145	M		X			X		X	X	X	X	
1146	M				X							
1147	M			X			X	X		X	X	
1148	M						X					X
1150	M		X	X				X				X
1151	M							X	X	X	X	
1152	M	X										X
1153	F							X	X	X	X	
1154	M		X	X		X		X	X	X	X	
1155	M										X	
1156	M	X	X	X		X		X	X		X	
1157	M					X	X	X		X	X	
1158	F	X		X		X	X		X	X	X	
1159	F	X	X		X					X		X
1160	F	X			X	X	X	X	X	X	X	
1161	F	X			X							X
1162	M						X		X		X	
1163	M								X	X	X	
1164	M											X
1165	M			X	X	X	X	X	X	X	X	
1166	F	X	X	X		X	X	X	X	X	X	
1167	F					X						X
1168	F		X		X	X		X	X	X	X	
1169	F		X				X					X
1170	F	X	X		X	X	X		X	X		X
1171	M		X					X		X	X	
1172	M				X						X	
1173	M											
1174	F											X
1175	M		X									X
1176	M						X	X	X	X	X	

X Captured