

**EVALUATION OF CAPTURE-RECAPTURE ESTIMATORS
USING A CYCLIC SNOWSHOE HARE POPULATION**

by

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ABSTRACT

Many theoretical capture-recapture estimation models have been introduced into applied field ecology in the last twenty years, but only a few of these models have been tested in field situations. The objective of this thesis was to evaluate capture-recapture estimators when applied to a cyclic snowshoe hare population in the Kluane Lake area in the Southern Yukon. The estimation models and model selection routine of program CAPTURE, and the Jolly-Seber open model were evaluated.

Two independent approaches were used to evaluate estimators: 1) Island populations of known size were used to determine estimator bias and study factors that affect hare capture probabilities, and 2) An individual-based spatial Monte Carlo simulation model was used to evaluate estimator robustness to sample biases caused by a cyclic snowshoe hare population.

Two islands were used for studies of estimator bias. Results from both islands suggest that the CAPTURE heterogeneity models M_h (jackknife), M_h (Chao), and M_{th} (time/heterogeneity) were approximately unbiased for the island population of hares. All other CAPTURE models displayed a negative bias. The program CAPTURE model selection routine picked models of different bias for each trapping period.

Island studies of variation in hare capture probabilities documented a strong relationship between hare movement patterns and capture probabilities on an individual and population level. The strong contribution of sampling factors such as trap placement, and time of sampling in the variation of hare capture probabilities was also documented.

A Monte Carlo simulation model was used to determine estimator robustness to trap saturation with increasing hare densities, uneven trap spacing, and other sample biases typical of a cyclic snowshoe hare population. All models except the jackknife heterogeneity (M_h) estimator showed increasing negative bias with increasing simulated hare density. The jackknife estimator was robust to biases caused by trap saturation, and showed an acceptable coefficient of variation. The program CAPTURE model selection routine performed poorly when selecting estimation models of different bias for each simulated hare density.

The results from the island studies and Monte Carlo simulation study were then compared to Kluane field data. Similar trends were evident in all the data sets.

This study concludes that the jackknife estimator (M_h) is the most robust to sampling variations in a cyclic snowshoe hare population. The poor performance of the program CAPTURE model selection routine was documented. Recommendations for future research are given.

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Chapter 1: General Introduction

Introduction

One of the most common techniques used in the study of small mammals is the estimation of abundance with capture-recapture techniques. In the past 20 years, a variety of estimation models based on complex statistical techniques have become available to biologists through microcomputer software packages such as CAPTURE (Otis et al. 1978) and JOLLY (Pollock et al. 1990). While these estimation models have created opportunities for more detailed and accurate estimates, they have also created the need for better sampling procedures and improved knowledge about the biological validity of assumptions made by estimation models (White et al. 1982; Begon, 1983).

The literature on capture-recapture methods is quite vast. Over 200 articles and 4 books have been produced on this subject in the last thirty years. Despite all this effort, only two papers test CAPTURE estimators with actual field data in which true parameter values are known (Hallet et al. 1991; Otis et al. 1978). Typically, the estimation models and model selection procedures for CAPTURE have been evaluated using capture probability distributions generated by Monte Carlo simulation. Monte Carlo simulation is a powerful technique to evaluate estimator robustness. However, it is difficult to evaluate accuracy with field data using this technique because capture probability distributions of animals are not known (Carothers, 1973). Davis and Winstead (1980) state "The failure of wildlife investigators to check population estimates against a known population is a deplorable situation". White(1992) suggests that innovative studies are needed to evaluate estimator accuracy in actual field situations.

The main objective of this thesis is to evaluate population estimators currently available to biologists for determining the abundance of snowshoe hare populations in the Kluane Lake area of the Yukon. For information about this project see Krebs et al. (1986). Because of the dynamic nature of this cyclic population estimation of abundance and model selection is a complex process. There are three specific objectives of this thesis: 1) evaluation of the accuracy of estimators on island populations of hares in which true population numbers are known, 2) evaluation of estimator robustness to variations in hare capture probabilities as a result of the hare cycle and, 3) re-evaluation of past trapping data from the Kluane project using information from previous chapters.

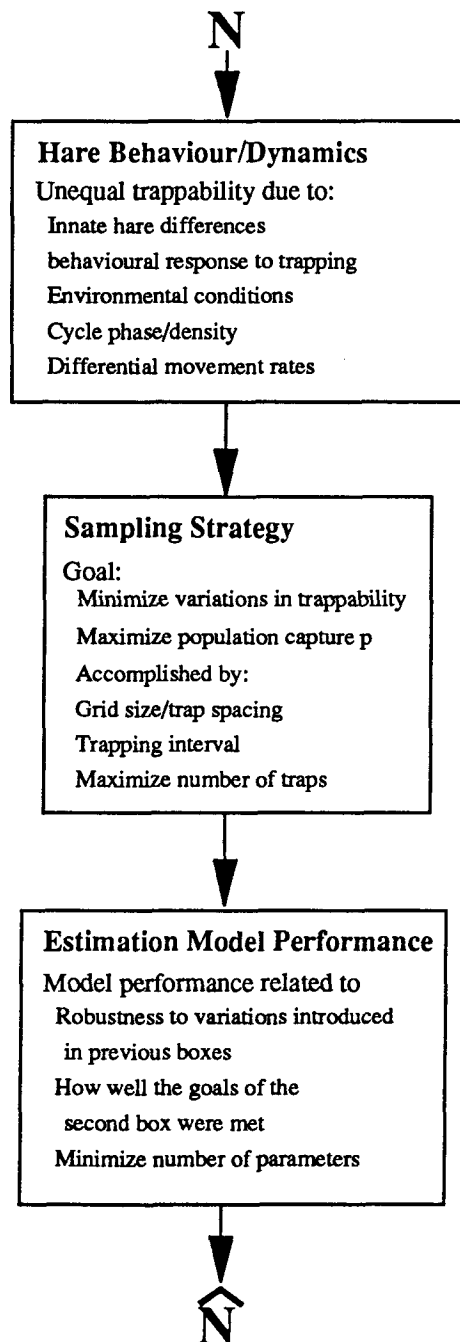
I will focus on estimation of animal abundance using estimation models within program CAPTURE and the general open model of Jolly-Seber. I will not address the estimation of survival rate or density in this thesis.

The problem of estimating snowshoe hare populations

Bias in population estimates is a consequence of unequal probabilities of capture of individual hares. When hares exhibit unequal probabilities of capture, a non-random sample of the population occurs. This leads to a negative bias with most capture-recapture estimators. Figure 1.1 summarizes the estimation process. I will first discuss factors that cause unequal probabilities of capture in snowshoe hare populations and then discuss models for estimation of population abundance.

Snowshoe hares exhibit unequal probability of capture (Krebs et al. 1986). Unequal probability can be dichotomized to two main factors (Cormack, 1966):

Figure 1.1. A graphical representation of the population estimation process using capture recapture methodology.



1) There is an innate distinct capture probability for each animal caused by biological factors. The population makes up a distribution of capture probabilities. This type of variation in capture probabilities is termed *heterogeneity* in program CAPTURE.

2) The probability of capture is based on prior capture experience of the animal. Animals change probability of capture depending on trapping experience. This type of variation is termed *behaviour* in program CAPTURE.

Eberhardt (1969) added a third factor;

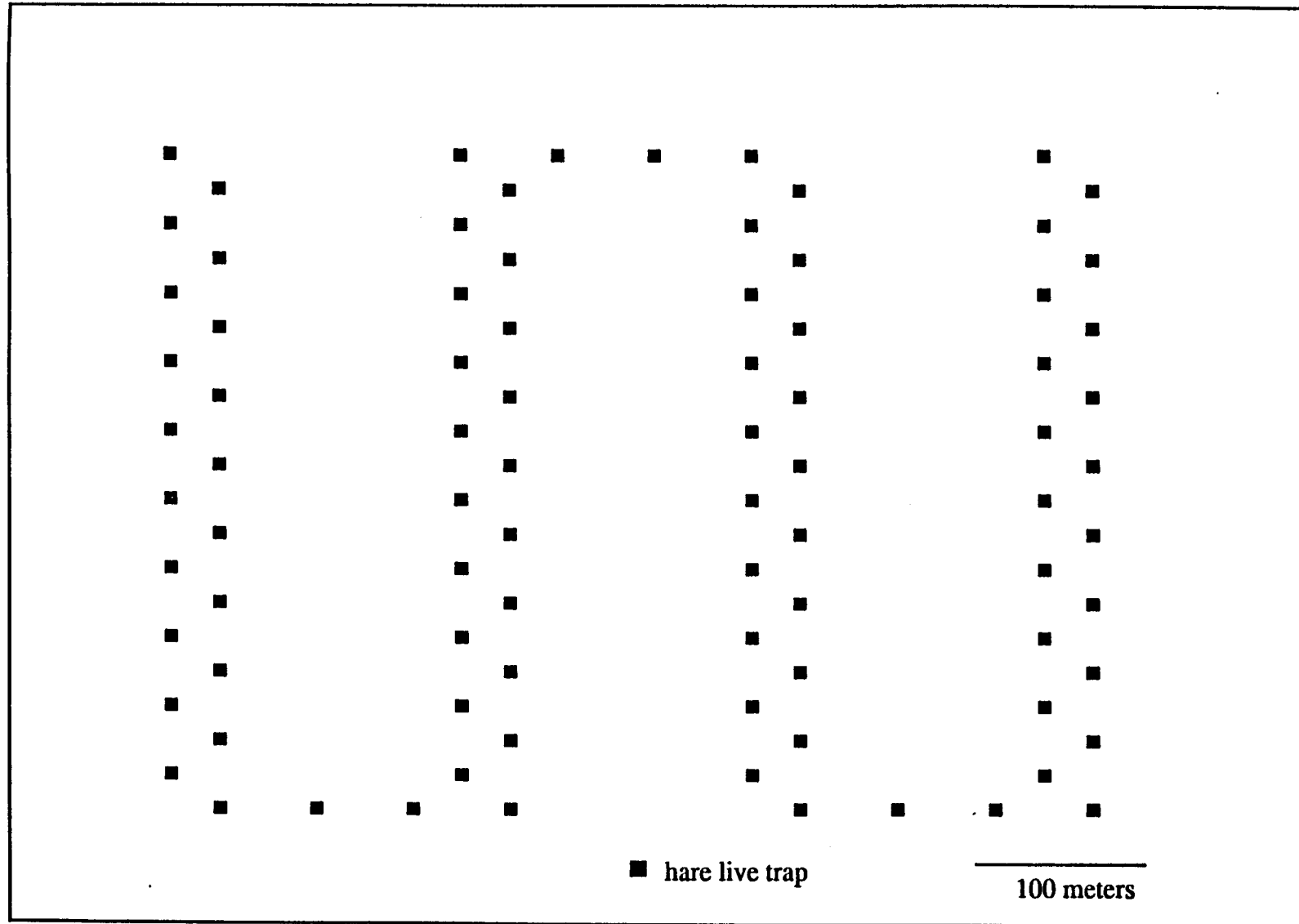
3) The capture probability depends on the relative opportunity to be caught. Capture probability is a function of the geographic locations of animals relative to traps.

The third factor pertains to how the hare population is sampled. Variations caused by sampling can be subdivided into sample error and sample bias error. Sample error relates to sample size and repeatability of a sample. Bias error relates to the randomness of the sample taken. In an ideal situation in which all animals in the population have equal access to empty traps, sample bias error would be caused mainly by individual variation in capture probabilities and behavioral response. This is rarely the case with field data, especially in the case of cyclic snowshoe hare populations.

Unequal access to traps may cause a high bias error in capture data. The typical Kluane live-trapping grid is composed of 86 traps spaced in an uneven four row pattern that covers 36 hectares (Figure 1.2). In this case an individual snowshoe hare's probability of capture is probably a function of where its home range is relative to the grid. The effect of uneven trap spacing may be very pronounced when hare densities are maximal and traps are saturated. At this time of the hare cycle, it is reported that hares may be trapped within minutes of traps being

Figure 1.2. The Kluane trapping grid design. Eighty six traps are spaced over 36 hectares.

Kluane grid setup



set (A.R.E. Sinclair, pers. comm.). A hare with a home range on the trap line has a much higher probability of being sampled than hares with home ranges between trap lines. The result is a sample with a high bias error which would be reflected as an increased heterogeneity of capture probabilities of individual hares.

In conclusion, hares exhibit unequal capture probabilities due to innate differences and previous trap experience. The population of hares makes up a capture probability distribution. Sampling factors such as trap spacing and sample size can cause further variations in hare capture probabilities. In the case of the hare cycle, sampling factors may be the main cause of unequal capture probabilities. It is essential to understand how sampling affects hare capture probabilities.

A review of estimation strategy

In capture recapture methodology, a model is a name given to a series of assumptions concerning the capture probabilities of the population being studied. For each model, a mathematical estimator of population size or related parameters is developed. The use of the term model in this case is different than the typical use of this term. The difference is a consequence of how the model is used. In capture-recapture studies, field data is put into a estimation model, and parameter estimates are produced. With a traditional model, such as a simulation model, parameters are put into the model to generate pseudo-data or specific predictions about the population being studied. This thesis mainly concerns estimation models.

An optimal estimation model should be accurate, precise, and robust. Bias, is a measure how close the estimate is to true parameter values, and is difficult to evaluate with normal field data in which true population sizes are not known. Precision is the repeatability of estimates

from a similar data set and has been evaluated mainly using Monte Carlo simulation. Robustness is a measure of how the estimator performs in terms of bias, even when the assumptions made about the capture probabilities are not true.

Therefore, an estimator should be able to account for or estimate variations in capture probabilities due to innate differences between animals, sample bias, and error. Intuitively, this could be done by building an estimator that estimates or accounts for most of the deviations that cause unequal probability of capture. However, a tradeoff exists between precision and accuracy. An estimation model that accounts for all possible variations within the data may have low bias, but will have low precision and be useless. This tradeoff between precision and accuracy is called the principle of parsimony. Simply stated, the precision of estimates decreases when more parameters are estimated. An optimal estimation model is not always the most unbiased, but the simplest model that explains capture probability variations within the data set.

Therefore, relying on highly sophisticated estimation models may not provide better inference if the data set has high sample bias and error (Lebreton et al. 1992). As shown in Figure 1.1, it is *essential* for a biologist to minimize variations introduced in the "Sampling strategy" box rather than rely on more sophisticated estimation models for reliable estimates (White et al. 1982).

A review of estimation models addressed in this thesis

This thesis will focus on the estimators in program CAPTURE (Otis et al. 1978). An analysis of the open Jolly-Seber model will also be included for comparison. These are the most commonly used estimation models for population estimation in field biology. The

modifications of the Jolly-Seber model used in programs JOLLYAGE (Pollock et al. 1990) and SURGE (Lebreton et al. 1991) will not be covered for they are mainly used in survival rate estimation. Estimation models can be dichotomized as open or closed based upon the assumptions made about the demography of the population being studied. With an open model such as the Jolly-Seber, emigration, immigration, deaths and births are allowed during the time the capture-recapture data is collected. In closed models, such as those found in program CAPTURE, no emigration, immigration, deaths, and births are allowed during the trapping period.

The Jolly-Seber model is the most widely used open model (Begon 1983). Simulation studies have shown that population estimates from this model are biased by unequal capture probabilities especially when the average population capture probability is below 0.5 (Gilbert, 1973). It is used mainly for population estimation when the assumption of population closure (and use of closed models) is not valid or for survival rate estimation in which it is more robust to violation of equal capture probabilities (Lebreton et al. 1992).

Closed models were developed to allow for relaxation of the assumption of equal capture probabilities. The assumption of closure provides a framework in which actual variations in capture probabilities can be addressed. Unlike open models, animals are trapped for a short duration of time (for example; 5 continuous trap nights) to minimize violation of the assumption of population closure.

Variation in capture probabilities can be subdivided to variation by time, behaviour, and heterogeneity. These sources of variation are the basis for program CAPTURE models (Table 1.1) (White et al. 1982). A comprehensive review of these models can be found in Otis et al.

Table 1: A review of estimation models implemented in program CAPTURE.
(Otis et al, 1978)

Model	Appropriate Estimator	Capture Probability Variation allowed:
M_0	Null (Otis et al, 1978)	None
M_h^*	Jackknife (Otis et al, 1978) (Chao,1989)	Heterogeniety: p varies individually, constant temporally
M_t^*	Darroch (1958) Chao (1989)	Time: p equal individually, but varies temporally
M_b	Zippin (1956)	Behaviour: p equal individually but changes equally for all individuals after capture
M_{tb}	Burnham (In press)	Time/Behaviour
M_{bh}^*	Generalized removal (Pollock, 1974) (Pollock and Otto, 1983)	Behaviour/Heterogeniety
M_{th}	Chao and Lee, (1991)	Time/Heterogeniety
M_{tbh}	None	Time/Behaviour Heterogeniety

*Two versions of this model are currently implemented following the works of Chao (1989).

(1978). More than one version of the heterogeneity, time, and behaviour/heterogeneity models are implemented. The assumptions of each model are described below:

M₀: Null Model The capture probabilities of all animals are assumed to be equal for the duration of the study.

M_h: Heterogeneity Model: Each animal is assumed to have an individual capture probability which is constant for the duration of the study. Individuals vary in this capture probability.

M_b: Behaviour Model: Every animal in the population has the same probability of capture which changes equally for each animal after it is caught.

M_t: Time Model: Every animal in the population has the same probability of capture for each trap night. However, this probability changes for the whole population each trap night.

M_{th}: Time/Heterogeneity Model: Assumptions of models M_t and M_h are allowed.

M_{bh}: Behaviour/Heterogeneity Model: Assumptions of models M_b and M_h are allowed.

M_{tb}: Time/Behaviour Model: Assumptions of models M_t and M_b are allowed.

M_{tbh}: Time/Behaviour/Heterogeneity Model: Assumptions of all models are allowed. No estimator has been found for this model.

Within the same trapping data set, variations due to heterogeneity, time, and behaviour probably can be found. It is not always obvious which factors are most dominant. For this reason the authors of program CAPTURE implemented a selection routine to choose the most appropriate model from a set of field data using a series of hierarchical series of chi-square hypothesis tests. In each test, the validity of a particular model is assessed by comparing the capture probability distribution of the data with a hypothetical distribution generated under the

particular model being tested.

As an example of how this routine works I will demonstrate the first of the eight hypothesis tests. The first test tests for heterogeneity of capture probabilities within the population. The null hypothesis is that there is no variation in capture probabilities and model M_0 is the appropriate model. The alternative hypothesis is that there is individual variation in capture probabilities and M_h is the appropriate model. The expected capture frequencies (f_j) for model M_0 are generated using the binomial formula where:

$$\hat{f}_j = \hat{N}_0 \binom{t}{j} p^j (1-p)^{t-j}$$

In this formula t is the number of trap nights, and j is the frequency of nights an animal was caught. N (estimated population number) and p (estimated population capture probability) are estimated under model M_0 . If H_0 is true then the test statistic (T) is approximately distributed as a chi-square random variable with $t-2$ degrees of freedom where:

$$T_1 = \sum_{j=1}^t \frac{(f_j - \hat{f}_j)^2}{\hat{f}_j}$$

This test determines whether observed capture frequencies can be explained by chance. If they can, then the observed distribution should fit a binomial distribution with independent trials. The other seven tests use a similar rationale with slightly more complicated test statistics. See Otis et al. (1978) for a more detailed discussion of these tests.

Many of the tests in the model selection routine are not independent. For instance, a test for time variation in capture probabilities may be influenced by a behavioral response within the population to trapping. An example of this would be if all the animals become

addicted to trapping ("trap happy") after first capture. The capture probability of the population would increase each successive night. This would be detected as time variation as well as a behavioral response. Determination of which model is most appropriate would be difficult if the researcher looked just at the hypothesis tests. To face this problem the authors of program CAPTURE have employed a discriminant function analysis in which the significance levels of the tests are compared and the appropriate model is selected (Otis et al. 1978).

The model selection procedure of program CAPTURE has been found to exhibit erroneous selection of models, especially with small populations that have low mean probabilities of capture (Menkins and Anderson, 1988). When population sizes are small, then the hypothesis tests employed lack power to reject the null hypothesis. This leads to type II errors and inappropriate model selection. Inappropriate model selection can be defined as selection of a model in which the assumptions of the model do not correspond to the capture probability variation in the data. An example of this would be selection of the null model (M_0) when individual hares in the population exhibit individual distinct capture probabilities and the heterogeneity model M_h is more appropriate. If an inappropriate model is selected, the resulting estimates have unknown bias and an unrealistically small or large variance (Otis et al. 1978).

While Monte Carlo simulation has been mainly used for such evaluation some field studies have shown similar results. One field study of opossums and raccoons (in which true parameter values were measured using radio telemetry) reported similar problems. In this case negatively-biased estimation models were usually selected (Hallet et al. 1991). Similar results were reported when data from penned cottontail rabbits (Eberhardt, 1969) were analyzed (Otis et al. 1978). In all these studies, low power of the hypothesis tests in the CAPTURE selection

routine was cited as the reason for inappropriate model selection.

The use of hypothesis tests to select sets of estimation models is fairly unique in the statistical literature. In most cases likelihood ratio tests are used to compare models. From these tests, parsimonious models are chosen using optimization equations such as the Akaike Information Criterion (Lebreton et al. 1992). For some of the models in program CAPTURE (such as the jackknife (M_h) estimator), likelihood ratio tests have not been developed precluding the use of this method (Otis et al. 1978).

To boost the power of the model selection routine in program CAPTURE a biologist may decide to increase the length of the trapping period. By doing this he or she is increasing sample size and power of each hypothesis test employed in the model selection routine. In doing this the assumption of population closure may be negated, and deleterious effects to the population may be caused by the trapping process. The effects of trapping on snowshoe hares are especially pronounced, since a hare spends an average of 8 hours in a trap during a trap night. Because of trap stress, the maximum length of a trapping period for snowshoe hares at Kluane is five days.

Optimal estimation models for cyclic snowshoe hare population

The cyclic snowshoe hare population at Kluane presents a challenging problem for estimation methodology. One of the principal uses of capture data is comparison of treatments and calculation of intrinsic rate of population increase. For these purposes, an estimation model that shows consistent relative bias throughout the snowshoe hare cycle is preferable over changing models that could show different biases with population size. However, if individual capture probabilities, as well as sample error and bias factors, change as a function of the cycle

as described above, then using a different model that fits each phase of the cycle may be more appropriate.

Techniques of estimator evaluation in this thesis

As described above, many sources of variation interact to cause unequal probabilities of capture within a population. Selection of appropriate models that account for capture probability variation also is problematic. It is also impossible to evaluate estimator accuracy using typical field data alone, since true population number is rarely known.

To obtain an evaluation of the estimation process it is essential to find means independent of the actual field data. Three separate techniques that are used in this thesis to evaluate estimation models and strategies. The techniques are: 1) Evaluation of estimator bias using island populations of hares of known size, 2) empirical studies of factors that affect hare capture probabilities, and 3) Monte Carlo simulation evaluation of estimator robustness to biases caused by the hare cycle. The conceptual basis for this approach is outlined in Figure 1.3.

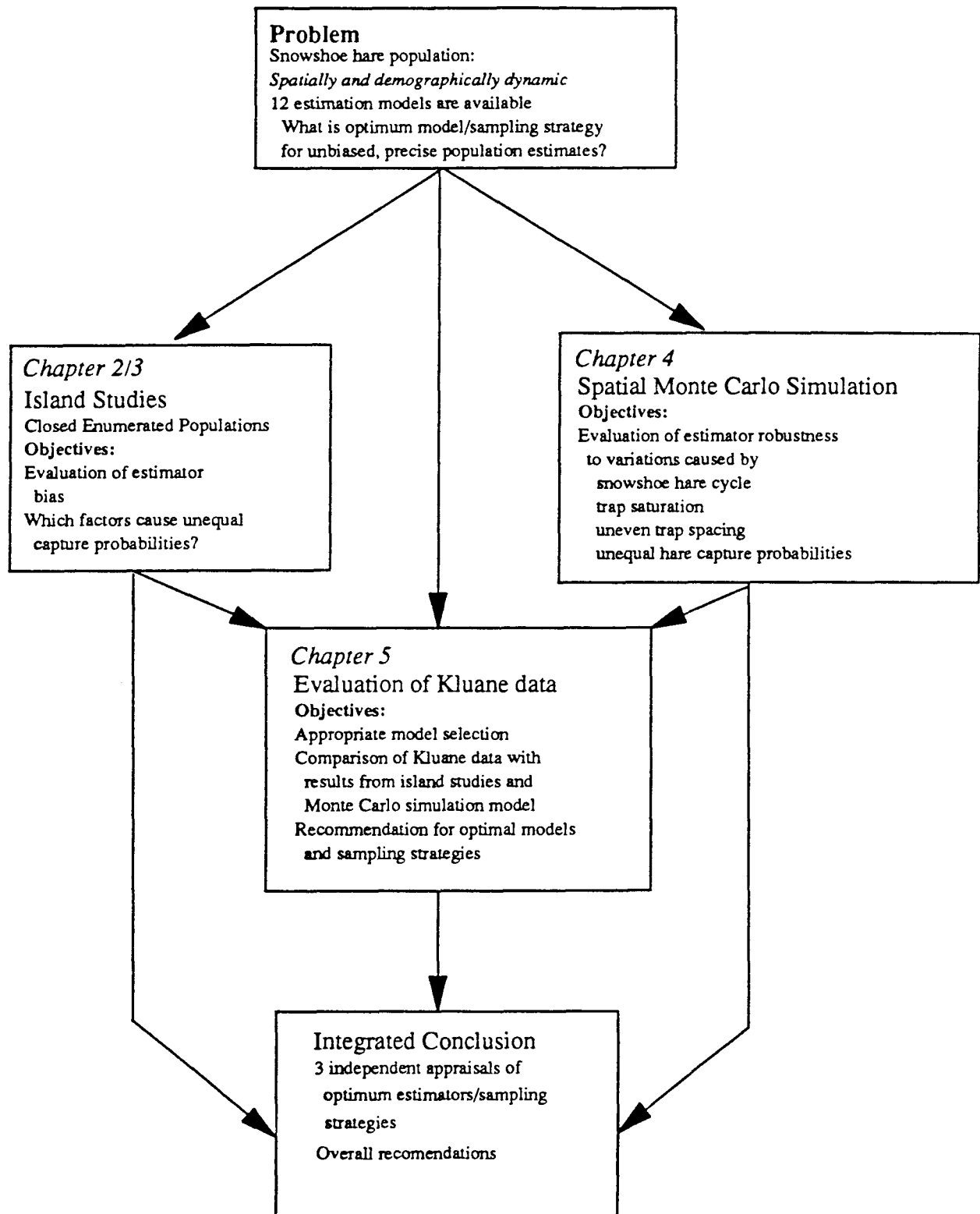
The second chapter of the thesis addresses accuracy of estimators. As described above, accuracy is very difficult to determine using only trapping data or Monte Carlo simulation. To study which estimator most accurately describes hare population numbers, two hare populations residing on large islands in the Kluane area were enumerated. Once populations were enumerated, periodic samples were undertaken, and then the estimated population sizes were compared for accuracy and precision. These results are discussed in Chapter 2.

The use of closed populations on islands also allowed insight into what innate, behavioural and sampling factors may cause differential capture probabilities. This study is discussed in Chapter 3.

Chapter 4 addresses estimator robustness when confronted with possible sample biases introduced by the snowshoe hare cycle. The main factors explored are bias due to trap saturation, and unequal trap spacing. I modified a spatial Monte Carlo simulation model first used by Zarnoch (1976) and later modified by Wilson (1983). Parameter values for the model were taken from Kluane trapping data and the results of the capture probability experiments in Chapter 3. The main objective of this simulation model was to create capture frequencies that could result from sampling biases caused by the snowshoe hare cycle. From this data, it could be determined what estimators are most robust to these sampling biases. Also, estimator precision, as well as the effectiveness of the CAPTURE model selection routine could be evaluated.

Chapter 5 examines the historical Kluane trapping data. Recommendations for appropriate estimation models and sampling techniques for the Kluane project are made.

Figure 1.3 A conceptual diagram of thesis chapters. Each chapter is an independent appraisal of estimation methodology.



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Chapter 2: Evaluation of Estimator Bias Using Island Populations of Known Size

Introduction

Over 200 manuscripts in the last twenty years have addressed the theoretical properties of population estimation models. Of these manuscripts, only two have attempted to compare the new models in program CAPTURE in actual field situations in which independent estimates of population size were available. In all other cases, evaluation of these models has been by Monte Carlo simulation in which a range of capture probability distributions are tested to determine robustness. Because the distributions of capture probabilities are seldom known in the field, Monte Carlo simulation has limited utility for the field biologist studying dynamic populations (Carothers, 1973). White and Nichols (1992) suggested that more studies in which true parameter values are known are needed in development of valid estimation models.

The two field studies of CAPTURE models have shown varying utility of some of the complex estimation models. One study was of a penned population of 135 cottontail rabbits (Edwards and Eberhardt, 1969), subsequently analyzed by Otis et al.(1978), in which none of the models performed adequately due to low population capture probabilities. Hallet et al. (1991) compared CAPTURE and Jolly-Seber models to an independent radio-telemetry estimator for a large population of opossums and raccoons. In this case, program CAPTURE appeared to show a substantial negative bias, and the authors recommended a combination of radio telemetry and the Jolly-Seber models as the optimum estimation methodology. From these studies it is evident that field appraisal of estimation models and factors that influence capture probabilities are needed to aid field biologists and statisticians in appraisal of new

theoretical methods.

In this chapter I present studies of estimator bias using island populations of known size. Knowledge of true population number at risk of capture is essential to a field evaluation of estimator bias. If a population of known number exists, and periodic samples are taken and estimates are made, an empirical determination of estimator bias is possible. Knowledge of true population number is impossible in most mainland trapping areas where animals disperse in and out of the grid area. Lack of closure between trapping periods is very noticeable with most Kluane data. For instance, 60 percent of snowshoe hares in the Kluane area were live-trapped once and never trapped again from 1976-1984.

Design of island studies

For this study I utilized entire island areas in which the trap coverage was even and continuous in all habitats, making the calculation of actual population at risk of capture feasible. Every animal was at risk of capture to some degree, and more valid inference could be gained into estimator bias, as well as differences in individual hare capture probabilities. A combination of radio telemetry and intensive sampling at the beginning and end of the study allowed me to track the population using a total enumeration method independent of the sampling process. The main objectives of the island studies are:

- 1) Evaluation of estimation model bias with closed island populations in which the true population number could be determined. Samples with minimal sample error and bias were taken with the idea that if an estimator fails to perform well in this "ideal" situation, its performance in a much more dynamic mainland situation will be unreliable.
- 2) Study of causes in differences in individual hare capture probabilities utilizing a

closed situation in which all hare fates are known. The relationship of movement rates, home range size and condition of hares to capture probabilities was addressed. The results of this analysis are discussed in Chapter 3.

There are assumptions inherent in studies of island populations. One is that the population behaves similarly to mainland populations. Collection of home range and other descriptive data allows a partial testing of this assumption.

Methods

Island descriptions

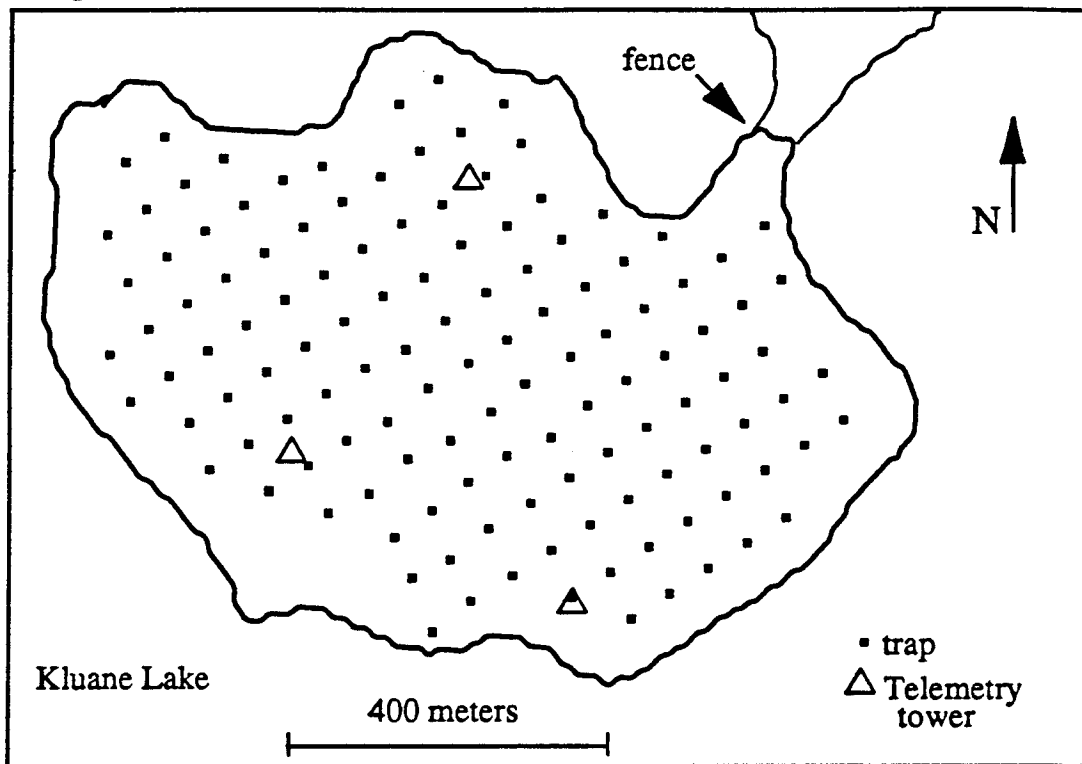
One goal of this study was evaluation of estimators in a natural, closed situation. To accomplish this, Jacquot and Dezadeash Islands in the Kluane area were used. These two islands were large enough (48 and 40 ha.) to support substantial hare populations, but still logistically possible to enumerate. By using two islands I could replicate experiments. Both islands were sampled from May to August 1991. Jacquot Island was also sampled from March to June 1992.

Jacquot Island

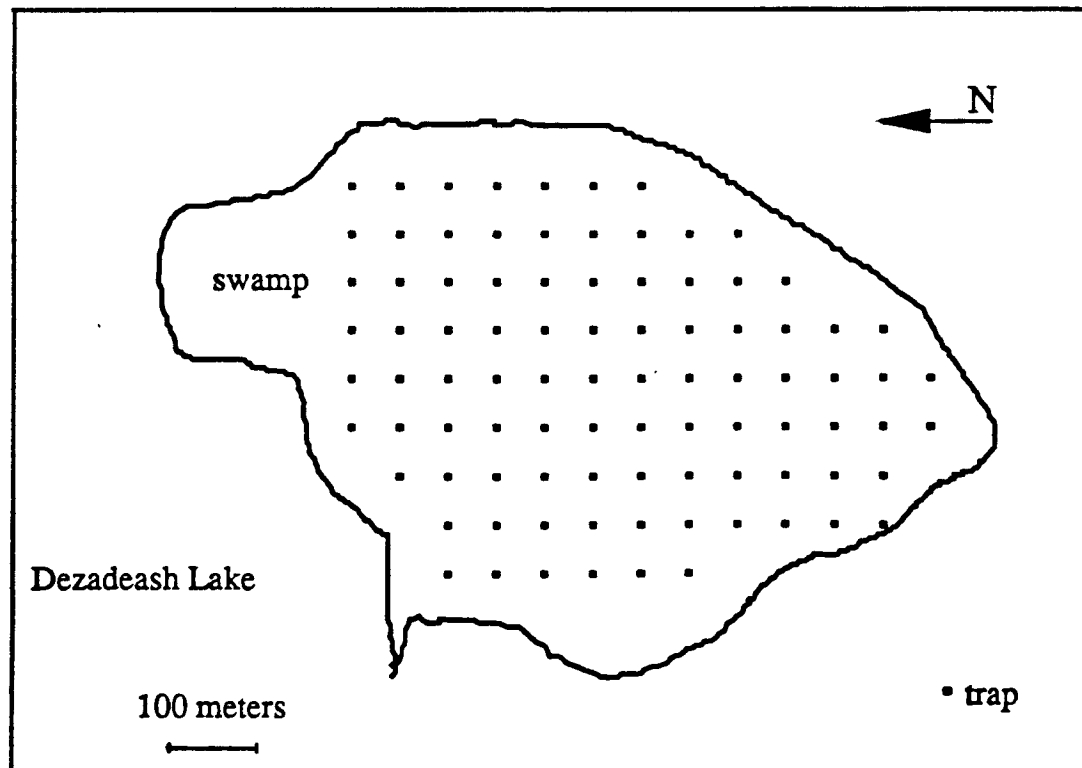
Jacquot Island is located in Kluane Lake, 6 kilometres northeast of Destruction Bay. The closest point of land is along the Talbot Arm, approximately 4 kilometres to the East. The southern peninsula of the island (Figure 2.1) was used for the study. This area could be easily separated from the main part of the island by a fence to ensure population closure in terms of movement. The southern grid is a mosaic of spruce (*Picea glauca*), willow (*Salix* spp.), and birch (*Betula glandulosa*) groves. The main habitat areas are slightly elevated from the lake by

Figure 2.1. Jacquot and Dezadeash Islands. Jacquot Island (48 ha) with "full island" traps stations and telemetry tower locations. Island areas not covered by trap stations are cliffs, or rocky shoreline. Traps were 55 meters apart. A fence with traps in it controlled emigration from the southern island. Dezadeash Island (40ha) with trap stations. The northern end was a swamp and was not surveyed. The traps were spaced 55 meters apart.

Jacquot Island



Dezadeash Island



bluffs. Access was by boat in summer, and car, ATV motorcycle, foot, or cross country ski across the ice in winter.

A grid composed of 240 trap stations spaced 40 meters apart across the southern peninsula of Jacquot Island (Figure 2.1) was initially surveyed. This trap spacing allowed for uniform and intensive initial sampling needed to enumerate the population. After the intensive sampling period, two sampling schemes were employed.

A "full island" sample on Jacquot Island consisted of 120 traps spaced 55 meters apart trapped for five nights. This represented the maximal logistical effort possible to trap the entire island area in one night. The data from this effort were used for estimator evaluation and empirical determination of the population capture probability distribution.

A secondary smaller grid scheme was employed by Todd Zimmerling in which 160 traps (40 meter spacing) in a 10 by 15 uniform grid were trapped. The data were utilized for continuous enumeration of the population and estimator evaluation. A Kluane mainland live trap grid design (see Chapter 4) was also trapped for five nights to study how uneven trap spacing affects hare capture frequencies in the data.

Dezadeash Island

Dezadeash Island (61 N, 137 W) is located approximately 70 kilometres south of Haines Junction, Yukon. It lies approximately 800 meters east of the western shore of Dezadeash Lake. The island consists of a mosaic of willow (*Salix* spp.), and open white spruce (*Picea glauca*). The island has minimal topographic relief. Access was by canoe from the western shore of Dezadeash Lake.

A grid encompassing 75 percent of the island area was surveyed on Dezadeash Island.

The northern end of Dezadeash consists of swampland in which summer hare habitation was minimal and was not surveyed. Traps were initially placed every 30 meters to allow for an initial intensive sample of the population for enumeration. After this initial period, a "full island" grid of 100 traps spaced 55 meters apart was trapped.

Surveying and trapping methods

Surveying was conducted by hand-held Silva compass with a sighting mirror and a 60 meter measuring tape. Cross checks were applied for every other line surveyed to insure accurate trap spacing. Lines were surveyed from one shoreline until the next shoreline was reached ensuring even spatial coverage across entire island areas. In this way, all animals that lived on the island were equally exposed to the live traps.

Hares were tagged with metal and plastic orange eartags to allow for sight confirmation of whether an animal was marked. Weight and right hind foot skeletal measurements were taken for use in condition index calculations. On Jacquot Island, animals were also radio collared for survival/movement monitoring. Animals which were less trappable were targeted for radio collars. At the end of the summer field season, animals were again exposed to an intensive trapping effort to account for all hare fates. Traps were baited with alfalfa cubes and apples.

A five day trapping period was used which is similar to Kluane project. Trapping was stopped for at least two days during a sampling period to minimize any deleterious effects on the population. Traps were set only in periods of stable weather conditions to minimize capture probability variation and adverse effects on the population.

Data from each sampling period were pooled for use with the Jolly-Seber estimator. The full open model implemented in program JOLLY (Pollock et al. 1990) was used for estimates.

Population enumeration

Enumeration of the trappable population was a primary objective of this study. This number is based on the number of animals known to be alive during a given trapping period as determined by the radio-collared population (regardless of whether they were trapped) and any additional animals caught during the given trapping period or subsequent trapping periods. At the end of the field season the population was trapped intensively to capture the entire marked population. If a hare was not caught at the end of the field season it was assumed that it died just after the last time it was trapped. In this case, the hare would only be included as part of the enumerated estimate until the date it was last trapped.

This technique is similar to the minimum-number-known-alive estimator (Krebs 1966) which is negatively biased (Pollock et al. 1990) when capture probabilities are low. The intensive sampling effort and complete closure of the island maximized overall capture probabilities, and minimized any negative bias of this method. It should also be noted, that due to this study design, the enumeration of this study is not strictly equivalent to MNA estimates. In a typical study, animals that had not been caught in the last trapping period would not be "targeted" for capture at the end of a study. Also, radio-collared animals that were not trapped in a given trapping period would not be included as part of the population estimate.

There is a chance that a portion of the hare population was untrappable and was never caught. This possibility was tested by having secondary visual markers on each animal, and having approximately 40 percent of the population always radio-collared on Jacquot Island. In the case of an untrappable segment, the enumerated estimate could be considered to be a lower bound for the actual true population number and it would be expected that a valid estimator

should match this number or exceed it.

To validate the technique of enumeration another estimate of population size was employed using the subpopulation of radio-collared animals (Hallet et al. 1991). The RADIO population estimate is calculated by first obtaining the capture probability of the radio-collared population:

$$\hat{p} = \frac{m'_i}{n'_i}$$

In this case, n'_i is the number of radio collared animals in the population and m'_i is the number of radio collared animals caught in trapping period i . To get an independent estimate of population size the following formula is used:

$$\hat{N} = \frac{n_i}{\hat{p}_i}$$

In this equation, n_i is the total number of animals (radio collared or non radio collared) caught during trapping period i . Variances are found as follows:

$$var(\hat{p}_i) = \frac{\hat{p}_i(1-\hat{p}_i)}{n_i}$$

$$var(\hat{N}_i) = (n_i/\hat{p}_i)^2 [var(\hat{p}_i)/(\hat{p}_i)^2]$$

This estimator assumes that radioed animals exhibit behaviour similar to non-radio collared animals. Also, it assumes that animals that are captured and radio collared exhibit behaviour similar to animals that have never been caught. The RADIO estimator is considered

conservative with respect to actual true population number (Hallet et al. 1991).

Evaluation of population estimators

Comparative bias of an estimator was calculated as the estimated value subtracted from the enumerated value divided by the enumerated value. Due to mortality of hares, the adult population of each island decreased through the summer. As a result, the actual number of hares on each island was different for each trapping period. Using comparative bias as a means of comparing estimators scaled the bias of estimators during each period to the actual number of animals present. This simplified the display and interpretation of estimator bias. Because the enumerated value is considered to be a lower bound on population number, a good estimator should exhibit zero to a positive comparative bias.

Results

Enumeration studies

Jacquot Island

On Jacquot Island a starting population of 56 adult hares was tagged and there were 950 recaptures of individuals throughout the field season which lasted from May to August 1991 (Figure 2.2). The full island grid was sampled twice (trapping periods 2 and 4) and slightly smaller grid area (which covered 70 percent of the island) three times (trapping periods 1,3, and 5) due to logistical constraints and to accommodate a simultaneous study by Todd Zimmerling. When the smaller grid was used, the enumerated estimate was adjusted for animals not on the grid as determined by previous trapping history. After the first month of trapping no untagged hares were caught (Figure 2.3). The average daily population capture probability was 0.41 (std. dev.=.05, n=5). No hares without orange eartags were observed, but poor visibility during the

Figure 2.2. A summary of the sample sizes on Jacquot during the 1991 and 1992 field seasons. The RADIO estimate has standard error bars. Mean nightly capture probabilities calculated with formula from Otis et al (1978) mentioned in the text. Initial trap dates were the first night of a 5 day trapping period.

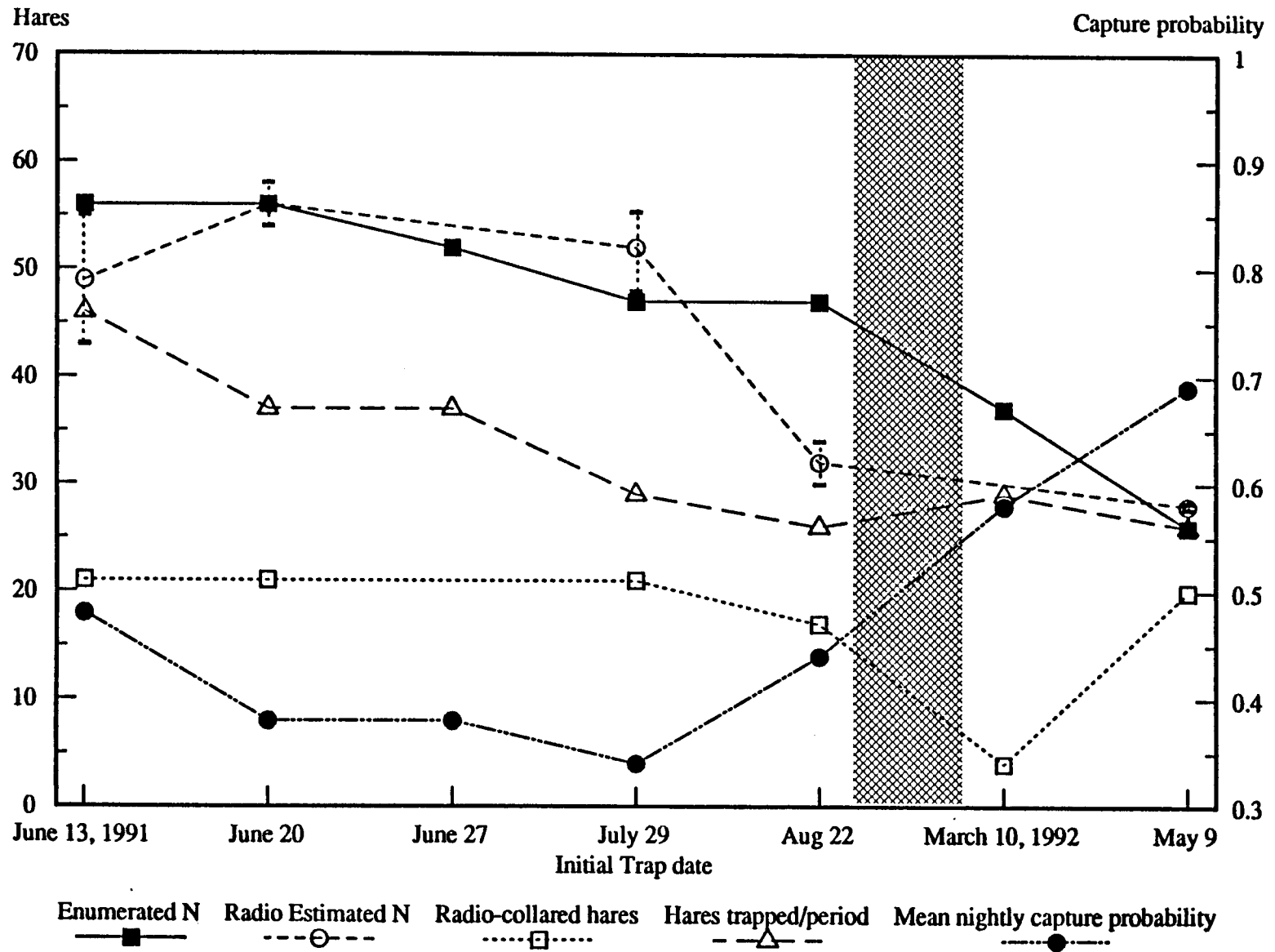
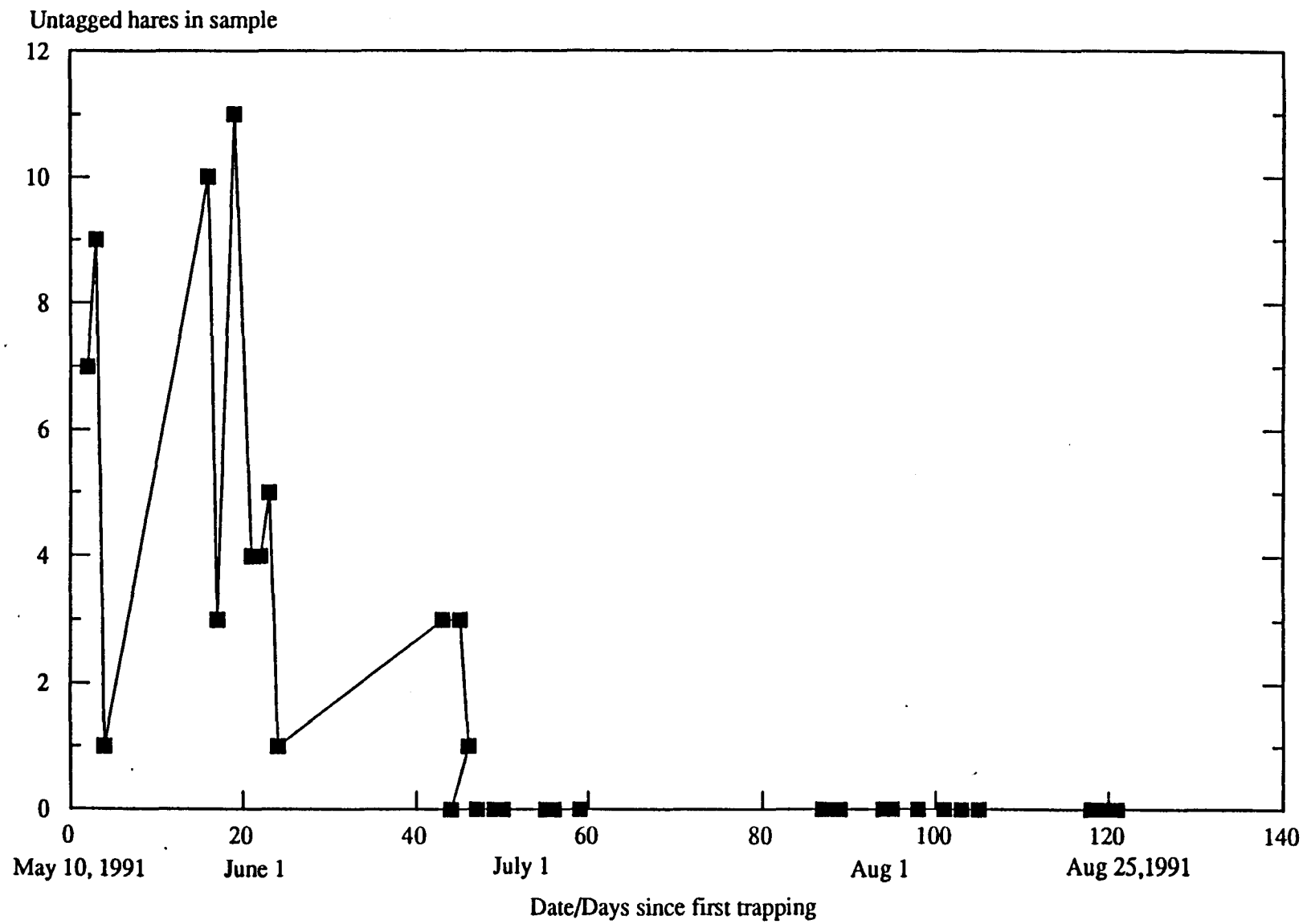


Figure 2.3. The number of new hares in a sample during the 1991 Jacquot Island field season. Each square represents a trapping effort.



summer months limited the effectiveness of this method. High rainfall limited sampling during most of July 1991.

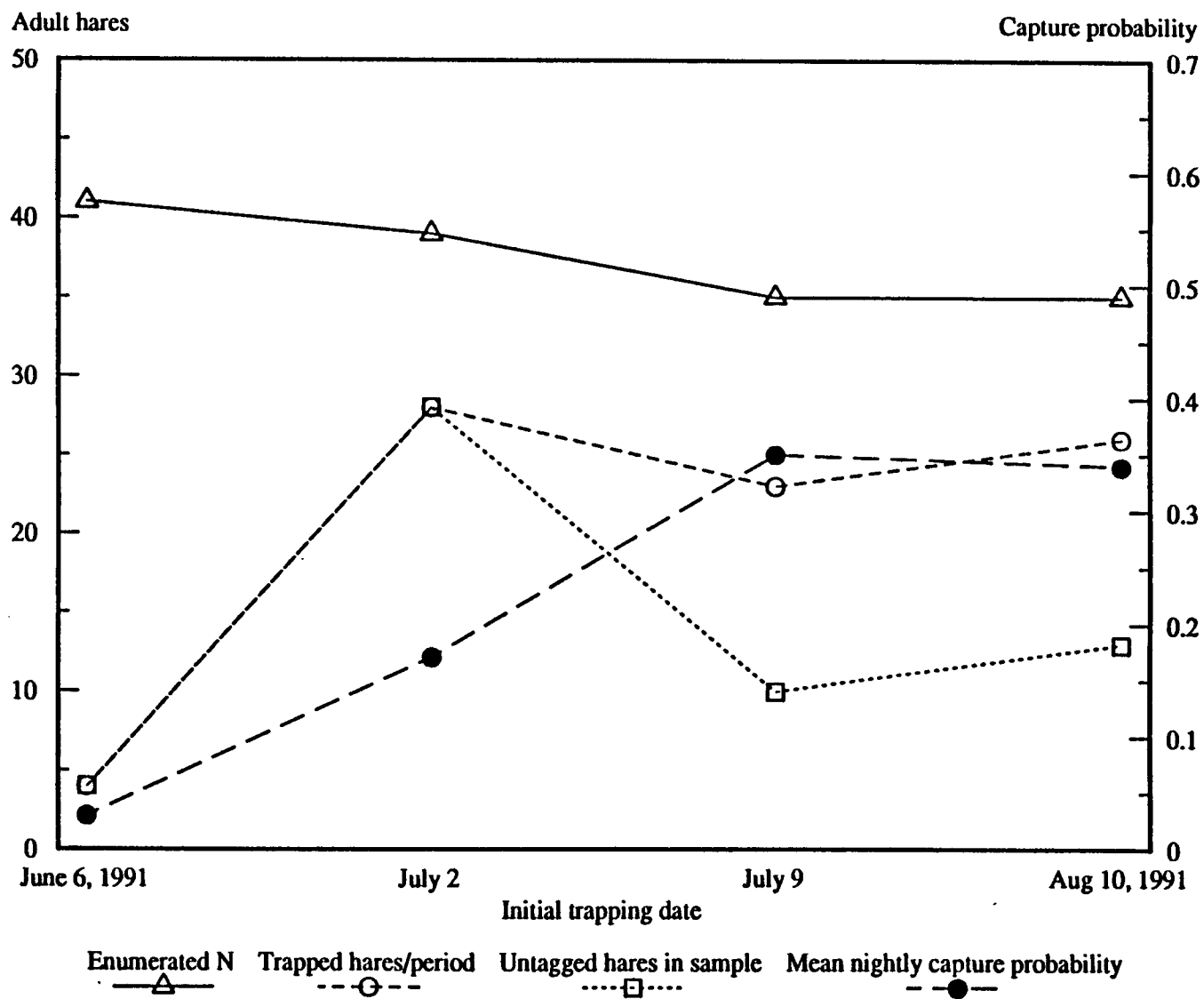
Because this is a natural population, births and deaths did occur. As a result, the enumerated adult population decreased as the summer progressed (Figure 2.2). During the 1991 field season, 28-day survival rates on Jacquot Island for radioed hares averaged 0.94 (0.87-0.99 95% confidence limits, $n=47$) using the Kaplan-Meier method (Pollock et al. 1989). The juvenile hare population increased during the 1991 field season but this segment of the population was ignored in the estimation of adult population size. At the end of the 1991 field season 6 adult hares had disappeared and these individuals were not included in the enumerated adult population number after the dates they were last trapped.

Jacquot Island was also sampled in March and May 1992 (trapping periods 6 and 7). During this time a starting population of 37 hares was captured 417 times. During the 1992 field season, mortality was high (Kaplan-Meier $s=0.76$ per 28 days, 0.5-0.89 95% confidence limits, $n=24$). The mean nightly capture probability was .63 (std. dev.=.04, $n=2$) (Figure 2.3). Substantial mortality occurred during April, and the population was reduced to 26 individuals. During this time 20 radio collars were used to keep track of hare fates.

Dezadeash Island

Four 5 day trapping periods were conducted on Dezadeash Island during the 1991 field season (June-August), and 41 individual hares were enumerated. Unlike Jacquot, new animals appeared in all four samples (Figure 2.4). The mean nightly capture probability of the population was 0.22 (std. dev.=.07, $n=4$). Radios were not used on the island so an estimate of survivability was gained from the Jolly-Seber model which was 0.92 (std err=.092). At the

Figure 2.4. A summary of sample sizes on Dezadeash Island during the 1991 field season. No RADIO estimate was possible due to lack of radio collars. Initial trapping date was the first night of a trapping period. Mean nightly capture probabilities were calculated with the formula from Otis et al (1978).



end of the summer, 5 hares had disappeared and were not included in the enumerated population number after the dates they were last trapped.

Validation of the enumeration technique

The RADIO estimates and the enumeration values of the Jacquot Island hare population were correlated ($r=.79, p=.1, n=5$), and 4/5 of enumeration values were within one standard error of the RADIO estimates (Figure 2.2). The RADIO estimates are considered to be conservative of actual population size, and Hallet et al.(1991) recommend that a valid estimator should at least exceed them.

Estimator Performance

General results

The CAPTURE models showed similar characteristics for both islands. In each case, models M_0 , M_b , M_t , $M_t(\text{Chao})$, M_{bh} , $M_{bh}(\text{Pollock})$, and M_{th} showed a negative bias relative to the enumeration estimate. Models M_h , $M_h(\text{Chao})$, and M_{th} showed a positive bias (Figures 2.5, 2.6 and table 2.1). The program CAPTURE model selection routine picked different models for each trapping occasion. The models picked by program CAPTURE showed an overall negative bias.

The Jolly-Seber model showed a slightly negative bias on Dezadeash Island and a positive bias on Jacquot Island. The low number of estimates available from this model (estimates of first and last trapping periods are not possible) made the evaluation of this model difficult.

Precision of an estimator can be indexed by the standard deviation of repeated bias estimates relative to the enumerated value (Table 1). This is similar to the straightness of the

given estimator line on Figures 2.5 and 2.6. In the case of Jacquot Island, models M_h , and M_{th} showed the largest standard deviations.

The precision of estimators on Dezadeash was highly influenced by the negative bias of all estimators during the first trapping period. After the first period estimators showed similar precision, with the exception of the two M_{bh} models, and the CAPTURE selected models, which exhibited high standard deviations.

The confidence interval coverage was fairly consistent for all the estimators except the M_{bh} models which fell outside the enumerated values in at least 50% of the trapping periods (Table 1). The width of confidence intervals was quite model dependent. The M_h (Chao), and M_{th} models all had quite large confidence intervals which could make interpretation of these estimates with field data difficult.

No estimator gave unbiased results when capture probability was below 0.1, which corresponds with the simulation results of Otis et al. (1978). Except for the first trapping period on Dezadeash Island, capture probabilities were above 0.35, which is the recommended sample size needed for populations less than 100 for use with estimation models (White et al. 1982).

During the 1992 spring field season on Jacquot Island all estimators produced nearly identical estimates of population. This was due to the high capture probabilities of all individuals in the population ($p=0.63$).

Sampling factors

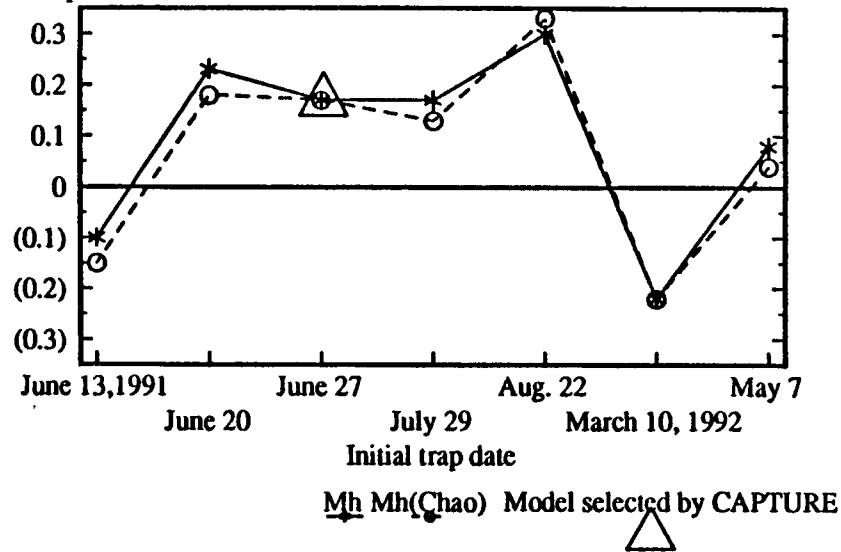
One 5 day trapping period in which the trap layout was similar to the Kluane mainland trapping grid was undertaken in July 1991 on Jacquot Island. All estimators showed a mean 11 percent negative bias compared with the grid sample taken the next week. The mean capture

Figure 2.5. Estimator comparative bias by trapping period on Jacquot Island. Comparative bias is the estimated value minus the enumerated value divided by the enumerated value. Models selected by program CAPTURE for a particular trapping period are enclosed by a large triangle.

Jacquot Island Estimator Bias 1991-92

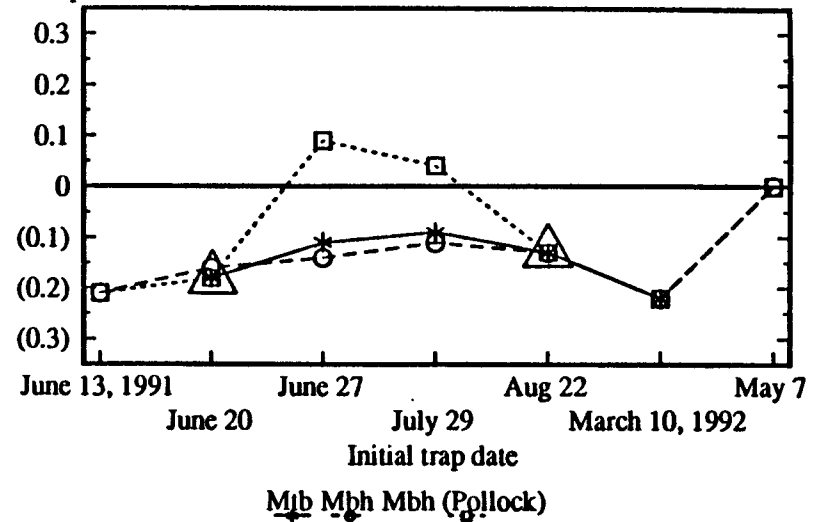
Heterogeneity Models

Comparative bias



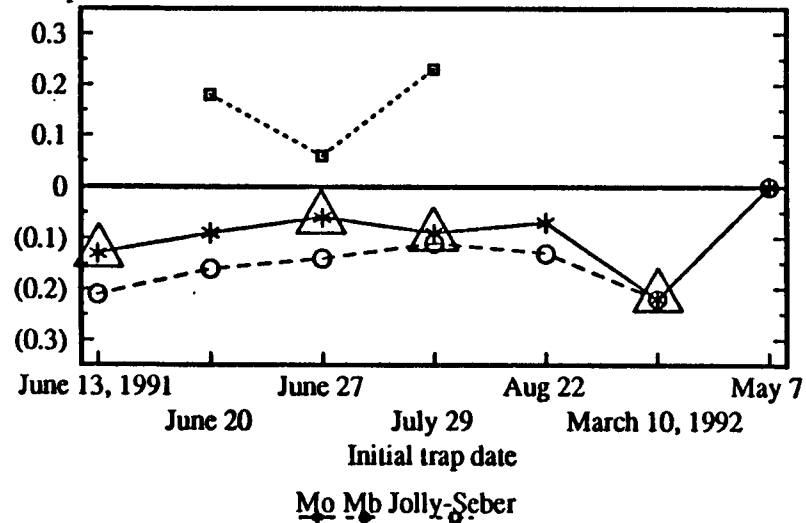
Other Models

Comparative bias



Null, Behaviour, and Jolly-Seber Models

Comparative bias



Time and Time/Heterogeneity Models

Comparative bias

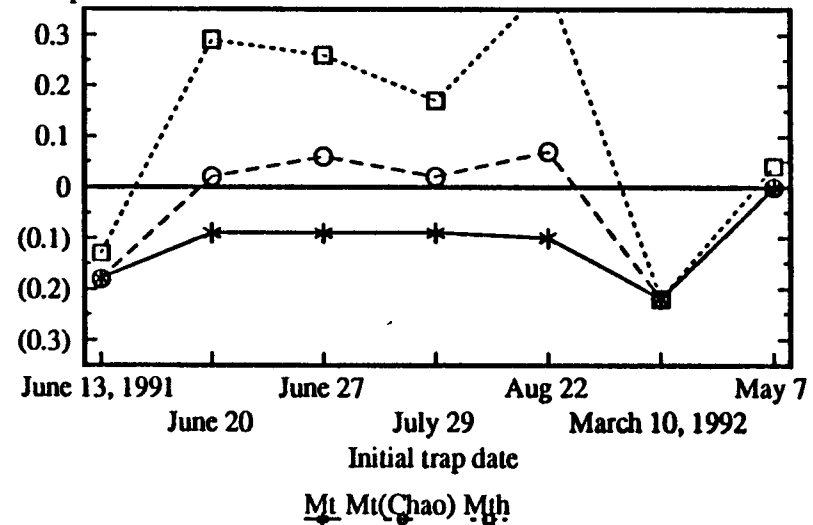
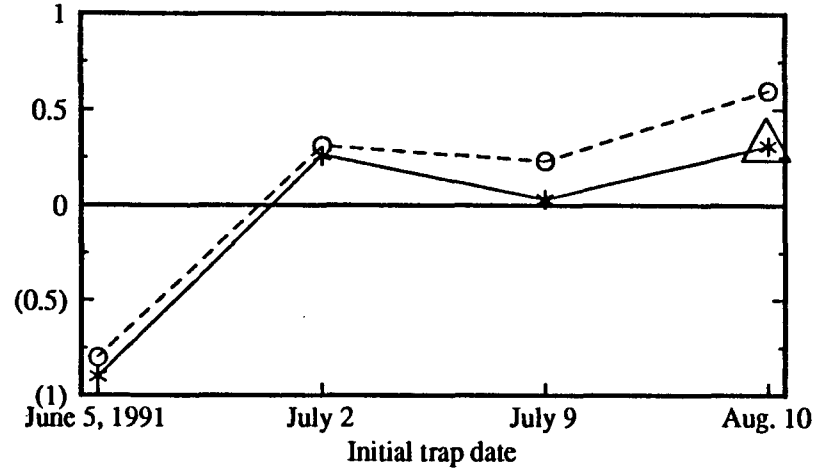


Figure 2.6. Estimator comparative bias by trapping period on Dezadeash Island. Comparative bias is the estimated value minus the enumerated value divided by the enumerated value. Models selected by program CAPTURE for a particular trapping period are enclosed by a large triangle.

Dezadeash Island Estimator Bias 1991

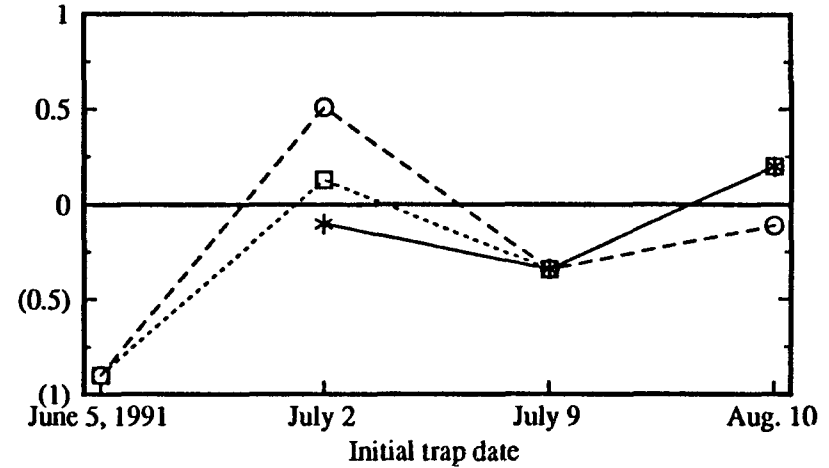
Heterogeneity Models

Comparative bias



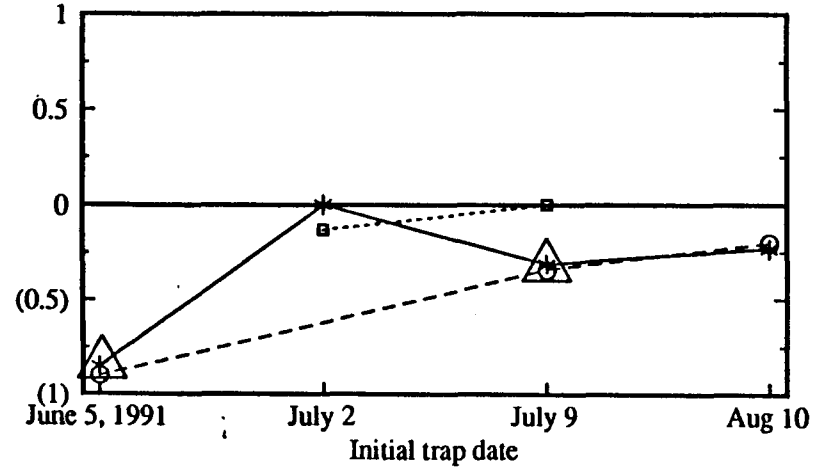
Other Models

Comparative bias



Null, Behaviour, and Jolly-Seber Models

Comparative bias



Time and Time/Heterogeneity Models

Comparative bias

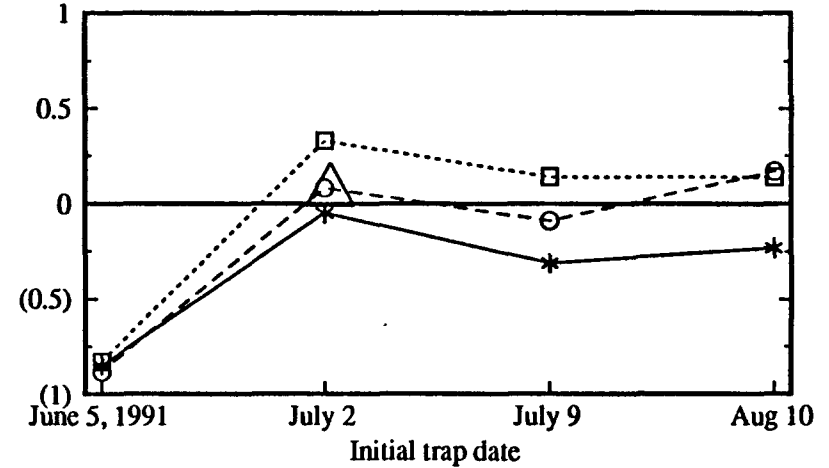


Table 2.1. Mean comparative bias of estimators for Jacquot and Dezadeash Island for the 1991 and 1992 field seasons. Comparative bias is the estimated value minus the enumerated value divided by the enumerated value. The 95% confidence interval coverage is the number of times the enumerated value was in the estimator's confidence interval. CAPTURE estimate is the bias of the models selected by CAPTURE for each trapping period (Bias was averaged in cases where CAPTURE picked more than one model) Sample sizes are n=4 for Dezadeash and n=7 for Jacquot.

Jacquot Island					
Model	Com. Bias	Std. Dev	95% CI Coverage		Ave. CI Width
			In	Out	
M_o	-0.09	0.06	6	1	8.7
M_b	-0.13	0.07	3	4	6.5
M_h	0.09	0.18	5	1	20.4
$M_h(\text{Chao})$	0.06	0.19	6	0	29.6
M_t	-0.10	0.07	4	2	7.0
$M_t(\text{Chao})$	-0.03	0.11	6	1	17.1
M_{bh}	-0.13	0.07	3	4	6.0
$M_{bh}(\text{Pollock})$	-0.08	0.12	3	4	8.1
M_{tb}	-0.14	0.05	-	-	-
M_{th}	0.11	0.22	5	1	33.9
CAPTURE	-0.07	0.12	9	5	11.3
Jolly-Seber	0.15	0.09	3	0	8.2

Dezadeash Island					
Model	Com. Bias	Std. Dev	95% CI Coverage		Ave. CI Width
			In	Out	
M_o	-0.34	0.36	1	3	15.3
M_b	-0.48	0.37	1	2	5.0
M_h	-0.07	0.56	3	1	28.7
$M_h(\text{Chao})$	0.08	0.61	4	0	81.7
M_t	-0.36	0.34	1	3	11.0
$M_t(\text{Chao})$	-0.17	0.47	3	1	17.5
M_{bh}	-0.21	0.58	2	2	6.0
$M_{bh}(\text{Pollock})$	-0.22	0.50	2	2	19.5
M_{tb}	-0.08	0.27	1	0	22.6
M_{th}	-0.05	0.52	3	1	46.5
CAPTURE	-0.11	0.48	5	2	47.4
Jolly-Seber	-0.06	0.09	2	0	33.0

probability was 0.25 as compared to 0.34 for a comparable grid sample. The frequencies of capture for the Kluane mainland trapping grid were significantly different from binomial distribution (chi-square=5.742, df=1, p=.01) implying inequality of capture probabilities within the population. The comparable grid sample did not vary significantly from a binomial distribution (chi-square=1.961, p=.1614, df=1). Both of these tests had low power, due to small sample sizes, and the results should be used only in terms of comparison between the grid and non-uniform trap spacing design. The estimators most robust to this possible sample bias are M_{th} and $M_h(\text{Chao})$ which displayed a +13% and -.05% bias.

Discussion

Validity of island studies

Population closure

A key assumption of the island studies is that the hare population is completely closed and all emigration, immigration, death and births are accounted for in the analysis. This assumption makes total enumeration of the island possible.

Births occurred on both islands during both field seasons. Juvenile hares could be easily recognized by their smaller size. The juvenile population was not considered in evaluation of estimators. A possible trap saturation effect occurred when juveniles filled traps, which could have caused increased heterogeneity of adult capture probabilities and a lowering of the population capture probability. During the 1992 field season on Jacquot Island trapping was stopped before juveniles entered the trappable population.

The most pronounced source of non-closure was mortality of hares due to predation and other causes. Survival was fairly high on Jacquot and Dezadeash during the summer of 1991.

During the 1992 field season, survival was low on Jacquot. The death of individuals was accounted for by constant adjustment of the enumerated population number. Dates of trapping for estimate analyses were always conducted in short time intervals to assure closure within trapping periods.

Dispersal from the island was impossible during the 1991 field season when water surrounded the island. During the 1992 season, one radio-collared animal dispersed from the island to the mainland area near the Talbot Arm across the ice of Kluane Lake. I skied around the island on the ice in search of tracks of any other dispersing or immigrating hares, and found none. If a hare dispersed, and was not caught for the rest of the season, it was not included in the enumerated count. I assumed that no hares arrived from the mainland or north end of the island.

Validity of comparison with mainland trapping grids

The island studies could be considered to be a simplification of a more dynamic system found on the Kluane mainland grids. Because movement is constrained on the island there may be differences in movement patterns, animal interactions, that could cause different trap behaviour than would occur in the mainland populations. One comparison of island and mainland hares is their home range sizes. If home range sizes are similar it can be generally assumed that hare spatial use between islands and mainland populations is similar. The mean home range size of snowshoe hares on Jacquot Island was 7.16 (std. dev=3.0, n=13) hectares, which is similar to mainland populations (David Hik, pers. comm). Further comparison of mainland and island hare populations is presented in Chapter 5.

The sampling scheme on the island was different from that used on the Kluane hare grids. The trap density was higher (120 traps/40 hectares) as compared to 86 traps/36 hectares. Theoretically, the main effect of a higher trap density is a lowering of the sample error or variance (Skalski and Robson, 1992). In this case, the island samples are more precise and more repeatable than a mainland sample. The advantage of the more precise island samples is that they allow a clearer comparison of estimators, as well as a more precise calculation of individual animal capture probabilities.

The trap layout on the islands was also different than mainland grids. The effect of different trap layouts was investigated by trapping a grid similar to the Kluane mainland grid layout. A general increase in heterogeneity of capture probabilities was noted (see results). Unfortunately, time constraints prevented replication of this comparison. The effect of uneven trap spacing on hare capture probabilities and estimates is explored further in Chapters 3 and 4.

CAPTURE estimator performance

Evaluation of estimators in this study was somewhat difficult due to the small number of replicates. The logistics of lake travel as well as inclement weather precluded getting more samples. However, on both islands estimators showed similar biases, and even though sample sizes are small, inference still can be made regarding optimal estimation models.

The examination of estimator bias is the most relevant result from the island studies. Estimator precision, which is the variance of the estimate around the true population value can also be determined. However, this attribute can also be addressed more powerfully with Monte Carlo Simulation where more replicates are possible.

I will now discuss the performance of each of the models of program CAPTURE in regards to bias. This discussion will focus on which estimators exhibited acceptable performance.

Non-heterogeneity estimators(M_0, M_{th}, M_b)

The non-heterogeneity estimators in program CAPTURE all showed an overall negative bias on both islands. One cause of this could be heterogeneity of capture probabilities. Otis et al. (1978) documented negative bias of all non-heterogeneity class estimators when heterogeneity was present within the population. Hallet et al. (1991) reported similar results with a study of opossums and raccoons.

The Jackknife Estimator (M_b)

The jackknife estimator was one of the least biased estimators for both Dezadeash and Jacquot Islands. It is considered by Otis et al. (1978) to be the most robust of the CAPTURE estimators to departures from the assumption of equal capture probabilities. It is recommended for occasions in which a large number of recaptures are present as in the case of this study. It should be noted that the performance characteristics of this model have been shown to change with decreasing capture probabilities. To test the usefulness of this model with lower capture probabilities a simulation approach will be used (Chapter 4).

The confidence intervals of the jackknife estimator were quite large. Otis et al. (1978) suggests that the confidence intervals of this estimator are only reliable when the majority of the population is trapped.

Chao's M_0 , M_{th} , and M_b

Models M_0 (Chao) and M_b (Chao) were developed after simulation results suggested that

the traditional M_h and M_l estimators showed negative biases when population capture probabilities were low (Chao 1989). Simulation results suggest that the Chao estimators are best when used with data of low capture probabilities, but biased when capture probabilities are high. They also have the largest variance of any estimators.

On both islands, the heterogeneity model M_h (Chao) showed a positive bias but also showed the highest standard deviations, and confidence interval widths. On Dezadeash Island, which was characterized by lower capture probabilities, it was the only estimator that showed an overall positive bias, and complete confidence interval coverage. However, because of the large standard deviations associated with estimates, use of this model is preferable only when capture probabilities are low.

On both islands the time model (M_l (Chao)) showed less bias than the traditional Darroch estimator. However, it was still negatively biased, possibly due to heterogeneity of capture probabilities in the hare population.

The time/heterogeneity model M_{lh} showed acceptable performance in terms of bias. It also showed a large standard deviations, which may suggest a lack of precision in estimates. Because it is estimating more parameters than other models a lack of precision is to be expected.

Program CAPTURE model selection routine

The program CAPTURE model selection routine picked negatively biased models for 3/4 and 5/7 of the trapping periods on Dezadeash and Jacquot Islands respectively. The general trend in results suggests that the heterogeneity class models were the least biased. However, heterogeneity models were only picked 2 out of 5 times on Jacquot Island and 1 out of 4 times

on Dezadeash Island. The negatively biased null model (M_0) was picked 3 out of 5 times on Jacquot and 3 out of 4 times on Dezadeash Island. From these results it can be surmised that the model selection routine is picking models of *different* bias for each trapping period. This again reflects the low power of the selection routine as documented in simulation studies by Menkins and Anderson (1988) and Otis et al. (1978). Unless capture probabilities are very high, or many trapping periods are employed, the model selection routine lacks power to select models of similar bias.

The Jolly-Seber model

The Jolly-Seber model displayed a bias comparable to many of the CAPTURE models. Most simulation results show a negative bias of this estimator when heterogeneity of capture probabilities are present. A positive bias is also possible when a trap happy segment of the population exists (Gilbert 1973).

One reason for the moderate bias of this model was that the mean Jolly Seber capture probability was .68 for Jacquot and .57 for Dezadeash (from the Jolly Seber capture probability formula). The Jolly Seber formula calculates capture probabilities for animals for the whole trapping period whereas the CAPTURE probabilities are for an individual trap night. When capture probabilities are above .5, Gilbert (1973) found that bias due to heterogeneity with the Jolly-Seber model was minimal. Unfortunately, in mainland studies average capture probability is below .5 frequently and the unbiased performance of this model cannot be expected.

Conclusion

The objective of the island studies was to evaluate estimation model bias in populations of known size. From this work, I found the heterogeneity class models, and the Jolly-Seber

model to be the least biased estimators of the island hare populations. The model selection routine of program CAPTURE picked models of different bias for each trapping period on both islands. Time of sampling plays a key role in estimator accuracy. I consider this the first step in estimator evaluation. To evaluate estimator performance in less ideal circumstances, a Monte Carlo simulation approach will be used (Chapter 4).

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Chapter 3: Empirical Studies of Factors Affecting Hare Capture Probabilities

Introduction

I present studies pertaining to hare capture probabilities in this chapter. Bias in population estimates is directly linked to unequal probabilities of capture between animals. Precision of population estimates is related to the mean capture probability of the population being trapped. Snowshoe hares exhibit unequal probabilities of capture (Krebs et al. 1986). However, very little is known about what individual attributes of hares may cause them to exhibit unequal capture probabilities. This information is essential in defining the link between biological causes of unequal capture probability, the sampling process, and estimator performance.

The main objective of this empirical study of capture probabilities is to detect general attributes of individuals, and sampling factors which could cause hares to exhibit unequal probabilities of capture on an individual and population level. The results of these tests are used to define key parameters for the Monte Carlo simulation model introduced in Chapter 4.

Hypotheses addressed

Otis et al. (1978) suggests that variation in capture probabilities can be classified into three factors; *heterogeneity*, *time*, and *behaviour*. These sources of variation provide a framework in which hypothesis concerning capture probabilities are addressed. I will propose the hypotheses addressed in this study in terms of these factors.

Heterogeneity variation relates to individual differences in animal's initial probability of capture. This type of variation can be caused by innate differences between animals or the way the population is sampled. Knowledge of the role that sampling plays in causing heterogeneity of hare probabilities of capture is essential in modelling grids with uneven trap spacing such as the Kluane trapping grid. Of particular interest in modelling is whether hares seek out traps or encounter them randomly. Most simulation evaluations of trapping grids have assumed that each animal on the trapping grid traverses the landscape, and encounter traps in a similar fashion (Skalski and Robson, 1992). The assumption of similar trap encounter rates among individual animals is probably biologically unrealistic, for snowshoe hares exhibit individual differences in movement rates and distances traversed in a given night. (D. Hik pers. comm.). It seems plausible that the distance which a hare traverses will affect its trap encounter rate and subsequent probability of capture. In this study the hypothesis that active hares should encounter more traps and display higher probabilities of capture than sedentary hares is tested. I was also interested in the area in which a hare was most vulnerable to trapping. More specifically, I tested if hares could be trapped outside of their core home range areas. I also investigated the effect of individual animal attributes, such as condition on capture probabilities.

Time variation relates to change in the mean capture probability of the population. I investigated the effect of forage availability, season of the year, and the presence of predators on trapping grids on mean population capture probabilities.

Behavioural variation is defined as further change in an animal's capture probability caused by learned experience with traps. Behavioral variation is very difficult to test in a field setting. Some general trends in behavioral variation are reported.

Conceptual base for study

The assumption that every individual on a given trapping grid has equal opportunity to be caught is essential to determine what factors affect hare capture probabilities. If this assumption is valid, empirical capture probabilities of hares can be calculated and compared to individual animal attributes. To minimize violation of this assumption each individual should have equal access to traps regardless of what habitat, or area their home range is in. The assumption of equal access of each hare to traps is not satisfied in most mainland trapping areas where animals disperse in and out of the trapping grid area. It would be difficult to tell if individuals were avoiding traps or had travelled off the grid and were not in risk of being trapped.

To study hare capture probabilities I utilized entire island areas in which the trap coverage was even in all habitat areas. This study was integrated with the empirical studies of estimator bias described in Chapter 2. Every animal was at risk of capture to some degree, and I could investigate differences in individual hare capture probabilities. During the radio-telemetry study, the number of traps outnumbered the population of hares by a four to one, thus minimizing potential biases associated with trap saturation and competition for traps.

Methods

As discussed in Chapter 2, Jacquot and Dezadeash Islands were trapped periodically to test estimators and to study hare capture probabilities. The "full island" trapping grids on the islands covered the full surface in an uniform pattern from shore to shore.

Factors which cause unequal hare capture probabilities within a trapping session were observed in two ways: 1) By correlating differences (heterogeneity) in individual capture probabilities with individual animal attributes, and 2) by measuring changes in the mean capture probability of the whole population. These changes in capture probability, which are usually termed time variation, were examined in relation to changes in the biology of the population and outside factors. Behavioral variation was studied by studied on an observational basis.

In this section I will first introduce the general conceptual basis and design of tests to detect trends in individual and population variation of capture probabilities. I will then detail the radio-telemetry, condition index, capture probability indexes, and trapping techniques used.

Factors affecting individual hare capture probabilities

It has been suggested that individual hares exhibit differential movement patterns (D. Hik, pers comm.). I hypothesise that the way in which a hare traverses its home range in a trap night should affect its trap encounter rate and its resulting capture probability. More specifically, animals that traverse large areas should encounter more traps and exhibit higher capture probabilities. Hares that are more sedentary should exhibit lower capture probabilities. To study differences in individual hare movement patterns an intensive radio-telemetry study was conducted in which radio-collared hares were tracked from 2100 to 0200 hours for ten nights from April to May 1992. During this time, movement indices were recorded and compared with capture probabilities as indexed by capture frequency in the full island sample.

In addition to studying movement patterns I was interested in the effect of hare condition on capture probabilities. If animal condition is related to capture probabilities, then food or stress may be partly what causes an animal to "risk" entering a live trap. I hypothesize that

animals in good condition should be less willing to be trapped than animals in poor condition. If condition is plotted against capture probability no animals in high condition should exhibit high capture probabilities. In addition, animals in low condition should not exhibit low capture probabilities.

Factors affecting individual differences in capture probabilities discussed previously relate to variation in probabilities caused by innate biological differences between animals. I was also interested in the role of sampling in causing variation of capture probabilities. Of particular interest was the effect of uneven trap spacing on individual hare capture probabilities. Hares seem to show preferences to certain traps within their home range. It seems reasonable that a hare would be trapped most often in the core area of its home range, because it is most active and present in this area, and would encounter this set of traps most often. This hypothesis was easily tested by comparing the size of a hare home range to the area in which traps were used. To quantify the trapping area a hare is usually trapped in I calculated an animal's "trapping range" treating the location of each trap used as a point. The trapping range was calculated using the minimum convex polygon method, which calculates the area defined by a polygon drawn from the outermost points within an area. This area was then compared to 95%, 85%, and successively smaller sizes of each hare home range using a paired t-test until a non-significant difference between the two areas was found. The largest percentage home range area that corresponded (non-significantly) to the trapping range was found to be the 75% home range area (see results). This area is termed the "core trapping range" and is used in the test described next.

If a hare is also attracted to the traps, then if given the opportunity, it should be able to be caught in traps outside of its core trapping range that are still within its home range. To test if hares could be trapped outside of their core trapping range ten nighttime "trapping trials" were conducted in which two lines of twenty traps spaced 40 meters apart were set at 2000 hours on a given night. The lines of traps set intersected different parts of each radio-collared hare's core trapping range which could be indexed by the number of traps included within this range. From the time the traps were set to 0200 hours radio-collared hare movements relative to the traps were recorded to allow observation of hare movement patterns. At 0200 hours traps were checked, and trapped animal numbers were recorded.

Sixteen hares were tracked during the trapping trials. All had at least one of the set traps within their 95% home range. Of the 16, 5 had no traps within their core trapping range. From trapping records of previous full island samples it was determined that these 5 hares had not previously used any of the 20 set traps either. I was interested if any of the 5 animals with would be trapped on the line of set traps. By using radio-telemetry I could test if the hares encountered the set traps, and chose not to be trapped or whether they never encountered the set traps. If hares are attracted to traps and can be trapped outside of their core trapping range area, then it would be expected that they would change their normal trapping patterns and be trapped in one of the 20 set traps.

Factors affecting population capture probabilities

It has been noticed that the population capture probabilities change for snowshoe hares with season (A.R.E. Sinclair, pers. comm). This is usually termed time variation. Because my field season went from early spring to late summer I could document whether capture

probabilities change during this time, and study some of the possible causes of these changes. Factors that affect hare population capture probabilities I investigated were; (1) mean changes in hare condition due to seasonal changes in vegetation and forage availability, and (2) the presence of predators on the trapping grid. If population capture probabilities are related to these causes, mechanisms which actually cause the changes in capture probabilities should be present also. A plausible mechanism for changes in mean population capture probabilities is changes in mean population movement patterns.

This relationship between mean population capture probabilities and population movement rates was observed on a nightly, and seasonal basis. On a nightly basis, times of peak animal capture were recorded using trap timers (discussed below) during each full island trap night. Movement indexes of animals were recorded using radio-telemetry techniques (discussed below) to find peak activity times. If population capture probability is related to movement rates, peak time of animal capture should relate to peak times of animal movement.

On a seasonal basis, mean nightly capture probabilities were related to mean nightly movement rates. Mean nightly movement rates were recorded using radio-telemetry movement monitoring sessions in April and May of 1992. Mean nightly capture probabilities were measured by the percentage of the whole population of hares caught on a given full island trap night. Factors that could cause changes in movement patterns of hares were monitored throughout the field season. These factors were changes in vegetation, and presence of predators on the trapping grid.

General Techniques

This section details the field and analysis techniques used to investigate the hypotheses proposed above.

Trapping grids

A "full island" sample on Jacquot Island consisted of 120 traps spaced 55 meters apart trapped periodically during the spring and summer of 1991 and 1992. A similar procedure was used on Dezadeash Island in 1991. The data from these efforts were used for calculation of population capture probabilities. The methods of trapping, and surveying of Jacquot Island are discussed in more detail in Chapter 2.

Calculation of individual hare capture probabilities

Capture probabilities of individual hares were calculated using individual animal's capture frequencies. The capture probability of an individual was estimated by the number of times trapped divided by the number of full island trap nights. In the case of Jacquot Island, there were eleven full island trap nights between March and May of 1992. Any animals that died before the seventh full island trapping occasion in mid-May were eliminated from the analysis to avoid biased probability calculations.

Mean population capture probabilities

Mean population capture probabilities were calculated using a modification of the following formula from Otis et al. (1978):

$$\bar{p} = \frac{n}{tN}$$

In this equation n is the total number of captures for a trapping period, t is the trapping period length, and N is the enumerated population number (described in chapter 2). This formula calculates average nightly capture probability of the population during a given trapping period which is most applicable to the models in Program CAPTURE. It should not be confused with the Jolly-Seber capture probability, which is the capture probability of individuals for the whole trapping period.

Hare Condition Index

Condition indices were calculated for individual hares using methods similar to O'Donoghue (1991). A power curve (SAS Proc NLIN) was fitted to weight and right hind foot length. Separate curves were generated for each sex, and only weights of females taken before late April were considered. The condition index is observed weight/predicted weight.

Times of Animal Capture

Eighty trap timers were manufactured and placed on traps to determine at what times during a given trap night animals were captured. These timers were constructed as a modification of those used by Barry et al. (1989). Tandy (Radio Shack Corporation) stick-on clocks were modified to allow for use as a stop watch. These LCD clocks were placed on 2.5 cm wood blocks and sealed with silicone. A plastic coated wire was mounted between the copper contacts of the clothes pin and attached to the trap door. When the trap was sprung the wire was pulled from the clothes pin, contact was made, and the stop watch started. The time of capture was calculated by subtracting the time when the trap was checked from the elapsed time on the stopwatch.

Radio-Telemetry Methods

The main emphasis of the 1992 Jacquot Island field season was investigation of animal home range and movement patterns in relation to capture probability. For this reason only Jacquot Island was sampled to allow for a more substantial radio-telemetry effort. The field season was also started earlier (March as compared to May) to gather data on early spring hare populations. These data were essential, for most of the Kluane trapping efforts are during this time.

Three null peak telemetry towers were placed on the highest points of Jacquot Island. The triangular design of the towers is the optimal geometric pattern to minimize error polygon size when bearings are taken (White 1990). The use of three towers allows for accurate determination of error polygon size. The actual location of towers relative to traps was evaluated using a GPS Pathfinder unit. To estimate actual tower location, GPS location of towers, and surrounding traps were taken for 5 successive days in August 1992.

Proper orientation of the towers was determined by placing transmitters at known angles from towers. Bearing estimates by telemeters were compared to compass bearings on towers using a mirror sight compass. At least twenty independent trials were conducted to ensure proper tower orientation and allow calculation of bearing error. This data was further verified by the GPS locations. Continuous tower calibration was assured by permanently placing at least three transmitters in known bearing locations. During every bearing session the "blind" telemeter took bearings on these transmitters, allowing continuous appraisal of tower calibration as well as telemeter efficiency.

Bearings were fed directly into a Toshiba T1000SE microcomputer and assessed using Program LOCATE (Nams 1990). Each telemeter recorded bearings and confidence in bearing on a scale of 1-4. A '1' was given if the signal was barely heard. A '2' was given if the signal was heard but there was no null found. A '3' was given if a null was found but it was greater than 3 degrees wide. A '4' was given if a very distinct null less than 5 degrees wide was found. Bearings were then reported to the central telemeter using walkie-talkies. The central telemeter would then assess the bearings for signal bounce and error polygon size.

A fundamental assumption in the estimation of home range is independence of animal locations. The minimal time interval between telemetry fixes needed for independence was determined by testing the autocorrelation (Swihart and Slade, 1985) of successive telemetry points. The time interval between successive locations in which there is no significant correlation is determined to be the minimal time interval needed for independence. From this test it was determined that the maximal number of points that can be collected and still be independent is once per day and twice per night.

The UTM locations of animals on the grid were calculated with program TRIANG (White and Garrot, 1984). Home ranges of animals were estimated using the harmonic mean estimator (Dixon and Chapman, 1980) implemented on the software program McPaal (M. Stuwe and C.E. Blohowiak, Conserv. Res. Cent., Natl. Zool. Park, Smithsonian Inst., Front Royal, Va., 1985). Only animals for which there were at least twenty independent locations were used in the analyses. The harmonic mean (Dixon and Chapman, 1980) was used for it is the most accurate of estimators available, and the most robust to differences in sample sizes (Boulanger and White, 1990).

Data were entered on site using dBASE and Lotus software programs, and were analyzed using SAS statistical package.

Radio-collared hare movement rate/trapping trials

As discussed previously, ten nighttime movement sessions were conducted in which radio-collared animal locations were determined every forty five minutes from approximately 1900 hrs to 0200 hrs. Also, ten nighttime movement sessions were conducted in which a small set of traps were opened to allow indirect observation of animal interactions at traps. At the end of each night, a map of animal movements was compiled using the mapping function on program LOCATE allowing assessment of animal movements relative to traps.

Every animal in the vicinity of the towers was radio-collared to allow observation of interactions within the population. During this time approximately 20 animals were available. Locations were initially assessed using the three-tower system. Animals that were in areas in which radio locations were imprecise were dropped from the session. Animals in good areas were tracked for the rest of the evening using the two-tower system. Only bearings in which the confidence ellipse was less than 0.1 hectare and average confidence rating was 3.5 were kept in the data set.

Movement rate indices were calculated by taking the cumulative distance between successive points divided by cumulative time of observations. This supplied an index of animal movement distances scaled for the duration of time between fixes, allowing comparison between animals (Siniff and Jessen, 1969). The limited scale of resolution with telemetry sampling limits the detection of small scale movement patterns. For this reason, movement rate should be thought of as an index of how much area a given animal covers in one trap night.

Results

Results of hypothesis concerning individual and population capture probabilities are grouped by the specific attribute being investigated.

Movement rates

Twenty nighttime movement-monitoring sessions were conducted in April and May. Individual hare movement rates were positively correlated ($r=0.6$, $p=.0163$, $n=15$) with capture probability measured over the 20 sessions (Figure 3.1). Movement rates were also weakly correlated with home range size ($r=.46$, $p=.07$, $n=13$).

There is one noticeable outlier in Figure 3.1, in which an animal with a low capture probability exhibited a high movement rate. This animal (#76) was an adult male first captured in 1991 which exhibited a moderate home range size (12 hectares). During some of the movement sessions this hare was observed chasing female hares in the grid area which may have contributed to its high movement rate. If this animal is eliminated from the analysis the correlation is more significant ($r=.849$, $p=.0001$, $n=14$).

On the population level, mean nightly movement rates of hares changed dramatically during May 1992 (Figure 3.2). The sudden decrease in movement rates might correspond with the availability of spring vegetation at this time, or with the presence of a lynx on the grid in late May.

Home range

Substantial mortality of collared hares occurred during the 1992 field season and as a result the sample size of radio-collared hares with enough independent points for home range estimation was small ($n=13$). All individuals had at least 27 independent points. Mean 95%

Figure 3.1. Movement rate index of hares as a function empirical capture probabilities. Movement rate is expressed as meters moved per minute(n=17).

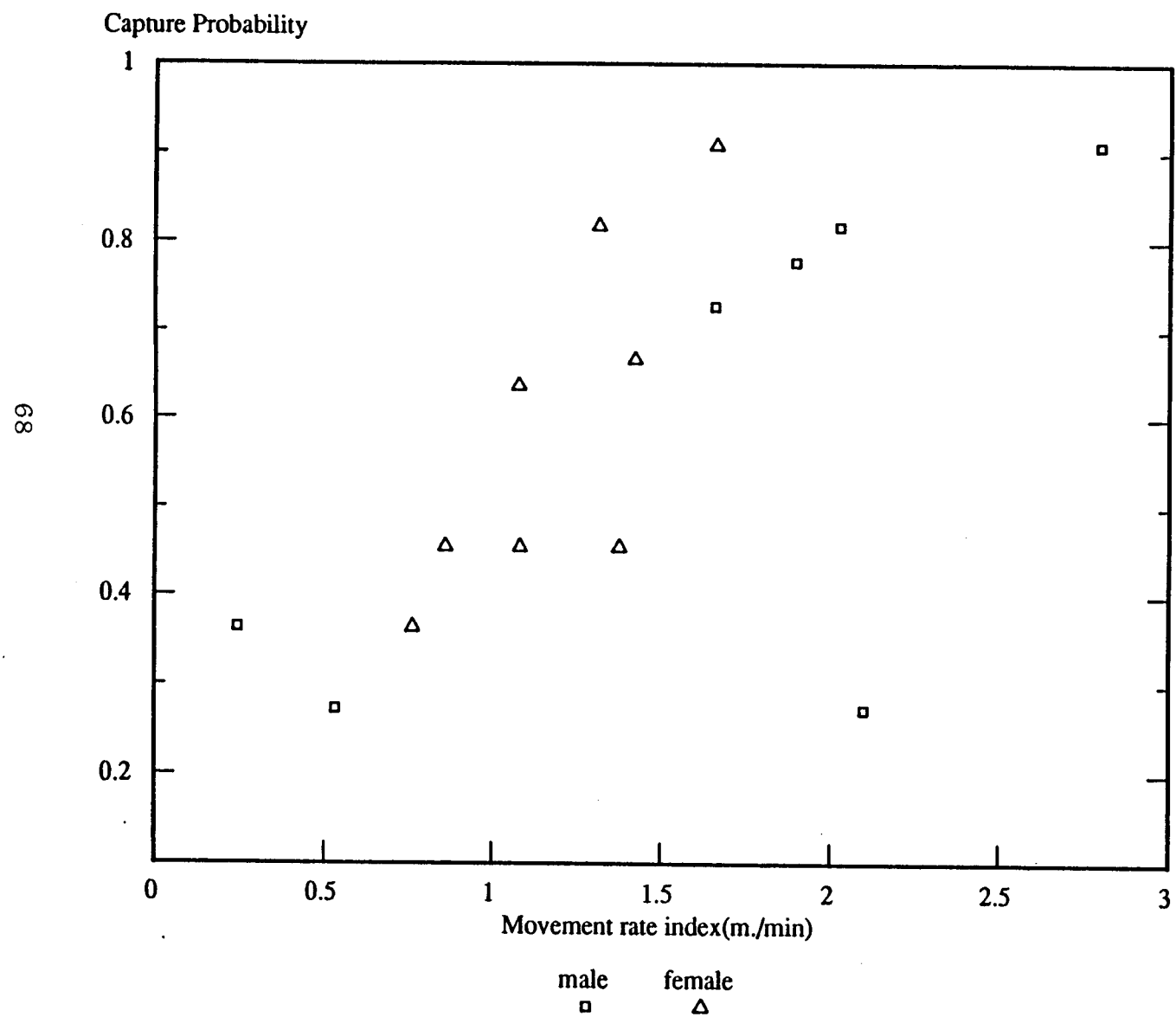
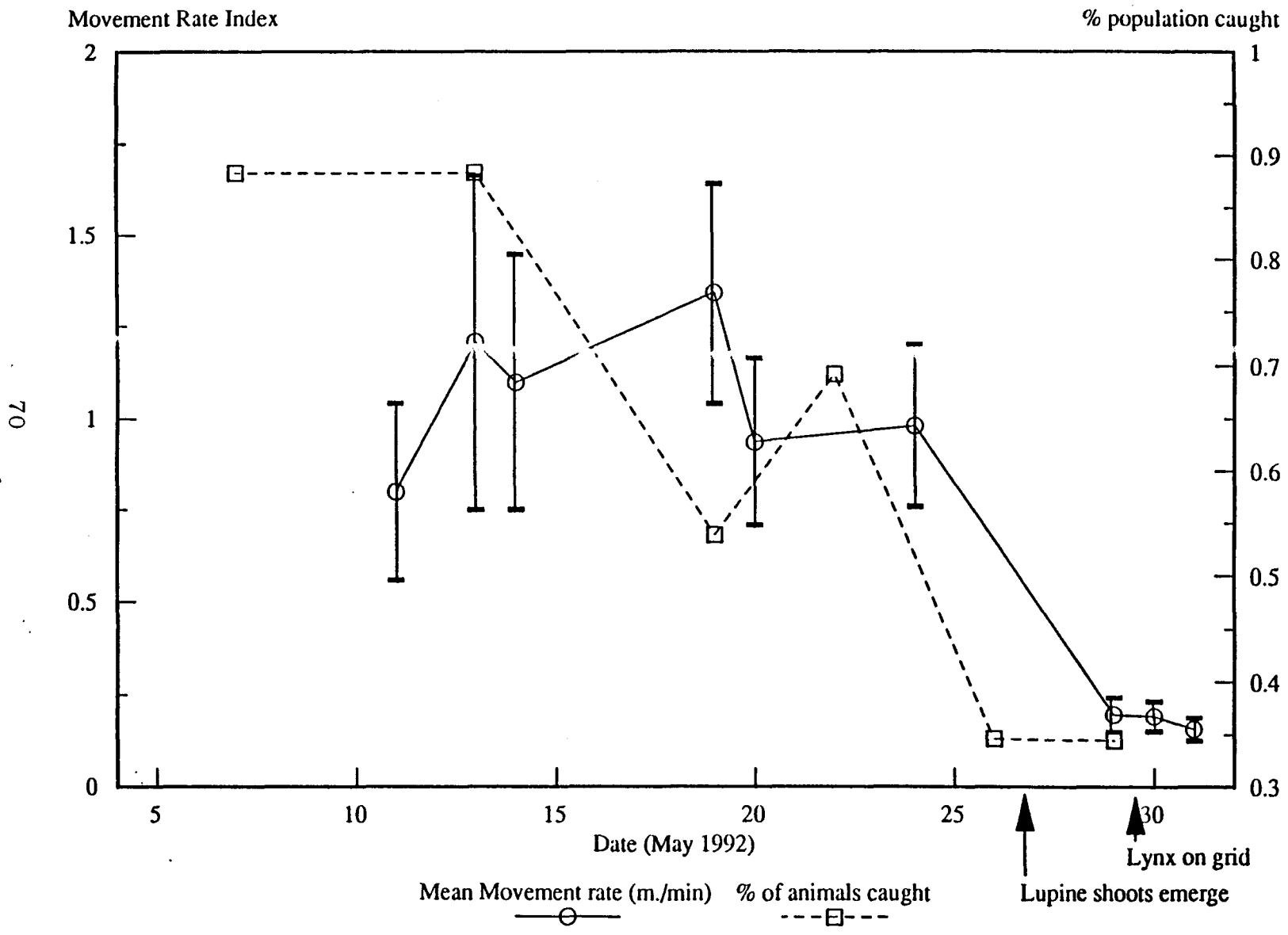


Figure 3.2. Index of population movement rates for the month of May 1992 compared to capture probabilities. Capture probability of the population is indexed by the percentage caught on a particular trap night. Movement rates are from the entire radioed population and are expressed as meters moved per minute. Each bar is one standard error from the mean.



home range sizes were 7.16 ± 3.04 ha. Capture probability was weakly correlated with 95% home range ($r=.527$, $p=.0637$, $n=13$).

Trapping trials

Radio-collared animals were always trapped within their 75% home range areas (paired t-test, $t=.63$, $p=.5$, $n=13$). Trapping ranges compared to home ranges are displayed in Figure 3.3. In no cases was an animal caught outside the 95% home range area as defined by telemetry sampling.

Trapping trials were conducted to observe individual animal movement patterns around traps and determine if animals would leave their core home range areas to be trapped. The time in which the trials were conducted (2100 to 0200 hrs) corresponds to the time of peak hare trap activity as shown in Figure 3.4. In Figure 3.4, hourly movement rates were calculated for the pooled population and overlaid on the maximal trapping times curves.

Animals showed variable activity patterns around traps. In Figure 3.5, each line represents the movement patterns of a radio-collared animal from 2100 to 0200 hrs. The animals with higher capture probabilities traversed large areas and were easily trapped whereas other animals showed more restricted movement, and did not patrol trap lines.

The objective of the trapping trials was to see if hares could be trapped away from their core trapping range. In these trials a line of traps was set intersecting various parts of hare home range. Sixteen animals were tracked during these trials. Of the 16 hares tracked, 5 had no set traps within their core trapping range. They also had not previously been trapped in any of the set traps. Only one of the 5 animals was trapped during the trapping trials. This hare was "transient" male (#71) who seemed to have no defined core home range area on the island.

Of the four other animals not trapped, they all ventured outside of their core trapping range at least once, but were not trapped. The sample size of this test is small and results should therefore be interpreted carefully. However the results suggest that in general hares are more likely to be trapped within their core trapping range.

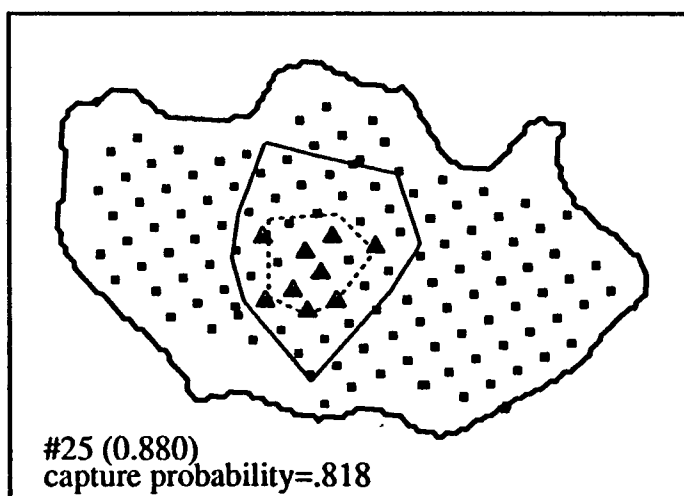
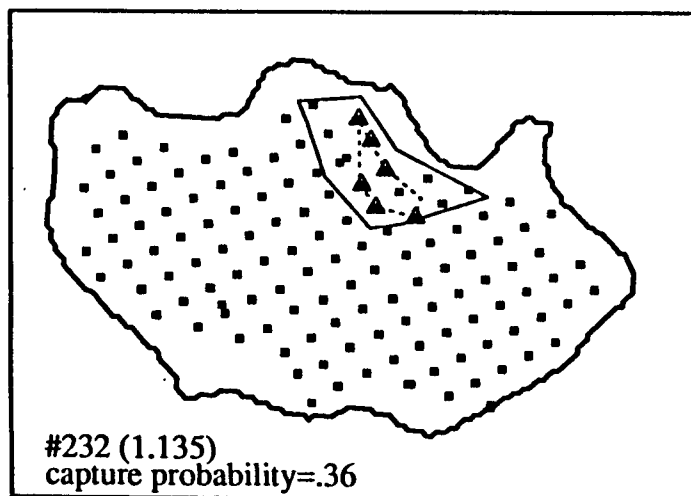
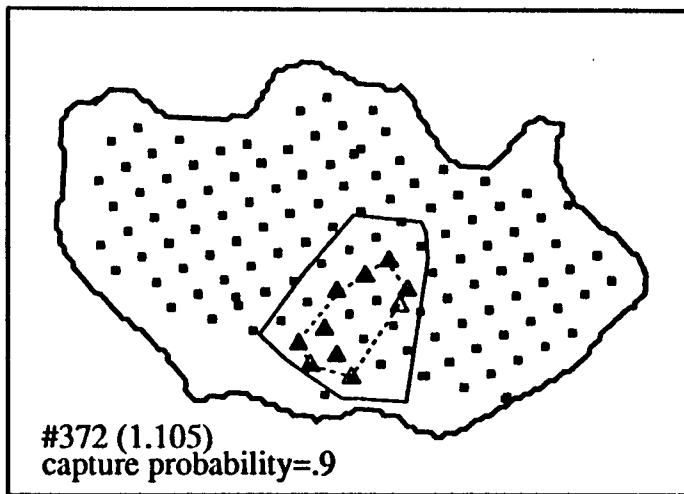
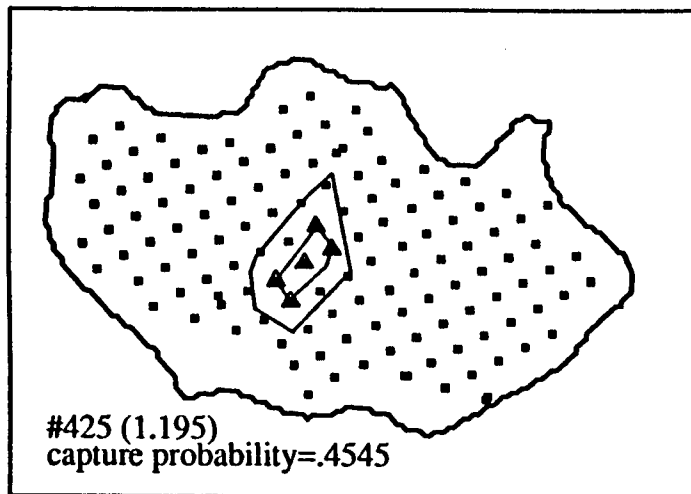
The trapping trials allowed me to observe changes in movement rates of the population of radio-collared hares also. One interesting observation was the sudden drop in animal activity when a lynx was present on the grid. On May 27, 1992 I noticed a sudden drop in animal movement and subsequent activity around traps. As I checked traps at 0300 hrs I was confronted with an adult lynx sitting on the trap line. Extrinsic factors such as the presence of predators probably affects capture probabilities. In May females started delivering their young. Before this time, movement rates of these animals dropped off and their capture probabilities also decreased (Figure 3.2).

In summary, the capture probability of an animal was a function of whether any traps were within its core trapping range. If traps are not located in areas an animal usually traverses, it probably will exhibit a lower capture probability.

Hare condition

In Figure 3.6 a weak trend in which hares of high condition do not exhibit high capture probabilities and low condition animals do not show low capture probabilities is evident. The relationship between individual hare capture probabilities and condition is quite weak. This relationship is most apparent in hares that are in extremely high or extremely poor condition. However, other attributes such as movement rates play a larger role in determining capture probabilities for the majority of the population.

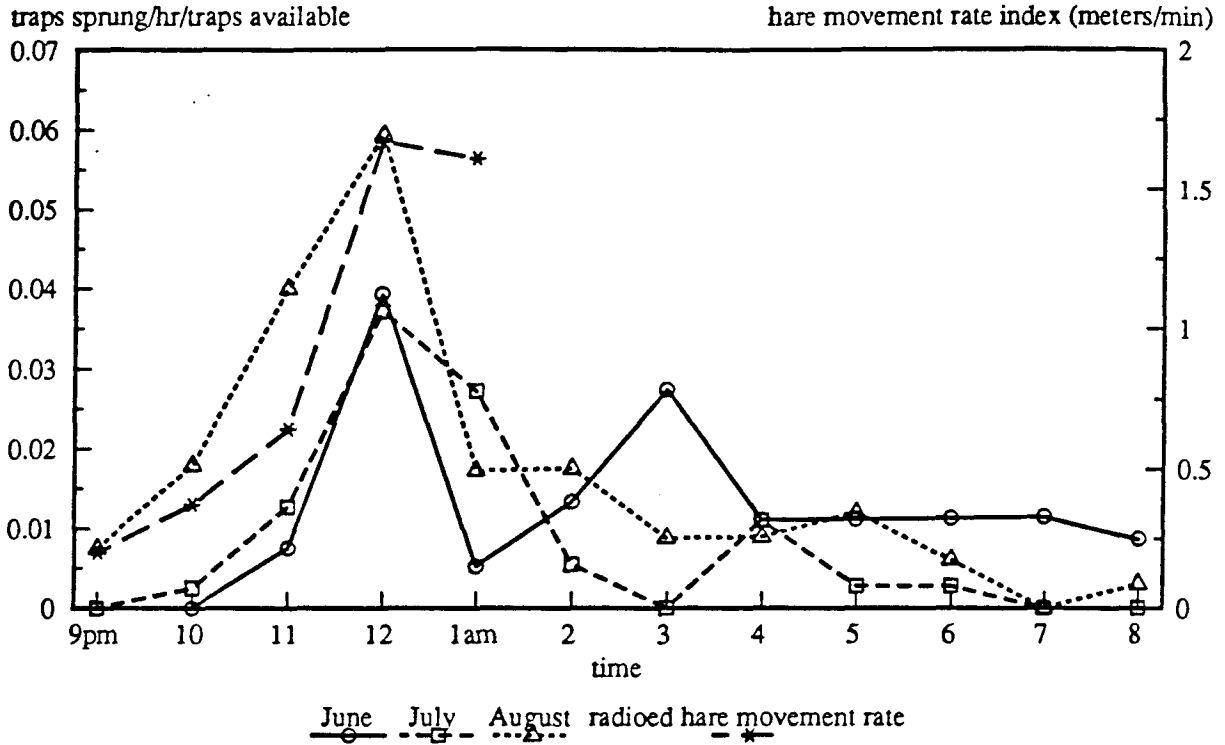
Figure 3.3. Home range and trapping range on Jacquot Island during the spring of 1992 for trap happy (#25 and #372) and trap shy (#232 and #425) animals.



———— home range trapping range ■ trap △ used trap

Figure 3.4. Trapping activity peaks. Number of traps sprung per hour per traps available for Jacquot Island and Dezadeash Island during the summer of 1991. Data from multiple trapping periods were pooled for each month due to small sample sizes (Jacquot Island: n(# of timed captures)=54 for June, n=40 for July, n=70 for August, Dezadeash Island n=115 for August, n=71 for July). Radioed hare movement rates on Jacquot Island are mean hourly movement rates nights for all hares tracked during May 1992.

Jacquot Island



Dezadeash Island

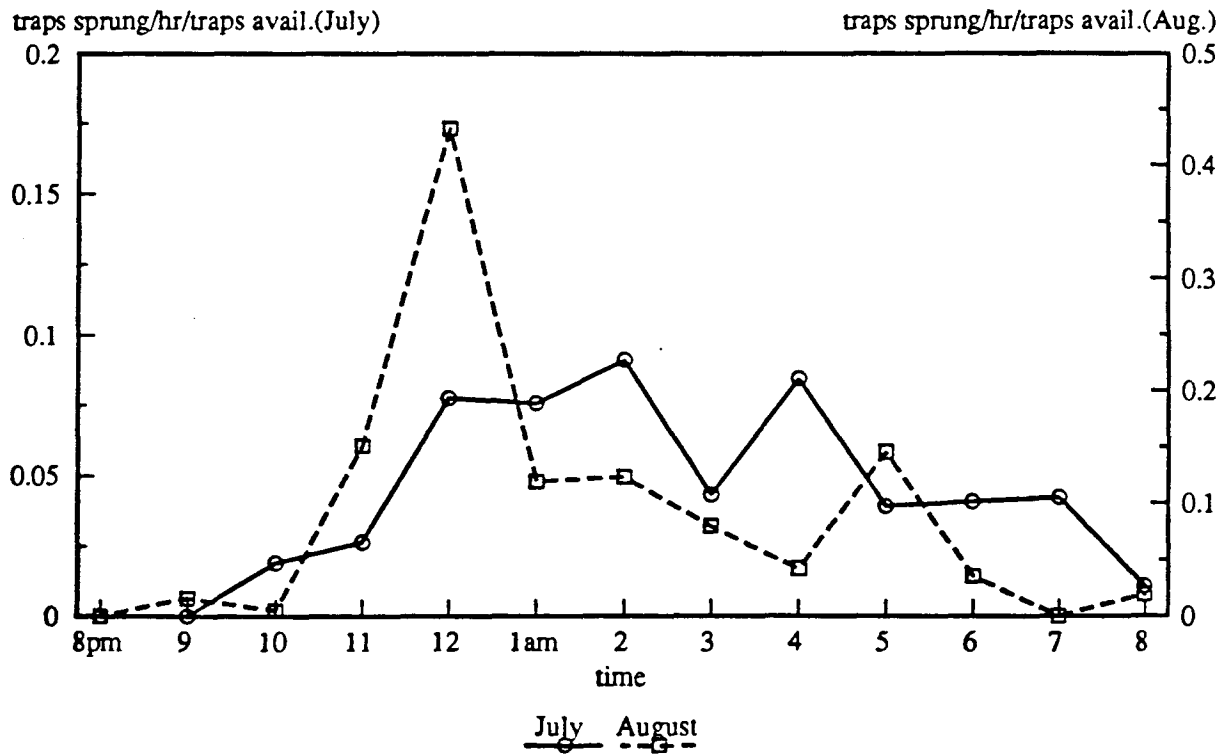
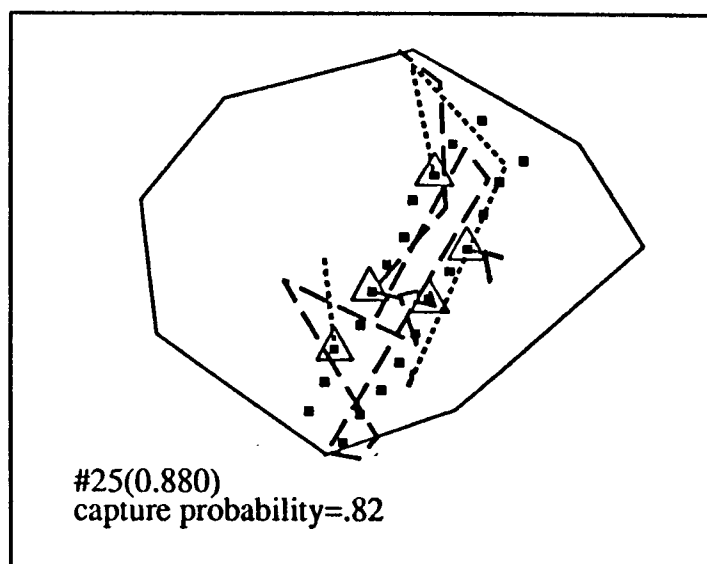
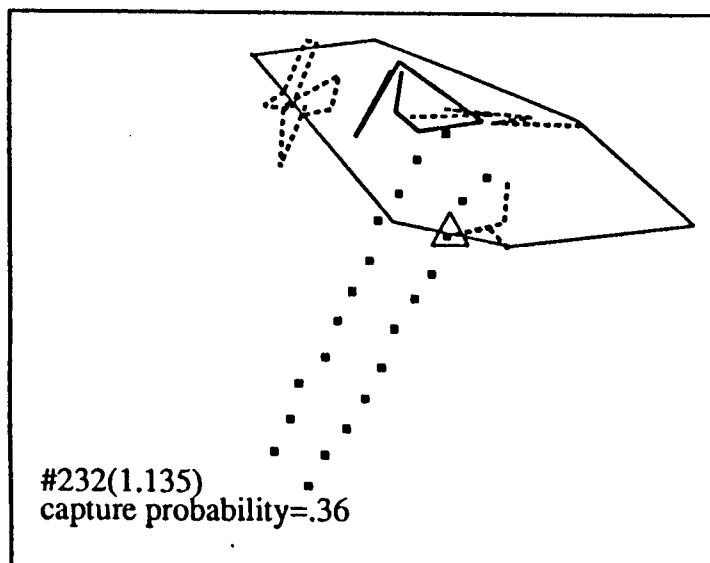
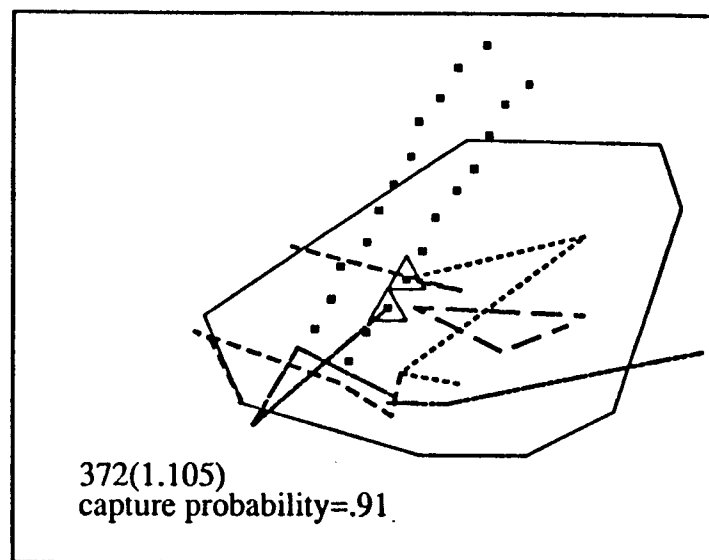
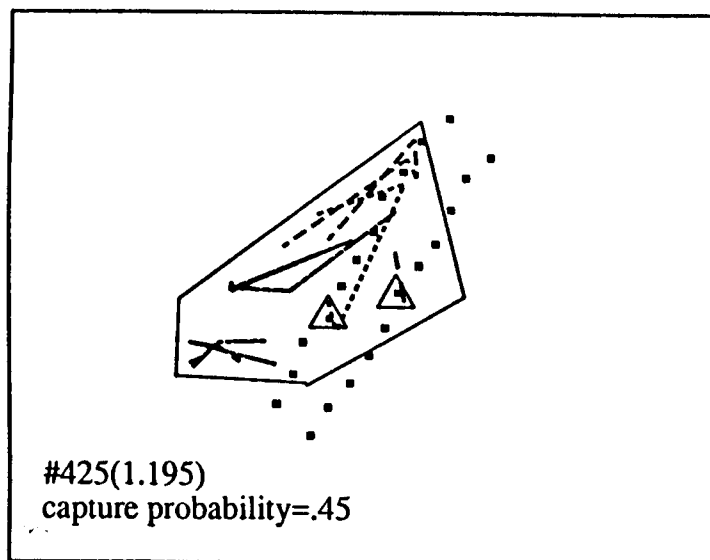


Figure 3.5. Movement patterns for trap-happy hares (#25 and #372) and trap-shy hares (#232 and #425). Each line represents movements monitored every 45 minutes from 9pm to 2am during the trapping trials in May, 1992. The line of traps were the traps set during the trapping trials.



■ trap

△ used trap

A seasonal change in capture probabilities could also be related to changes in mean population condition (Figure 3.7). The results in Figure 3.7 suggest that hares in poorer condition in winter may be more willing to enter traps hence increasing capture probabilities. This relationship is very weak. Other factors probably play a more important role in determining capture probabilities of the population.

Times of capture

Hares showed a diurnal peak in trapping activity regardless of season (Figure 3.4) on both islands. On Jacquot Island this corresponds to times of peak animal movement measured using radio-telemetry. In all cases most hares were trapped about midnight. Juvenile hares were included for this analyses. The trap activity is weakly bimodal for hares in June and July on Jacquot, and July on Dezadeash. The bimodal pattern could be attributed to the fact that hares have two periods of activity each night. However, in all cases the highest peak occurred during the first activity period. The increased height of the peak for August on both islands is due to greater numbers of juveniles being trapped. Trap saturation caused by juvenile hares in August could have caused the bimodal effect to be obscured.

Discussion

Validity of study

In chapter 1 of this thesis three explanations of unequal probability of capture are given. The first two relate to innate differences in individual capture probabilities, and learned variation in capture probabilities. The third factor, unequal access to traps, is probably a significant factor in most capture-recapture studies. However during the 1992 field season in which hare capture probabilities were studied, 30 adult hares had 120 traps available during

Figure 3.6. Condition indices of hares versus empirical capture probabilities. Condition indices were calculated from right hind foot and weight of individual hares. Power curves (SAS Proc NLIN) generated expected weights, and condition index is simply the observed weight/expected weight. Power curve formulas are: Males; $\text{Pred. weight} = \text{RHF}^{1.35} + 576.37$ and Females(before May 1); $\text{Pred. weight} = \text{RHF}^{1.446} + 123$

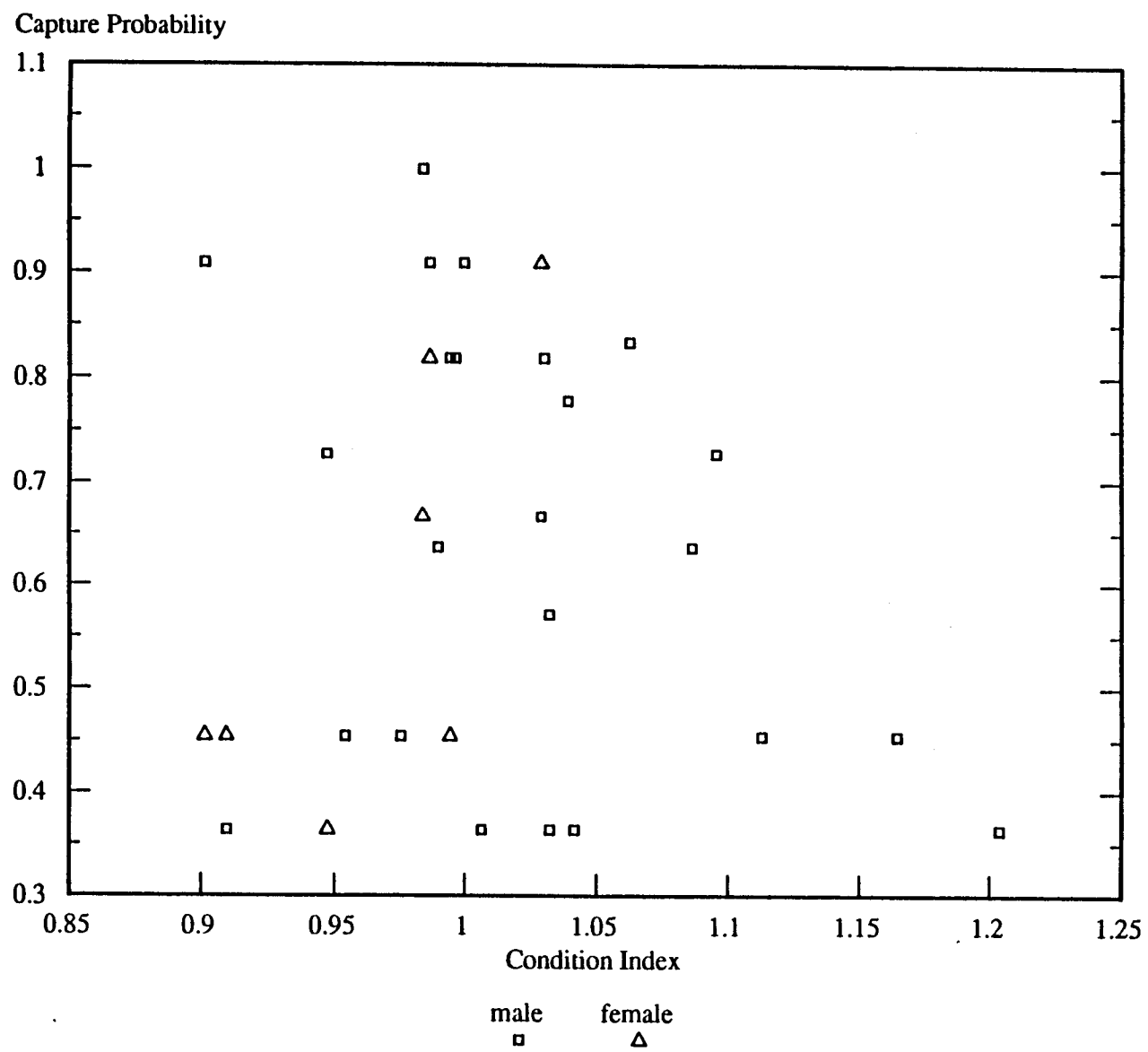
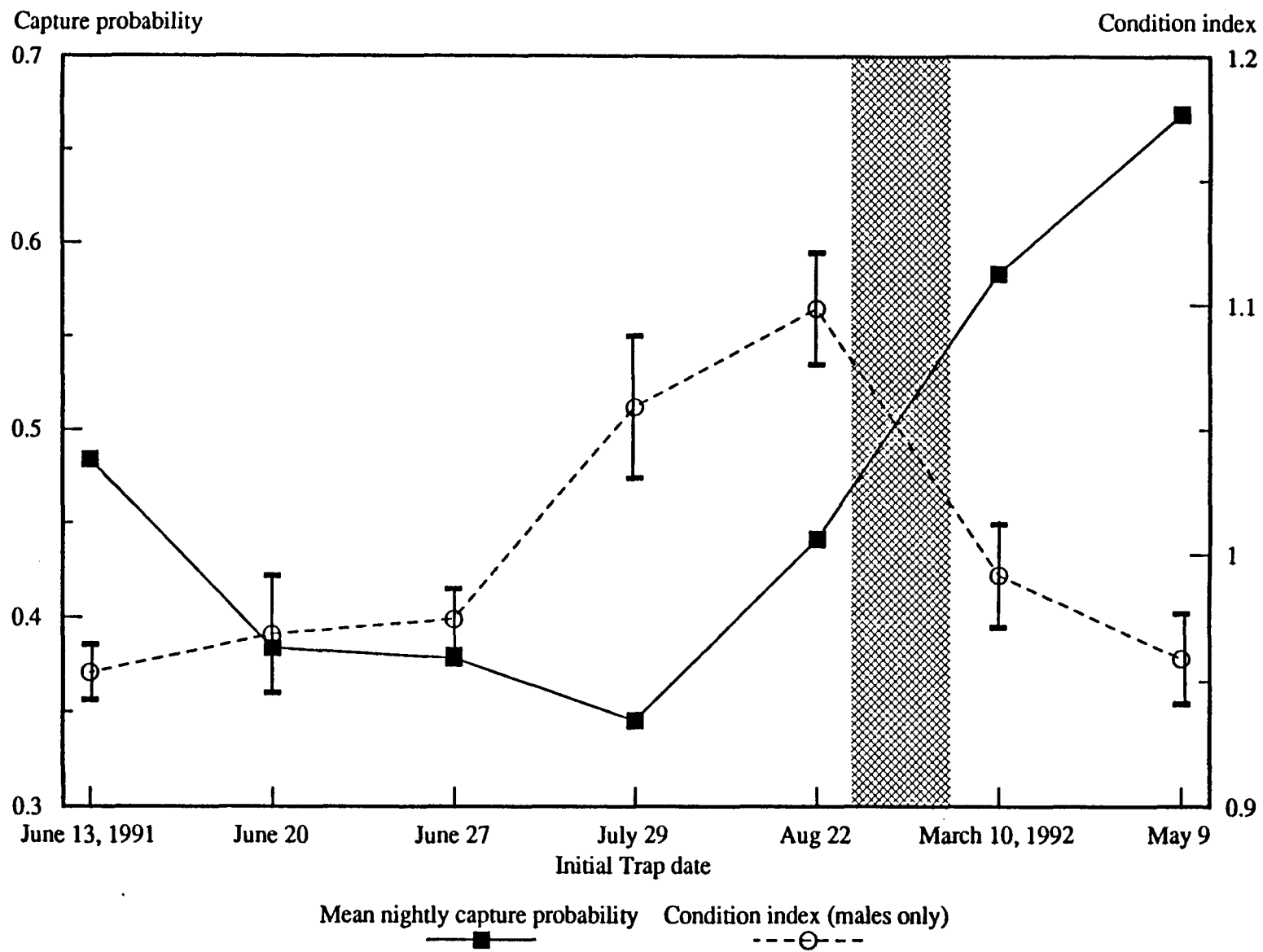


Figure 3.7. Mean condition of male population and capture probabilities by date. Bars on condition indicate one standard error from the mean. Condition index is observed weight over expected weight. Capture probabilities from Otis et al. (1978)



each trap night. Most of the radio-collared animals had at least 6 traps within their core home range. This intensive sampling effort minimized biases associated with trap saturation. It is important to note that this does not mean that every animal encountered the same number of empty traps in a given night. As discussed previously, differences in movement patterns might cause different trap encounter rates. The major point is that the population was exposed to similar trapping effort and trends concerning capture probabilities could be addressed.

Factors affecting individual capture probabilities

Heterogeneity variation

The process in which an individual animal is trapped can be dichotomized into (1) trap encounter, and (2) given a trap is encountered, the decision to enter the trap. My radio-telemetry results suggest that hares that traverse larger areas exhibit higher capture probabilities. Figure 3.5 represents typical movements for animals during peak trap activity time (2100 to 0200 hrs). Hares that exhibited lower movement rates (#232 and #425) probably encountered one or two traps in a given night. If hares prefer a small subset of traps within their home range (Figure 3.3), differential movement patterns may explain why individuals exhibit low capture probabilities.

Extreme attraction to traps was exhibited by a small subset of the hare population. An example of this was patrolling of trap lines by animal number 25 (Figures 3.3 and 3.5). The patrolling of trap lines was also evident from snow tracking in the spring of 1992. Hare number 25 was also caught twice in a given night on four different occasions. After it was released it ran directly into the next open trap down the line. The extreme attraction to trap exemplified by number 25 was not observed in other hares. Hares such as number 25

obviously seek traps out; however, in no instance were they caught outside of their core trapping ranges.

What actually causes an animal to decide to enter a trap is difficult to determine in a field setting. The relationship between movement rates and capture probabilities could be due to differences in encounter rates. Possibly, the animals that exhibit higher movement rates are also the "risk takers" and are also more willing to be trapped. The only way to test the "risk taker" hypothesis would be in a more controlled setting. With the design of this experiment, the relationship between movement rates and capture probabilities can only be attributed to differential trap encounter rates.

I noted a weak relationship between condition and capture probability. In this case one could speculate that animals in poor condition are more willing to risk being trapped for the reward of the apple bait. This relationship suggests that other factors additional to differential movement patterns may effect hare capture probabilities.

Non-uniform trap spacing such as on Kluane grids exaggerates differences in hare capture probabilities. The results of the trapping trials suggest that a hare is reluctant to leave its core home range area to enter traps. In this case, an individual hare's capture probability becomes a function of its movement rate, and where its home range is relative to the line of traps.

In conclusion, my results suggest that hares do exhibit individual variations in capture probabilities. The movement they exhibit towards traps is not random as is suggested in many simulation studies of trapping grid design (Skalski and Robson, 1992). The relationship between movement rates and capture probabilities, as well as hare fidelity to traps within their

home range suggests that there is a strong relationship between how a population is sampled and variation in capture probabilities.

Factors affecting population capture probabilities

Time variation

A primary goal of any capture-recapture experiment is to maximize the capture probability of the population. Hares exhibited a much higher probability of capture in the early spring as compared to the summer on Jacquot Island. It is important to note that during this time the population may still be exhibiting unequal capture probabilities. However, due to the high capture probabilities, all models gave similar estimates. Due to these factors it is preferable to sample at this time compared with mid-summer.

Changes in population movement rates are related to changes in capture probabilities. Another question relates to the causes of changes in movement rates. One plausible explanation for what actually causes changes in movement rates that also relates to condition is a shift in hare foraging strategies with season. That is, hares are more "hungry" in early spring, and must traverse larger areas to find adequate forage for sustenance and are more prone to be trapped. The lower condition of the population at this time suggests the population may be less risk-adverse. As summer progresses, and alternative foods become available, hares traverse smaller areas to find forage and may thus show lower capture probabilities.

Change in animal condition and foraging patterns were very apparent on Jacquot. In early spring, some hares would actually visit the Jacquot cabin in daylight to eat alfalfa scraps from the bait bags. As new vegetation emerged, no hares were observed near the cabin, and radio-collared hares exhibited little daytime movements. Factors such as pregnancy of female

hares, and the presence of predators on the trapping grid complicate these results. A year-round radio-telemetry/trapping study would be needed to verify these relationships.

In conclusion, I suggest that changes in movement and foraging patterns interact to cause changes in hare capture probabilities with season. Other factors such as presence of predators, breeding behaviour, and weather can also affect these relationships. The overall suggestion from these results is that it is best to sample snowshoe hares in early spring.

Behaviour variation

Behaviour variation can be defined as a change in animal capture probability due to prior capture experience. It is very difficult to study behaviour on an individual level since an initial capture probability of an animal is needed to make subsequent comparisons. If a response towards trapping is occurring then the animal's capture probability will change after initial capture making the calculation of any initial capture probability impossible (It is impossible to calculate a probability with only one observation). As a result, trends concerning behaviour can only be addressed on an observational basis.

The effect of behaviour was most noticeable on Dezadeash Island. This population had not been previously trapped in five years (C. Krebs. per comm). Only four animals were caught in the first five days of trapping. I actually observed one animal approach a trap, sniff it, and then move away, not knowing how to enter the trap. In subsequent trapping occasions the group of hares initially caught plus a new group was caught each trap night. In this case it seems that hares were more trappable once they learned how to enter the traps, and the location of traps on their home ranges.

Another noticeable trend was the effect of pre-baiting or locking traps open before a given trapping session. In all cases either of these techniques will increase the number of animals caught on the initial trap night. I have not tested this trend in a rigorous way, however it has also been observed on Kluane grids also (Sabine Schweiger, pers. comm.). This evidence also suggests that hares capture probability changes once it has found a trap, or entered a trap within its home range.

I speculate that the capture probability of hares changes depending on their prior capture experience. My results suggest that initial capture probabilities are lower, as a result of animals lack of knowledge of where a trap is, and how to enter it. After an initial capture, the probability of capture is affected by factors previously discussed. To test this hypothesis a more controlled observational study of hares would be needed.

Conclusion

In this study I found a direct relationship between animal movement patterns and heterogeneity of capture probabilities. This relationship could be seen on an individual and on a population level. I also observed time and behavioral variation in capture probabilities.

The results of this study document the contribution of sampling, and differential animal movements in determining capture frequencies in snowshoe hare trapping data. In most evaluations of trapping design it is assumed that animals move in an entirely random fashion and the only factor determining unequal capture probabilities is innate or behavioral differences between animals (Skalski and Robson, 1992). Furthermore, most Monte Carlo simulation models used for estimator evaluation completely ignore the trapping process (Otis et al. 1978). This study indicates that sampling and animal movements are important elements and that valid

simulation models or evaluations of trapping design should take these factors into account.

The results of this study indicate key elements of the capture-recapture process to be considered in a Monte Carlo simulation model introduced in Chapter 4. Individual hare movement patterns relative to traps, and variations in capture probabilities are simulated in this model. The results of this study combined with the Monte Carlo simulation model provide a theoretical interface between the biology of the population being studied, the trapping process, and estimator performance.

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Chapter 4: Evaluation of Estimator Robustness to Sample Biases Caused by a Cyclic Snowshoe Hare Population

Introduction

Monte Carlo simulation has been used extensively for testing capture-recapture estimators (Otis et al. 1978, Menkins and Anderson, 1978). In these simulations a variety of hypothetical capture frequencies are used to determine robustness of estimators. While such studies have been helpful in discerning which estimators are the most robust, they have not helped the field biologist decide which particular estimator may be optimal for the population being studied. The reason for this is that there is little knowledge about innate capture probability variation among animals, and the role of sampling in determining the actual capture frequencies in the field data. As a result, most biologists have trouble applying the results of Monte Carlo simulation to the actual animals being studied (Carothers, 1973).

Capture frequencies of hares in trapping data are determined by the capture probabilities of the animals, and the fashion in which the population is sampled. Many factors could possibly be creating sampling biases on Kluane grids. First, snowshoe hares exhibit extreme population fluctuations as a result of their 10 year population cycles. On a given area densities of hares can vary from 20 to 400 individuals. Secondly, the trap spacing on Kluane grids is irregular which may cause the probability of capture of each hare to be dependent on where its home range is on the grid. Thirdly, biological differences between hares may make certain individuals more trap prone. Fourthly, I found that hares exhibit differential movement patterns, which were correlated with hare capture probability (Chapter 3).

It is possible that particular estimation models could be more robust to these sample biases and produce less biased estimates. It is difficult to determine empirically the importance, or the magnitude of bias caused by the factors mentioned above, because in a typical field situation true population size and distributions of hare capture probabilities are not known.

To explore the effects of sampling biases I modified an individual-based Monte Carlo simulation model first introduced by Zarnoch (1969) and later modified by Wilson (1980). This model simulates individual hare movement patterns, hare capture probability differences, trap layout, and the trapping process. This model allows me to simulate plausible sampling situations found on Kluane grids, and produce capture frequencies from which population estimates are made from. Because the true number of hares in the model is known, insight into estimator biases is possible. The objectives of the simulations are:

- 1) Determine potential biases due to trap saturation caused by varying densities of hares on a trapping grid.
- 2) From these results, determine which models are most robust to variations caused by the hare cycle, grid setup, and hare capture probability differences.

In determining the optimal model for snowshoe hare data it is important to consider the design of the Kluane experiment and the time series nature of the data. The main objective of the Kluane experiment is comparison of treatments on trapping grids during the snowshoe hare cycle. For this reason, an optimal model is one that shows constant relative bias throughout the hare population cycle. If such a model is used, unbiased calculation of rates of increase, and comparisons between treatments are possible regardless of absolute population density. It should be noted that in this case *consistent* bias at any hare density is more important than

unbiased model performance at one particular hare density. Furthermore, a model that is slightly biased, but exhibits high precision is preferable to an unbiased, imprecise model.

Variation in densities of hares as a result of the cycle could cause changes in the capture frequencies of hares in the data. In this case, different models may be optimal at different phases of the hare cycle. The program CAPTURE model selection routine will be evaluated to determine if the models it picks exhibit consistent bias throughout the cycle.

This model was built with the objective of simulating what I feel are the most plausible sources of sampling biases. The parameters are based on the previously discussed telemetry studies, the work of David Hik on Kluane grids, and past Kluane trapping data.

I will first detail the conceptual basis and structure of the simulation model. After that I will explain how the parameter values for the model were chosen from empirical data. I will then explain the criteria for evaluation of estimation models using the simulated data.

Methods

Simulation methods

General computer methods

Data were generated using the simulation model described below. The simulation model produced input files which were then fed into program CAPTURE. These programs produced estimates which were then evaluated. The FORTRAN base code for program CAPTURE was modified so that it would produce abridged data files for later analysis.

The actual simulation model was a modified version of a program produced by Zarnoch (1969) and later modified by Wilson (1982). The model is written in FORTRAN (See appendix 1). I used the basic structure of this program. The movement simulations, underlying capture

probability model and trapping process were modified to simulate the Kluane system.

All programs were run on a SUN SPARC station. A master driver file was written in a UNIX shell script to call programs, and keep track of simulations.

This model simulated three components of the capture-recapture process: 1) Differential hare movement patterns, 2) differences in individual hare capture probabilities and, 3) the trapping process. The methods for simulating these three components are described below.

Hare movement patterns

Hares exhibit differences in the amount of habitat they traverse in a given night (Chapter 3). Some hares are sedentary and cover very little area in a given night whereas others traverse very large areas, rarely repeating a given movement pattern. These differences in movements patterns were positively correlated with an individual animal's probability of capture. Also, hares tend to remain in the center of their home range and are most often trapped there. A main objective of this model was to simulate differences in hare movement patterns. I needed a movement model that takes into account each individual hare's path, and simulates differences in the way which individual animals traverse the landscape.

The modelling of animal movement rates has seen much theoretical attention. The bivariate normal model has been used previously to model animal locations on a trapping grid (Zarnoch, 1969, Wilson, 1980). With this model an animal is moved at each time interval according to a bivariate normal distribution centred over the animals home range center. This method is unsatisfactory for my purposes because the prior position or path of an animal is ignored, and so animals are made to "jump" biologically unrealistic distances.

Another movement model, the random walk, has the advantage that an animal's path is taken into account, and differences in animals can be simulated by changing probabilities of movement in a given direction at each time step (Holgate, 1971). Various mathematical methods such as Ornstein-Uhlenbeck diffusion processes and Markov Chains have been used to derive probabilities of movement for random walks. However, many of these applications are computationally intensive, and hard to relate to the actual biology of the animal being described.

I chose a correlated random walk model developed by Bovet and Benhamou (1988) and further refined by Benhamou (1989) to describe hare movements. This method is computationally simple, and the parameters used in the random walk can be derived from actual movement patterns measured in the field. An animal's movement within its home range is determined by two parameters; its sinuosity (S_b) and central tendency (k).

Sinuosity (S_b) is the tendency of the animal to turn while travelling across a landscape. It ranges from 0 to 1. An animal with a low sinuosity has a tendency to move forward and traverse large areas whereas an animal with a high sinuosity has a tendency to turn frequently and traverse smaller areas. The central tendency factor (k) determines how far an animal will on average travel from its home range center and also varies from 0 to 1. Both these parameters apply directly to differential movement patterns and home range use of hares discussed previously.

The basic sequence in which an animal moves according to this model is determined by the following equations (for more detail see Benhamou (1989)). The equations for these parameters are:

$$\sigma_b = S_b \sqrt{P} \quad (1)$$

$$\sigma_i = \sigma_b (1 + k \frac{dD_i}{P}) \quad (2)$$

$$D_{i+1} = [(X_{i+1} - X_0)^2 + (Y_{i+1} - Y_0)^2]^{1/2} \quad (3)$$

$$dD_{i+1} = D_{i+1} - D_i \quad (4)$$

$$\alpha_i = N(0, \sigma_i) \quad (5)$$

$$\theta_{i+1} = \theta_i + \alpha_i \quad (6)$$

$$X_{i+1} = X_i + P \cos \theta_{i+1} \quad (7)$$

$$Y_{i+1} = Y_i + P \sin \theta_{i+1} \quad (8)$$

The computational sequence in which a hare is moved will now be described. Numbers in parenthesis pertain to particular equations being described. A hare is in its home range center (X_0, Y_0) initially. It moves from its center on the first time step ($i=1$) in a random angle for a step length P . Its path after the initial random step is determined by the parameters σ_b , dD_i , σ_i , and α_i . σ_b is determined by the step length (P) and the hare's sinuosity (S_b) and is fixed for the simulation (1). σ_i varies with the distance of the hare from its home range center. It is determined by the central tendency (k), step length (P), and dD_i (2). The parameter dD_i is the change in the hares distance from its home range center between time step i and $i+1$ (3 and 4). Note how the ratio of dD_i/P will vary between 0 and 1. If the animal's step from i to $i+1$ is directly away from the home range center then this ratio is equal to 1, otherwise it is less than one. In this way σ_i varies with each step the animal takes (2).

The angle and distance of travel for each step is determined by a random variable, α_i , which is generated from a normal distribution with mean 0 and variance σ_i (5). Note that the magnitude of σ_i determines the variance of α_i . The turning angle of a hare is determined by the previous angle turned as well as α_i (6). Therefore, when α_i is large the animal will have a tendency to turn more frequently in its path. When α_i is small it will tend to continue in a straight line. As a hare gets farther from its center, α_i will tend to increase (as σ_i increases) causing the animal to turn more frequently and not cross over the home range boundary. How quickly this happens is dependent on k , the animal's central tendency and sinuosity (S_b). Finally, the hares new coordinates are determined using trigometric functions (7 and 8). The process is repeated for each time step in the simulation.

The sources of variation in hare movement I wished to simulate was the area traversed in a given trap night. This could be accomplished by varying the sinuosity (S_b) alone. The central tendency factor (k) was held constant at .5 which scaled the simulated path to the range of sizes of hare home ranges observed on Kluane trapping grids. Step length P , was set constant at 10 meters. In setting these parameters constant I assumed that all hares show a similar central tendency, but some will wander further from the home range center dependent on the sinuosity parameter (S_b).

The unit of information available from the Kluane project that pertains to hare spatial patterns is home range size. For this reason, sinuosity (S_b) was set proportional to the observed home range size. This was accomplished using a set of equations developed by Benhamou (1989). Using simulations Benhamou determined the distribution of points generated by the random walk models was most closely approximated by a circular bivariate exponential

distribution. The home range area was then defined as the .95 probability density of an animals location from the center. With this relation the home range area (*HRA*) could then be related to the standard deviation (δ) of points from the home range center by the following equation (for more details see Benhamou, 1989):

$$HRA = 7.5\pi\delta^2 \quad (9)$$

Given this relation, sinuosity (S_b) and central tendency (k) were related to δ using simulations. In these simulations a range of S_b and k values were used to generate data sets with varying standard deviations (δ) of the X and Y locations from the home range center. By adjusting a function $g(k, S_b) = ak^{-1}S_b^{-2}$ to the observed values of δ using the least squares method he obtained the following equation:

$$\delta = \frac{1.92}{k.S_b^2} \quad (10)$$

This formula allows the user to vary both k and S_b to obtain desired home range sizes. In the case of the hare simulations, I assumed k was constant at .5, and S_b was determined by the hares home range size. Rather than repeat the whole process of obtaining equation 10, I modified the equations so that the only parameter related to home range area was S_b . So the constants were combined to calculate sinuosity (S_b) from observed or assessed home range size by the following equation.

$$S_b = \frac{4.27}{(HRA)^{1/4}} \quad (11)$$

I assumed that an animal's tendency to turn or wander from its home range center is proportional to its home range size. I also assumed that all animals on their home range have a central tendency. These assumptions are biologically reasonable. My empirical studies

showed a relationship between home range size and movement pattern. All animals displayed a central tendency while some animals wandered more from this center area which would be reflected in differences in sinuosity. The assumption of a circular home range is a simplification. However it is adequate to describe an animals basic central tendency and area traversed within one given trap night.

The size of the home range areas used to calculate sinuosity (S_b) in the simulations was determined from empirical data. Boutin (1984) reported hares had a mean home range size of 6.9 (std. dev.=3.7) hectares. The hares on Jacquot had a mean home range size of 7.16 (std. dev.=3.04) hectares. D. Hik (per. comm.) reported similar home range sizes for the hares on Kluane grids.

The home range sizes for the hares in the simulation were generated for each simulation as a normally distributed random variable with mean 7.0 and standard deviation 3.5 hectares. No home ranges smaller than 1 hectare were allowed as this would be biologically unreasonable. Generation of home range sizes with each simulation avoided any initial state biases.

Animals were moved for 100 time steps. At each time step they moved 10 meters. So for a given night each hare moved 1000 meters. This is the mean movement distance of a snowshoe hare (D. Hik, pers. comm.) on the Kluane grids. I assumed that what determines the area an animal traverses is not actual distance moved, but the straightness of the individual hares path. This assumption is biologically reasonable. It has been documented that more sedentary hares seem to travel in tight "loops" in small areas, whereas less sedentary individuals tend to have longer "loops" (D. Hik, pers comm.). Therefore, an adequate simulation of areas

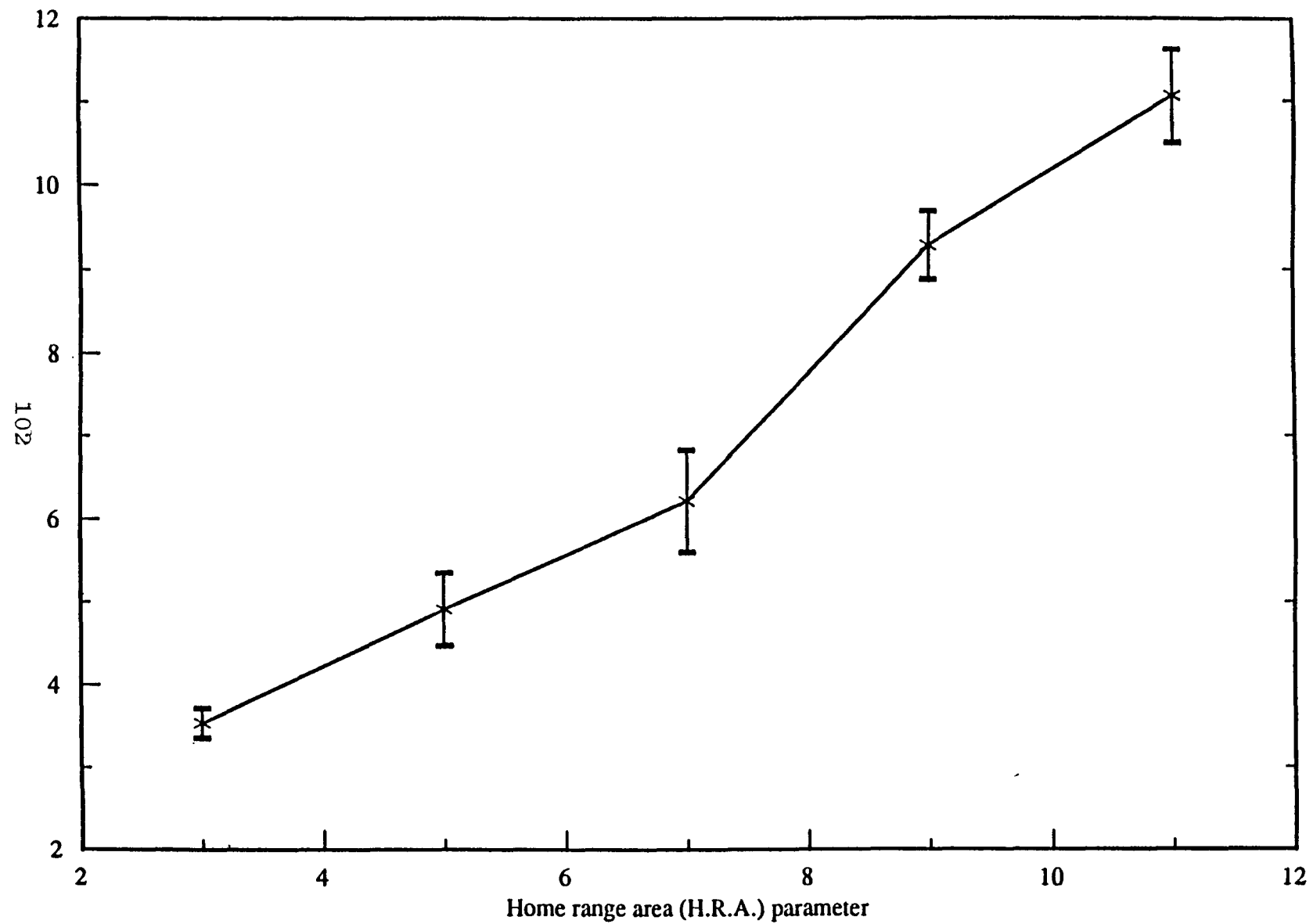
covered in one trap night can be obtained by varying sinuosity alone and keeping the step length constant.

The results from Jacquot Island (Chapter 3) suggest that hares were seldom trapped off their home range areas. Therefore, it was essential that the home range areas from simulated data actually corresponded to the input parameter (*HRA*). To test if the data generated actually corresponded to the hare home range size parameter (*HRA*) in the random walk model seven simulated data sets of 2000 step (10 meter spacing) paths were generated for hare home range areas (*HRA*) of 3, 5, 7, 9, and 11 hectares. Each data set generated was subsampled every twentieth step to provide independence between points. Independence of points is a fundamental assumption for unbiased home range estimation. This resulted in a data set of 100 points for each simulated data set. A home range area was then estimated from the simulated data sets using the 95% harmonic mean home range estimator as implemented in program McPaal (M Stuwe and C.E. Blohowiak, Conserv. Res. Cent. Natl. Zool. Park, Smithsonian Inst., Front Royal, Va., 1985). The home range areas estimated from the simulated data were then compared to the home range area (*HRA*) parameter in the random walk model. As seen in Figure 4.1 the simulated and estimated areas correspond well with a slight tendency for the random walk model to produce a larger home range area than the home range area parameter (*HRA*). The imprecision of most home range estimators (Boulanger and White, 1990), may be the reason for this discrepancy. Never the less, the model seems to generated a suitable range of home range sizes that correspond to the home range parameter.

To determine how well the random walk model simulated actual hare movements within its home range I compared data simulated to actual hare movements observed using a radio

Figure 4.1: A comparison of home range areas (in hectares) generated by random walk model (H.R.A. parameter) and home ranges estimated from the resulting simulated data (in hectares). Each data set consisted of 100 independent points. Home ranges were estimated using the 95% harmonic mean home range estimator. Seven data sets were generated for each home range area. The bars around each point are one standard error from the mean.

Estimated home range area (from simulated data)



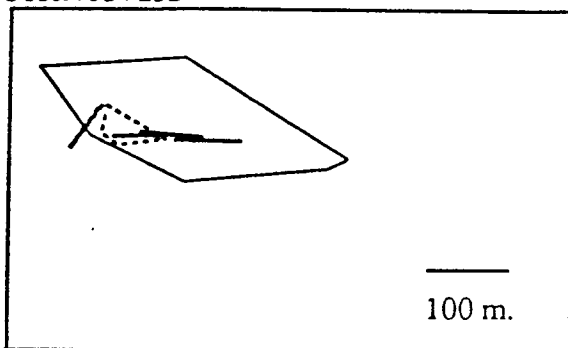
telemetry on Jacquot Island (Chapter 3). This comparison was difficult, for the resolution of data produced by the random walk model is much higher than paths observed using radio telemetry on Jacquot Island. The reason for the difference in resolution is that the unit of movement in the random walk model is a step length (10 meters) whereas the unit of observation of a radio-collared hare was where its location was every 45 minutes. The radio telemetry data displays the general area covered, not minute scale movements.

Therefore, when I compared the movements generated by the model to observed movements the actual objective of the random walk simulation had to be considered. The main objective of the random walk model was not to simulate exact movement patterns of hares but to simulate *differences* in movement patterns between animals that could affect trap encounter rates and subsequent capture probabilities. Minute scale movements were secondary in importance to actual areas an animal would cover in a given trap night.

The results from Jacquot Island (Chapter 3) suggest that animals exhibit a central tendency as a function of home range size, and that they are most likely to be trapped in core areas. Therefore, the criteria for acceptable model performance was if the animals "wandered" as a function of their home range size. These attributes are hard to compare (Siniff and Jessen, 1969) and therefore visual inspection of generated and observed paths was the best test given the objectives of the simulation. For this test I used animals that have been previously used as examples in Chapter 3. Data were generated for hares with high and low sinuosities as reflected by large and small home range sizes. I simulated ten different paths for each type and compared them to maps generated from the Jacquot data. An example of these tests are displayed in Figures 4.2 and 4.3. The criteria for acceptable performance were if the simulated

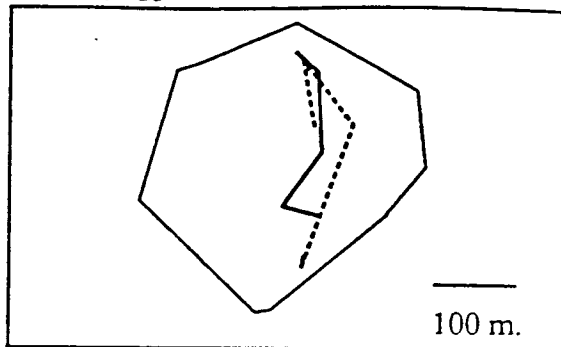
Figures 4.2 and 4.3: Hare movement patterns generated by the random walk model compared to observed paths on Jacquot Island in the spring of 1992. The top boxes on each page contain the paths observed using radio telemetry (in meters) on Jacquot Island during the spring of 1992 (Chapter 3). Fixes were taken on each animal every 45 minutes from 2100 to 0200 hours. Below these boxes are simulated paths from the random walk model using the hares observed home range to determine its sinuosity (S_p). Paths of 500 meters (10 meter steps) were generated for each hare which is roughly equivalent to the distance that a radio collared hare would travel during a telemetry monitoring session.

Observed #232



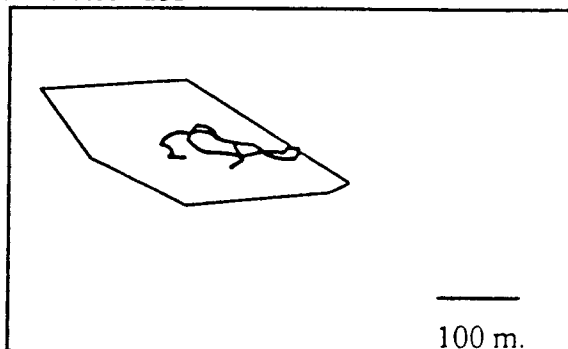
Home range = 5.2 hectares

Observed #25



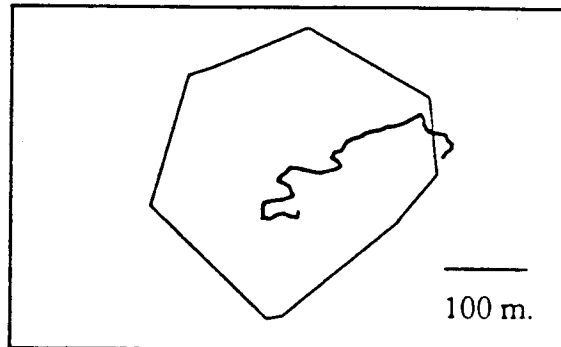
Home range = 12.86 hectares

Simulated #232



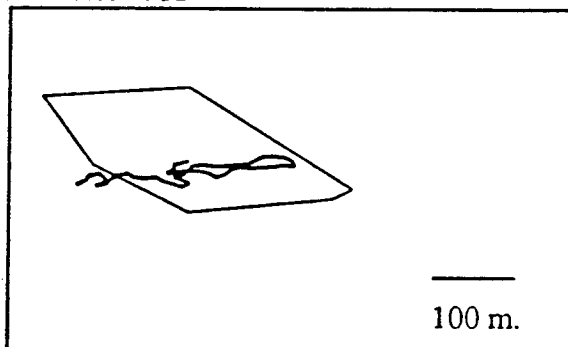
Sinuosity (Sb)=.26

Simulated #25



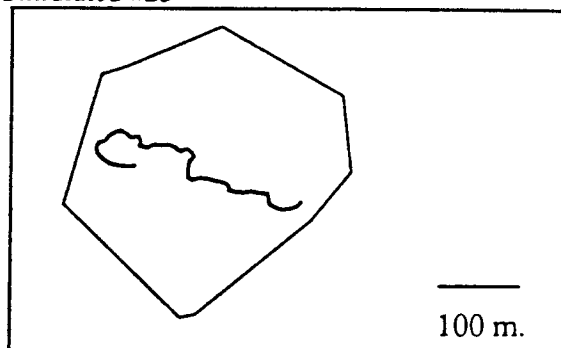
Sinuosity(Sb)=.19

Simulated #232



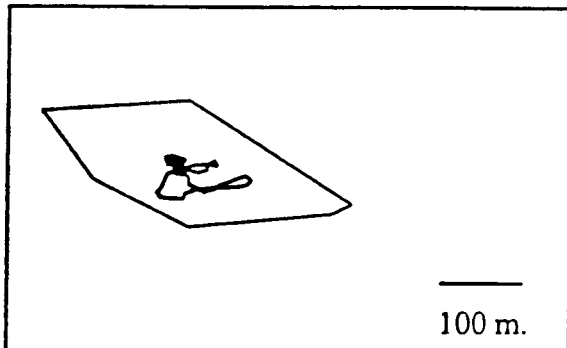
Sinuosity (Sb)=.26

Simulated #25



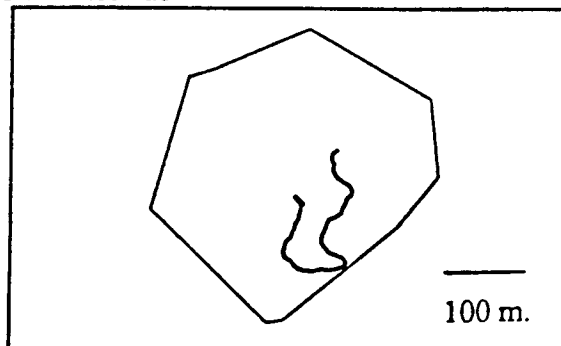
Sinuosity(Sb)=.19

Simulated #232



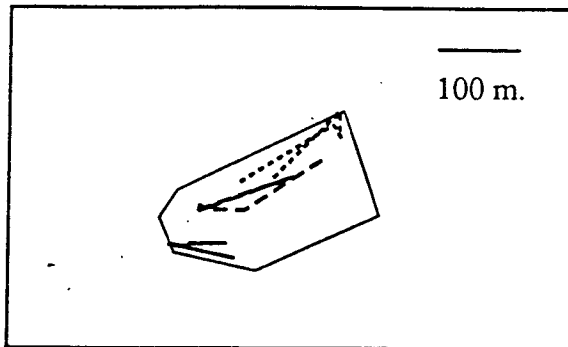
Sinuosity (Sb)=.26

Simulated #25



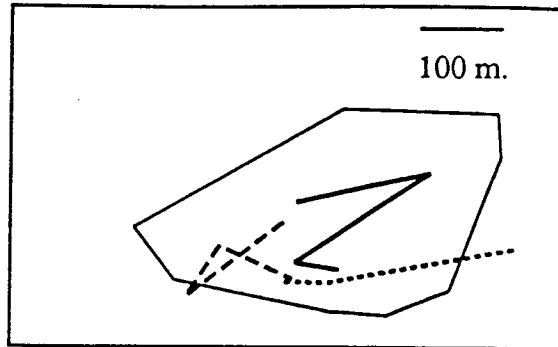
Sinuosity(Sb)=.19

Observed #425



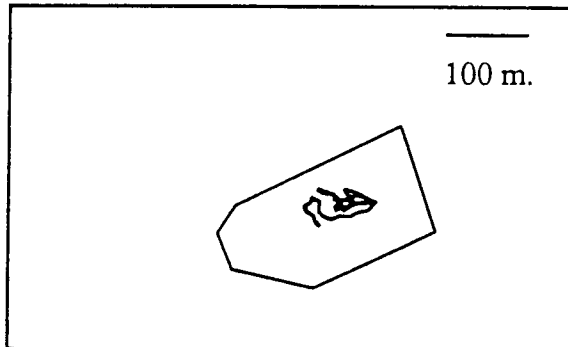
Home range = 4.06 ha.

Observed #372



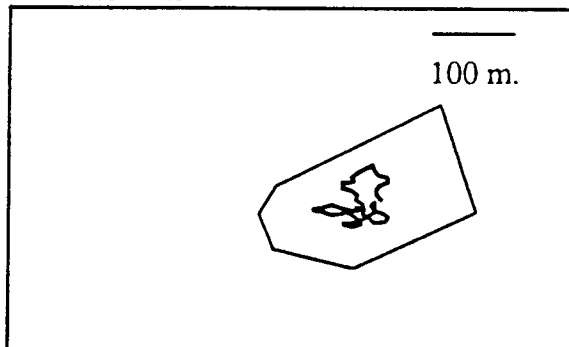
Home range = 11.27 ha.

Simulated #425



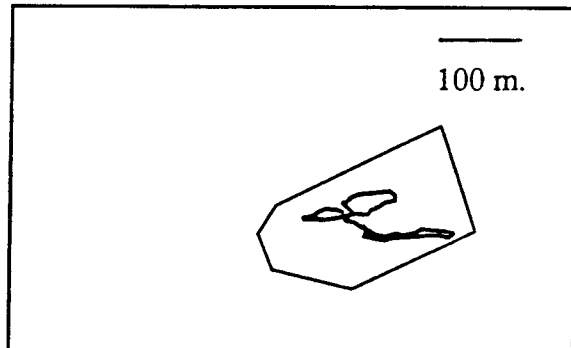
Sinuosity(Sb) = .3

Simulated #425



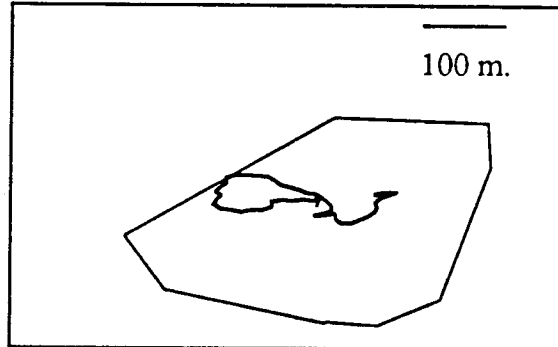
Sinuosity (Sb) = .3

Simulated #425



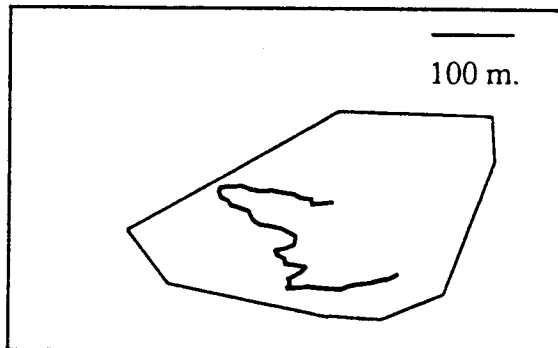
Sinuosity(Sb) = .3

Simulated #372



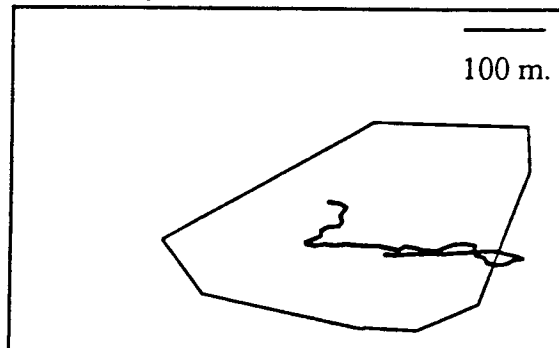
Sinuosity(Sb)=.23

Simulated #372



Sinuosity(Sb)=.23

Simulated #372



SinuositySb)=.23

hares traversed the same size area as the corresponding empirical hares. From visual inspection, the simulations seem like an adequate approximation.

Capture probabilities of hares

The experiments on Jacquot and Dezadeash suggested that differential movement patterns accounted for differences in hare capture probabilities. It was also possible that individual hare capture probabilities changed as a function of prior trapping experience (behaviour). Also, some individuals had tendencies to be trapped independent of past experience and movement pattern (heterogeneity).

The main purpose of this model is to simulate possible sample and estimator biases associated with the snowshoe hare cycle. The role of individual variation in hare capture probabilities plays a role in determining the magnitude of these biases. To simulate changes and differences in hare capture probabilities I used a modified version of a simulation model developed by K. Burnham and programmed by K. Wilson (1982). This model allows the user to simulate heterogeneity, behaviour, time, and all combinations of these factors to produce capture probabilities for individual animals.

I was limited in the number of simulations that I could do. Because of this I could only simulate two different underlying capture probability models. The most valid underlying simulation model is most likely variation of capture probabilities with time, behaviour and heterogeneity. However, the stochasticity of this model could make it hard to discern the effects of trap saturation and other simulated effects on estimates.

The objectives of this simulation were two fold: 1) to determine robustness of estimators to sample biases brought on by changes in hare density and the Kluane sampling design, and

2) biases brought on by biological differences between animals. The equal probability simulation model would be best to detect which models are most robust to changes in density. The more stochastic time/behaviour/heterogeneity simulation model would be a good test of which estimators can handle the extremes of capture probabilities in a hare population. In reality, the true underlying model could be somewhere in the range between the equal capture probability model and the model in which capture probabilities change with time, behaviour and heterogeneity. All these sources of capture probability variation were evident on Jacquot Island (Chapter 3) and so it is also biologically reasonable to use this model. This treatment will be abbreviated as model M_{tbh}

No simulation program is needed to simulate capture probabilities when all capture probabilities are equal. To simulate variation of capture probabilities with behaviour and heterogeneity I used a slightly modified version of K. Burnham's simulation model.

I will first describe model M_{tbh} in a conceptual format and then detail the mathematical equations. An individual (i) is assigned an capture probability (p_{ij}) for the first trap night (j) from a population distribution determined by an heterogeneity effect (B_i) and a time effect (Y_j). An effect is a randomly generated variable from a centred probability distribution. The capture probability of the hare varies each trap night only by a time effect (Y_j) until it is trapped. Once it is trapped its capture probability decreases or increases as determined by a behaviour effect (V_{ij}). The initial distribution of capture probabilities, and the distribution of changes in capture probabilities is assumed to be approximately normal or slightly centred and is approximated by a beta distribution (discussed below). The actual equations are now detailed.

$$\theta_{ij} = \theta + (B_i - \bar{B}) + (Y_j - \bar{Y}) \text{ for } j=1 \quad (12)$$

$$\theta_{ij} = \theta_{i,j-1} + V_{ij}Z_{ij} + (Y_j - \bar{Y}) \text{ for } j>1 \quad (13)$$

$$p_{ij} = \frac{e^{\theta_{ij}}}{1 + e^{\theta_{ij}}} \quad (14)$$

In equation 12, θ_{ij} is a capture probability for individual i on trapping occasion (or trap night) j . θ is the mean capture probability effect and is proportional to the mean capture probability input for the simulation. B_i is a heterogeneity effect, and B is the mean effect for the population. Y_j is a time effect that is generated each trap night affecting each individual equally and Y is the mean effect for the population. For subsequent trap nights, ($j>1$) the capture probability effect is defined by equation 13. In equation 13, the capture probability from the previous trap night ($\theta_{i,j-1}$) plus a behavioural effect (V_{ij}) and time effect determine an individuals capture probability. The inclusion of V_{ij} is determined by Z_{ij} that is equal to 1 if an animal has been trapped on occasion $j-1$, and is equal to 0 otherwise. So if the animal was not trapped on the previous trapping occasion ($j-1$), then the behaviour term (V_{ij}) has no effect.

So for each individual hare (i) on each trap night (j) an effect (θ_{ij}) is generated. To assure the capture probability effects are contained between 0 and 1 θ_{ij} is scaled into a probability (p_{ij}) using a logistic transform equation (14).

Each effect was generated from a beta distribution. For my simulation I used beta parameters $a=2$ and $b=2$ to simulate the heterogeneity effect. This produced a slightly centred distribution with mean .5 and variance .05. I chose this to produce a wide scatter of initial capture probabilities. The behaviour and time effects were simulated with beta parameters $a=6$ and $b=19$. These produced a normal distribution with mean .24 and variance .07. I chose these

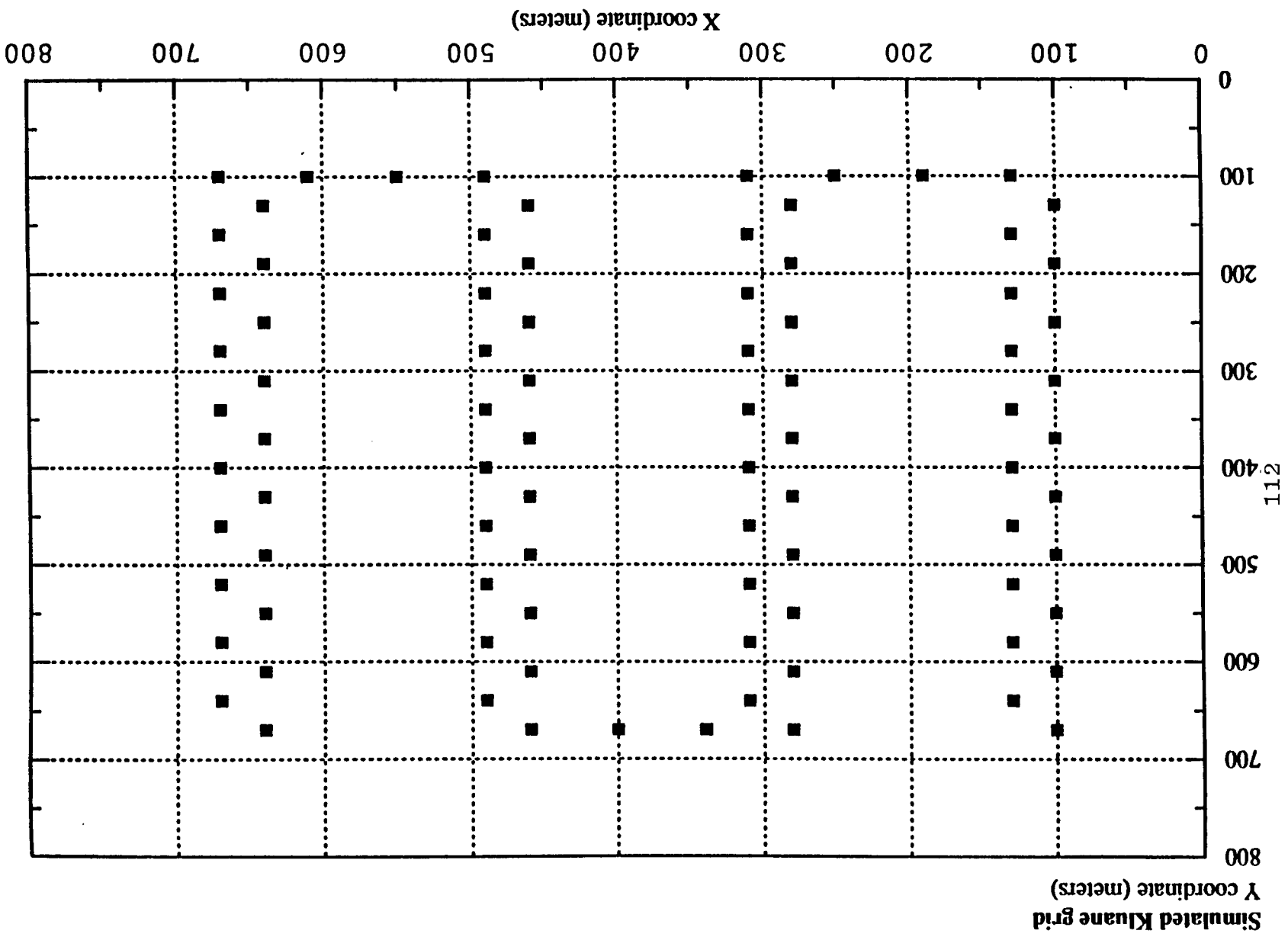
parameters to make the effect of trapping time centred, with occasional larger effects. It is impossible to actually determine what the values of these parameters are empirically. These effects are my "best guess" at what the distributions may be.

The trapping process

A set pattern of traps mimicking the Kluane setup was employed for each simulation (Figure 4.4). At the beginning of a simulation animals were placed on the grid in a random spatial distribution. Individual hares are assigned capture probabilities dependent on the underlying capture probability model. Each hare is moved by the given random walk model for a time step i . At each time step the distance of each hare from each trap on the grid is evaluated. The order in which hares are evaluated is randomized so that hares with low "eartag" numbers are not considered first to be trapped. If a hare's location is within the capture radius of a trap it is possibly trapped dependent on its probability of capture. If the hare's probability of capture is greater than a randomly generated uniform probability, then it is captured. The trap, as well as the hare, is no longer considered in the trapping process for the rest of the given trap night. If the hare is not within a capture radius of a trap, or its probability of capture is less than the random uniform probability, it continues on its path. At the end of the trap night captured hares numbers are recorded and stored. This process is repeated for each trap night.

Hares are allowed to wander out of the grid area. It is important to note that their initial positions are on, or within 25 meters of the grid area. This initial condition simulates heterogeneity caused by animals living on the edge of the grid. However, because the smallest animal home range size allowed was 1 hectare, even animals that had home ranges on the edge

Figure 4.4: The Kluane grid setup used in the simulation. This is an exact replica of the setup used currently.



of the grid would traverse the grid area and encounter traps and could therefore be considered part of the trappable population.

Choice of simulation parameters

Densities of hares

The main objective of this model was to simulate possible sampling biases at different hare densities. To determine what densities are actually found on Kluane grids I used Kluane data. I found the densities ranged from 10 (Sulphur) to 400 (Hungry Lake) hares dependent on the phase of the cycle for data from November 1985 to October 1992. I chose to simulate hare densities of 20, 50, 100, 200, and 400 on the trapping grids.

Capture probabilities

Results from previous chapters indicate that the mean capture probability of the population during a sampling period has a large effect on bias and accuracy of estimates. I was interested in mimicking the Kluane experiment, so I analyzed data from three grids to determine the range of capture probabilities usually observed. I used data from trapping periods that occurred in the spring or late fall, and had at least five successive trap nights. The probabilities were calculated using the formula:

$$\bar{p} = \frac{n}{t\hat{N}}$$

In this formula, n is the total captured in a trapping period, t is the trapping period, and N is the estimated population number. I used the M_h estimate for population size because it is usually the highest estimate, and will therefore make p the lower bound on the actual capture probability. It is important to remember that this value for p is an estimate. Estimated lower bounds on mean capture probabilities per trap night were .15 (range .08-.22) for Beaver Pond,

.45 (range .34-.57) for Sulphur, and .19 (range .1-.24) for Hungry Lake for trapping between November 1985 and October 1992. From these data I chose to simulate data capture probabilities of .23 and .35, which represent the mean values found on most Kluane grids. I also simulated a mean capture probability of .1 to determine estimator performance at the lowest observed mean capture probability level. The method in which capture probability parameters were chosen to produce the simulated data capture probabilities is detailed below.

The lower (.1) capture probability simulations were very difficult. Program CAPTURE estimations would continuously "get stuck" creating astronomical error messages and freezing the simulations. This is a problem with the UNIX version of the program CAPTURE code. It is far beyond the scope or objective of this thesis to fix. As a result, I will only detail these simulations when applicable.

Capture radius, hare density, and mean data capture probabilities

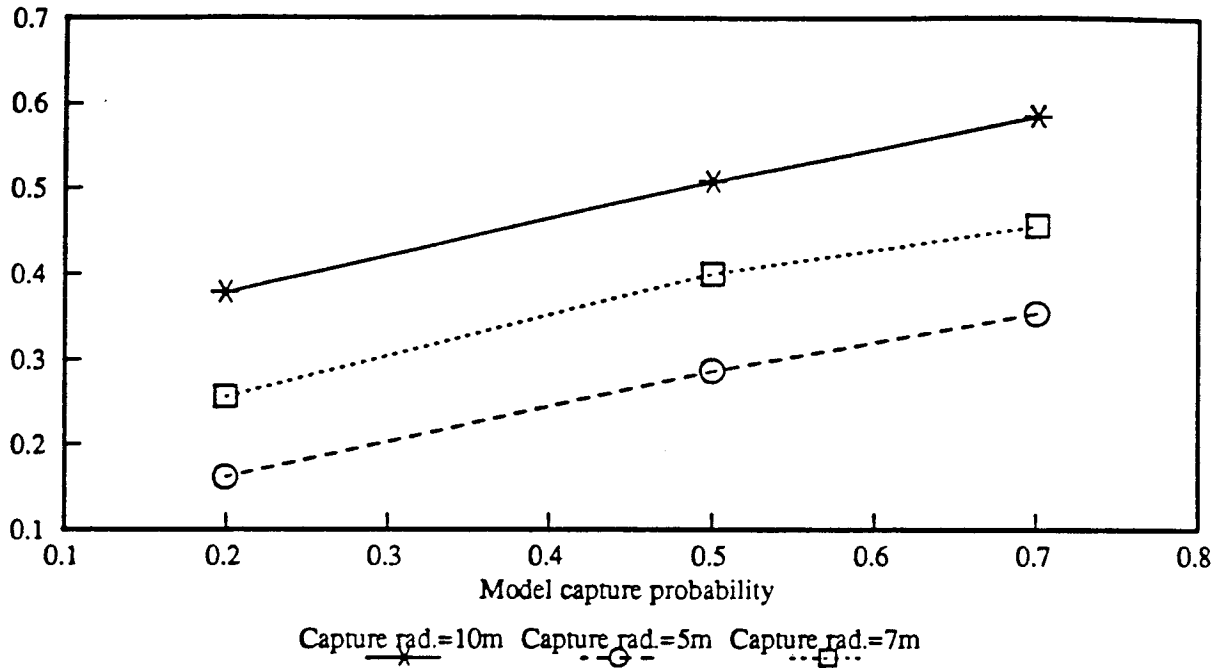
In each simulation, a mean capture probability for the population is an input parameter. Capture probabilities are then assigned to individual hares based on which capture probability model is being used. The mean capture probability parameter does not necessarily reflect the mean capture probability in the simulated data. I found that the capture probability in the simulated data is very dependent on the capture radius of the traps and population density being simulated (Figure 4.5).

I kept the capture radius of traps constant for each simulation treatment. Previous users of this model (Wilson 1982) have employed an iterative routine to change the capture radius of traps with each simulation so that the capture probability in the data will always approximately equals the capture probability parameter input into the model. This method is

Figure 4.5: An example of the effects of population density (hares/39.06 hectares) and capture radius on mean capture probability in the simulated data. The upper graph demonstrates the influence of capture radius on capture probability in the simulated data for a simulated population size of 50 hares. The lower graph documents changes in simulated data capture probability as hare density increases and traps become saturated.

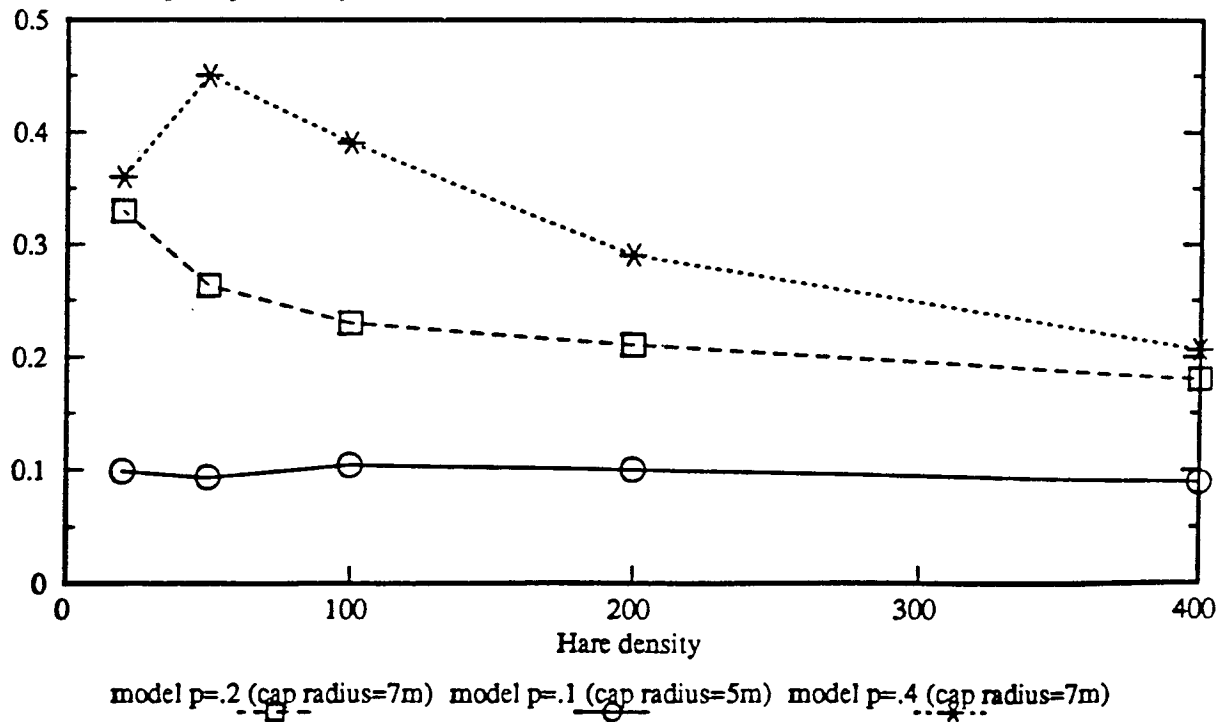
Data capture probability vs capture radius for N=50 hares

Mean data capture probability



Data capture probability vs population density

Mean data capture probability



biologically unrealistic because the attraction of a hare to a trap becomes a function of population density. With this routine, at low hare densities the capture radius usually is large (for example; 20 meters) and a hare is possibly trapped if it is within 20 meters of the trap. At high densities the capture radius is small (for example; 2 meters), so a hare would be possibly trapped if it were within 2 meters of the trap. I found no evidence that a hare will be more or less attracted to a trap as a function of population density. It is much more biologically reasonable to assume that hares are attracted to traps independent of density.

A trend of decreasing mean capture probability as a function of increasing hare density is apparent in data from all Kluane grids. A plausible explanation for this is that as the number of hares increases, the traps become saturated allowing less individuals the opportunity to be caught, and as a result the mean capture probability of the population decreases. By keeping the capture radius of traps fixed this effect was simulated (Figure 4.5).

To determine the best combinations of input capture probabilities and capture radiuses to use that allows the mean capture probability input to generate an equivalent range of capture probabilities in the output data I did a series of simulations. In these simulations capture radius was varied until mean capture probability input would approximately equal capture probability output as calculated in the formula described previously . This was done for a range of hare densities. (Figure 4.5) I found the optimal capture radius for the model was 7 meters for the .2 and .4 simulation, and 5 meters for the .1 capture probability simulations. This set of combinations produces a range of capture probabilities that is observed on Kluane grids.

Number of simulations run

In this study there were 45 different combinations of parameters simulated. More

specifically, there were 5 hare densities (20, 50, 100, 200, 400), 3 different mean capture probabilities (.1,.2,.4) and two underlying capture probability models (equal and M_{tbb}). For each combination of parameters 1000 simulations were run. This was the optimum number of simulations to allow for comparable results between treatments. Each parameter combination simulated took 10 to 20 hours of continuous CPU time on a SUN SPARC station to run. The density of hares being simulated, and the complexity of the underlying capture probability model was the main factor in determining the time for each treatment.

Criteria for evaluation of estimation models

An optimal estimation model should show low bias and high precision. Related to this is the robustness of a model, or how much its performance changes when its underlying assumptions are not true. Unlike most field situations, true population size is known and therefore bias can be determined. It is expressed as percent relative bias which is:

$$P.R.B. = \frac{E(\hat{N}) - N}{N} \times 100$$

In this equation the mean estimate from the simulations is equated to the true value.

Precision is indexed by the coefficient of variation. The formula for coefficient of variation is:

$$C.V. = \frac{\theta}{E(\hat{N})} \times 100$$

In this equation $E(N)$ is the mean estimated population number for the particular estimation model and θ is the mean standard deviation of N .

Results and Discussion

It is important to interpret the results of the simulations in terms of the precise objectives

of the simulation model. For this reason, I will first summarize the criteria for estimation model evaluation. Then I will discuss results pertaining to specific models and model selection routines.

Interpreting estimator bias and precision

Bias

It is important to remember the objectives of the simulation when interpreting the results pertaining to bias. The main objective of the simulations is to determine robustness of models to sampling biases caused by changes in hare density and the Kluane trapping design. To address this the simplest (equal probability of capture) and the most complex (variation by heterogeneity, time, and behaviour) were used. The assumption I am making is that the actual underlying capture probability distribution is somewhere between these two extremes and a good estimator should be robust to both underlying models.

It is erroneous to assume that the results from any particular simulation reflects the actual bias that may be found in the field. Instead, as stated in the objectives, this simulation model should be used to compare models, and theorize what possible biases in estimates could result from the sampling biases simulated.

The criteria for appraisal of bias is therefore as follows. First, an adequate model should exhibit constant bias as density increases which would infer that it is robust to trap saturation biases. The effect of trap saturation would be most noticeable with the simulations in which hares had equal probability of capture. Second, because edge effects were minimal, (ie. all hares had home range centers on, or within 25 meters of the edge of the grid) a model should not exhibit an extreme negative bias. The simulations with all hares having equal capture

probabilities of capture represents a very simple sampling situation which probably does not occur in the real world. In this case the sources of bias are only the differential movement patterns of hares and unequal trap spacing, and a slight edge effect. If an estimator exhibits negative bias with this simulation, it probably will exhibit an even more negative bias in the real world.

Precision

The precision of an estimator is the repeatability of its estimates from similar data sets. Usually more complex models exhibit lower precision than simpler models because they are estimating more parameters. Also precision usually increases as sample size increases and sample error decreases. In the case of these simulations, the precision is indexed by the coefficient of variation of particular estimates.

The degree of precision needed in estimates relates to the objectives of the particular study. In the case of the Kluane study the estimates are mainly used for assessing general trends in populations. In this case, an estimator of fairly high precision is desirable. Pollock et al 1990. states that a coefficient of variation of 20 percent or less is usually adequate for most capture recapture studies. This should be the upper bound for any estimator used with the Kluane data.

The criteria for evaluation of precision is therefore as follows. An estimator should have a mean coefficient of variation that is below 20 percent for the simulations. A more desirable estimator should show a decreasing coefficient of variation as density increases which would reflect increasing precision. A low coefficient of variation, and the characteristic of consistent bias at all hare densities are the two main criteria in determining the usefulness of an estimator

with snowshoe hare data.

Model-specific results

Three levels of capture probability, .1, .2 and .4 were simulated. In general, results from the .2 and .4 capture probability level were very similar. The results from the .1 capture probability were erratic with all models (except models M_{bh} (Pollock) and M_b) showing unacceptable coefficients of variation above 30%. The .1 simulations represent the extreme lower end of capture probabilities Kluane grids, and as a result I will not focus the discussion on these results. Because the simulation probability of .2 simulations represent the usual capture probability range found on Kluane grids, they are discussed in more detail. The results with capture probability equal to .4 can be thought of as upper bound on estimator performance.

The results for each model type are discussed below. The results are summarized graphically in Figures 4.6 through 4.13. The results are described only in figures. Tables with exact numbers would be meaningless in this case since the actual biases and coefficients of variation should only be interpreted in terms of comparison between models.

Heterogeneity Models

The heterogeneity models of Burnham and Overton, (1978) and Chao, (1989) displayed the least bias with both underlying models of capture probability. They also showed a generally acceptable coefficient of variation with exception of the $N=20$ simulations with capture probability equal to .2 (Figures 4.6 and 4.8).

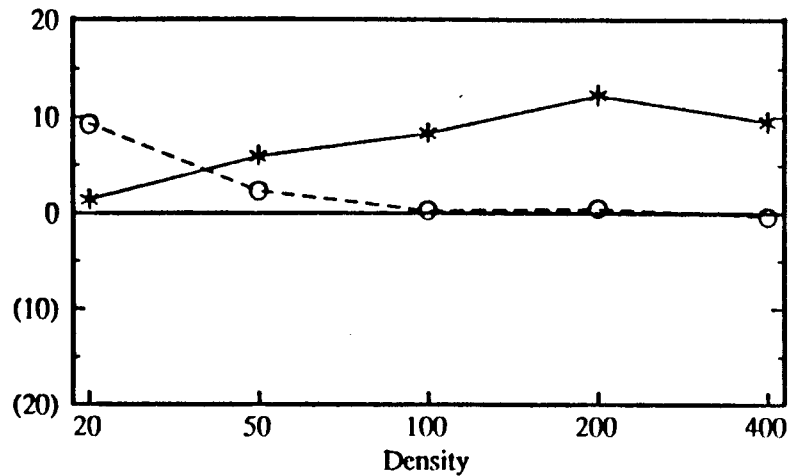
The jackknife estimator (M_b) of Burnham and Overton (1978) showed a positive bias with the equal probability capture simulations and a slightly negative bias with the more complex M_{bh} simulations. Unlike most estimators, it showed a slight increasing positive trend

Figures 4.6 and 4.7: The results from simulations in which all animals had equal probability of capture of .2 was simulated. Figure 4 displays bias and Figure 5 displays precision as reflected by coefficient of variation. Density expressed hares/39.06 hectares.

Results: Equal hare capture probabilities, mean $p=.2$

Heterogeneity Models

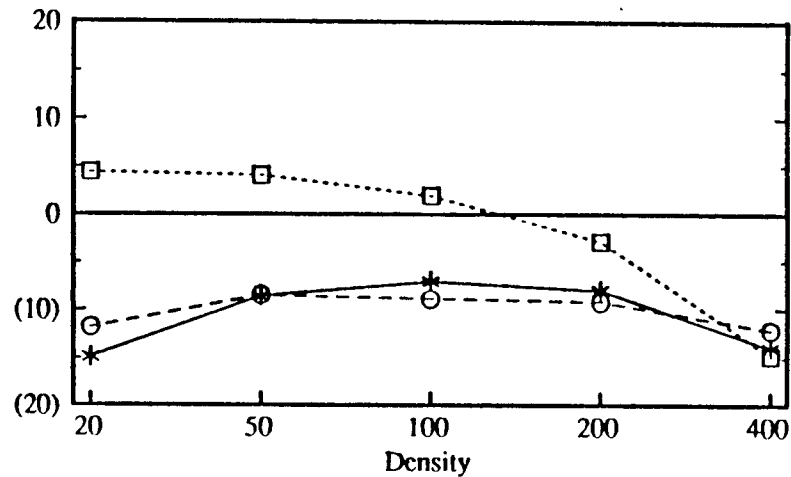
% Bias



M_h $M_h(\text{Chao})$

Other Models

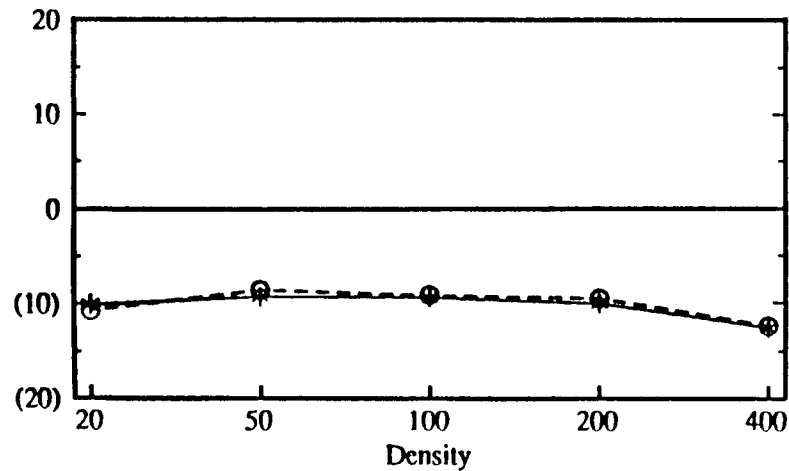
% Bias



M_b M_{bh} $M_{bh}(\text{Pollock})$

Null and Behaviour Models

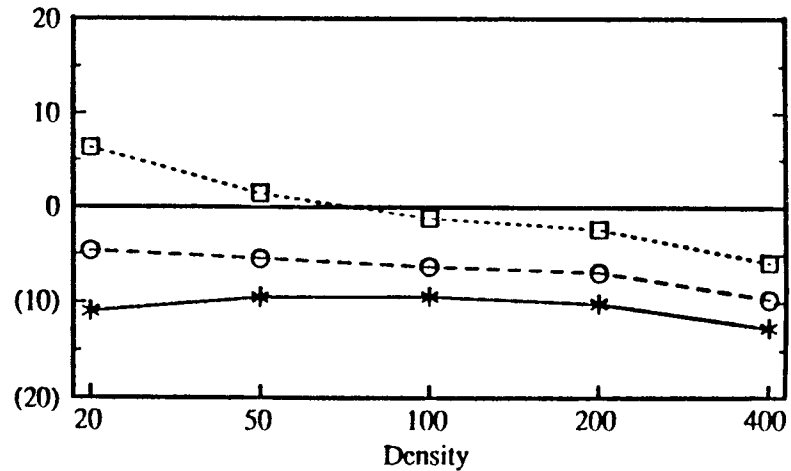
% Bias



M_o M_b

Time and Time/Heterogeneity Models

% Bias

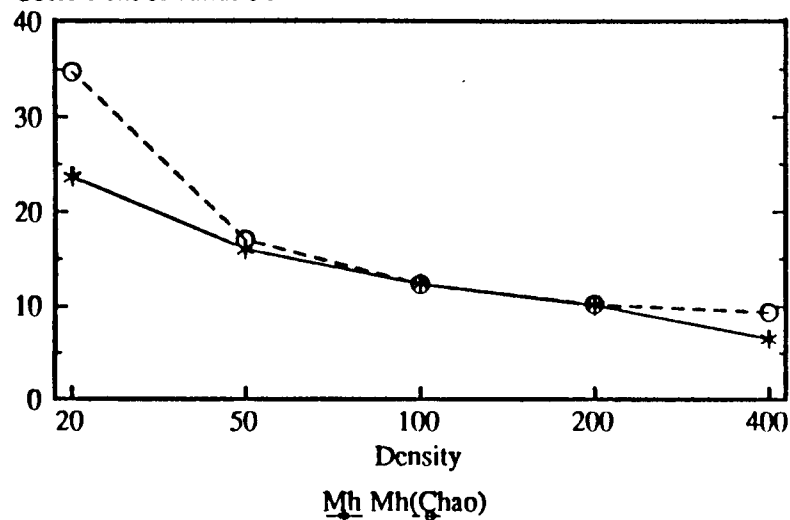


M_t $M_t(\text{Chao})$ M_{bh}

Results: Equal hare capture probabilities, mean $p=.2$

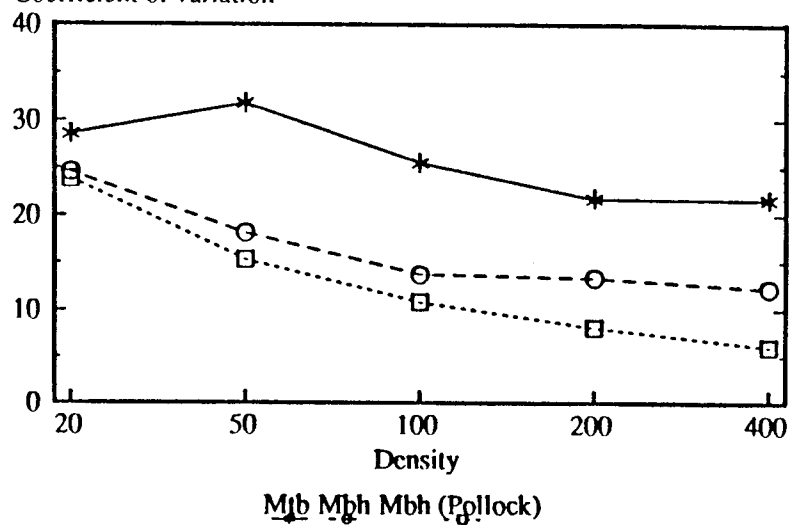
Heterogeneity Models

Coefficient of variation



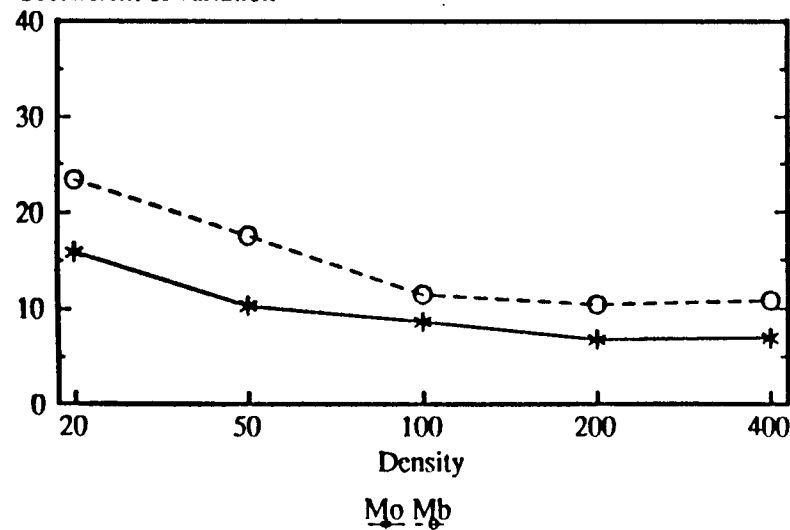
Other Models

Coefficient of variation



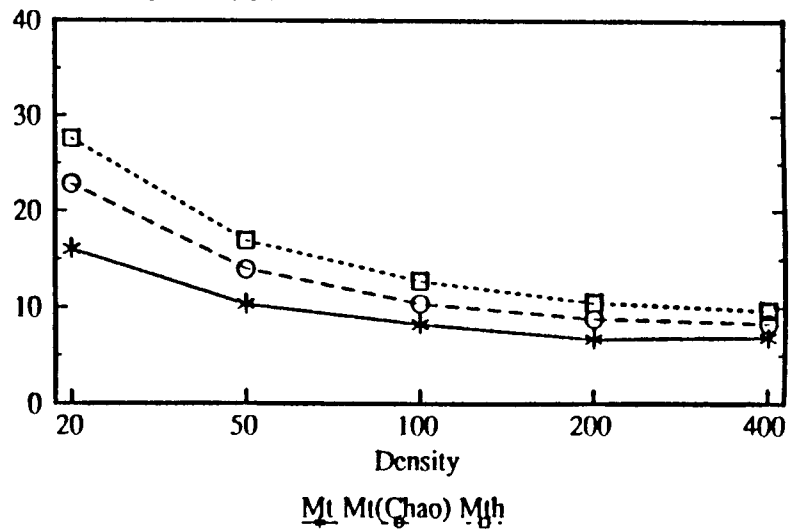
Null and Behaviour Models

Coefficient of variation



Time and Time/Heterogeneity Models

Coefficient of variation

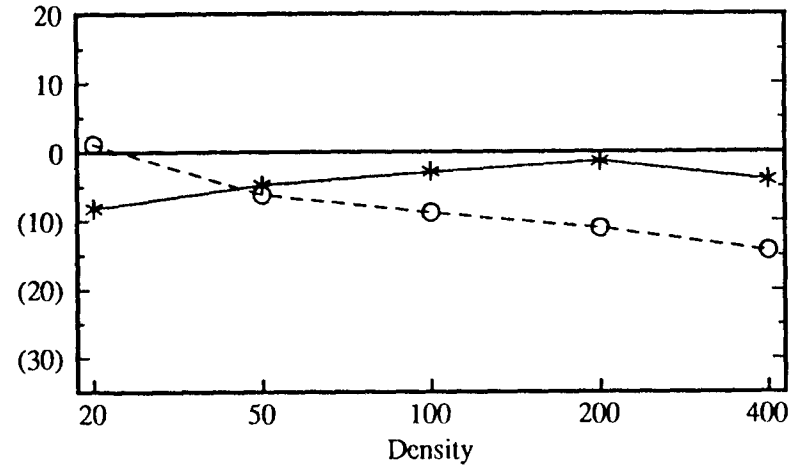


Figures 4.8 and 4.9: The results from simulations in which model M_{tbh} was the underlying capture probability model. A mean capture probability of .2 was assigned to each animal. Density expressed hares/39.06 hectares.

Results: Mtbh underlying capture probability model, mean $p=.2$

Heterogeneity Models

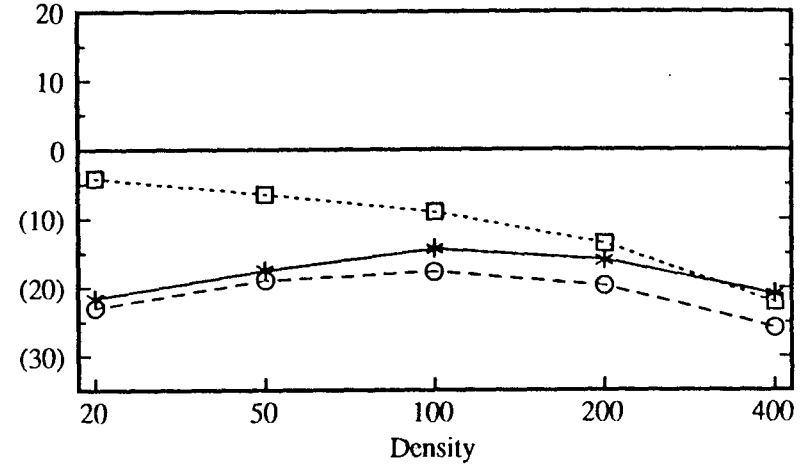
% Bias



Mh Mh(Chao)

Other Models

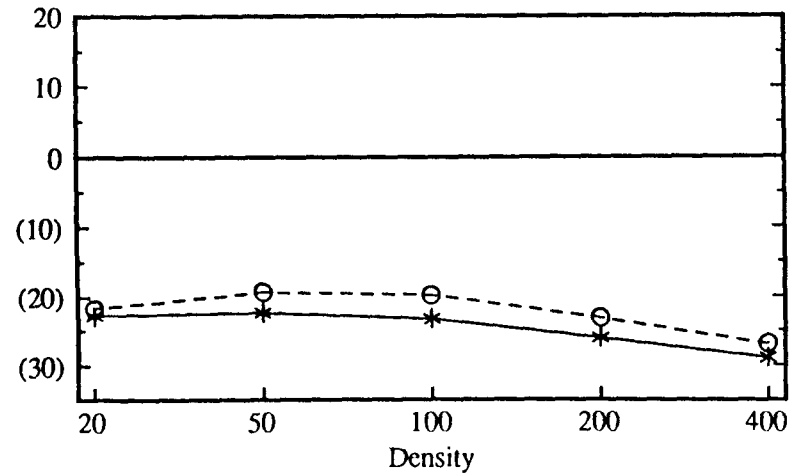
% Bias



Mb Mbh Mbh(Pollack)

Null and Behaviour Models

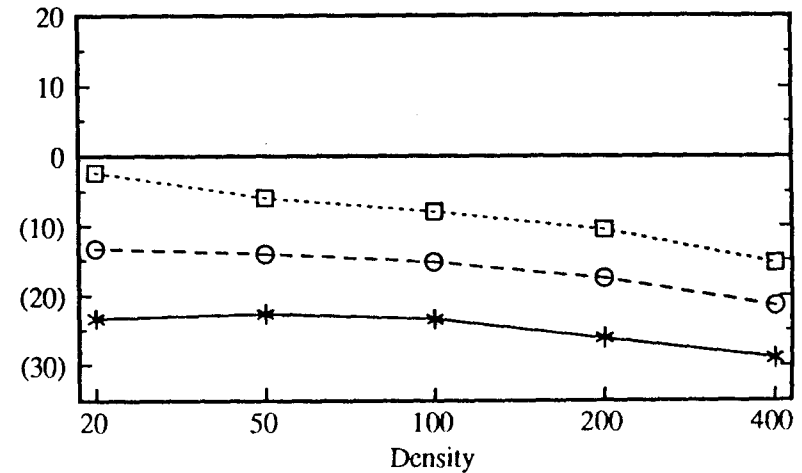
% Bias



Mo Mb

Time and Time/Heterogeneity Models

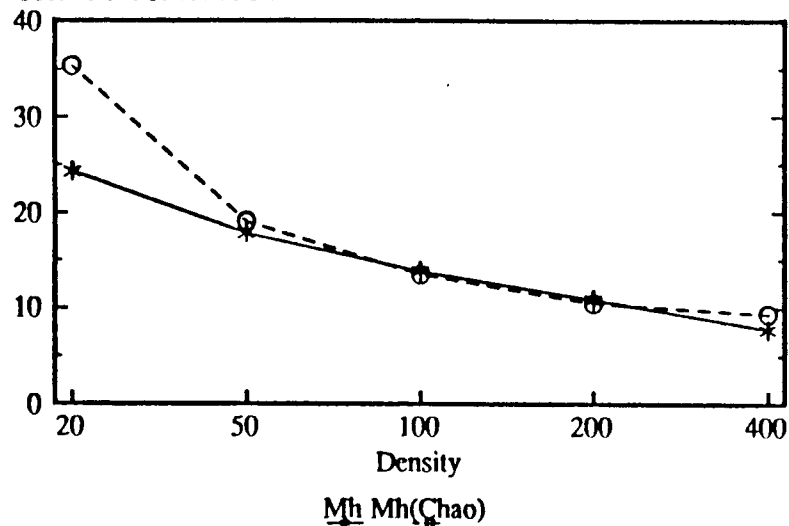
% Bias



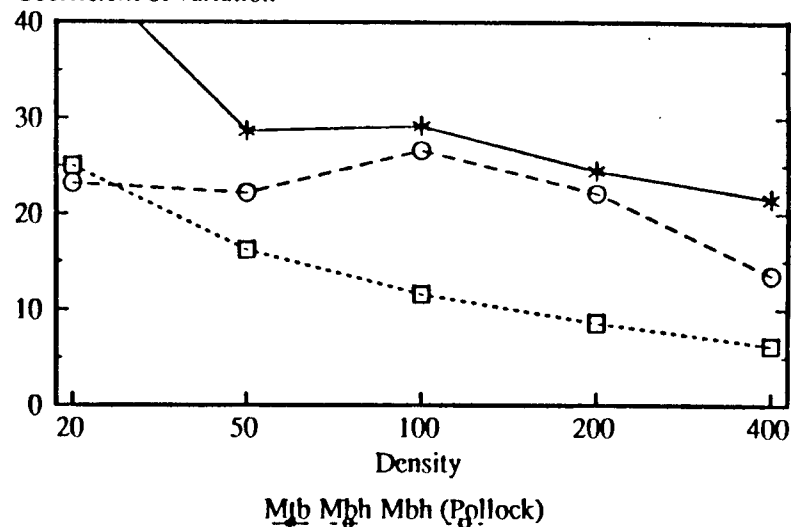
Mt Mt(Chao) Mbh

Results: Mtbh underlying capture probability model, mean $p=.2$

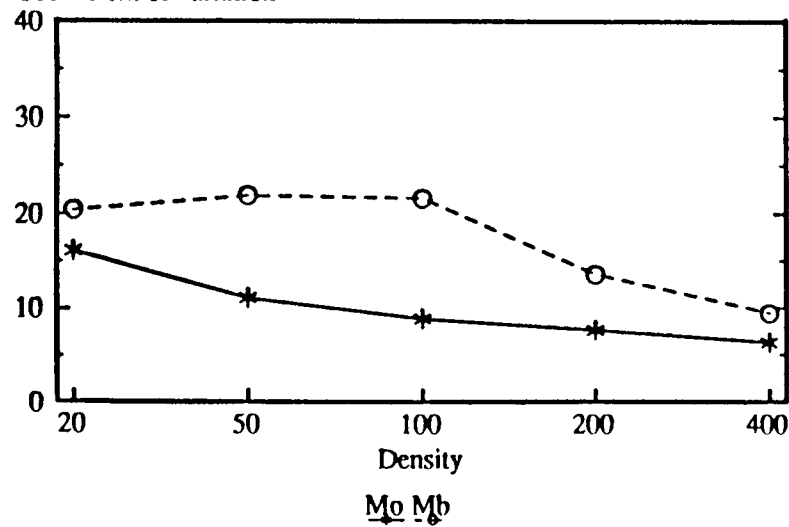
Heterogeneity Models
Coefficient of variation



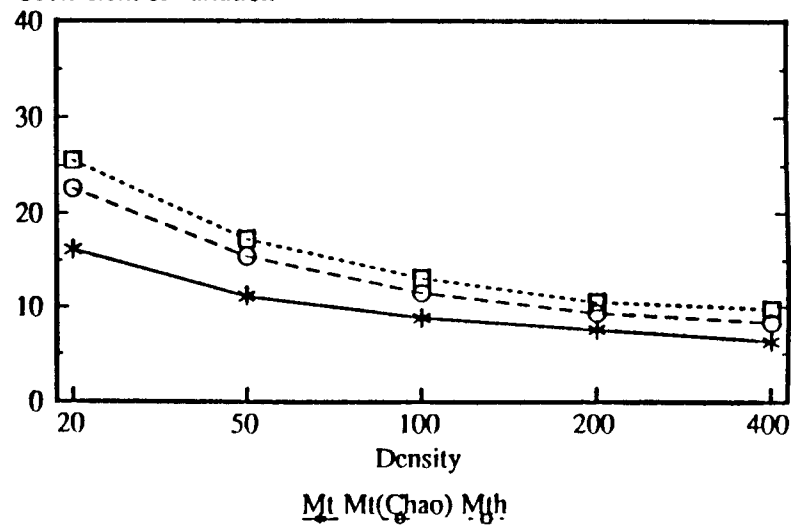
Other Models
Coefficient of variation



Null and Behaviour Models
Coefficient of variation



Time and Time/Heterogeneity Models
Coefficient of variation

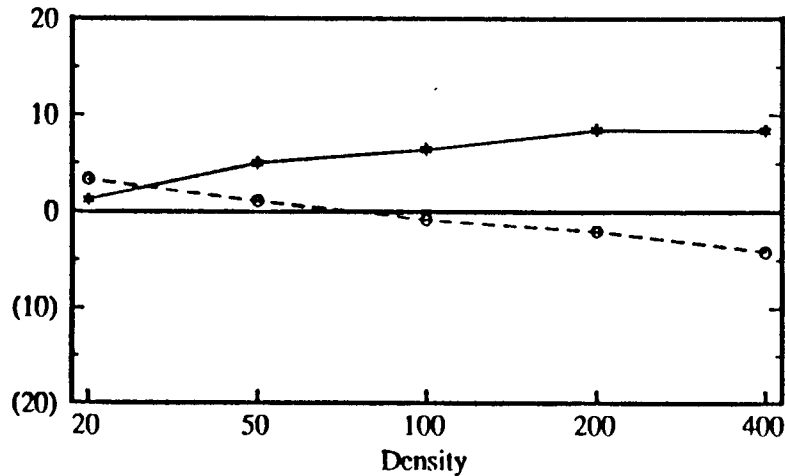


Figures 4.10 and 4.11: The results from simulations in which all animals had equal probability of capture. A capture probability of .4 was assigned to each animal. Density expressed hares/39.06 hectares.

Results: Equal hare capture probabilities, mean $p=.4$

Heterogeneity Models

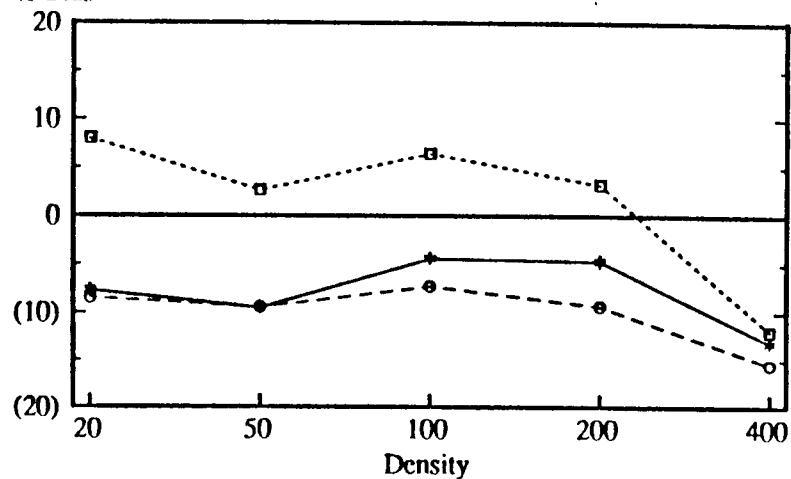
% Bias



M_h $M_h(\text{Chao})$

Other Models

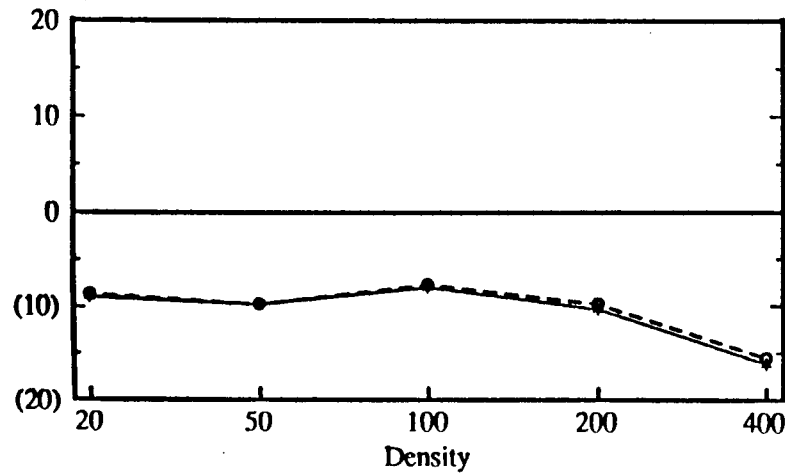
% Bias



M_b M_{bh} $M_{bh}(\text{Pollack})$

Null and Behaviour models

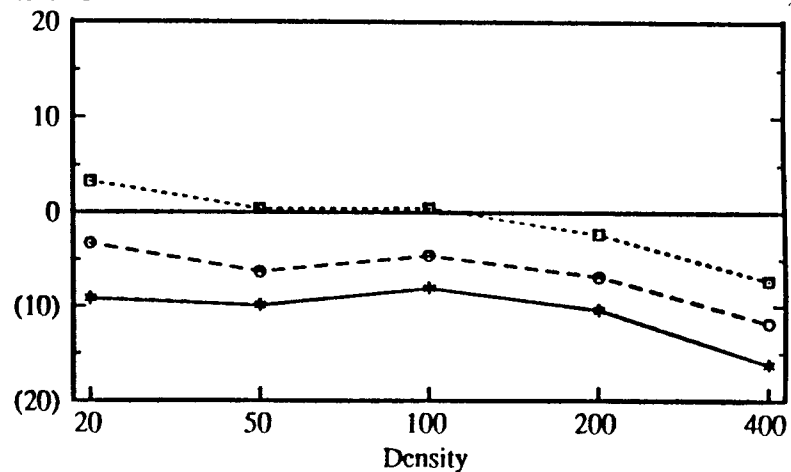
% Bias



M_o M_b

Time and Time/Heterogeneity Models

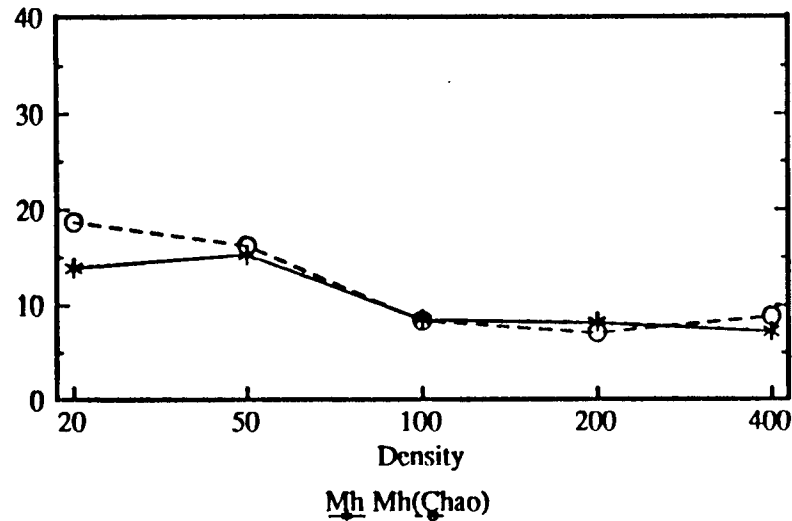
% Bias



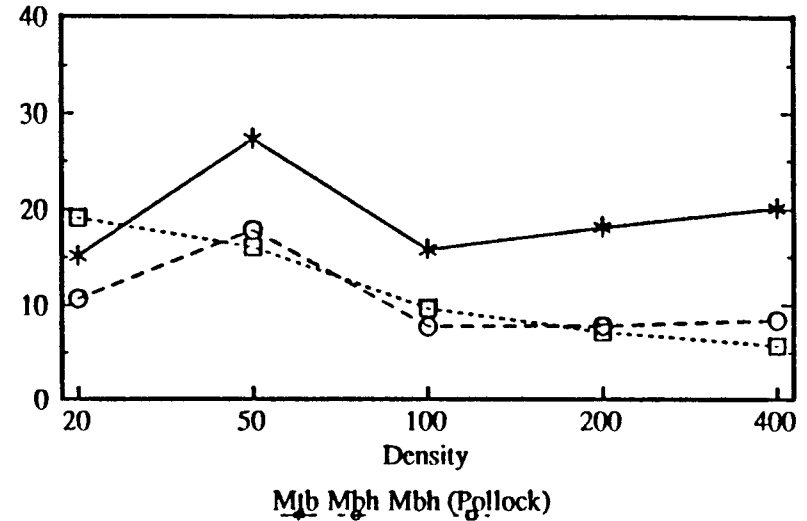
M_t $M_t(\text{Chao})$ M_{bh}

Results: Equal hare capture probabilities, mean $p=.4$

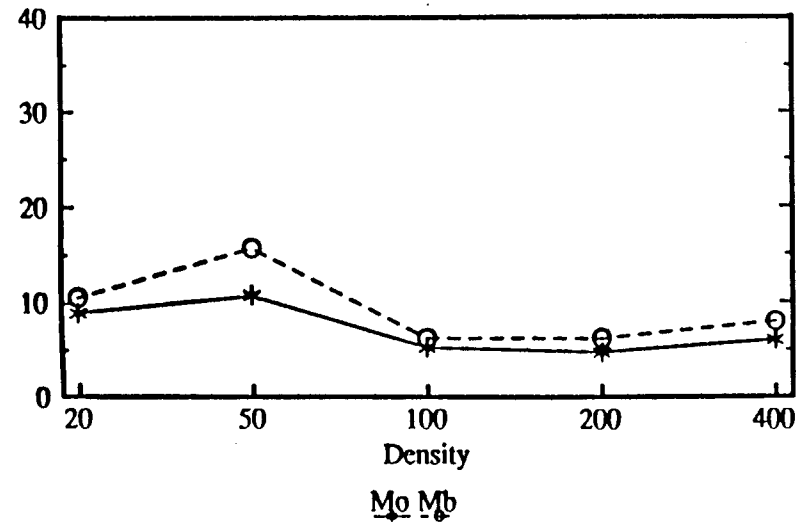
Heterogeneity Models



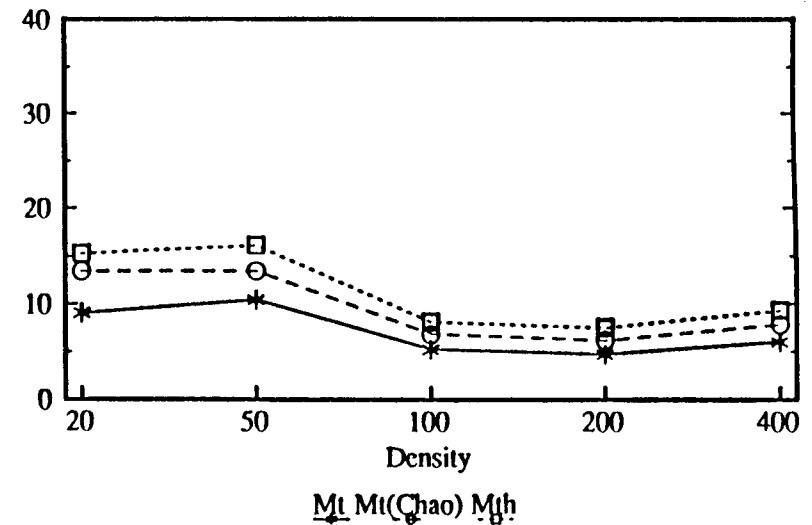
Other Models



Null and Behaviour Models



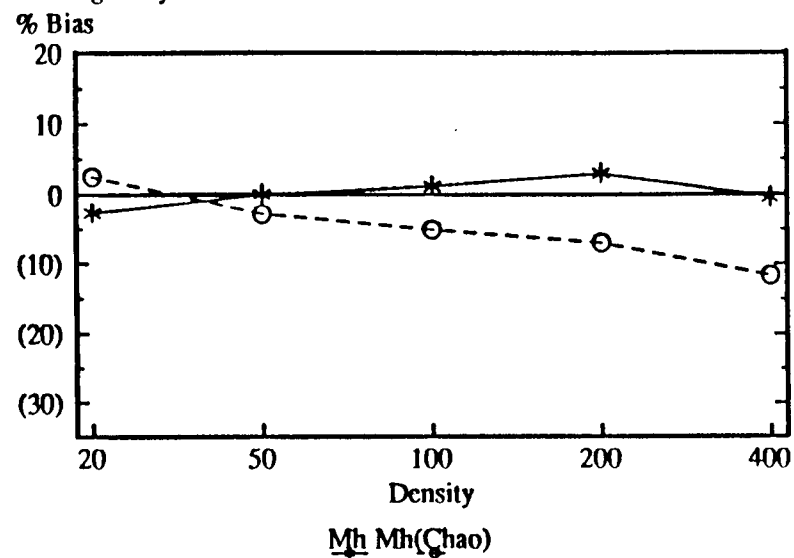
Time and Time/Heterogeneity Models



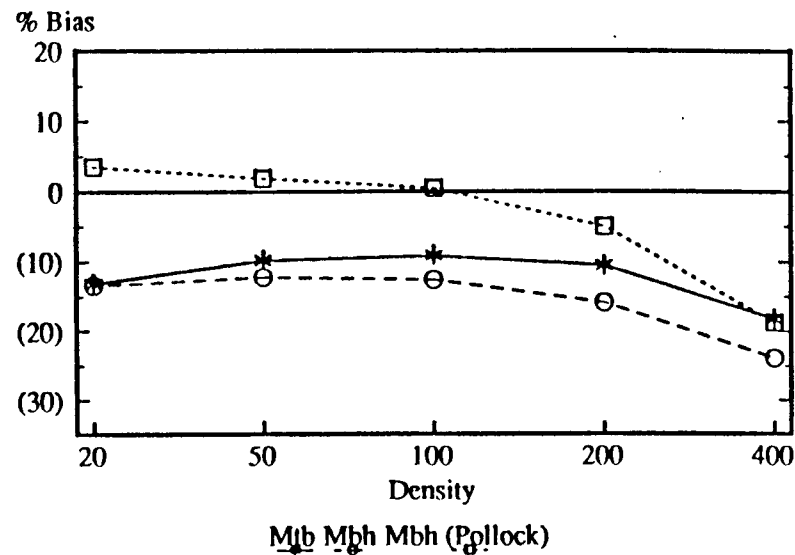
Figures 4.12 and 4.13: The results from simulations in which M_{tbb} was the underlying capture probability model. A mean capture probability of .4 was simulated. Density expressed hares/39.06 hectares.

Results: Mtbh underlying capture probability model, mean $p=.4$

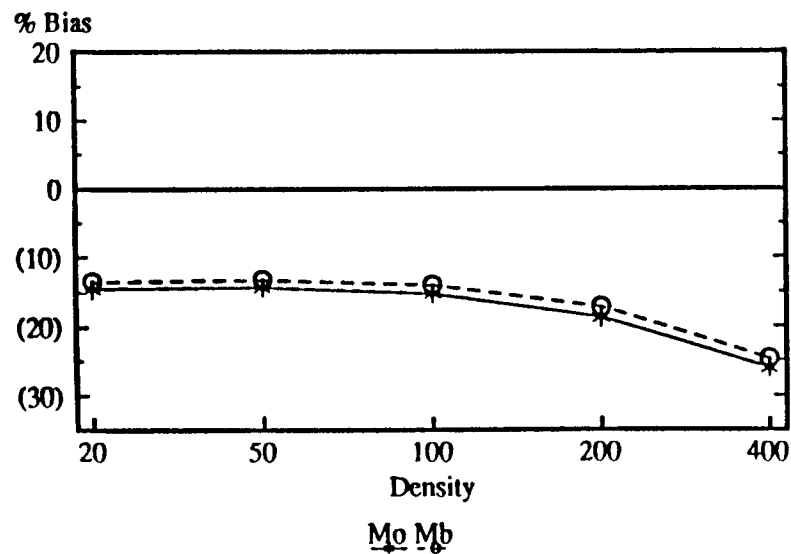
Heterogeneity Models



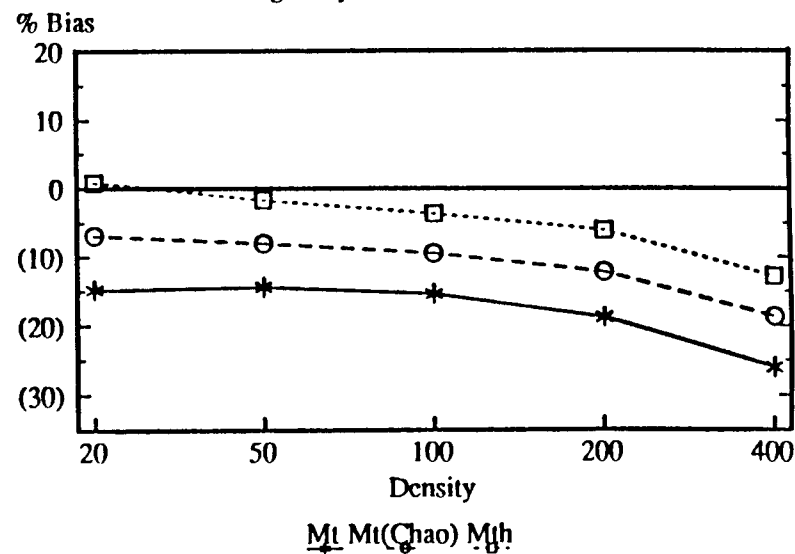
Other Models



Null and Behaviour Models

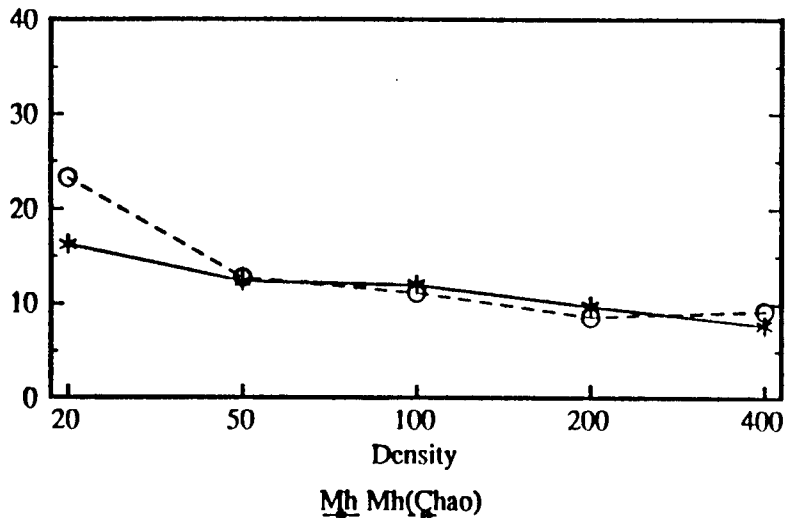


Time and Time/Heterogeneity Models

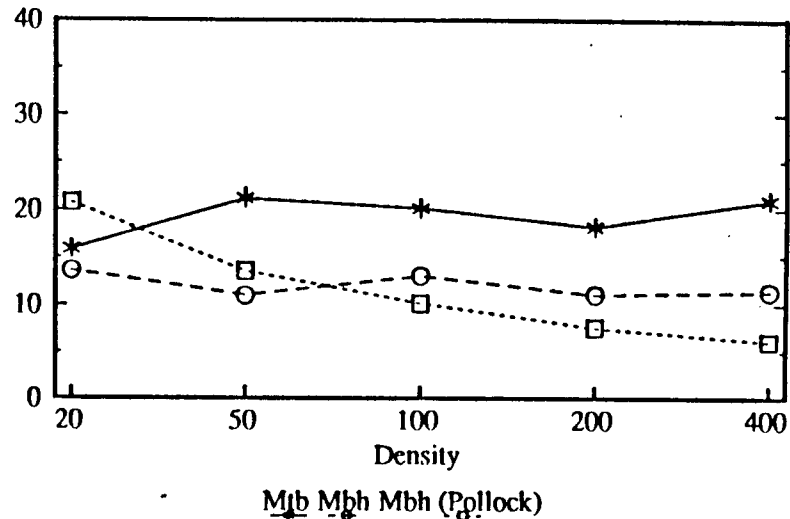


Results: Mtbh underlying capture probability model, mean $p=.4$

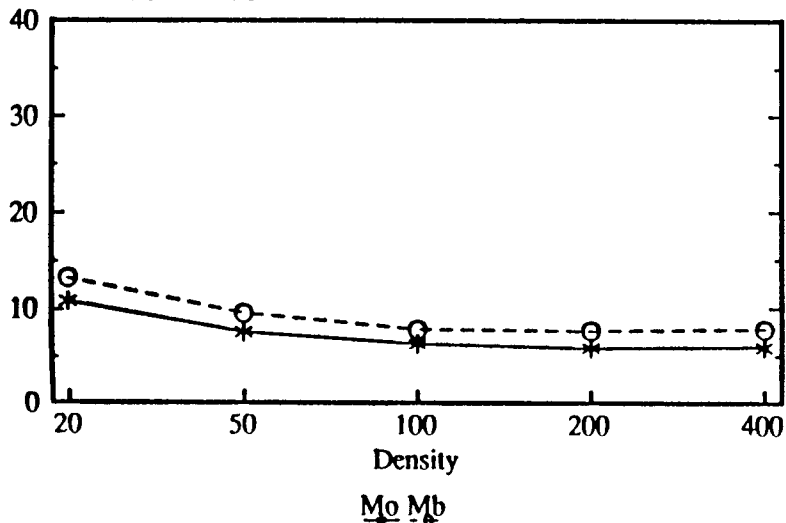
Heterogeneity Models
Coefficient of variation



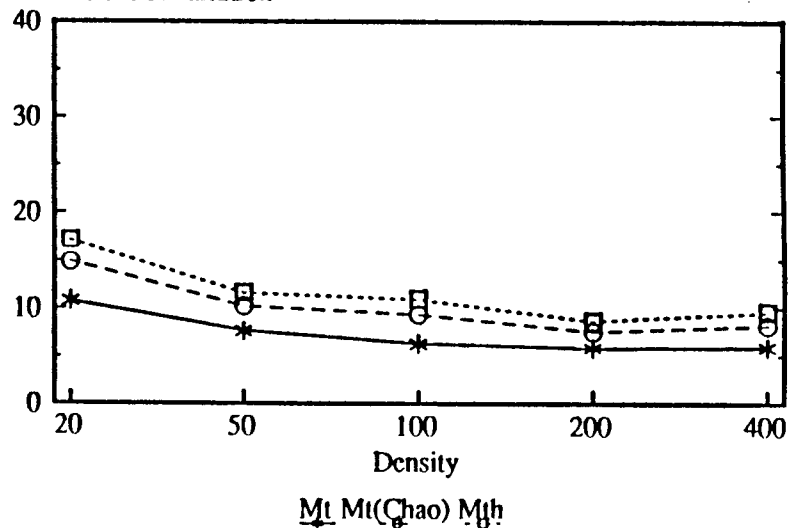
Other Models
Coefficient of variation



Null and Behaviour Models
Coefficient of variation



Time and Time/Heterogeneity Models
Coefficient of variation



in bias with increasing density with the equal capture probability model. With the M_{tbb} model it showed virtually no change in bias with density. Otis et al (1978) comments that the jackknife is the most robust of estimators to variation of capture probabilities which these results seem to reflect. It is also commented that its performance is best in experiments in "which a many animals are caught a relatively large number of times". My results agree with these comments as the jackknife estimator coefficient of variation decreased substantially as density increased. Chao (1989) reported that the jackknife estimator shows a substantial negative bias when capture probabilities are low. I found that the jackknife estimator did show an even (at all densities) 10% negative bias when a .1 mean capture probability (equal capture probability model) was simulated. However, it was still one of the best estimators at this capture probability showing the least bias and one of the lowest coefficients of variation (mean =15%) of any of the estimators. The characteristics of even bias with density, and an approximately unbiased performance suggest this estimator is best for the stated objectives especially at densities greater than 20 hares.

The heterogeneity estimator, M_h of Chao (1989) performed in a similar fashion as the jackknife estimator in terms of general bias and precision. It did show sensitivity to change in density, with an increasing negative bias as density increased especially with the M_{tbb} capture probability model at $p=.2$ (Figure 4.8.) It also showed a very high coefficient of variation (35%) when population number was small ($N=20$) when the underlying capture probability model was M_{tbb} (Figure 4.9). This estimator was developed because the jackknife heterogeneity estimator has been documented to underestimate population size when capture probabilities are low. However with the .1 capture probability simulations (equal capture

probability model) this estimator showed a decreasing positive (+40% at $n=50$ to +10% at $n=400$) bias. It also showed a very large coefficient of variation (greater than 27% for all hare densities) with this simulation. Chao (1989) does report a large standard error with this estimator which she attributes to low capture probabilities in the data this estimator is usually used with. Based on the results from my simulations, the Chao estimator offers a mediocre performance as compared to the jackknife estimator.

Null and behaviour Models

The null (M_0) and behaviour (M_b) models performed very similarly and will therefore be discussed together. Both models displayed a significant negative bias (-10 to -30%). They also showed a increasing negative bias as density increased. The null model showed a low coefficient of variation (12%) with both underlying capture probability models. The behaviour model (M_b) showed an intermediate coefficient of variation (15%).

The consistent negative bias of these models could be due to the presence of heterogeneity within the population (Otis et al. 1978), possibly caused by uneven trap spacing and trap saturation. Otis et al comments that model M_0 is the least robust of any of the CAPTURE estimators, and will exhibit a substantial negative bias if capture probabilities vary among animals. In any case, these models seemed to be the most negatively biased of all models in program CAPTURE.

Time models

The time models of Darroch (1958) (M_t) and Chao (1989) (M_t (Chao)) showed a substantial negative bias that increased with density. Each showed acceptable coefficient of variation.

The time model of Chao (1989) was designed for use with data that has lower capture probabilities. With lower capture probabilities the Darroch (1958) estimator has shown a significant negative bias. Based on these simulations, this model is an improvement from the Darroch estimator, but it is still is not robust to biases caused by increasing density.

Behaviour/heterogeneity models

The behaviour/heterogeneity models of Pollock (1974) (M_{bh}) and Pollock and Otto (1983) (M_{bh} (Pollock)) showed similar performance characteristics. The Pollock and Otto (1983) estimator showed an overall positive bias with the equal capture probability simulations (Figure 4.6), and a negative bias with the M_{bh} simulations (Figure 4.8). The Pollock (1974) estimator showed a negative bias with both underlying capture probability models. Both estimators showed an increasing negative bias as density increased.

The Pollock estimator showed a large coefficient of variation (25%) with both capture probability models (Figures 4.7 and 4.9). The Pollock and Otto estimator showed a slightly better performance showing an acceptable coefficient of variation in all simulations.

Overall, both estimators showed a mediocre performance despite their more complex structure. The substantial trend of increasing negative bias with increasing density is most noteworthy.

Time/behaviour models

Model M_{tb} showed the most erratic performance of any estimator as noted by the large coefficient of variation (40%) in all simulations. It showed a negative bias that increased as density increased. G. White (pers. comm.) commented that this estimator exhibits poor performance especially when data does not conform to the underlying assumptions of the M_{tb}

model.

Time/heterogeneity models

Model M_{th} was designed by Chao and Lee (1989) for data with low capture probabilities. It showed a roughly unbiased performance for data at low densities. However as density increased it showed an increasing negative bias. Also, at lower densities it showed a large coefficient of variation (27%). Overall, this estimator showed a mediocre performance due to increasing negative bias at higher densities.

Program Capture model selection routine

Figure 4.14 displays the effect of increasing density on the model selection routine of program CAPTURE for all simulations run. Only models M_o and M_h are displayed. As evident in Figure 4.14, one of these models was chosen in the majority of the simulations. See Otis et al. (1978) and chapter 1 for a review of the program CAPTURE model selection routine.

As noted in the previous discussion of model bias, the heterogeneity model (M_h) showed a positive (+10%) bias when the equal capture probability model was used, and a slightly negative (-5%) bias when model M_{tth} was used. Model M_o showed a slightly negative (-10%) bias with the equal capture probability model and a large negative bias (-25%) when model M_{tth} was used. These results suggest that these two models vary markedly in terms of bias when confronted with identical data sets.

For the simulations in which all animals have equal probability of capture the model selection routine only picks model M_h occasionally when the population is large (greater than 200) and capture probability equal to .4. Model M_o was picked for the majority of other occasions.

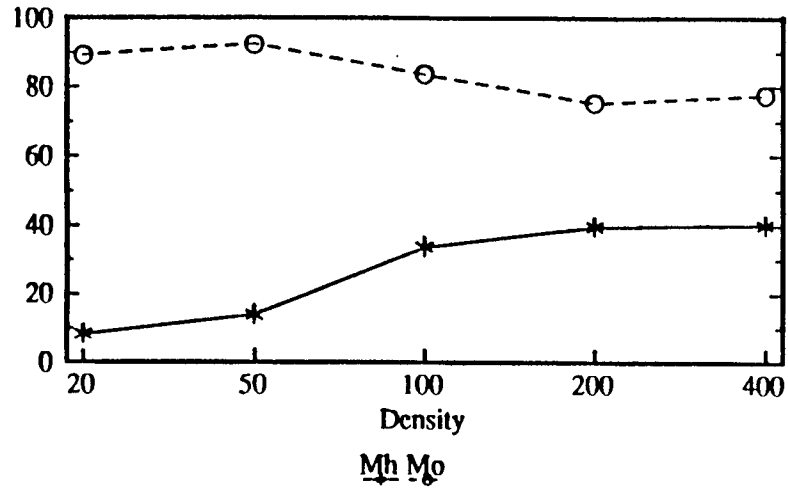
Figure 4.14: Performance of the program CAPTURE model selection routine with changing hare density. Percentages of frequencies when model M_0 and model M_h were selected are displayed. The effect of changing underlying capture probability models and mean capture probabilities are displayed. Density expressed hares/39.06 hectares.

Program CAPTURE model selection routine performance

P equal for all individuals

Mean p. =.2

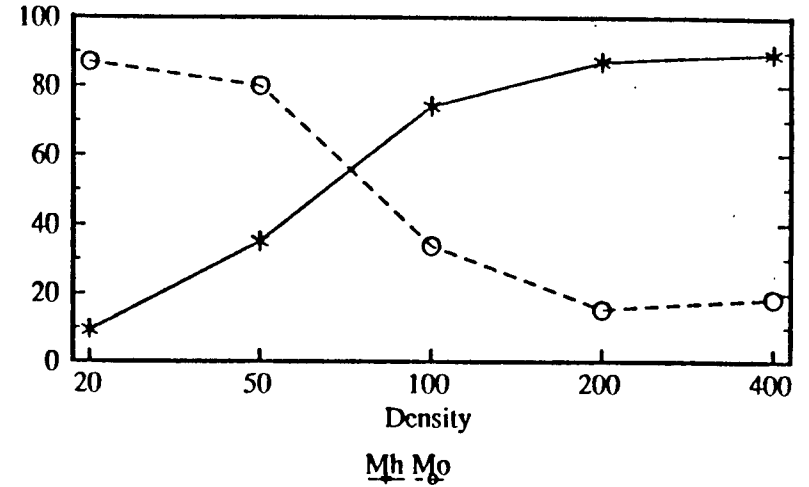
% Model selected



Underlying capture probability model: Mtbh

Mean p. =.2

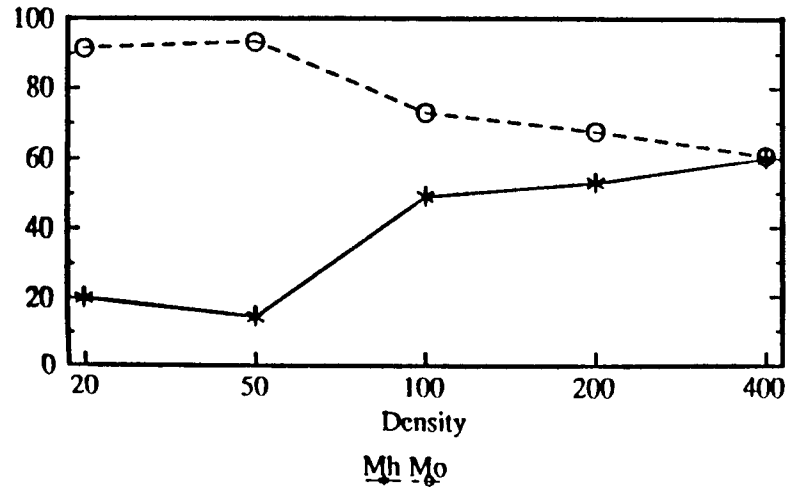
% Model selected



P equal for all individuals

Mean p. =.4

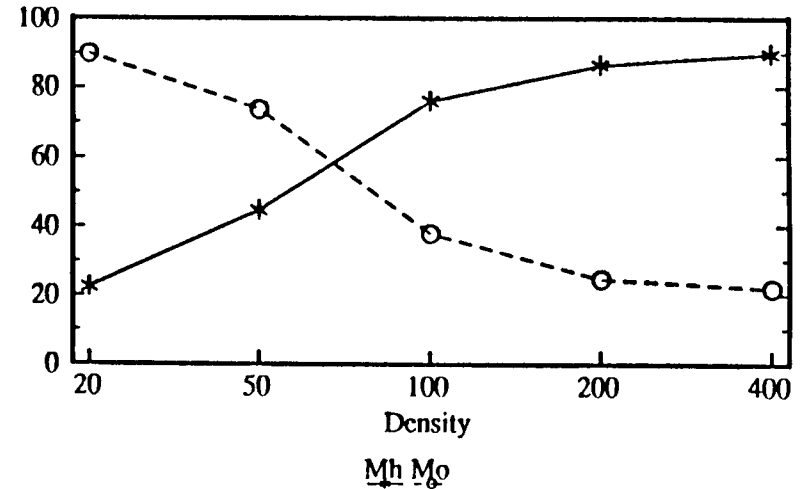
% Model selected



Underlying capture probability model: Mtbh

Mean p. =.4

% Model selected



For the simulation in which M_{ubh} was the underlying capture probability model, model M_h was picked only after the population was above 100. Model M_o was picked for the majority of the other occasions.

These results suggest that the program CAPTURE model selection routine picks models of different bias at different hare densities. In general, the routine picks the negatively biased model M_o at lower densities and the less biased model M_h at higher densities.

The trend in the graphs in Figure 4.14 can be explained in terms of power of statistical tests. When all capture probabilities are equal, the only source of variation in capture probabilities would be due to sampling biases. It would therefore take a large sample size or population size for the model selection routine not to choose the null model. With the simulation in which M_{ubh} is the underlying model a larger "effect size" or variation in capture probabilities is present and therefore the null model is rejected at lower sample sizes.

The actual shape of these curves in Figure 4.14 could represent the extremes of model selection trends actually found in the field. The important thing to note is that dependent on density, and capture probability of the population, models of different bias are selected as a function of density, not of the underlying capture probability distribution in the population.

The lack of power of the program CAPTURE model selection routine has also been documented by Menkins and Anderson (1978) and Hallet et al (1991). In these studies lack of power was related to mean capture probability of the population. No studies have related lack of power to changing density of animals on a grid.

In conclusion, the model selection routine of program CAPTURE selected models of different bias as a function of hare density. As stated in the introduction, the optimal model(s)

for estimation of densities is one that displays a constant bias throughout the hare cycle. The model selection routine of CAPTURE fails in terms of this criteria. Use of the routine could cause errors in comparisons between grids at different densities, as well as calculation of population rates of increase for it may pick models of different bias dependent on density of the population. From these results it is best to use one model of consistent bias such as model M_h , than use the program CAPTURE model selection routine with cyclic snowshoe hare populations.

Conclusion

Estimators showed markedly different performance characteristics as a function of hare density and underlying capture probability models. All models showed a negative bias except the heterogeneity estimators when capture probabilities were equal among animals. When capture probabilities varied with time, behaviour and heterogeneity all models showed a negative bias.

All models showed an increasing negative bias with increasing density with the exception of the jackknife heterogeneity estimator (M_h). From the results of these simulations, the jackknife estimator is the most robust to variations caused by uneven trap spacing and increasing hare density.

The program CAPTURE model selection routine lacked the power to select an estimator or estimators of consistent bias at different hare densities. These results suggest that it is a better strategy to use one estimator that displays a consistent bias at different hare densities than rely on the program CAPTURE model selection routine.

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Chapter 5: Conclusion

Introduction

The main objective of this thesis was to evaluate capture-recapture estimation models when used with a cyclic snowshoe hare population. My approach was to explore estimator bias and precision using experiments that were separate from the Kluane field data. I used two approaches: 1) Island populations of known size to determine estimator bias and explore factors that cause unequal capture probabilities and, 2) Monte Carlo simulation to evaluate estimator robustness to variations in capture probabilities caused by sampling biases. In this concluding chapter, I will integrate my findings from these two approaches with data from the Kluane project. Recommendations for optimal estimation models will be made, as well as suggestions for further research.

Both the island studies and the Monte Carlo simulation model are simplifications of the more demographically complex mainland snowshoe hare population. Each study independently tested estimator performance with plausible sources of variation in capture probabilities found on the mainland Kluane grids. For instance, the island studies tested estimators with trap behaviour, and innate differences in capture probabilities found in a natural hare population. The simulation studies tested estimators with plausible sampling biases such as uneven trap spacing and trap saturation found on the mainland grids. Individually, each of the results of these studies are limited in application to mainland hare populations. However, together each of these studies suggest similar optimal estimation models, and highlight the limitations of the capture-recapture approach.

Comparison of Kluane field data to results of island and simulation studies

I will first describe the general demographics of the three Kluane grids used in the analysis. I will then compare the results from the Kluane grids to my results focusing on similarities between these studies. The Jolly-Seber open model has also been included for comparison.

Kluane field data attributes

The population of hares on each of the Kluane grids shows specific attributes in terms of mean capture probabilities, and population size (Figures 5.1, 5.2, and 5.3). The lower bound on mean capture probabilities found on Sulphur, Beaver Pond and Hungry Lake trapping grids are .45, .15, .19, respectively. (See chapter 4 for the calculation of these mean capture probabilities). Densities of hares on these grids differ with Sulphur showing lower densities (20-150 hares) and Hungry Lake showing higher densities (150-500 hares). Hungry Lake is a food addition grid which may cause additional variation in hare capture probabilities.

Comparison of CAPTURE estimation models

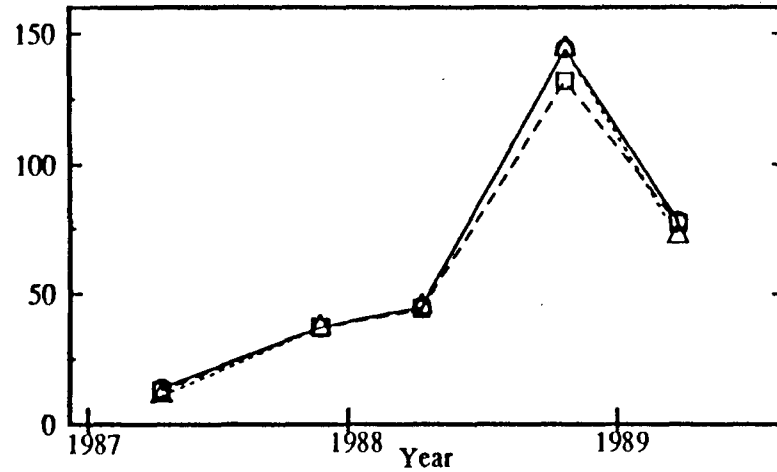
The estimates from the Kluane grids and the results from the island studies and Monte Carlo simulation model show important similarities. In a given trapping period or simulation, each estimation model gives estimates of similar magnitude when compared with other estimation models (Figures 5.1, 5.2, and 5.3). For instance, in all cases the heterogeneity estimators show the highest estimates whereas the null and behaviour estimators show the lowest estimates. This is particularly noticeable at peak densities. For any given trapping period, each estimation model is probably giving an estimate of *different* bias relative to other models. More importantly, it could be surmised that each estimation model's bias is consistently unique

Figures 5.1, 5.2, and 5.3 A comparison of estimates from program CAPTURE models for Sulphur, Beaver Pond, and Hungry Lake trapping grids in the Kluane Lake area.

CAPTURE estimates from Sulphur

Heterogeneity Models

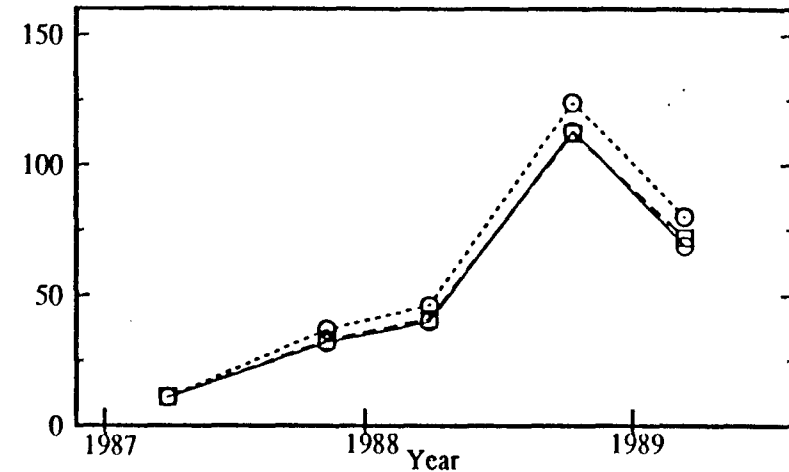
Estimate



M_h $M_h(\text{Chao})$

Other Models

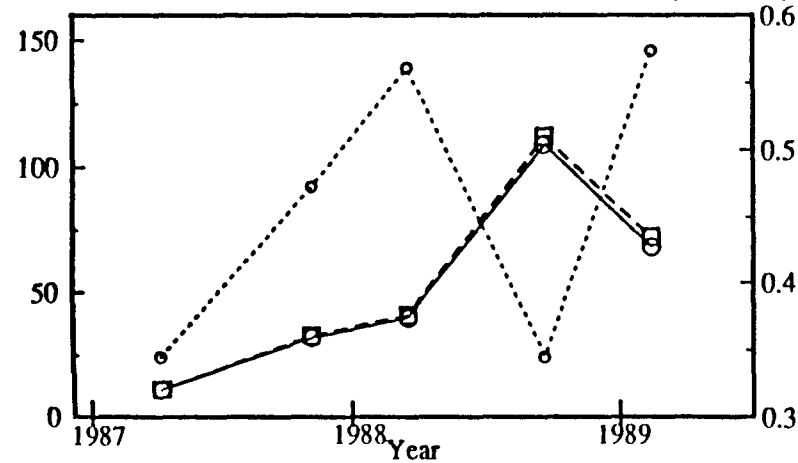
Estimate



M_{lb} M_{bh} $M_{bh}(\text{Pollock})$

Null and Behavioral Models, Capture Probability

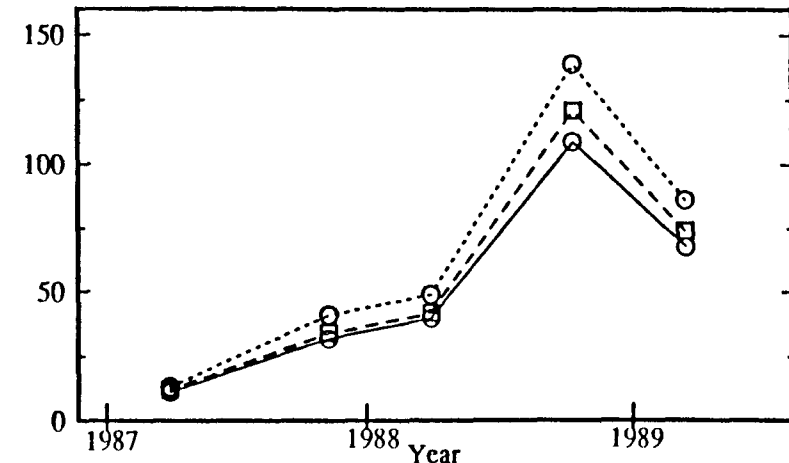
Estimate



M_o M_b Mean capture probability

Time and Time/Heterogeneity Models

Estimate

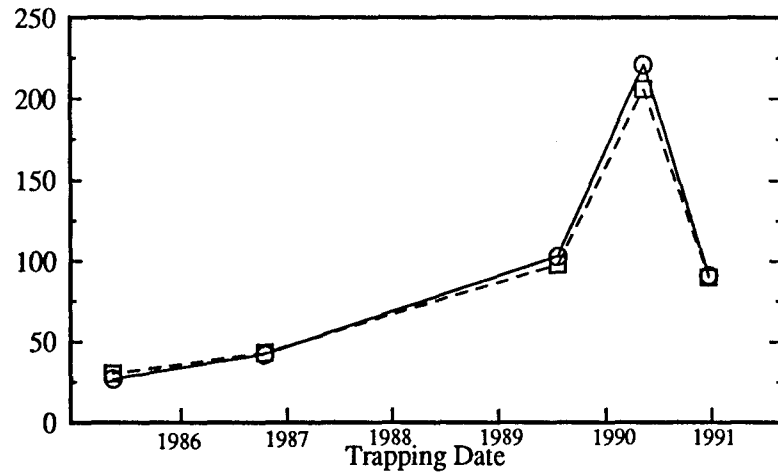


M_t $M_t(\text{Chao})$ M_{th}

CAPTURE estimates from Beaver Pond

Heterogeneity Models

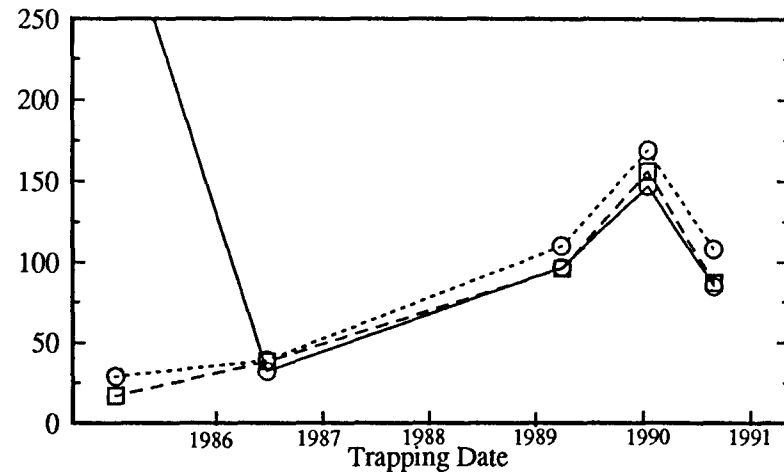
Estimate



M_h $M_h(Chao)$

Other Models

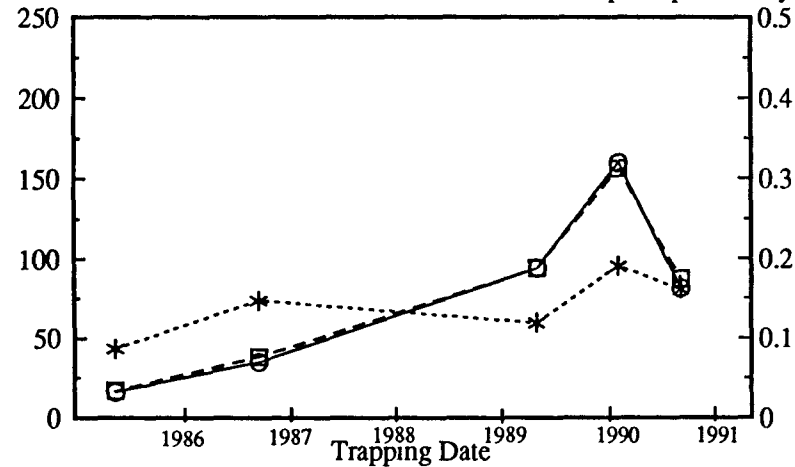
Estimate



M_b M_{bh} M_{bh} (Pollock)

Null and Behavior models, capture probabilities

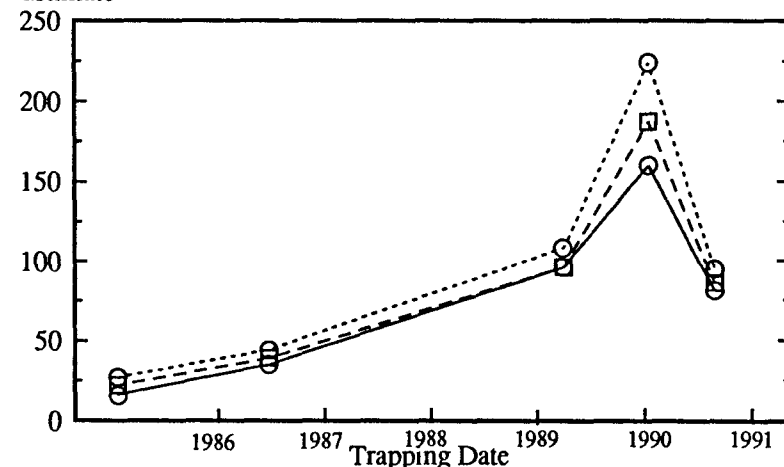
Estimate



M_0 M_b Capture probability

Time and Time/Heterogeneity Models

Estimate

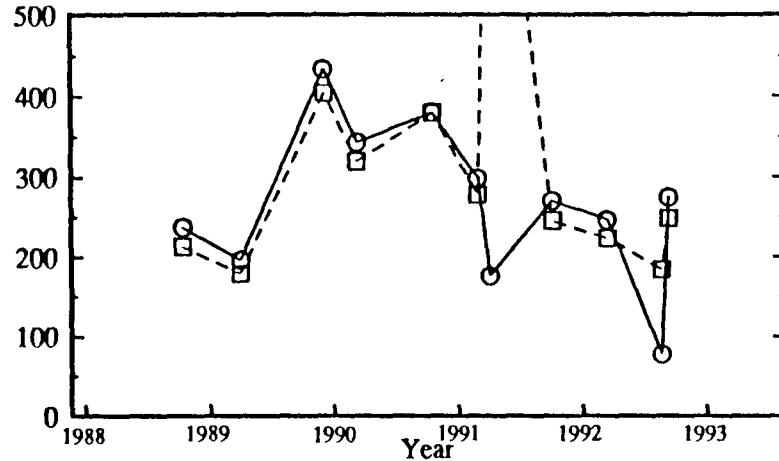


M_t $M_t(Chao)$ M_{th}

CAPTURE estimates from Hungry Lake

Heterogeneity Models

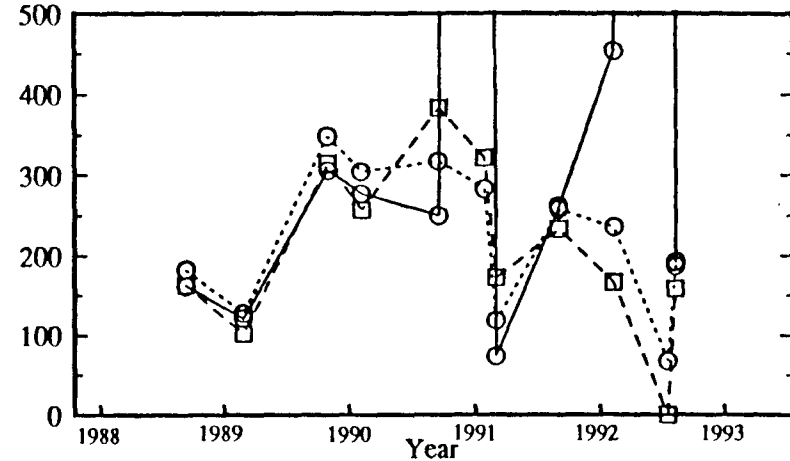
Estimate



M_h $M_h(\text{Chao})$

Other Models

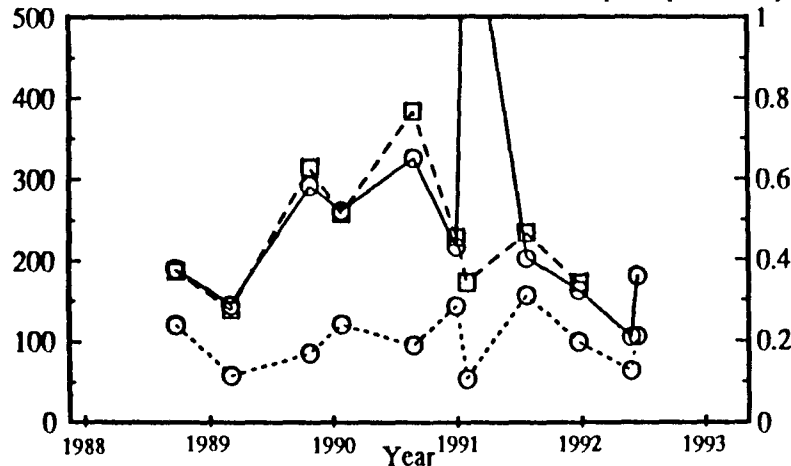
Estimate



M_b M_{bh} $M_{bh}(\text{Pollack})$

Null and Behavioral models, Capture probability

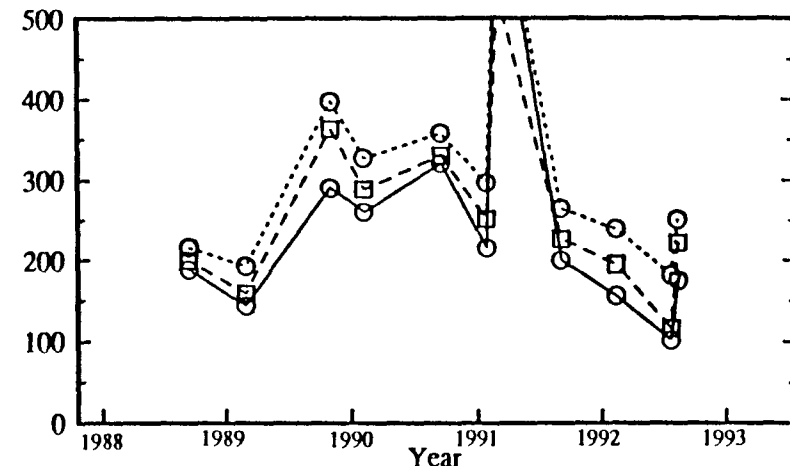
Estimate



M_0 M_b Capture probability

Time and Time/Heterogeneity Models

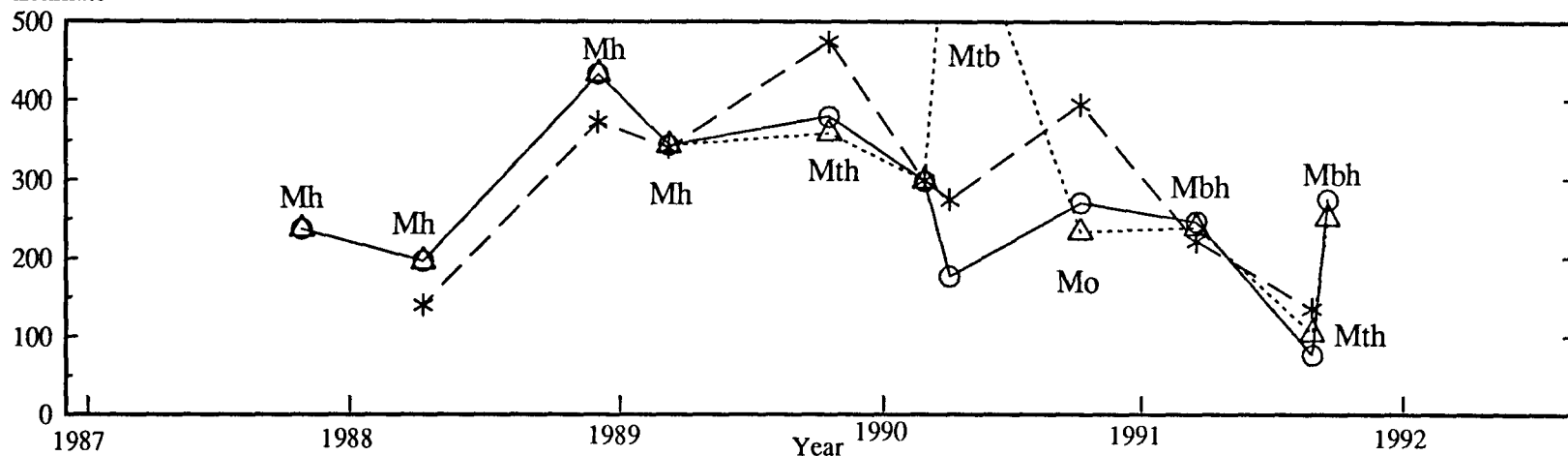
Estimate



M_t $M_t(\text{Chao})$ M_{th}

Figure 5.4. A comparison of estimates from the jackknife estimator (M_h), models selected by program CAPTURE, and the Jolly-Seber model for three Kluane mainland grids.

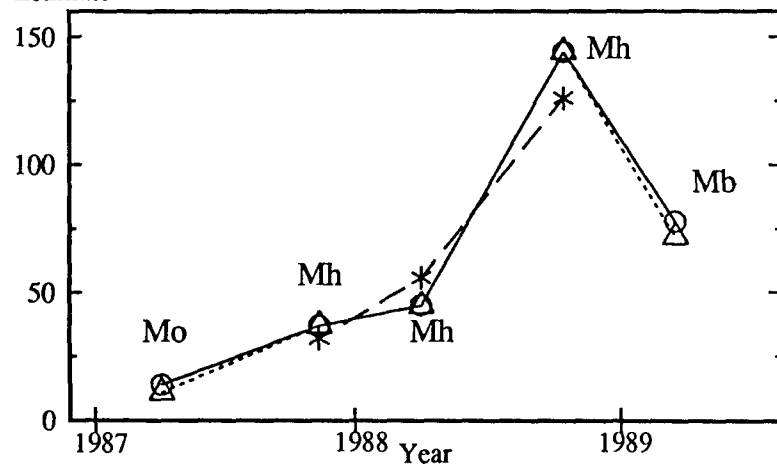
Hungry Lake
Estimate



Mh (jackknife) CAPTURE model selected Jolly-Seber

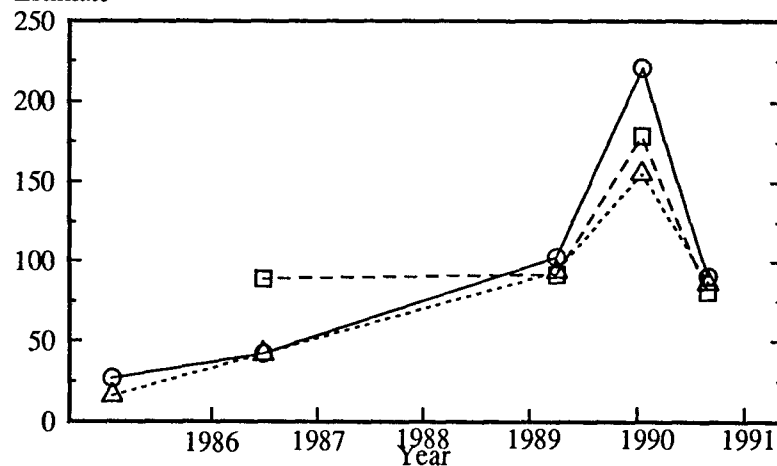
M_: Model selected by CAPTURE

Sulphur
Estimate



Mh (jackknife) CAPTURE model selected Jolly-Seber

Beaver Pond
Estimate



Mh (jackknife) Jolly-Seber CAPTURE model selected

for any given density of animals given the results of the Monte Carlo simulation model. The simulation model also documented the increasing negative bias of most estimators with increasing densities. Given these findings, it is probably preferable to use just one model for all densities, regardless of what actual bias that model exhibits.

Jolly-Seber model

The Jolly-Seber model showed comparable estimates to the heterogeneity estimators of program CAPTURE when capture probabilities were above .2 such as with the Sulphur grid and Hungry Lake during some of the later trapping periods (Figure 5.4). At other times it showed lower estimates that were similar to the null and behavioral models. The Jolly-Seber models has been shown to exhibit a negative bias with lower capture probabilities which may be reflected in these results (Gilbert, 1973)

CAPTURE model selection routine

The program CAPTURE model selection routine picked different models on each trapping occasion (Figure 5.4). In general it picked model M_h at higher densities or when capture probabilities are higher. For example M_h was picked for the majority of peak densities on Sulphur, Beaver Pond, and Hungry Lake. At lower densities, other models such as M_b , and M_o were picked.

The trend in Kluane field data in which heterogeneity models are picked at higher densities and null or behavioral models are picked at lower densities is also reflected in the Monte Carlo simulation model results (Chapter 4). In chapter 4, I suggested that the cause of this trend was lack of power in the CAPTURE model selection routine at low densities to pick the appropriate model. The most important point to note here is that the selection routine is

picking models with *different* bias for each trapping period.

Recommendations for the Kluane project

Optimal Estimation models

An optimal estimation model should be approximately unbiased and precise. In the particular case of the snowshoe hare cycle, it is also important that an estimator show consistent bias regardless of hare density on the trapping grid. In terms of bias, the island studies results suggest that the jackknife (M_h) estimator is one of the most robust to variations in capture probabilities typical of snowshoe hare populations. In terms of precision, it exhibited a moderate coefficient of variation in the simulation study. Except at low densities, the coefficient of variation was under 20 percent which is usually considered acceptable. It was also the only estimator robust to changing hare densities retaining a consistent bias regardless of density.

Other estimators all showed increasing negative bias as density increased in the simulation studies. The newer complex estimators (M_{lh} , M_{th} , and M_{bh}) also showed an increasing negative bias with density, as well as unacceptable coefficients of variation. The Jolly-Seber model exhibited unbiased performance only when capture probabilities were high. I cannot say that the jackknife estimator is always the most unbiased, however it seems to be the most robust to variations typical of snowshoe hare population and therefore its use is recommended.

Program CAPTURE model selection routine

This study shows the limited utility of this routine for estimating numbers in cyclic populations. With the simulated data, and Kluane Data it picked models of varying bias as a

function of density. Given this, the use of this routine will lead to biased comparison between grids of different densities, and biased calculations of intrinsic rates of increase. It is a better strategy to use one model that exhibits constant bias, such as the jackknife M_h estimator, than use the program CAPTURE model selection routine.

Optimal Sampling

The results from the capture probability experiments (Chapter 3) documented the dynamic nature of snowshoe hare populations in terms of sampling conditions. Capture probabilities vary markedly in terms of individual movement patterns, time of year, and trap pattern used. The recommendations that I will make correspond to optimum strategies in terms of 1)time of sampling, 2)grid design, and, 3)trapping period length.

In terms of time of sampling, the island studies and Monte Carlo simulation model suggest that sampling in times of highest mean capture probability will result in the most reliable estimates. The times of highest capture probability seem to be the early spring and late fall. The results from Dezadeash Island suggest that when sampling a population previously not trapped it is very important to trap initially during one of these periods when hares are most prone to be trapped. During mid-summer capture probabilities are lower and as a result population estimates will most likely be of poorer quality.

In terms of grid design, the Kluane trapping grid seems to cause a slightly more negative bias with most estimation models (Chapter 2). The sample size of this comparison was small so these results are not conclusive. To explore the effect on population estimates of this design a simulation study as done in Chapter 4 with a uniform grid instead of the Kluane grid should be done. The same strategy in terms of optimal estimation model strategy applies to optimal

sampling designs. It is best to stay with a design of consistent bias then change designs in the middle of an experiment even if the new design is less biased. For this reason, I recommend that the trapping grid design of Kluane experiment should be retained for the duration of the study. Newer studies should use the Monte Carlo simulation model in Chapter 4 to explore the optimal trapping grid design for snowshoe hare populations.

The trapping period length at Kluane is five days. In terms of estimator performance, increasing this period would probably cause estimates of higher precision (Otis et al. 1978). However, from the trap timers it was found that a hare spends an average of 8 hours in a live trap in a given trap night. Obviously, if a trapping period is longer than 5 days detrimental effects to the population could occur. Also, the radio telemetry movement studies showed widespread movement patterns of snowshoe hares making population closure a consideration in trapping period length. If the total time for a trapping period (including nights off) is much more than a week the assumption of closure would become dubious. For these reasons, a five day trap period is recommended.

Recommendations for future research

A trend that is also obvious from the island studies, simulation studies, and Kluane data is the similarity of estimates between many of the estimation models. In capture-recapture research, more complex theoretical estimation models are being produced on a yearly basis, but few studies are attempting to actually test these estimators with real data. The results from this study suggest that these newer estimators offer little improvement over older methods. For example, models M_{lb} , M_{lh} , and M_{bh} showed little or no improvement over the older jackknife estimator with snowshoe hare populations. Capture-recapture estimation models are an attempt

to integrate theoretical statistics with actual biology of animals. For this reason, the utility of these models can be determined only by studies that actually incorporate the biology of the animals being studied. More research is needed to determine whether the underlying assumptions made by the newer estimators apply to wild populations. These studies must be specific to the populations being studied and the sampling regime being used.

The program CAPTURE model selection routine showed minimal utility in this study mainly due to lack of power in the hypothesis tests used to select models. This problem has been also documented by Menkins and Anderson (1988). Further work is needed in developing a more reliable model selection routine. One improvement would be a model selection routine that calculates or gives an index of the power of its tests for the sample size of data being analyzed. In this way, the biologist has some reference to the credibility of the routine.

The importance of sampling procedure is also apparent from this study. When designing a study biologists should use spatial simulation models to scale the trapping grid to the general movement patterns of the population studied. By doing this, the use of more complex models can possibly be avoided.

Finally, biologists need to become aware that estimation is a statistical topic that requires a rigorous approach if good estimates are desired. Biologists should not use estimation programs such as CAPTURE as a "black box". The results of this study document possible biases introduced by "black box" routines such as the program CAPTURE model selection routine. Simulation models such as the one used in this study that link the actual biology of the animal to the estimation process should be more available for use with biologists. In this way, the biologist can gain an approximation of the variance and bias associated with the

estimates for the population studied.

The availability of compact, powerful microcomputers now will allow biologists to use more complex estimation models. This can lead to more precise results and predictions in applied field ecology. However, this will occur only if theoretical statisticians and biologists work together to merge theoretical techniques with the constraints of applied field ecology.

Literature Cited

- Gilbert, R. 1973. Approximations of the bias in the Jolly-Seber capture-recapture model. *Biometrics* 29:501-526.
- Menkins, G. E., and S. H. Anderson. 1988. Estimation of Small Mammal Population Size. *Ecology* 69(6); 1952-1959.
- Otis, D., K. Burnham, G. White, and D. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Mon.* 62:133.

Appendix 1:

Monte Carlo Simulation model

This model was originally written by Zarnoch (1976) and was modified by Ken Wilson (1982). I used only a small part of the actual code in my simulations. I will outline other features of this model. For more details concerning this model see the references listed below. I acquired the code for this program from Dr. Ken Wilson at Colorado State University (Dept of Wildlife Biology, Ft. Collins, CO 80523). Dr. Wilson is writing a version of this model for IBM PC computers. The additional features of this model are:

- 1) Animals can be moved by bivariate normal, uniform, and other probability distributions. Their home range centers can be simulated by uniform, fixed, random, clustered, and combinations of the above. The distribution of animals in a cluster can be simulated by a variety of probability distributions
- 2) Traps can be fixed, or placed by various probability distributions. Traps can be activated or inactivated for each trapping occasion.
- 3) The capture radius of traps can be adjusted iteratively so that the expected number of captures approximately equals the population size and capture probabilities being simulated.
- 4) Output files can be generated for other estimation programs such as TRANSECT.

The following changes were made to the code:

- 1) The MAIN program was modified to accept input from the standard input stream (unit=5). The trapping process was modified for random walk model. (Subroutine HRPAR was disabled)
- 2) Subroutine RANDWALK was added to simulate animal movements. This subroutine is detailed in this thesis.
- 3) Subroutine MTBH was modified. This modification is detailed in the text in this thesis.
- 4) Subroutine TRAP was modified to support the RANDWALK subroutine.
- 5) Subroutine RANDOM was modified to allow standard utm coordinates. In the previous setup, all coordinates are centered around an axis (0,0). This subroutine may need to be modified if random clustered animal patterns are simulated.
- 6) Subroutine RANO and subroutine RANNOR were added to generate uniform random and normal random numbers

7) Subroutine HRPAR was modified so that a distribution of home ranges is generated for each simulation

Model References:

Benhamou, S. 1989 An olfactory orientation model for mammals movements in their home ranges. *J. Theor. Biol.* 139:379-388

Wilson, K.R. 1983. Evaluation of a new trapping web design and analysis method for estimating density of small mammal populations. M.S. Thesis, Utah State Univ., Logan. 188pp.

Zarnoch, S.J. 1976. Evaluation of estimators of population size based on simulation techniques. PhD. Thesis, Virginia Polytechnique Inst. and State Univ., Blacksburg, 191pp.

C
C
C MARK-RECAPTURE DATA SIMULATOR.
C LARGE SAMPLE SIZE.
C REFERENCE: ZARNOCH, S. J. 1976.
C EVALUATION OF ESTIMATORS OF POPULATION SIZE BASED ON
C SIMULATION TECHNIQUES.
C PH.D. DISSERTATION.
C VIRGINIA POLYTECHNIC INSTITUTE AND STATE UNIVERSITY.
C 191 PAGES.
C VERSION MODIFIED BY KENNETH R. WILSON. 1982.
C UTAH COOPERATIVE WILDLIFE RESEARCH UNIT
C UTAH STATE UNIVERSITY
C CURRENT VERSION MODIFIED BY JOHN G. BOULANGER, 1993
C DEPT. OF ZOOLOGY
C UNIVERSITY OF BRITISH COLUMBIA
C IN DETAIL:
C SUBROUTINE TRAP, MTBH, RANDOM, MODIFIED
C SUBROUTINES RANDWALK, RANO, RANNOR ADDED
C MAIN MODEL MODIFIED
C REF: ESTIMATION OF CYCLIC SNOWSHOE HARE POPULATIONS
C MSC THESIS, UNIVERSITY OF BRITISH COLUMBIA
C*****
C LEGEND FOR VARIABLES USED IN THE SIMULATOR.
C*****
C***** THE LETTER D AFTER A VARIABLE NAME MEANS THAT VARIABLE IS NO LONGER
C USED IN THE CURRENT VERSION OF THE MODEL.
C
C NAME TITLE CHOSEN FOR THE SIMULATIONS TO BE RUN.
C
C NSEG ARRAY OF UP TO 10 ELEMENTS WHICH INDICATES THE NUMBER OF LINES
C IN EACH GROUPING OF DATA WHEN IDATA.GT.1. EXAMPLE: IF THERE
C ARE 3 GROUPINGS OF THE DATA, AND THE FIRST GROUPING COVERS
C FROM LINE 1 TO LINE 27, AND THE SECOND FROM LINE 28 TO LINE 56
C AND THE THIRD FROM LINE 56 TO 83. THEN NSEG(1)=27, NSEG(2)=29,
C AND NSEG(3)=27. ALL OTHER GROUPINGS WOULD BE 0 IN THIS CASE.
C
C NSIMS THE NUMBER OF SIMULATIONS OF TRAPPING EXPERIMENTS WHICH ARE TO
C BE PERFORMED ON THIS SET UP. EACH SIMULATION MUST HAVE A NEW
C SET OF DATA CARDS.
C THE MAXIMUM NUMBER OF SIMULATIONS PER SET UP IS 999.
C
C ISIM THE NUMBER OF THE CURRENT SIMULATION IN PROCESS.
C
C IIX THE INITIAL RANDOM NUMBER GENERATOR SEED.
C THIS MUST BE AN ODD NUMBER OF NINE OR LESS DIGITS.
C
C IX THE RANDOM NUMBER GENERATOR SEED AT ANY SPECIFIC POINT
C IN THE SIMULATION.
C
C JIX ALLOWS FOR INPUT OF RANDOM NUMBER BY USER OR FROM COMPUTER
C TIME CLOCK.
C 0 = RANDOM NUMBER ENTERED BY COMPUTER CLOCK.
C 1 = USER ENTERS RANDOM NUMBER.
C
C C A CONSTANT USED AS A PARAMETER FOR THE LENGTH OF A SIDE
C OF THE SQUARE STUDY GRID.
C
C NTPER THE NUMBER OF TRAPPING PERIODS FOR THE SIMULATION.
C
C ITROP THE TRAPPING OPTION. THIS OPTION ALLOWS THE SELECTION
C OF A VARIETY OF TRAPPING PATTERNS TO BE USED OVER THE COURSE OF
C THE TRAPPING PERIODS. THIS IS ACCOMPLISHED BY ACTIVATING
C OR DEACTIVATING CERTAIN TRAPS ON A GIVEN TRAPPING PERIOD
C IN ORDER TO ACHIEVE THE SPECIFIC TRAPPING PATTERN.
C 0 = ALL TRAPS ARE ACTIVATED FOR ALL TRAPPING PERIODS.
C 1 = ALL TRAPS HAVE THE SAME ACTIVATION SCHEME OVER THE

C
C TRAPPING PERIODS. ONE PARAMETER CARD MUST ACCOMPANY THE
C ITROP CARD IN THE DATA INDICATING THE ACTIVATION
C SCHEME. THE FORMAT IS 2011.
C EXAMPLE: IF THERE ARE TEN TRAPPING PERIODS AND
C ALL TRAPS ARE TO BE ACTIVATED EVERY
C OTHER TRAPPING PERIOD STARTING THE
C FIRST ACTIVATION IN TRAPPING PERIOD 1,
C THEN THE DATA CARD WOULD BE
C 1010101010.
C
C 2 = ALL TRAPS WITHIN ANY SPATIAL PATTERN HAVE THE SAME
C ACTIVATION SCHEME OVER THE TRAPPING PERIODS.
C A CARD MUST ACCOMPANY THE ITROP CARD IN THE DATA
C FOR EACH OF THE FIVE TRAP PATTERN GROUPS WHICH ARE
C NOT SPECIFIED TO BE ZERO IN THE DATA INPUT: TR, TU,
C TRC, TUC, AND TF. THE FORMAT FOR EACH CARD IS 2011.
C EXAMPLE: IF THERE ARE TEN TRAPPING PERIODS AND
C (1) TRAPS IN THE RANDOM PATTERN ARE TO BE
C ACTIVATED FOR ALL TEN TRAPPING PERIODS,
C (2) TRAPS IN THE UNIFORM PATTERN ARE TO BE
C ACTIVATED FOR ALL TEN TRAPPING PERIODS,
C (3) TRAPS IN THE RANDOMLY CLUSTERED PATTERN
C ARE TO BE ACTIVATED EVERY OTHER TRAPPING
C PERIOD STARTING THE FIRST ACTIVATION IN
C TRAPPING PERIOD 1,
C (4) TRAPS IN THE UNIFORMLY CLUSTERED PATTERN
C ARE TO BE ACTIVATED EVERY OTHER TRAPPING
C PERIOD STARTING THE FIRST ACTIVATION IN
C TRAPPING PERIOD 2, AND
C (5) TRAPS IN THE FIXED PATTERN ARE TO BE
C ACTIVATED EVERY TRAPPING PERIOD EXCEPT
C TRAPPING PERIOD 1,
C THEN THE DATA CARDS FOR THIS EXAMPLE
C ARE, RESPECTIVELY,
C 1111111111
C 1111111111
C 1010101010
C 0101010101
C 0111111111.
C
C PBAR THE OVERALL AVERAGE PROBABILITY OF CAPTURE DURING TRAPPING
C PERIOD 1 FOR ALL ANIMALS IN THE POPULATION.
C
C ICPB,ICPG,ICPL PARAMETER FOR CHOOSING TYPE OF BETA DISTRIBUTION
C DESIRED FOR REPRESENTING CAPTURE PROBABILITIES.
C ICPB-BETA OF LOGISTIC TRANSFORM EQTN.
C ICPG-GAMMA OF LOGISTIC TRANSFORM EQTN.
C ICPL-LAMBDA OF LOGISTIC TRANSFORM EQTN.
C 1 = ALPHA AND BETA ARE POSITIVE WHOLE NUMBERS.
C 2 = ALPHA=1.0, BETA GREATER THAN 0.
C 3 = ALPHA GREATER THAN 0., BETA=1.0.
C 4 = ALPHA LESS THAN OR EQUAL TO BETA, WHERE BOTH
C ARE ON THE INTERVAL 0,1.
C
C ALPHB,BETAB ALPHA AND BETA VALUES FOR BETA(HETEROGENEITY) TERM OF
C LOGISTIC TRANSFORM EQTN (SEE ICPB ABOVE).
C
C ALPHG,BETAG ALPHA AND BETA VALUES FOR GAMMA(TIME) TERM OF LOGISTIC
C TRANSFORM EQTN (SEE ICPG ABOVE).
C
C ALPHL,BETAL ALPHA AND BETA VALUES FOR LAMBDA(BEHAVIOR) TERM OF
C LOGISTIC TRANSFORM EQTN (SEE ICPL ABOVE).
C
C IUHR OPTION FOR UNIFORM HOME RANGE.
C 0 = BIVARIATE NORMAL DISTRIBUTION.
C 1 = UNIFORM DISTRIBUTION.
C 2 = U-SHAPED DISTRIBUTION.
C 3 = BIVARIATE NORMAL WITH INCREASED CAPTURE PROBABILITY

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C FOR EXCURSIONS OUTSIDE 95% HOME RANGE AREA.
C
C PEXC PROBABILITY OF CAPTURE DURING AN EXCURSION OUTSIDE 95% HOME RANGE.
C
C IHRPAR THE HOME RANGE MOVEMENT PARAMETERS OPTION.
C 0 = ALL ANIMALS HAVE THE SAME PARAMETERS. ONE
C PARAMETER CARD MUST ACCOMPANY THE IHRPAR CARD
C IN THE DATA.
C 1 = THE SPATIAL PATTERN GROUPS OF ANIMALS HAVE DIFFERENT
C PARAMETERS. A CARD MUST ACCOMPANY THE IHRPAR CARD
C IN THE DATA FOR EACH OF THE FIVE ANIMAL PATTERN GROUPS
C WHICH ARE NOT SPECIFIED TO BE ZERO IN THE DATA INPUT:
C NR, NU, NRC, NUC, AND NF.
C 2 = THE PARAMETERS FOR ALL ANIMALS IN THE RANDOM OR
C UNIFORM PATTERN ARE READ FROM INDIVIDUAL PARAMETER
C CARDS. THE PARAMETERS FOR ALL RANDOMLY CLUSTERED
C ANIMALS ARE THE SAME AND ARE READ FROM A
C SINGLE PARAMETER CARD. THE PARAMETERS FOR ALL
C UNIFORMLY CLUSTERED ANIMALS ARE THE SAME AND ARE
C READ FROM A SINGLE PARAMETER CARD. THE PARAMETERS
C FOR ALL ANIMALS IN THE FIXED PATTERN ARE READ
C FROM INDIVIDUAL PARAMETER CARDS. THUS, ALL
C ANIMALS IN EITHER THE RANDOM PATTERN, UNIFORM PATTERN,
C OR FIXED PATTERN MAY HAVE DIFFERENT PARAMETERS.
C THOSE IN THE RANDOMLY CLUSTERED PATTERN MUST
C HAVE THE SAME PARAMETERS. THOSE IN THE UNIFORMLY
C CLUSTERED PATTERN MUST HAVE THE SAME PARAMETERS.
C
C ICPRAD INDICATES WHETHER CAPRAD IS FIXED OR ALLOWED TO VARY.
C 0 = FIXED
C 1 = VARIES
C
C CAPRAD CAPTURE RADIUS OR TRAP RADIUS FOR THE ANIMALS.
C
C CAPFIX STORES CAPRAD FROM TRAPPING PERIOD OF PREVIOUS SIMULATION, FOR
C USE AS STARTING VALUE OF NEXT SIMULATION. NOT USED IF IDATA=1
C OR IF ISIM=KGROUP.
C
C AP A MATRIX, (2000,3), WHICH SHOWS THE TYPE OF PATTERN EACH ANIMAL
C IS IN AND THE CENTER OF ACTIVITY OF EACH ANIMAL.
C THE ROWS REPRESENT ANIMALS.
C THE FIRST COLUMN INDICATES THE SPATIAL PATTERN OF
C THAT ANIMAL. THE FOURTH DIGIT TO THE LEFT OF THE DECIMAL
C POINT IS THE CODE FOR THE ANIMAL'S SPATIAL PATTERN.
C 1 = RANDOM PATTERN.
C 2 = UNIFORM PATTERN.
C 3 = RANDOMLY CLUSTERED PATTERN.
C 4 = UNIFORMLY CLUSTERED PATTERN.
C 5 = FIXED PATTERN.
C THE THREE DIGITS IMMEDIATELY TO THE LEFT
C OF THE DECIMAL POINT INDICATE TO WHICH CLUSTER AN
C ANIMAL BELONGS IF IT IS IN EITHER A RANDOMLY CLUSTERED OR
C UNIFORMLY CLUSTERED PATTERN.
C THE SECOND AND THIRD COLUMNS INDICATE THE CENTER OF
C RESPECTIVELY.
C
C NR THE NUMBER OF ANIMALS IN A RANDOM PATTERN.
C
C NU THE NUMBER OF ANIMALS IN A UNIFORM PATTERN.
C THIS MUST BE A SQUARE OF AN INTEGER.
C
C NRC THE NUMBER OF RANDOM CLUSTERS OF ANIMALS.
C
C NUC THE NUMBER OF UNIFORM CLUSTERS OF ANIMALS.
C THIS MUST BE A SQUARE OF AN INTEGER.
C

C NF THE NUMBER OF ANIMALS IN A FIXED PATTERN.
C
C NNRC THE NUMBER OF ANIMALS IN THE RANDOMLY CLUSTERED PATTERN.
C
C NNUC THE NUMBER OF ANIMALS IN THE UNIFORMLY CLUSTERED PATTERN.
C
C IOPNRC THE OPTION FOR THE TYPE OF PROBABILITY DISTRIBUTION OF THE
C NUMBER OF ANIMALS IN A RANDOMLY CLUSTERED PATTERN.
C 1 = POISSON.
C 2 = GEOMETRIC.
C 3 = BINOMIAL.
C 4 = NEGATIVE BINOMIAL.
C 5 = DISCRETE UNIFORM.
C 6 = CONSTANT.
C
C VINRC THE VARIANCE OF X IN THE BIVARIATE NORMAL DISTRIBUTION
C FOR THE DETERMINATION OF THE CENTER OF ACTIVITY OF
C ANIMALS IN A RANDOMLY CLUSTERED PATTERN.
C
C V2NRC THE VARIANCE OF Y IN THE BIVARIATE NORMAL DISTRIBUTION
C FOR THE DETERMINATION OF THE CENTER OF ACTIVITY OF
C ANIMALS IN A RANDOMLY CLUSTERED PATTERN.
C
C RHONRC RHO IN THE BIVARIATE NORMAL DISTRIBUTION FOR THE DETERMINATION
C OF THE CENTER OF ACTIVITY OF ANIMALS IN A RANDOMLY
C CLUSTERED PATTERN.
C
C PINRC THE FIRST PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
C NUMBER OF ANIMALS IN A RANDOMLY CLUSTERED PATTERN.
C THE DISTRIBUTION MAY HAVE ONLY ONE PARAMETER.
C
C P2NRC THE SECOND PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
C NUMBER OF ANIMALS IN A RANDOMLY CLUSTERED PATTERN.
C THIS IS EQUAL TO ZERO IF THE DISTRIBUTION
C HAS ONLY ONE PARAMETER.
C
C IOPNUC THE OPTION FOR THE TYPE OF PROBABILITY DISTRIBUTION OF THE
C NUMBER OF ANIMALS IN A UNIFORMLY CLUSTERED PATTERN.
C 1 = POISSON.
C 2 = GEOMETRIC.
C 3 = BINOMIAL.
C 4 = NEGATIVE BINOMIAL.
C 5 = DISCRETE UNIFORM.
C 6 = CONSTANT.
C
C VINUC THE VARIANCE OF X IN THE BIVARIATE NORMAL DISTRIBUTION
C FOR THE DETERMINATION OF THE CENTER OF ACTIVITY OF
C ANIMALS IN A UNIFORMLY CLUSTERED PATTERN.
C
C V2NUC THE VARIANCE OF Y IN THE BIVARIATE NORMAL DISTRIBUTION
C FOR THE DETERMINATION OF THE CENTER OF ACTIVITY OF
C ANIMALS IN A UNIFORMLY CLUSTERED PATTERN.
C
C RHONUC RHO IN THE BIVARIATE NORMAL DISTRIBUTION FOR THE DETERMINATION
C OF THE CENTER OF ACTIVITY OF ANIMALS IN A UNIFORMLY
C CLUSTERED PATTERN.
C
C PINUC THE FIRST PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
C NUMBER OF ANIMALS IN A UNIFORMLY CLUSTERED PATTERN.
C THE DISTRIBUTION MAY HAVE ONLY ONE PARAMETER.
C
C P2NUC THE SECOND PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
C NUMBER OF ANIMALS IN A UNIFORMLY CLUSTERED PATTERN.
C THIS IS EQUAL TO ZERO IF THE DISTRIBUTION
C HAS ONLY ONE PARAMETER.
C
C TP A MATRIX, (2000,3), WHICH SHOWS THE TYPE OF PATTERN EACH TRAP

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C IS IN AND THE LOCATION OF EACH TRAP.
 C THE ROWS REPRESENT TRAPS.
 C THE FIRST COLUMN INDICATES THE SPATIAL PATTERN OF
 C THAT TRAP. THE FOURTH DIGIT TO THE LEFT OF THE DECIMAL
 C POINT IS THE CODE FOR THE TRAPS SPATIAL PATTERN.
 C 1 - RANDOM PATTERN.
 C 2 - UNIFORM PATTERN.
 C 3 - RANDOMLY CLUSTERED PATTERN.
 C 4 - UNIFORMLY CLUSTERED PATTERN.
 C 5 - FIXED PATTERN.
 C THE THREE DIGITS IMMEDIATELY TO THE LEFT
 C OF THE DECIMAL POINT INDICATE TO WHICH CLUSTER A
 C TRAP BELONGS IF IT IS IN EITHER A RANDOMLY CLUSTERED OR
 C UNIFORMLY CLUSTERED PATTERN.
 C THE SECOND AND THIRD COLUMNS INDICATE THE LOCATION OF
 C THE TRAP, ITS X AND Y COORDINATES, RESPECTIVELY.
 C
 C TR THE NUMBER OF TRAPS IN A RANDOM PATTERN.
 C
 C TU THE NUMBER OF TRAPS IN A UNIFORM PATTERN.
 C THIS MUST BE A SQUARE OF AN INTEGER.
 C
 C ITRFIX TRAP LOCATIONS FIXED FOR EACH GROUPING OF THE SIMULATION.
 C 0-TRAP LOCATIONS CALCULATED FOR EACH SIMULATION RUN.
 C 1-TRAP LOCATIONS FIXED FOR EACH GROUPING OF THE DATA.
 C
 C G LENGTH OF A SIDE OF THE TRAPPING GRID.
 C
 C TRC THE NUMBER OF RANDOM CLUSTERS OF TRAPS.
 C
 C TUC THE NUMBER OF UNIFORM CLUSTERS OF TRAPS.
 C THIS MUST BE A SQUARE OF AN INTEGER.
 C
 C TF THE NUMBER OF TRAPS IN A FIXED PATTERN.
 C
 C TW THE NUMBER OF TRAPS IN A WEB PATTERN.
 C
 C LINES THE NUMBER OF LINES IN THE WEB PATTERN.
 C
 C ITL THE NUMBER OF TRAPS/LINE IN THE WEB PATTERN.
 C
 C TSP THE TRAP SPACING OR DISTANCE BETWEEN TRAPS IN THE WEB PATTERN.
 C
 C NTRC THE NUMBER OF TRAPS IN THE RANDOMLY CLUSTERED PATTERN.
 C
 C NTUC THE NUMBER OF TRAPS IN THE UNIFORMLY CLUSTERED PATTERN.
 C
 C IOPTRC THE OPTION FOR THE TYPE OF PROBABILITY DISTRIBUTION OF THE
 C NUMBER OF TRAPS IN A RANDOMLY CLUSTERED PATTERN.
 C 1 - POISSON.
 C 2 - GEOMETRIC.
 C 3 - BINOMIAL.
 C 4 - NEGATIVE BINOMIAL.
 C 5 - DISCRETE UNIFORM.
 C 6 - CONSTANT.
 C
 C V1TRC THE VARIANCE OF X IN THE BIVARIATE NORMAL DISTRIBUTION
 C FOR THE DETERMINATION OF THE LOCATION OF TRAPS IN A
 C RANDOMLY CLUSTERED PATTERN.
 C
 C V2TRC THE VARIANCE OF Y IN THE BIVARIATE NORMAL DISTRIBUTION
 C FOR THE DETERMINATION OF THE LOCATION OF TRAPS IN A
 C RANDOMLY CLUSTERED PATTERN.
 C
 C RHOTRC RHO IN THE BIVARIATE NORMAL DISTRIBUTION FOR THE DETERMINATION
 C OF THE LOCATION OF TRAPS IN A RANDOMLY CLUSTERED PATTERN.

C P1TRC THE FIRST PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
 C NUMBER OF TRAPS IN A RANDOMLY CLUSTERED PATTERN.
 C THE DISTRIBUTION MAY HAVE ONLY ONE PARAMETER.
 C
 C P2TRC THE SECOND PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
 C NUMBER OF TRAPS IN A RANDOMLY CLUSTERED PATTERN.
 C THIS IS EQUAL TO ZERO IF THE DISTRIBUTION
 C HAS ONLY ONE PARAMETER.
 C
 C IOPTUC THE OPTION FOR THE TYPE OF PROBABILITY DISTRIBUTION OF THE
 C NUMBER OF TRAPS IN A UNIFORMLY CLUSTERED PATTERN.
 C 1 - POISSON.
 C 2 - GEOMETRIC.
 C 3 - BINOMIAL.
 C 4 - NEGATIVE BINOMIAL.
 C 5 - DISCRETE UNIFORM.
 C 6 - CONSTANT.
 C
 C V1TUC THE VARIANCE OF X IN THE BIVARIATE NORMAL DISTRIBUTION
 C FOR THE DETERMINATION OF THE LOCATION OF TRAPS IN A
 C UNIFORMLY CLUSTERED PATTERN.
 C
 C V2TUC THE VARIANCE OF Y IN THE BIVARIATE NORMAL DISTRIBUTION
 C FOR THE DETERMINATION OF THE LOCATION OF TRAPS IN A
 C UNIFORMLY CLUSTERED PATTERN.
 C
 C RHOTUC RHO IN THE BIVARIATE NORMAL DISTRIBUTION FOR THE DETERMINATION
 C OF THE LOCATION OF TRAPS IN A UNIFORMLY CLUSTERED PATTERN.
 C
 C P1TUC THE FIRST PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
 C NUMBER OF TRAPS IN A UNIFORMLY CLUSTERED PATTERN.
 C THE DISTRIBUTION MAY HAVE ONLY ONE PARAMETER.
 C
 C P2TUC THE SECOND PARAMETER FOR THE PROBABILITY DISTRIBUTION OF THE
 C NUMBER OF TRAPS IN A UNIFORMLY CLUSTERED PATTERN.
 C THIS IS EQUAL TO ZERO IF THE DISTRIBUTION
 C HAS ONLY ONE PARAMETER.
 C
 C NTOTAL THE TOTAL NUMBER OF ANIMALS IN THE SIMULATION.
 C
 C NTRAPS THE TOTAL NUMBER OF TRAPS IN THE SIMULATION.
 C
 C PHR A MATRIX, (2000,3), WITH THE HOME RANGE MOVEMENT PARAMETERS.
 C THE ROWS REPRESENT ANIMALS AND THE COLUMNS REPRESENT THE
 C PARAMETERS OF THE BIVARIATE NORMAL DISTRIBUTION. THE
 C FIRST COLUMN IS THE VARIANCE OF X, THE SECOND COLUMN IS THE
 C VARIANCE OF Y, AND THE THIRD COLUMN IS RHO.
 C
 C RWPARG A MATRIX(2000,4), WITH THE PARAMETERS FOR THE RANDOM WALK
 C MODEL. THE FIRST ELEMENT IS THE ANIMALS LAST X LOCATION
 C THE SECOND ELEMENT IS THE ANIMALS LAST Y LOCATION. THE THIRD
 C ELEMENT IS THE PREVIOUS THETA VALUE. THE FOURTH ELEMENT
 C IS THE ANIMALS LAST DISTANCE FROM ITS HOME RANGE CENTER. THIS
 C ARRAY IS ONLY ACTIVE IN SUBROUTINE TRAP
 C
 C STEP A VARIABLE FOR THE STEP LENGTH OF ANIMALS IN THE RANDOM
 C WALK MODEL
 C
 C KL THE CENTRAL TENDENCY FACTOR IN THE RANDOM WALK MODEL
 C THIS SHOULD BE CHOSEN FOR A GIVEN RANGE OF SINOUSITIES
 C SEE SUBROUTINE RANDWALK FOR INFORMATION ABOUT THIS
 C PARAMETER
 C
 C IOT A MATRIX, (500,10), WHICH IDENTIFIES THE TRAPS WHICH ARE
 C TO BE ACTIVATED.
 C 0 - TRAP NOT ACTIVATED DURING THAT TRAPPING PERIOD.
 C 1 - TRAP ACTIVATED DURING THAT TRAPPING PERIOD.

model

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C      THE ROWS REPRESENT TRAPS AND THE COLUMNS REPRESENT
C      TRAPPING PERIODS.
C      THUS, THE MAXIMUM NUMBER OF TRAPS ALLOWED IS 500 AND THE MAXIMUM
C      NUMBER OF TRAPPING PERIODS ALLOWED IS 20.
C
C T      A MATRIX, (2000,40), WHICH HAS THE DATA FOR ALL TRAPPING PERIODS.
C      THE ROWS REPRESENT ANIMALS. EACH GROUP OF FOUR COLUMNS
C      REPRESENTS DATA FROM ONE TRAPPING PERIOD. THE FIRST COLUMN
C      OF THE GROUP INDICATES WHICH TRAP CAPTURED THAT ANIMAL.
C      A ZERO INDICATES THAT THE ANIMAL WAS NOT CAPTURED DURING THAT
C      TRAPPING PERIOD. THE SECOND AND THIRD COLUMNS OF
C      THE GROUP INDICATE THE LOCATION OF THE ANIMAL.
C      FOR THAT TRAPPING PERIOD, ITS X AND Y COORDINATES, RESPECTIVELY.
C      THUS, THE MAXIMUM NUMBER OF ANIMALS ALLOWED IS 2000 AND
C      THE MAXIMUM NUMBER OF TRAPPING PERIODS IS 10. THE FOURTH
C      IS THE MOVE DURING THE TRAPPING PERIOD THE ANIMAL WAS CAUGHT.
C
C PC      A MATRIX, (2000,10), WHICH HAS THE PROBABILITY OF CAPTURE
C      FOR ALL ANIMALS DURING ALL TRAPPING PERIODS.
C      THE ROWS REPRESENT ANIMALS AND THE COLUMNS REPRESENT
C      TRAPPING PERIODS.
C
C ICPROB  OPTION FOR OUTPUT OF DETAILED CAPTURE PROBABILITIES.
C          0 = NO OUTPUT.
C          1 = DETAILED OUTPUT FOR MODEL MTBH PRODUCED.
C
C IRED    OPTION FOR REDUCED OUTPUT.
C          0 = NORMAL OUTPUT.
C          1 = REDUCED OUTPUT.
C          2 = EXTREMELY REDUCED OUTPUT.
C          3 = NO OUTPUT
C
C ICAPTX  OPTION FOR OUTPUT OF X MATRIX FOR POPULATION ESTIMATES USING
C      PROGRAM CAPTURE. FILE NAME = 'XMATRX.DAT', FILE NUMBER = 14.
C      FILE MAY NEED TO BE EDITED BEFORE USE IN PROGRAM CAPTURE.
C          0 = NO OUTPUT.
C          1 = OUTPUT DESIRED.
C
C ICPRED  OPTION FOR OUTPUT OF XY-REDUCED DATA FILE FOR USE IN POPULATION
C      AND DENSITY ESTIMATES FOR PROGRAM CAPTURE. CAN'T BE USED WITH
C      WEB TYPE(TW) DATA, ICAPTX MUST BE USED FOR TW. FILE NAME = 'XRED.DA
C      FILE NUMBER = 15. FILE MAY NEED EDITING BEFORE USE IN PROGRAM
C      CAPTURE.
C          0 = NO OUTPUT.
C          1 = OUTPUT DESIRED.
C
C ITRANS  OPTION FOR OUTPUT OF DATA FILE FROM WEB TRAPPING DATA(TW) FOR
C      DENSITY ESTIMATES FROM PROGRAM TRANSECT. CAN ONLY BE USED WITH
C      WEB TYPE DATA. FILE NAME = 'TRANS.DAT', FILE NUMBER = 16.
C      FILE WILL NEED EDITING BEFORE USE IN PROGRAM TRANSECT.
C          0 = NO OUTPUT.
C          1 = OUTPUT DESIRED.
C
C MINTAB  OPTION FOR OUTPUT TO DATAFILE FOR USE IN PLOTTING ANIMAL AND
C      TRAP LOCATIONS FOR THE FIRST SIMULATION ON PROGRAM MINTAB.
C
C IDATA   INDICATES HOW MANY GROUPINGS OF INPUT DATA EXIST, EXAMPLE
C      IF IDATA=5, AND NSIMS=500 THEN EACH 100 RUNS HAVE A NEW DATA
C      INPUT. ALL GROUPINGS EXIST IN THE INPUT FILE SIMIN.DAT. HEAD-
C      ING INFORMATION EXISTS IN SIMHEAD.DAT.
C
C ILOC    OPTION FOR OUTPUT OF DATA FILE CONTAINING ANIMAL LOCATIONS
C      , MOVEMENTS, AND CAPTURES.
C          0 = NO OUTPUT
C          1 = OUTPUT DESIRED
C
C IN      INPUT FILE NUMBER. USE 5 FOR TERMINAL INPUT, OTHERWISE ANY

```

```

C      NUMBERS BUT 13-17.
C
C IN1     FILE NUMBER OF HEADING INFO ONLY, IF ALL DATA INPUT FROM ONE
C      FILE THEN IN1=IN.
C
C OUT     OUTPUT FILE NUMBER. USE 6 FOR TERMINAL OUTPUT, OTHERWISE ANY
C      NUMBERS BUT 13-17.
C
C SIMIN.DAT INPUT FILE FOR ALL DATA WHEN IDATA=1, IF IDATA.GT.1 THEN
C      FILE OCCURS SEVERAL GROUPINGS OF DATA DEPENDING ON VALUE
C      OF IDATA.
C
C SIMHEAD.DAT INPUT FOR HEADING INFO ONLY IF IDATA.GT.1, REFERENCED BY
C      IN1.
C
C SIMOUT.DAT GENERAL OUTPUT FILE FOR ANIMAL & TRAP LOCATIONS, ETC.
C
C XMATRIX.DAT OUTPUT FILE FOR ICAPTX, FOR PROGRAM CAPTURE.
C
C XRED.DAT   OUTPUT FILE FOR ICPRED, FOR PROGRAM CAPTURE.
C
C MINTAB.DAT OUTPUT FILE FOR MINTAB, FOR PLOTTING ANIMAL LOCATIONS ON
C      FACILITIES WITH MINTAB CAPABILITIES.
C
C TRANS.DAT  OUTPUT FILE FOR ITRANS, FOR PROGRAM TRANSECT.
C
C *****
C DATA FORMAT.
C EVERY ***** INDICATES A POSSIBILITY OF AT LEAST ONE DATA CARD.
C A NOTE AT THE END OF EACH ***** STATEMENT INDICATES THE EXACT
C NUMBER OF CARDS. IN AN ?IF? RELATIONSHIP NO CARDS ARE
C SUBMITTED WHEN THE ?IF? RELATIONSHIP DOES NOT HOLD.
C *****
C NOTE*****THE SYMBOL *D* INDICATES THE VARIABLE IS DELETED FROM THE MODEL.
C
C ***** NAME
C      (A15)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE, NO
C      MATTER HOW MANY SIMULATIONS ARE TO BE PERFORMED
C      ON THIS SET UP.
C
C ***** IF(IN1.NE.IN.AND.IDATA.GT.1)
C      NSEG(10)
C      (10(I2,IX))
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE, NO
C      MATTER HOW MANY SIMULATIONS ARE TO BE PERFORMED
C      ON THIS SET UP.
C
C ***** MINTAB
C      (I1)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** ICAPTX
C      (I1)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** ICPRED
C      (I1)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** ITRANS
C      (I1)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** NSIMS
C      (I3)

```


5

ALL THE FOLLOWING STATEMENTS MUST BE EXAMINED AND CARDS
SUBMITTED IF APPLICABLE FOR EACH SIMULATION IN THE SET UP.

```
C ***** IUHR
C          (I1)
C          NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
```

```
C ***** IF (NUC.NE.0.AND.IOPNUC.EQ.1)
C      P1NUC
```

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C      (F7.3)
C      IF (NUC.NE.0.AND.IOPNUC.EQ.2)
C      P1NUC
C      (F7.3)
C      IF (NUC.NE.0.AND.IOPNUC.EQ.3)
C      P1NUC,P2NUC
C      (I3,1X,F7.3)
C      IF (NUC.NE.0.AND.IOPNUC.EQ.4)
C      P1NUC,P2NUC
C      (I3,1X,F7.3)
C      IF (NUC.NE.0.AND.IOPNUC.EQ.5)
C      P1NUC,P2NUC
C      (I3,1X,I3)
C      IF (NUC.NE.0.AND.IOPNUC.EQ.6)
C      P1NUC
C      (I3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (NF.NE.0)
C      AP (K,1),AP (K,2),AP (K,3)
C      (F6.1,1X,F7.3,1X,F7.3)
C      NOTE: NF CARDS MUST ACCOMPANY THE DATA HERE.
C
C ***** TR,TU,TRC,TUC,TF,TW
C      (I3,1X,I3,1X,I3,1X,I3,1X,I3,1X,I3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (TU.NE.0.OR.TW.NE.0)
C      ITRFIX
C      (I1)
C      NOTE ONLY ONE CARD MUST ACCOMPANY THE DATA HERE
C
C ***** IF (TU.NE.0)
C      G
C      (F6.1)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (TRC.NE.0)
C      IOPTRC,VITRC,V2TRC,RHOTRC
C      (I1,1X,F6.3,1X,F6.3,1X,F6.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (TRC.NE.0.AND.IOPTRC.EQ.1)
C      P1TRC
C      (F7.3)
C      IF (TRC.NE.0.AND.IOPTRC.EQ.2)
C      P1TRC
C      (F7.3)
C      IF (TRC.NE.0.AND.IOPTRC.EQ.3)
C      P1TRC,P2TRC
C      (I3,1X,F7.3)
C      IF (TRC.NE.0.AND.IOPTRC.EQ.4)
C      P1TRC,P2TRC
C      (I3,1X,F7.3)
C      IF (TRC.NE.0.AND.IOPTRC.EQ.5)
C      P1TRC,P2TRC
C      (I3,1X,I3)
C      IF (TRC.NE.0.AND.IOPTRC.EQ.6)
C      P1TRC
C      (I3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (TUC.NE.0)
C      IOPTUC,VITUC,V2TUC,RHOTUC
C      (I1,1X,F6.3,1X,F6.3,1X,F6.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C

```

```

C ***** IF (TUC.NE.0.AND.IOPTUC.EQ.1)
C      P1TUC
C      (F7.3)
C      IF (TUC.NE.0.AND.IOPTUC.EQ.2)
C      P1TUC
C      (F7.3)
C      IF (TUC.NE.0.AND.IOPTUC.EQ.3)
C      P1TUC,P2TUC
C      (I3,1X,F7.3)
C      IF (TUC.NE.0.AND.IOPTUC.EQ.4)
C      P1TUC,P2TUC
C      (I3,1X,F7.3)
C      IF (TUC.NE.0.AND.IOPTUC.EQ.5)
C      P1TUC,P2TUC
C      (I3,1X,I3)
C      IF (TUC.NE.0.AND.IOPTUC.EQ.6)
C      P2TUC
C      (I3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (TF.NE.0)
C      TP (K,1),TP (K,2),TP (K,3)
C      (F6.1,1X,F7.3,1X,F7.3)
C      NOTE: TF CARDS MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (TW.NE.0)
C      LINES,ITL,TSP
C      (I4,1X,I4,1X,F6.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.0.AND.IUHR)
C      IF (NR.NE.0.OR.NU.NE.0.OR.NRC.NE.0.OR.NUC.NE.0.OR.NF.NE.0)
C      PHR (I,1),PHR (I,2),PHR (I,3)
C      (F7.3,1X,F7.3,1X,F7.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.1.AND.NR.NE.0.AND.IUHR)
C      PHR (I,1),PHR (I,2),PHR (I,3)
C      (F7.3,1X,F7.3,1X,F7.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.1.AND.NU.NE.0.AND.IUHR)
C      PHR (I,1),PHR (I,2),PHR (I,3)
C      (F7.3,1X,F7.3,1X,F7.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.1.AND.NRC.NE.0.AND.IUHR)
C      PHR (I,1),PHR (I,2),PHR (I,3)
C      (F7.3,1X,F7.3,1X,F7.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.1.AND.NUC.NE.0.AND.IUHR)
C      PHR (I,1),PHR (I,2),PHR (I,3)
C      (F7.3,1X,F7.3,1X,F7.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.1.AND.NF.NE.0.AND.IUHR)
C      PHR (I,1),PHR (I,2),PHR (I,3)
C      (F7.3,1X,F7.3,1X,F7.3)
C      NOTE: ONLY ONE CARD MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.2.AND.NR.NE.0.AND.IUHR)
C      PHR (I,1),PHR (I,2),PHR (I,3)
C      (F7.3,1X,F7.3,1X,F7.3)
C      NOTE: NR CARDS MUST ACCOMPANY THE DATA HERE.
C
C ***** IF (IHRPAR.EQ.2.AND.NU.NE.0.AND.IUHR)

```

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C PROGRAM TO SIMULATE SMALL MAMMAL MOVEMENT AND TRAPPING CREATED BY ZARNOC
C AND MODIFIED BY KEN WILSON AND JOHN BOULANGER.

```

C
      INTEGER TR,TU,TRC,TUC,TF,TW,OUT,NSEG(10)
      REAL DH(2,3),DT(2,10),ML(3),MU(3),XLAM(10),DLAM(10),PCTOT(10)
      REAL AVEPC(10),TCAP(10),EXCAP(10),CPRAD(10),KL
      CHARACTER NAME*40,FILEN*25,OUTN*25,HDFILE*25
      COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3
1),PC(1000,10)
      COMMON/R/ IX
      COMMON/B/BETA(1000),GAMMA(10),XLAMHD(1000,10),NTOTAL,NTPER,PHAR,
1ICPB,ALPHB,BETAB,ICPG,ALPHG,BETAG,ICPL,ALPHL,BETAL,AVEBET,AVEGAM,
2PEXC,PCTOT,STEP
C
C*****
C
C  OPENS VARIOUS INPUT AND OUTPUT FILES DESCRIBED IN DOCUMENTATION
C  AND ENTERS NAME OF THE SIMULATION RUNS.
C*****
C
C
C
C
      IDATA=1
      IN=5
      IN1=IN
      OUT=2
      FILEN='simbunin'
      OUTN='simbunout'
      IF(IN.NE.5) OPEN(IN,FILE=FILEN,STATUS='OLD')
      IF(OUT.NE.6) OPEN(OUT,FILE=OUTN,STATUS='NEW')
      IF(IN1.NE.IN) OPEN(IN1,FILE=HDFILE,STATUS='OLD')
      READ(IN1,'(A40)') NAME
      IF(IN1.NE.IN) THEN
        KGR=0
        READ(IN1,'(10(I2,1X))') (NSEG(I),I=1,IDATA)
      END IF
      READ(IN1,'(I1)') NOOUT
      READ(IN1,'(I1)') MINTAB
      OPEN(13,FILE='M'//NAME(1:5)///'.DAT',STATUS='NEW')
      READ(IN1,'(I1)') ICAPTX
      IF(ICAPTX.NE.0) OPEN(14,FILE='XM'//NAME(1:5)///'.DAT',STATUS='NEW')
      READ(IN1,'(I1)') ICPRED
      IF(ICPRED.NE.0) OPEN(15,FILE='XR'//NAME(1:5)///'.DAT',STATUS='NEW')
      READ(IN1,'(I1)') ITRANS
      READ(IN1,'(I1)') ITRN2
      IF(ITRANS.NE.0) THEN
        OPEN(16,FILE='TR'//NAME(1:5)///'.DAT',STATUS='NEW')
        OPEN(18,FILE='PC'//NAME(1:5)///'.DAT',STATUS='NEW')
      END IF
      IF(ITRN2.NE.0) THEN
        OPEN(19,FILE='LO'//NAME(1:5)///'.DAT',STATUS='NEW')
      END IF
      READ(IN1,'(I1)') ILOC
      IF(ILOC.NE.0) OPEN(17,FILE='LC'//NAME(1:5)///'.DAT',ACCESS='SEQUENTIAL'
1,STATUS='NEW',FORM='UNFORMATTED',RECORDTYPE='FIXED',RECL=18)
      READ(IN1,'(I1)') JIX
      READ(IN1,'(I3)') NSIMS
      IF(IN1.NE.IN) THEN
        IGROUP=NSIMS/IDATA
        KGROUP=IGROUP
      END IF
      KGRP=0
      ISIM=0
      READ(IN,'(I1)') ICPROB
      READ(IN,'(I1)') IRED
C
C*****
C
C  READS IN THE RANDOM NUMBER GENERATOR SEED.
C*****

```

```

C
  IF (JIX.NE.0.AND.ISIM.EQ.1) THEN
    READ(IN,'(I9)') IIX
    IX=IIX
    GO TO 402
  END IF
  IF (IN1.NE.IN) THEN
    IF (ISIM.EQ.1.OR.ISIM.EQ.KGRP) THEN
      Y--(SECNDS(9999999.0))
      IIX=IFIX(Y/2.)*2+1
      IX=IIX
    ELSE
      IIX=IIX+(ISIM*52)
      IX=IIX
    END IF
  ELSE IF (IN1.EQ.IN) THEN
    Y--(SECNDS(9999999.0))
    IIX=IFIX(Y/2.)*2+1
    IX=IIX
  END IF

C*****
C  READS IN PARAMETERS AND OPTIONS.
C*****
C
402  READ(IN,'(F6.1)') C
    READ(IN,'(I2)') NTPER
    READ(IN,'(I1)') ITROP
    READ(IN,'(F4.2)') PBAR
    READ(IN,'(I1)') ICPB
    READ(IN,'(2F11.7)') ALPHB,BETAB
    READ(IN,'(I1)') ICPG
    READ(IN,'(2F11.7)') ALPHG,BETAG
    READ(IN,'(I1)') ICPL
    READ(IN,'(2F11.7)') ALPHL,BETAL
    READ(IN,'(I1)') IUHR
    IF (IUHR.EQ.3) READ(IN,'(F4.1)') PEXC
    READ(IN,'(I1)') IHRPAR
    READ(IN,'(I1)') ICPRAD
    READ(IN,'(F6.2)') CPRAD(1)
    IF (ISIM.GT.1.AND.ISIM.LE.KGROUP) CPRAD(1)=CAPFIX
    CAPRAD=CPRAD(1)
    READ(IN,'(I2)') NMOVES
    IF (IUHR.EQ.4) THEN
      READ(IN,'(I3)') STEP
      READ(IN,'(F4.2)') KL
    END IF

C*****
C  INITIALIZES VARIABLES.
C*****
C
    NNRC=0
    NNUC=0
    NTRC=0
    NTUC=0

C
C  READS IN AND SETS UP THE POPULATION ACCORDING TO THE SPATIAL
C  PATTERN DESIRED.
C*****
C
    K=0
    READ(IN,'(I3,1X,I3,1X,I3,1X,I3,1X,I3,1X,I3)') NR,NU,NRC,NUC,NF
    READ(IN,'(I4)') NEXTOT
    IF (NR.EQ.0) GO TO 500
    CALL RANDOM(C,K,NR,AP)
500  IF (NF.EQ.0) GO TO 504

```

```

    DO I=1,NF
      K=K+1
      READ(IN,'(F6.1,1X,F7.3,1X,F7.3)') AP(K,1),AP(K,2),AP(K,3)
    END DO

C*****
C  READS IN AND SETS UP THE TRAPS ACCORDING TO THE SPATIAL
C  PATTERN DESIRED.
C*****
C
504  K=0
    READ(IN,'(I3,5(1X,I3))') TR,TU,TRC,TUC,TF,TW
508  IF (TF.EQ.0) GO TO 509
    DO I=1,TF
      K=K+1
      READ(IN,'(F6.1,1X,F7.3,1X,F7.3)') TP(K,1),TP(K,2),TP(K,3)
    END DO
400  NTOTAL=NR+NU+NNRC+NNUC+NF
    NTOTAL=NEXTOT
    NTRAPS=TR+TU+NTRC+NTUC+TF+TW
    DO K=1,NTOTAL
      NT=NTPER*4
      DO L=1,NT
        T(K,L)=0.0
      END DO
    END DO

C
C*****
C  READS IN THE HOME RANGE MOVEMENT PARAMETERS VAR(X),VAR(Y),
C  AND RHO OF THE DISTRIBUTION CHOSEN AND SETS THEM INTO PHR.
C*****
C
    IF (NTOTAL.EQ.0) GO TO 910
    CALL HRPAR(NTOTAL,NR,NU,NRC,NNRC,NUC,NNUC,NF,IHRPAR,DH)

C
C  PERFORMS THE TRAPPING PROCESS FOR ALL TRAPPING PERIODS.
C*****
C
911  IF (NTPER.EQ.0.OR.NTOTAL.EQ.0) GO TO 913
    DO I=1,NTPER
      CALL HRMOVM-disabled by John Boulanger 5/93
      PCTOT(I)=0.0
      CALL MTBH(I)
      CALL TRAP(NTOTAL,I,NTRAPS,NMOVES,CAPRAD,NTPER,TCAP,STEP,KL)

C
C*****
C  IDENTIFIES THE TRAPPING EXPERIMENT NUMBER.
C*****
C
    IF (IRED.EQ.3) GO TO 1008
    IF (IRED.EQ.2.AND.ISIM.GT.1) GO TO 1000
913  WRITE(OUT,863)
863  FORMAT(//)
    DO I=1,2
      WRITE(OUT,862)
862  FORMAT(' ',T10,'*****')
    END DO
    WRITE(OUT,863)
1000 WRITE(OUT,'(1X,T47,A33,3X,I3)') 'SIMULATION OF TRAPPING EXPERIMEN
    1T',ISIM
    WRITE(OUT,863)
    IF (IRED.EQ.2.AND.ISIM.GT.1) GO TO 1002
    DO I=1,2
      WRITE(OUT,862)
    END DO

```

```

C
C*****
C PRINTS THE DATA INPUT.
C*****
C
1002 IF (IRED.EQ.2.AND.(ISIM.EQ.1.OR.ISIM.EQ.KGRP)) THEN
      GO TO 1003
      ELSE IF (IRED.EQ.2) THEN
      GO TO 1010
      END IF
1003 WRITE(OUT,'(1H1,T51,A)') NAME
      WRITE(OUT,'(//,1X,T60,A)') 'THE DATA INPUT'
      WRITE(OUT,'(1X,A,14)') 'IDATA=' ,IDATA
      WRITE(OUT,'(1X,A,11)') 'MINTAB=' ,MINTAB
      WRITE(OUT,'(1X,A,11)') 'ICAPT=' ,ICAPT
      WRITE(OUT,'(1X,A,11)') 'ICPRE=' ,ICPRE
      WRITE(OUT,'(1X,A,11)') 'ITRAN=' ,ITRAN
      WRITE(OUT,'(1X,A,11)') 'ILOCA=' ,ILOCA
      WRITE(OUT,'(1X,A,11)') 'ICPROB=' ,ICPROB
      WRITE(OUT,'(1X,A,13)') 'NSIMS=' ,NSIMS
      WRITE(OUT,'(1X,A,11)') 'IRED=' ,IRED
      WRITE(OUT,'(1X,A,11)') 'IIX=' ,IIX
      WRITE(OUT,'(1X,A,11)') 'IIC=' ,IIC
      WRITE(OUT,'(1X,A,12)') 'NTPER=' ,NTPER
      WRITE(OUT,'(1X,A,11)') 'ITROP=' ,ITROP
      WRITE(OUT,'(1X,A,14)') 'PBAR=' ,PBAR
      WRITE(OUT,'(1X,A,11)') 'ICPB=' ,ICPB
      WRITE(OUT,'(1X,2(A,F11.7))') 'ALPHB=' ,ALPHB, ' BETAB=' ,BETAB
      WRITE(OUT,'(1X,A,11)') 'ICPG=' ,ICPG
      WRITE(OUT,'(1X,2(A,F11.7))') 'ALPHG=' ,ALPHG, ' BETAG=' ,BETAG
      WRITE(OUT,'(1X,A,11)') 'ICPL=' ,ICPL
      WRITE(OUT,'(1X,2(A,F11.7))') 'ALPHL=' ,ALPHL, ' BETAL=' ,BETAL
      WRITE(OUT,'(1X,A,11)') 'IUHR=' ,IUHR
      IF (IUHR.EQ.3) WRITE(OUT,'(1X,A,14)') 'PEXC=' ,PEXC
      WRITE(OUT,'(1X,A,11)') 'IHRPAR=' ,IHRPAR
      WRITE(OUT,'(1X,A,14)') 'INITIAL CAPRAD=' ,CAPRAD(1)
      WRITE(OUT,'(1X,A,12)') 'NMOVES=' ,NMOVES
      IF (IUHR.EQ.4) THEN
      WRITE(OUT,'(1X,A,13)') 'STEP=' ,STEP
      WRITE(OUT,'(1X,A,14)') 'KL=' ,KL
      END IF
      WRITE(OUT,'(1X,A,13,4X,A,13,4X,A,13,4X,A,13,4X,A,13)') 'NR=' ,NR,
1NU=' ,NU, 'NRC=' ,NRC, 'NUC=' ,NUC, 'NF=' ,NF
      WRITE(OUT,'(1X,A,14)') 'NEXTOT=' ,NEXTOT
      IF (NRC.EQ.0) GO TO 626
      WRITE(OUT,'(1X,A,11,3X,A,14,4X,A,13,4X,A,13,4X,A,13)') 'IOPNRC=' ,I
1OPNRC, 'VINRC=' ,VINRC, 'V2NRC=' ,V2NRC, 'RHONRC=' ,RHONRC
      GO TO(614,616,618,620,622,624),IOPNRC
614 WRITE(OUT,'(1X,A,14)') 'PINRC=' ,PINRC
      GO TO 626
616 WRITE(OUT,'(1X,A,14)') 'PINRC=' ,PINRC
      GO TO 626
618 IP1NRC=PINRC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'PINRC=' ,IP1NRC, 'P2NRC=' ,P2NRC
      GO TO 626
620 IP1NRC=PINRC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'PINRC=' ,IP1NRC, 'P2NRC=' ,P2NRC
      GO TO 626
622 IP1NRC=PINRC
      IP2NRC=P2NRC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'PINRC=' ,IP1NRC, 'P2NRC=' ,IP2NRC
      GO TO 626
624 IP1NRC=PINRC
      WRITE(OUT,'(1X,A,13)') 'PINRC=' ,IP1NRC
626 IF (NUC.EQ.0) GO TO 640
      WRITE(OUT,'(1X,A,11,4X,A,14,4X,A,14,4X,A,14,4X,A,14)') 'IOPNUC=' ,I
1OPNUC, 'VINUC=' ,VINUC, 'V2NUC=' ,V2NUC, 'RHONUC=' ,RHONUC

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GO TO(628,630,632,634,636,638),IOPNUC
628 WRITE(OUT,'(1X,A,14)') 'PINUC=' ,PINUC
      GO TO 640
630 WRITE(OUT,'(1X,A,14)') 'PINUC=' ,PINUC
      GO TO 640
632 IP1NUC=PINUC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'PINUC=' ,IP1NUC, 'P2NUC=' ,P2NUC
      GO TO 640
634 IP1NUC=PINUC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'PINUC=' ,IP1NUC, 'P2NUC=' ,P2NUC
      GO TO 640
636 IP1NUC=PINUC
      IP2NUC=P2NUC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'PINUC=' ,IP1NUC, 'P2NUC=' ,IP2NUC
      GO TO 640
638 IP1NUC=PINUC
      WRITE(OUT,'(1X,A,13)') 'PINUC=' ,IP1NUC
640 IF (NF.EQ.0) GO TO 643
      K=NR+NU+NNRC+NNUC+1
      KK=K+NF-1
      DO I=K,KK
        WRITE(OUT,'(1X,A,13,4X,A,14,4X,A,14,4X,A,14,4X,A,14)') 'AP('
1,I,',1)=' ,AP(I,1), 'AP(' ,I,',2)=' ,AP(I,2), 'AP(' ,I,',3)=' ,AP(I,3)
      END DO
643 WRITE(OUT,'(1X,A,13,4X,A,14,4X,A,14,4X,A,14,4X,A,14)') 'T
1R=' ,TR, 'TU=' ,TU, 'TRC=' ,TRC, 'TUC=' ,TUC, 'TF=' ,TF, 'TW=' ,TW
      WRITE(OUT,'(1X,A,11)') 'ITRFX=' ,ITRFX
      IF (TU.NE.0) WRITE(OUT,'(1X,A,14)') 'G=' ,G
      IF (TW.NE.0) THEN
        WRITE(OUT,'(1X,A,14)') 'LINES=' ,LINES
        WRITE(OUT,'(1X,A,14)') 'ITL=' ,ITL
        WRITE(OUT,'(1X,A,14)') 'TSP=' ,TSP
      END IF
      IF (TRC.EQ.0) GO TO 658
      WRITE(OUT,'(1X,A,11,4X,A,14,4X,A,14,4X,A,14,4X,A,14)') 'IOPTRC=' ,IO
1PTRC, 'V1TRC=' ,V1TRC, 'V2TRC=' ,V2TRC, 'RHOTRC=' ,RHOTRC
      GO TO(646,648,650,652,654,656),IOPTRC
646 WRITE(OUT,'(1X,A,14)') 'P1TRC=' ,P1TRC
      GO TO 658
648 WRITE(OUT,'(1X,A,14)') 'P1TRC=' ,P1TRC
      GO TO 658
650 IP1TRC=P1TRC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'P1TRC=' ,IP1TRC, 'P2TRC=' ,P2TRC
      GO TO 658
652 IP1TRC=P1TRC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'P1TRC=' ,IP1TRC, 'P2TRC=' ,P2TRC
      GO TO 658
654 IP1TRC=P1TRC
      IP2TRC=P2TRC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'P1TRC=' ,IP1TRC, 'P2TRC=' ,IP2TRC
      GO TO 658
656 IP1TRC=P1TRC
      WRITE(OUT,'(1X,A,13)') 'P1TRC=' ,IP1TRC
658 IF (TUC.EQ.0) GO TO 672
      WRITE(OUT,'(1X,A,11,4X,A,14,4X,A,14,4X,A,14,4X,A,14)') 'IOPTUC=' ,IO
1PTUC, 'V1TUC=' ,V1TUC, 'V2TUC=' ,V2TUC, 'RHOTUC=' ,RHOTUC
      GO TO(660,662,664,666,668,670),IOPTUC
660 WRITE(OUT,'(1X,A,14)') 'P1TUC=' ,P1TUC
      GO TO 672
662 WRITE(OUT,'(1X,A,14)') 'P1TUC=' ,P1TUC
      GO TO 672
664 IP1TUC=P1TUC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'P1TUC=' ,IP1TUC, 'P2TUC=' ,P2TUC
      GO TO 672
666 IP1TUC=P1TUC
      WRITE(OUT,'(1X,A,13,4X,A,14)') 'P1TUC=' ,IP1TUC, 'P2TUC=' ,P2TUC
      GO TO 672

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668 IP1TUC=P1TUC
IP2TUC=P2TUC
WRITE(OUT, '(1X,A,I3,4X,A,I3)') 'P1TUC=', IP1TUC, 'P2TUC=', IP2TUC
GO TO 672
670 IP1TUC=P1TUC
WRITE(OUT, '(1X,A,I3)') 'P1TUC=', IP1TUC
672 IF (TF.EQ.0) GO TO 675
K=TR+TU+NTRC+NTUC+1
KK=K+TF-1
DO I=K, KK
WRITE(OUT, '(1X,A,I3,A,F6.1,4X,A,I3,A,F7.3,4X,A,I3,A,F7.3)') 'TP(
1', I, '1)=' , TP(I,1), 'TP(' , I, ' , 2)=' , TP(I,2), 'TP(' , I, ' , 3)=' , TP(I,3)
END DO
675 IF (IUHR.EQ.1) GO TO 800
IF (IHRPAR.NE.0) GO TO 677
WRITE(OUT, '(1X,A,F7.2,4X,A,F7.2,4X,A,F7.3)') 'PHR(I,1)=' , PHR(1,1)
1', 'PHR(I,2)=' , PHR(1,2), 'PHR(I,3)=' , PHR(1,3)
677 IF (IHRPAR.NE.1) GO TO 687
IF (NR.EQ.0) GO TO 679
WRITE(OUT, '(1X,A,F7.2,4X,A,F7.2,4X,A,F7.3)') 'PHR(I,1)=' , PHR(1,1)
I, 'PHR(I,2)=' , PHR(I,2), 'PHR(I,3)=' , PHR(I,3)
679 IF (NU.EQ.0) GO TO 681
I=NR+1
WRITE(OUT, '(1X,A,F7.2,4X,A,F7.2,4X,A,F7.3)') 'PHR(I,1)=' , PHR(I,1)
1', 'PHR(I,2)=' , PHR(I,2), 'PHR(I,3)=' , PHR(I,3)
681 IF (NRC.EQ.0) GO TO 683
I=NR+NU+1
WRITE(OUT, '(1X,A,F7.2,4X,A,F7.2,4X,A,F7.3)') 'PHR(I,1)=' , PHR(I,1)
I, 'PHR(I,2)=' , PHR(I,2), 'PHR(I,3)=' , PHR(I,3)
683 IF (NUC.EQ.0) GO TO 685
I=NR+NU+NNRC+1
WRITE(OUT, '(1X,A,F7.3,4X,A,F7.3,4X,A,F7.3)') 'PHR(I,1)=' , PHR(I,1)
I, 'PHR(I,2)=' , PHR(I,2), 'PHR(I,3)=' , PHR(I,3)
685 IF (NF.EQ.0) GO TO 687
I=NR+NU+NNRC+NNUC+1
WRITE(OUT, '(1X,A,F7.3,4X,A,F7.3,4X,A,F7.3)') 'PHR(I,1)=' , PHR(I,1)
I, 'PHR(I,2)=' , PHR(I,2), 'PHR(I,3)=' , PHR(I,3)
687 IF (IHRPAR.NE.2) GO TO 800
IF (NR.EQ.0) GO TO 689
DO I=1, NR
WRITE(OUT, '(1X,A,I3,A,F7.2,4X,A,I3,A,F7.2,4X,A,I3,A,F7.3)') 'PHR
1(' , I, ' , 1)=' , PHR(I,1), 'PHR(' , I, ' , 2)=' , PHR(I,2), 'PHR(' , I, ' , 3)=' , PHR(
2I,3)
END DO
689 IF (NU.EQ.0) GO TO 691
K=NR+1
KK=K+NU-1
DO I=K, KK
WRITE(OUT, '(1X,A,I3,A,F7.3,4X,A,I3,A,F7.3,4X,A,I3,A,F7.3)') 'PHR
1(' , I, ' , 1)=' , PHR(I,1), 'PHR(' , I, ' , 2)=' , PHR(I,2), 'PHR(' , I, ' , 3)=' , PHR(
2I,3)
END DO
691 IF (NRC.EQ.0) GO TO 693
IF (NNRC.EQ.0) GO TO 960
I=NR+NU+1
WRITE(OUT, '(1X,A,F7.2,4X,A,F7.2,4X,A,F7.3)') 'PHR(I,1)=' , PHR(I,1)
1', 'PHR(I,2)=' , PHR(I,2), 'PHR(I,3)=' , PHR(I,3)
GO TO 693
960 WRITE(OUT, '(1X,A,F7.3,4X,A,F7.3,4X,A,F7.3)') 'PHR(I,1)=' , DH(1,1),
1'PHR(I,2)=' , DH(1,2), 'PHR(I,3)=' , DH(1,3)
693 IF (NUC.EQ.0) GO TO 695
IF (NNUC.EQ.0) GO TO 962
I=NR+NU+NNRC+1
WRITE(OUT, '(1X,A,F7.3,4X,A,F7.3,4X,A,F7.3)') 'PHR(I,1)=' , PHR(I,1)
1', 'PHR(I,2)=' , PHR(I,2), 'PHR(I,3)=' , PHR(I,3)
GO TO 695
962 WRITE(OUT, '(1X,A,F7.3,4X,A,F7.3,4X,A,F7.3)') 'PHR(I,1)=' , DH(2,1),

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1'PHR(I,2)=' , DH(2,2), 'PHR(I,3)=' , DH(2,3)
695 IF (NF.EQ.0) GO TO 800
K=NR+NU+NNRC+NNUC+1
KK=K+NF-1
DO I=K, KK
WRITE(OUT, '(1X,A,I3,A,F7.2,4X,A,I3,A,F7.1,4X,A,I3,A,F7.3)') 'PHR
1(' , I, ' , 1)=' , PHR(I,1), 'PHR(' , I, ' , 2)=' , PHR(I,2), 'PHR(' , I, ' , 3)=' , PHR(I,
23)
END DO
800 IF (NTRAPS.EQ.0.OR.NTPER.EQ.0) GO TO 812
IF (ITROP.NE.1) GO TO 802
WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (IOT(1,J), J=1, NTPER)
GO TO 812
802 IF (ITROP.NE.2) GO TO 812
IF (TR.EQ.0) GO TO 804
WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (IOT(1,J), J=1, NTPER)
804 IF (TU.EQ.0) GO TO 806
I=TR+1
WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (IOT(1,J), J=1, NTPER)
806 IF (TRC.EQ.0) GO TO 808
IF (NTRC.EQ.0) GO TO 990
I=TR+TU+1
WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (IOT(1,J), J=1, NTPER)
807 GO TO 808
990 WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (DT(1,I), I=1, NTPER)
808 IF (NTUC.EQ.0) GO TO 991
I=TR+TU+NTRC+1
WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (IOT(1,J), J=1, NTPER)
GO TO 810
991 WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (DT(2,I), I=1, NTPER)
810 IF (TF.EQ.0) GO TO 811
I=TR+TU+NTRC+NTUC+1
WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (IOT(1,J), J=1, NTPER)
811 IF (TW.EQ.0) GO TO 812
I=TR+TU+NTRC+NTUC+TF+1
WRITE(OUT, '(1X,A,20I1)') 'IOT(I,J)=' , (IOT(1,J), J=1, NTPER)
IF (IDATA.NE.1) THEN
WRITE(OUT, '(1X,A,I3)') 'IDATA=' , IDATA
DO K=1, IDATA
WRITE(OUT, '(1X,A,I2,A,I3)') 'NSEG(' , I, ' )=' , NSEG(K)
END DO
END IF
812 CONTINUE
C
C*****
C PRINTS THE OUTPUT.
C*****
C
1010 IF (IRED.EQ.2) THEN
GO TO 1900
ELSE
WRITE(OUT, '(1H1,T47,A,3X,I3)') 'SIMULATION OF TRAPPING EXPERIMENT
1', ISIM
END IF
1900 WRITE(OUT, '(A,A,3X,I11)') 'O', 'INITIAL RANDOM NUMBER GENERATOR SEE
1D', IIX
WRITE(OUT, '(A,A,10X,I3)') 'O', 'NUMBER OF ANIMALS IN RANDOM PATTERN
1N', NR
WRITE(OUT, '(A,A,9X,I3)') ' ' , 'NUMBER OF ANIMALS IN UNIFORM PATTERN
1N', NU
WRITE(OUT, '(A,A,9X,I3)') ' ' , 'NUMBER OF ANIMALS IN RANDOM CLUSTER
1S', NNRC
WRITE(OUT, '(A,A,8X,I3)') ' ' , 'NUMBER OF ANIMALS IN UNIFORM CLUSTER
1RS', NNUC
WRITE(OUT, '(A,A,11X,I3)') ' ' , 'NUMBER OF ANIMALS IN FIXED PATTERN
1', NF

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WRITE(OUT,'(A,A,22X,I3)') ' ', 'TOTAL NUMBER OF ANIMALS', NTOTAL
WRITE(OUT,'(A,A,9X,I3)') '0', 'NUMBER OF RANDOM CLUSTERS OF ANIMAL
1S', NRC
WRITE(OUT,'(A,A,8X,I3)') ' ', 'NUMBER OF UNIFORM CLUSTERS OF ANIMA
1LS', NUC
IF (IRED.EQ.2.AND.(ISIM.EQ.1.OR.ISIM.EQ.KGRP)) THEN
GO TO 1112
ELSE IF (IRED.EQ.2) THEN
GO TO 1111
END IF
1112 WRITE(OUT,'(A,A,12X,I3)') '0', 'NUMBER OF TRAPS IN RANDOM PATTERN'
1, TR
WRITE(OUT,'(A,A,11X,I3)') ' ', 'NUMBER OF TRAPS IN UNIFORM PATTERN
1', TU
WRITE(OUT,'(A,A,11X,I3)') ' ', 'NUMBER OF TRAPS IN RANDOM CLUSTERS
1', NTRC
WRITE(OUT,'(A,A,10X,I3)') ' ', 'NUMBER OF TRAPS IN UNIFORM CLUSTER
1S', NTUC
WRITE(OUT,'(A,A,13X,I3)') ' ', 'NUMBER OF TRAPS IN FIXED PATTERN',
1TF
WRITE(OUT,'(A,A,13X,I3)') ' ', 'NUMBER OF TRAPS IN A WEB PATTERN',
1TW
WRITE(OUT,'(A,A,24X,I3)') ' ', 'TOTAL NUMBER OF TRAPS', NTRAPS
WRITE(OUT,'(A,A,11X,I3)') '0', 'NUMBER OF RANDOM CLUSTERS OF TRAPS
1', TRC
WRITE(OUT,'(A,A,10X,I3)') ' ', 'NUMBER OF UNIFORM CLUSTERS OF TRAP
1S', TUC
IF (IUHR.EQ.1) GO TO 18139
C WRITE(OUT,'(A,A,10X,F5.2)') '0', 'TRAP RADIUS FOR TRAPPING PERIOD
C 11', TRPBAR
18139 IF (NRC.EQ.0) GO TO 580
WRITE(OUT,'(A,T24,A)') '0', 'THE PROBABILITY DISTRIBUTION OF THE N
UMBER OF ANIMALS IN A RANDOMLY CLUSTERED PATTERN'
GO TO (410,411,412,413,414,415), IOPNRC
410 WRITE(OUT,'(A,T45,A,3X,F7.3)') ' ', 'POISSON DISTRIBUTED WITH PARA
1METER', P1NRC
GO TO 580
411 WRITE(OUT,'(A,T42,A,3X,F7.3)') ' ', 'GEOMETRICALLY DISTRIBUTED WIT
1H PARAMETER', P1NRC
GO TO 580
412 IP1NRC=P1NRC
WRITE(OUT,'(A,T37,A,3X,I3,3X,A,3X,F7.3)') ' ', 'BINOMIALLY DISTRIB
1UTED WITH PARAMETERS', IP1NRC, 'AND', P2NRC
GO TO 580
413 IP1NRC=P1NRC
WRITE(OUT,'(A,T32,A,3X,I3,3X,A,3X,F7.3)') ' ', 'NEGATIVE BINOMIAL
1Y DISTRIBUTED WITH PARAMETERS', IP1NRC, 'AND', P2NRC
GO TO 580
414 IP1NRC=P1NRC
IP2NRC=P2NRC
WRITE(OUT,'(A,T35,A,3X,I3,3X,A,3X,I3)') ' ', 'DISCRETE UNIFORMLY D
1ISTRIBUTED WITH PARAMETERS', IP1NRC, 'AND', IP2NRC
GO TO 580
415 IP1NRC=P1NRC
WRITE(OUT,'(A,T55,A,3X,I3)') ' ', 'CONSTANT EQUAL TO', IP1NRC
580 IF (NUC.EQ.0) GO TO 581
WRITE(OUT,'(A,T24,A)') '0', 'THE PROBABILITY DISTRIBUTION OF THE N
UMBER OF ANIMALS IN A UNIFORMLY CLUSTERED PATTERN'
GO TO (420,421,422,423,424,425), IOPNUC
420 WRITE(OUT,'(A,T45,A,3X,F7.3)') ' ', 'POISSON DISTRIBUTED WITH PARA
1METER', P1NUC
GO TO 581
421 WRITE(OUT,'(A,T42,A,3X,F7.3)') ' ', 'GEOMETRICALLY DISTRIBUTED WIT
1H PARAMETER', P1NUC
GO TO 581
422 IP1NUC=P1NUC
WRITE(OUT,'(A,T37,A,3X,I3,3X,A,3X,F7.3)') ' ', 'BINOMIALLY DISTRIB

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1UTED WITH PARAMETER', IP1NUC, 'AND', P2NUC
GO TO 581
423 IP1NUC=P1NUC
WRITE(OUT,'(A,T32,A,3X,I3,3X,A,3X,F7.3)') ' ', 'NEGATIVE BINOMIAL
1Y DISTRIBUTED WITH PARAMETERS', IP1NUC, 'AND', P2NUC
GO TO 581
424 IP1NUC=P1NUC
IP2NUC=P2NUC
WRITE(OUT,'(A,T35,A,3X,I3,3X,A,3X,I3)') ' ', 'DISCRETE UNIFORMLY D
1ISTRIBUTED WITH PARAMETERS', IP1NUC, 'AND', IP2NUC
GO TO 581
425 IP1NUC=P1NUC
WRITE(OUT,'(A,T55,A,3X,I3)') ' ', 'CONSTANT EQUAL TO', IP1NUC
581 IF (TRC.EQ.0) GO TO 582
WRITE(OUT,'(A,T25,A)') '0', 'THE PROBABILITY DISTRIBUTION OF THE N
UMBER OF TRAPS IN A RANDOMLY CLUSTERED PATTERN'
GO TO (430,431,432,433,434,435), IOPTRC
430 WRITE(OUT,'(A,T42,A,3X,F7.3)') ' ', 'POISSON DISTRIBUTED WITH PARA
1METER', P1TRC
GO TO 582
431 WRITE(OUT,'(A,T42,A,3X,F7.3)') ' ', 'GEOMETRICALLY DISTRIBUTED WIT
1H PARAMETER', P1TRC
GO TO 582
432 IP1TRC=P1TRC
WRITE(OUT,'(A,T37,A,3X,I3,3X,A,3X,F7.3)') ' ', 'BINOMIALLY DISTRIB
1UTED WITH PARAMETERS', IP1TRC, 'AND', P2TRC
GO TO 582
433 IP1TRC=P1TRC
WRITE(OUT,'(A,T32,A,3X,I3,3X,A,3X,F7.3)') ' ', 'NEGATIVE BINOMIAL
1Y DISTRIBUTED WITH PARAMETERS', IP1TRC, 'AND', P2TRC
GO TO 582
434 IP1TRC=P1TRC
IP2TRC=P2TRC
WRITE(OUT,'(A,T35,A,3X,I3,3X,A,3X,I3)') ' ', 'DISCRETE UNIFORMLY D
1ISTRIBUTED WITH PARAMETERS', IP1TRC, 'AND', IP2TRC
GO TO 582
435 IP1TRC=P1TRC
WRITE(OUT,'(A,T55,A,3X,I3)') ' ', 'CONSTANT EQUAL TO', IP1TRC
582 IF (TUC.EQ.0) GO TO 546
WRITE(OUT,'(A,T25,A)') '0', 'THE PROBABILITY DISTRIBUTION OF THE N
UMBER OF TRAPS IN A UNIFORMLY CLUSTERED PATTERN'
GO TO (440,441,442,443,444,445), IOPTUC
440 WRITE(OUT,'(A,T45,A,3X,F7.3)') ' ', 'POISSON DISTRIBUTED WITH PARA
1METER', P1TUC
GO TO 546
441 WRITE(OUT,'(A,T42,A,3X,F7.3)') ' ', 'GEOMETRICALLY DISTRIBUTED WIT
1H PARAMETER', P1TUC
GO TO 546
442 IP1TUC=P1TUC
WRITE(OUT,'(A,T37,A,3X,I3,3X,A,3X,F7.3)') ' ', 'BINOMIALLY DISTRIB
1UTED WITH PARAMETERS', IP1TUC, 'AND', P2TUC
GO TO 546
443 IP1TUC=P1TUC
WRITE(OUT,'(A,T32,A,3X,I3,3X,A,3X,F7.3)') ' ', 'NEGATIVE BINOMIAL
1Y DISTRIBUTED WITH PARAMETERS', IP1TUC, 'AND', P2TUC
GO TO 546
444 IP1TUC=P1TUC
IP2TUC=P2TUC
WRITE(OUT,'(A,T35,A,3X,I3,3X,A,3X,I3)') ' ', 'DISCRETE UNIFORMLY D
1ISTRIBUTED WITH PARAMETERS', IP1TUC, 'AND', IP2TUC
GO TO 546
445 IP1TUC=P1TUC
WRITE(OUT,'(A,T55,A,3X,I3)') ' ', 'CONSTANT EQUAL TO', IP1TUC
546 CONTINUE
IF (NTOTAL.EQ.0) GO TO 900
1111 IF (IRED.EQ.2.AND.(ISIM.EQ.1.OR.ISIM.EQ.KGRP)) THEN
GO TO 1113

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ELSE IF(IRED.EQ.2) THEN
  GO TO 1004
END IF
1113 WRITE(OUT,' (A,T51,A)') ' ', 'DISTRIBUTION PATTERN OF ANIMALS'
  WRITE(OUT,' (A,T43,A,5X,A,6X,A,9X,A)') '0', 'ANIMAL NUMBER', 'PATTER
IN CODE', 'X', 'Y'
  NTOT=NTOTAL
  IF(IRED.EQ.1.OR.(IRED.EQ.2.AND.ISIM.GT.1)) NTOT=10
  DO I=1,NTOT
    WRITE(OUT,' (A,T49,I3,11X,F8.3,5X,F8.3,3X,F7.3)') ' ', I, AP(I,1), A
  1P(I,2), AP(I,3)
  END DO
900 IF(NTRAPS.EQ.0) GO TO 901
  NTRAP=NTRAPS
  IF(IRED.EQ.1.OR.(IRED.EQ.2.AND.ISIM.GT.1)) NTRAP=10
  IF(IRED.NE.0) THEN
    WRITE(OUT,' (//,T52,A)') ' DISTRIBUTION PATTERN OF TRAPS'
  ELSE
    WRITE(OUT,' (1H1,T52,A)') 'DISTRIBUTION PATTERN OF TRAPS'
  END IF
  WRITE(OUT,' (A,T44,A,6X,A,6X,A,9X,A)') '0', 'TRAP NUMBER', 'PATTERN
1CODE', 'X', 'Y'
  DO I=1,NTRAP
    WRITE(OUT,' (A,T49,I3,11X,F8.3,5X,F7.3,3X,F7.3)') ' ', I, TP(I,1), T
  1P(I,2), TP(I,3)
  END DO
  IF(NTPER.EQ.0) GO TO 901
  IF(IRED.NE.0.AND.ITROP.EQ.0) THEN
    WRITE(OUT,' (//,T59,A)') ' ALL TRAPS ACTIVATED FOR EACH TRAPPING
1PERIOD'
    GO TO 901
  END IF
  WRITE(OUT,' (1H1,T59,A)') 'TRAP ACTIVATION'
  WRITE(OUT,' (A,T47,A)') '0', '0-TRAP DEACTIVATED DURING TRAPPING PE
1RIOD'
  WRITE(OUT,' (A,T47,A)') ' ', '1-TRAP ACTIVATED DURING TRAPPING PERI
1OD'
  WRITE(OUT,' (A,T35,A,5X,A)') '0', 'TRAP NUMBER', 'TRAPPING PERIOD'
  WRITE(OUT,' (A,T49,20I3)') ' ', (J,J=1,NTPER)
  WRITE(OUT,' (A)') '0'
  DO I=1,NTRAP
    WRITE(OUT,' (A,T39,I3,7X,20I3)') ' ', I, (IOT(I,J),J=1,NTPER)
  END DO
901 IF(NTOTAL.EQ.0) GO TO 902
  IF(IRED.NE.0) THEN
    WRITE(OUT,' (//,T39,A)') ' HOME RANGE PARAMETERS FOR DISTRIBUTION
1CHOSEN'
  ELSE
    WRITE(OUT,' (1H1,T39,A)') 'HOME RANGE PARAMETERS FOR DISTRIBUTION
1CHOSEN'
  END IF
  WRITE(OUT,' (A,T49,A,3X,A,4X,A,6X,A)') ' ', 'ANIMAL NUMBER', 'VAR(X)
1', 'VAR(Y)', 'RHO'
  DO I=1,NTOT
    WRITE(OUT,' (A,T51,I3,8X,F7.2,3X,F7.1,3X,F7.3)') ' ', I, PHR(I,1), P
  1HR(I,2), PHR(I,3)
  IF(IHRPAR.EQ.0) THEN
    WRITE(OUT,' (1X,A)') 'ALL ANIMALS HAVE THE SAME HOME RANGES'
    GO TO 902
  END IF
  END DO
  GO TO 902
902 IF(NTPER.EQ.0.OR.NTOTAL.EQ.0) GO TO 903
1004 FCAP=0.0
  TAVEPC=0.0
  DO J=1,NTPER
    IF(IRED.NE.0) THEN

```

```

    WRITE(OUT,' (//,T58,A,1X,I2)') ' TRAPPING PERIOD', J
    IF(IRED.EQ.2.AND.(ISIM.EQ.1.OR.ISIM.EQ.KGRP)) THEN
      GO TO 1005
    ELSE IF(IRED.EQ.2) THEN
      GO TO 1006
    END IF
  ELSE
    WRITE(OUT,' (1H1,T58,A,1X,I2)') 'TRAPPING PERIOD', J
  END IF
1005 WRITE(OUT,' (A,T20,A,3X,A,7X,A,10X,A,4X,A,4X,A)') ' ', 'ANIMAL NUM
1BER', 'PROBABILITY OF CAPTURE', 'X', 'Y', 'TRAPPING CODE', 'NMOVE'
  DO I=1,NTOTAL
    K=(4*J)-3
    L=K+1
    M=L+1
    IF((IRED.EQ.1.OR.(IRED.EQ.2.AND.ISIM.GT.1)).AND.I.GT.10) GO TO 905
    WRITE(OUT,' (A,T25,I3,18X,F4.2,12X,F7.3,4X,F7.3,4X,F7.3,6X,F7.3
1)') ' ', I, PC(I,J), T(I,L), T(I,M), T(I,K), T(I,(J*4))
  905 END DO
1006 WRITE(OUT,' (1X,A,F7.3)') ' AVERAGE PROB=', AVEPC(J)
  WRITE(OUT,' (A,F4.0)') ' TOTAL CAPTURED=', TCAP(J)
  WRITE(OUT,' (A,F7.3)') ' EXPECTED NUMBER OF CAPTURES=', EXCAP(J)
  WRITE(OUT,' (A,I2,A,F9.3)') ' CAPTURE RADIUS FOR PERIOD ', J, ' =',
1CPRAD(J)
  FCAP=FCAP+TCAP(J)
  TAVEPC=TAVEPC+AVEPC(J)
  END DO
  TAVEPC=TAVEPC/NTPER
  WRITE(OUT,' (1X,/,A,F7.3)') 'AVERAGE PROB FOR SIMUL=', TAVEPC
C
C*****
C PRINTS DETAILED CAPTURE PROBABILITIES FOR MODEL MTBH.
C REFERENCE: OTIS ET. AL. 1978. STATISTICAL INFERENCE FROM
C CAPTURE DATA ON CLOSED ANIMAL POPULATIONS.
C WILDL. MONOGR. 62:1-135.
C*****
C
  IF(IRED.EQ.2.AND.(ISIM.EQ.1.OR.ISIM.EQ.KGRP)) THEN
    GO TO 1009
  ELSE IF(IRED.EQ.2) THEN
    GO TO 1008
  END IF
1009 IF(ICPROB.NE.0) THEN
  WRITE(OUT,' (1H0,T45,A)') 'DETAILED CAPTURE PROBABILITIES FOR MOD
1EL MTBH'
  WRITE(OUT,' (A,T20,A,3X,A,3X,A)') ' ', 'TRAPPING PERIOD',
1'TIME EFFECT', 'TRNSTIME'
  DO J=1,NTPER
    EGAM=EXP(GAMMA(J))
    XGAM=EGAM/(1+EGAM)
    WRITE(OUT,' (A,T27,I2,9X,F8.3,5X,F8.3)') ' ', J, GAMMA(J), XGAM
  END DO
  WRITE(OUT,' (A,T30,A,F8.3)') ' ', 'AVERAGE TIME EFFECT=', AVEGAM
  WRITE(OUT,' (1H0,T20,A,3X,A,3X,A)') 'ANIMAL NUMBER', 'HETER. EFFE
1CT', 'TRNSHETER'
  DO I=1,NTOT
    EBET=EXP(BETA(I))
    XBET=EBET/(1+EBET)
    WRITE(OUT,' (A,T25,I4,8X,F8.3,6X,F8.3)') ' ', I, BETA(I), XBET
  END DO
  WRITE(OUT,' (A,T25,A,F8.3)') ' ', 'AVERAGE HETER. EFFECT=', AVEBET
  WRITE(OUT,' (1H0,T59,A)') 'BEHAVIOR EFFECT'
  WRITE(OUT,' (A,/,T20,A,A)') ' ', 'EACH PAIR OF NUMBERS ARE A TRAPP
1ING PERIOD', ' THE BOTTOM NUMBER IS THE TRANSFORMED EFFECT.'
  WRITE(OUT,' (A,/,T10,A)') ' ', 'ANIMAL NUMBER'
  DO I=1,NTOT
    DO J=1,NTPER

```


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      DLAM(J)=XLAMBDA(I,J)
      IF (DLAM(J).EQ.99.0) DLAM(J)=0.0
      ELAM=EXP(DLAM(J))
      XLAM(J)=ELAM/(1+ELAM)
      END DO
      WRITE(OUT,' (A,T14,I4,7X,<NTPER>(F8.3))' ) ' ',I,(DLAM(J),J=1,NTP
1ER)
      WRITE(OUT,' (A,T25,<NTPER>(F8.3))' ) ' ',(XLAM(J),J=1,NTPER)
      END DO
      END IF
C
C*****
C CALLS VARIOUS OUTPUT FILES, IF DESIRED.
C*****
C
1008 IF (ICAPTX.NE.0) CALL XMATRIX(NAME,NTPER,ISIM,NTOTAL,FCAP)
      IF (ICPRED.NE.0) CALL CAPXYRED(NTRAPS,ISIM,NAME,NTPER,
1NTOTAL,TU,G,FCAP)
      IF (ILOCL.NE.0) CALL ANLCN(NTOTAL,NTPER)
      IF (ISIM.LE.MINTAB) CALL MINITAB(NTRAPS,NTOTAL,NTPER,OUT)
903  WRITE(OUT,' (I1)' )
C RETURNS TO NEXT SIMULATION
      IF (IDATA.GT.1) THEN
        IF (ISIM.EQ.KGROUP) THEN
          KGR=KGR+1
          KGRP=KGROUP+1
          ISEG=0
          KGROUP=IGROUP+KGROUP
          DO I=1,KGR
            ISEG=ISEG+NSEG(I)
          END DO
        END IF
        IF (KGR.EQ.0) THEN
          REWIND(IN)
        ELSE
          REWIND(IN)
          DO I=1,ISEG
            READ(IN,' (I1)' )
          END DO
        END IF
      END IF
      IF (ISIM.EQ.10.OR.ISIM.EQ.25.OR.ISIM.EQ.50.OR.ISIM.EQ.KGRP) THEN
        PRINT *,(CHAR(7),I=1,3)
      END IF
      IREM=MOD(ISIM,5)
      IF (IREM.EQ.0) PRINT *,CHAR(7)
723  GO TO 731
732  STOP
      END
      SUBROUTINE RNDWLK (STEP,KL,I,XO,YO,VARX,VARY,UTMX,UTMY
1,THETA,DIFFD,NX,NY)
C*****
C RANDOM WALK MODEL BASED ON WORK OF BENHAMOU:
C REF: J. THEOR. BIOL. 139:379-88
C*****
      COMMON/R/ IX
      REAL KL,NX,NY
      STD=((VARX+VARY)/2)**.5
      SB=(1.92/(KL*STD))**.5
      SIGMAB=SB*(STEP**.5)
      IF (I.EQ.1) PDIST=0.0
      IF (I.GT.1) PDIST=((UTMX-XO)**2+(UTMY-YO)**2)**.5
C If first iteration or animal close to center than spit in;
C another direction;
      IF (PDIST.LT.STEP) THEN

```

```

      THETA=RANO(IX)*(3.14*2.)
      UTMX=XO
      UTMY=YO
      ELSE
C Sigmai is changed dependant on change in distance from center;
      SIGMAI=SIGMAB*(1+(KL*(DIFFD/STEP)))
C A normal variate is generated dependant on value of sigmai;
      R1=RANNOR(IX)
      LAMBDAI=(SIGMAI*R1)
C Theta1 is direction of animals path, changed dependant on lambdai;
      THETA=THETA+LAMBDAI
      END IF
C Animals new location and distance from home range center calc;
      NX=UTMX+(STEP*COS(THETA))
      NY=UTMY+(STEP*SIN(THETA))
      DIST=((NX-XO)**2+(NY-YO)**2)**.5
      DIFFD=DIST-PDIST
      UTMX=NX
      UTMY=NY
      RETURN
      END
C
C*****
      SUBROUTINE MTBH(I)
C
C*****
C CALCULATES THE PROBABILITY OF CAPTURE FOR EACH ANIMAL USING THE MODEL
C M(TBH) AND A LOGISTIC TRANSFORM EQUATION OF THE FORM :
C  $P(I,J) = \exp(\theta(I,J) / (1 + \exp(\theta(I,J))))$ , WHERE
C  $\theta(I,J) = \theta(I) + (\beta(I) - \text{AVERAGE } \beta(I)) + (\gamma(J) - \text{AVERAGE } \gamma(J))$ 
C  $\lambda(I,J) = \lambda(I) * \lambda(J)$ 
C THETA-PBAR FOR THE SIMULATION.
C  $\beta(I)$ =HETEROGENEITY EFFECT FOR I=1,NTOTAL, USES PARAMETER ICPB.
C  $\gamma(J)$ =TIME EFFECT FOR J=1,NTPER, USES PARAMETER ICPG.
C  $\lambda(I,J)$ =BEHAVIOR EFFECT FOR I=1,NTOTAL AND J=1,NTPER, USES
C PARAMETER ICPL.
C 2(I,J)=0, IF ANIMAL HAS NOT BEEN CAUGHT, AND 1 IF CAUGHT.
C THIS LOGISTIC TRANSFORM EQUATION ASSURES P(I,J)'S ARE ON THE
C INTERVAL (0,1).
C THIS ALGORITHM HAS BEEN MODIFIED AS OF 7/93: THE CHANGES ARE:
C 1) HETEROGENEITY EFFECT IS ONLY A DETERMINANT OF ANIMAL
C CAPTURE PROBABILITY WHEN TRAPPING OCCASION J=1.
C 2) ANIMAL KEEPS BASE CAPTURE PROBABILITY EFFECT FROM PREVIOUS TRAP OCCASION
C CHANGE DETERMINED BY BEHAVIOUR EFFECT (IF ANIMAL CAUGHT IN PREVIOUS
C OCCASION(J-1) AND TIME EFFECT.
C 3) BEHAVIOUR EFFECT CAN BE NEGATIVE (TRAP SHY) OR POSITIVE (TRAP HAPPY)
C ZIJ IS DETERMINED BY PREVIOUS TRAP NIGHT ONLY
C
C REFERENCE: BURNHAM,KENNETH P. 1981. MEMORANDUM ON A UNIFIED
C CONCEPTUAL VERSION OF THE EIGHT MODELS IN OTIS ET. AL.
C OTIS ET. AL. 1978. STATISTICAL INFERENCE FROM CAPTURE
C DATA ON CLOSED ANIMAL POPULATIONS. WILDL. MONOGR. 62:1-135.
C*****
C
C
      REAL LAMVAR,Z(1000,10),LAMLN,PCTOT(10)
      COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3)
1,PC(1000,10)
      COMMON/R/ IX
      COMMON/B/BETA(1000),GAMMA(10),XLAMBDA(1000,10),NTOTAL,NTPER,PBAR,
1ICPB,ALPHB,BETAB,ICPG,ALPHG,BETAG,ICPL,ALPHL,BETAL,AVEBET,AVEGAM,
2PEXC,PCTOT
      M=((I-1)*4)-3
      ZTHETA=ALOG(PBAR/(1-PBAR))

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IF (I.EQ.1) THEN
  SUMBET=0.0
  SUMLAM=0.0
  AVELAM=0.0
  SUMGAM=0.0
  CTLAM=0.0
  DO J=1,NTOTAL
    DO K=1,NTPER
      XLAMB0(J,K)=99.0
      Z(J,K)=0.0
    END DO
  END DO
END IF
IF (I.EQ.1) THEN
  DO J=1,NTOTAL
10    CALL CAPROB(ICPB,BETVAR,ALPHB,BETAH)
      IF (BETVAR.EQ.0.0.OR.BETVAR.EQ.1.) GO TO 10
      BETLN=ALOG(BETVAR/(1.-BETVAR))
      BETA(J)=BETLN
      SUMBET=SUMBET+BETA(J)
    END DO
    DO K=1,NTPER
20    CALL CAPROB(ICPG,GAMVAR,ALPHG,BETAG)
      IF (GAMVAR.EQ.0.0.OR.GAMVAR.EQ.1.) GO TO 20
      GAMLN=ALOG(GAMVAR/(1.-GAMVAR))
      GAMMA(K)=GAMLN
      SUMGAM=SUMGAM+GAMMA(K)
    END DO
    AVEGAM=SUMGAM/FLOAT(NTPER)
    AVEBET=SUMBET/FLOAT(NTOTAL)
    GO TO 50
  END IF
  IF (I.GT.1) THEN
    DO J=1,NTOTAL
      IF (T(J,M).NE.0.0) THEN
C IF T(J,M).NE.0, ANIMAL WAS CAPTURED LAST TIME OR IF XLAMB0.NE.99.0
C MEANS THE ANIMAL HAD BEEN PREVIOUSLY CAUGHT-modified so that only last
C capture occasion matters-
30    CALL CAPROB(ICPL,LAMVAR,ALPHL,BETAL)
        IF (LAMVAR.EQ.0.0.OR.LAMVAR.EQ.1.) GO TO 30
        LAMLN=(ALOG(LAMVAR/(1.-LAMVAR))) *-1
        XLAMB0(J,I)=LAMLN
        CTLAM=CTLAM+1
        Z(J,I)=1.0
        SUMLAM=SUMLAM+XLAMB0(J,I)
      END IF
    END DO
    AVELAM=SUMLAM/FLOAT(CTLAM)
  END IF
50  DO J=1,NTOTAL
      IF (PC(J,I).EQ.999.9) THEN
        PC(J,I)=PEXC
      ELSE
C IF FIRST TRAP OCCASION P DET BY PBAR(ZTHETA) HETEROGENIETY EFFECT
C (BETA) AND TIME EFFECT (GAMMA)
        IF (I.EQ.1) THEN
          THETA=ZTHETA+(BETA(J)-AVEBET)+(GAMMA(I)-AVEGAM)+
1 (XLAMB0(J,I)-AVELAM)*Z(J,I)
C IF I>1 THEN P DET BY LAST PC, TIME EFFECT, AND BEHAVIOUR EFFECT
        ELSE
          ZTHETA=ALOG(PC(J,I-1)/(1.-PC(J,I-1)))
          THETA=ZTHETA+(GAMMA(I)-AVEGAM)+(XLAMB0(J,I)
1 -AVELAM)*Z(J,I)
        END IF
        PC(J,I)=EXP(THETA)/(1+EXP(THETA))
      END IF
      PCTOT(I)=PCTOT(I)+PC(J,I)

```

```

END DO
RETURN
END
SUBROUTINE CAPROB(I,VAR,A,B)
C *****
C CALCULATES CAPTURE PROBABILITIES FOR EACH ANIMAL ACCORDING TO A BETA
C DISTRIBUTION OR UNIFORM DISTRIBUTION, GIVEN A AND B
C *****
C
COMMON/R/ IX
GO TO (10,20,30,40),I
10  Z1=0.0
    Z2=0.0
    IALPH=IFIX(A)
    IBETA=IFIX(B)
    ISA=IALPH+1
    ISAB=IALPH+IBETA
    DO J=1,IALPH
12    RAN1=RANO(IX)
        IF (RAN1.EQ.0.0) GO TO 12
        Z1=Z1-ALOG(RAN1)
    END DO
    DO K=ISA,ISAB
14    RAN2=RANO(IX)
        IF (RAN2.EQ.0.0) GO TO 14
        Z2=Z2-ALOG(RAN2)
    END DO
    VAR=Z1/(Z1+Z2)
    GO TO 50
20  VAR=1-(1-RANO(IX))**(1/B)
    GO TO 50
30  VAR=RANO(IX)**(1/A)
    GO TO 50
40  VAR=A+(B-A)*RANO(IX)
50  RETURN
END

SUBROUTINE TRAP(NTOTAL,I,NTRAPS,NMOVES,CAPRAD,NTPER,TCAP,STEP,KL)
C *****
C PERFORMS THE TRAPPING PROCESS FOR A GIVEN TRAPPING PERIOD.
C modified for random walk simulations-may need some revision if other
C movement models are used
C *****
C
COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3),
1 PC(1000,10)
COMMON/R/ IX
INTEGER AVEC(1000),TVEC(500),CAPT
REAL TCAP(10),RWPAR(1000,4)
CALL RANVEC(AVEC,NTOTAL)
TCAP(I)=0.0
NN=I*4
MM=NN-1
MN=MM-1
DO XX=1,NTOTAL
  RWPAR(NTOTAL,1)=0.0
  RWPAR(NTOTAL,2)=0.0
  RWPAR(NTOTAL,3)=0.0
  RWPAR(NTOTAL,4)=0.0
END DO
DO L=1,NTRAPS
  TVEC(L)=IOT(L,I)*L
END DO
DO JJ=1,NMOVES
  DO K=1,NTOTAL

```

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CALL RNDWLK(STEP,KL,JJ,AP(K,2),AP(K,3),PHR(K,1),PHR(K,2),
1RWPAR(K,1),RWPAR(K,2),RWPAR(K,3),RWPAR(K,4),T(K,MN),T(K,MM))
ICOUNT=0
IF(JJ.NE.1) THEN
IF(T(K,NN).NE.0) GO TO 1
END IF
DO L=1,NTRAPS
IF(TVEC(L).EQ.0) GO TO 2
SDIST=((T(AVEC(K),MN)-TP(L,2))**2)+((T(AVEC(K),MM)-TP(L,3))**2)
IF(SDIST.GT.(CAPRAD**2)) GO TO 2
IF(ICOUNT.EQ.0) GO TO 5
IF(SDIST.GT.CAPSD) GO TO 2
CAPSD=SDIST
CAPT=L
GO TO 2
5 CAPSD=SDIST
ICOUNT=1
CAPT=L
2 END DO
IF(ICOUNT.EQ.0) GO TO 1
PROB=RANO(IX)
IF(PROB.LE.PC(AVEC(K),I)) THEN
T(AVEC(K),(MN-1))-CAPT
T(AVEC(K),NN)-FLOAT(JJ)
TVEC(CAPT)=0
TCAP(I)=TCAP(I)+1.
END IF
1 END DO
END DO
RETURN
END

```

```

SUBROUTINE RANDOM(C,K,N,Z)

```

```

C*****
C DISTRIBUTES ANIMALS OR TRAPS IN A RANDOM PATTERN
C modified so that all coordinates are positive-
C adjust to fit specifications of study area
C*****
C

```

```

REAL Z(1000,3)
COMMON/R/ IX
ADJC=C-75
DO I=1,N
K=K+1
Z(K,1)=1000.0

```

Cthis was originally ...-c/2 I eliminated c/2 to keep #'s positive

```

1 Z(K,2)=(ADJC*RANO(IX))
IF(Z(K,2).LT.75.0) GO TO 1
2 Z(K,3)=(ADJC*RANO(IX))
IF(Z(K,3).LT.75.0) GO TO 2
END DO
RETURN
END
SUBROUTINE UNI(C,K,N,Z)

```

```

C*****
C DISTRIBUTES ANIMALS IN A UNIFORM PATTERN
C*****
C

```

```

REAL Z(1000,3)
M=SQRT(FLOAT(N))
R=C/M
CONST=(R/2)-(C/2)
DO I=1,M

```

```

R1=((I-1)*R)+CONST
DO J=1,M
K=K+1
Z(K,1)=2000.0
Z(K,2)=R1
Z(K,3)=((J-1)*R)+CONST
END DO
END DO
RETURN
END
SUBROUTINE UNITR(G,K,N,Z)

```

```

C*****
C DISTRIBUTES TRAPS IN A UNIFORM PATTERN ACCORDING TO PARAMETER G.
C*****
C

```

```

REAL Z(500,3)
M=SQRT(FLOAT(N))
R=G/(M-1)
CONST=-(G/2.)
DO I=1,M
R1=((I-1)*R)+CONST
DO J=1,M
K=K+1
Z(K,1)=2000.0
Z(K,2)=R1
Z(K,3)=((J-1)*R)+CONST
END DO
END DO
RETURN
END
SUBROUTINE RANDCL(C,K,N,IOP,V1,V2,RHO,Z,KK,P1,P2)

```

```

C*****
C READS IN THE PARAMETER(S) OF A SPECIFIED DISTRIBUTION WITH WHICH IT
C DETERMINES THE NUMBER OF ANIMALS OR TRAPS IN A RANDOM CLUSTER
C PATTERN. THEN IT DISTRIBUTES THE ANIMALS OR TRAPS ACCORDING TO A
C SPECIFIED BIVARIATE NORMAL DISTRIBUTION.
C*****
C

```

```

REAL Z(1000,3)
INTEGER X
COMMON/R/ IX
P2=0.0
CH=C-100.
CL=100.
CHN=-1*CH
KK=0
DO I=1,N
A=(C*RANO(IX))
B=(C*RANO(IX))
GO TO(10,11,12,13,14,15),IOP
10 IF(I.GT.1) GO TO 20
READ(5,'(F7.3)')P1
CALL POISSN(P1,X)
GO TO 16
11 IF(I.GT.1) GO TO 21
READ(5,'(F7.3)')P1
CALL GEO(P1,X)
GO TO 16
12 IF(I.GT.1) GO TO 22
READ(5,'(I3,1X,F7.3)')NB,P2
P1=NB
22 CALL BINOM(NB,P2,X)
GO TO 16
13 IF(I.GT.1) GO TO 23
READ(5,'(I3,1X,F7.3)')K,P2

```

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```

REAL Z(1000,3)
INTEGER X
COMMON/R/ IX
P2=0.0
CH=C/2
M=SQRT(FLOAT(N))
R=C/M
CONST=(R/2)-CH
CHN=-1*CH
KK=0
DO I=1,M
  DO J=1,M
    AA=CONST+((I-1)*R)
    BB=CONST+((J-1)*R)
    GO TO(10,11,12,13,14,15),IOP
    IF(I.GT.1.OR.J.GT.1) GO TO 20
    READ(5,'(F7.3)')P1
    CALL POISSN(P1,X)
    GO TO 16
    IF(I.GT.1.OR.J.GT.1) GO TO 21
    READ(5,'(F7.3)')P1
    CALL GEO(P1,X)
    GO TO 16
    IF(I.GT.1.OR.J.GT.1) GO TO 22
    READ(5,'(I3,1X,F7.3)')NB,P2
    P1=NB
    CALL BINOM(NB,P2,X)
    GO TO 16
    IF(I.GT.1.OR.J.GT.1) GO TO 23
    READ(5,'(I3,1X,F7.3)')K,P2
    P1=K
    CALL NBINOM(K,P2,X)
  
```

```

      INTEGER X
      COMMON/R/ IX
      X=0
      B=EXP(-P)
      TR=1.0
1    R=RANO(IX)

```

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```

      TR=TR*R
      IF (TR-B) 3,2,2
    2 X=X+1
      GO TO 1
    3 RETURN
      END
      SUBROUTINE GEO(P,X)

```

```

C
C*****
C GENERATES A GEOMETRIC VARIATE ACCORDING TO THE SPECIFIED PARAMETER: P.
C
C REFERENCE: NAYLOR, T. H., J. L. BALINTFY, D. S. BURDICK, AND
C             K. CHU. 1966.
C             COMPUTER SIMULATION TECHNIQUES.
C             PAGES 102-104.
C*****
C

```

```

      INTEGER X
      COMMON/R/ IX
    10 R=RANO(IX)
      IF (R.EQ.0.0) GO TO 10
      X=ALOG(R)/ALOG(1-P)
      RETURN
      END
      SUBROUTINE BINOM(N,P,X)

```

```

C
C*****
C GENERATES A BINOMIAL VARIATE ACCORDING TO THE SPECIFIED PARAMETERS: N,P.
C
C REFERENCE: SCHMIDT, J. W. AND R. E. TAYLOR. 1970.
C             SIMULATION AND ANALYSIS OF INDUSTRIAL SYSTEMS.
C             PAGES 275-276.
C*****
C

```

```

      INTEGER X
      COMMON/R/ IX
      X=0
      DO I=1,N
      R=RANO(IX)
      IF (R.GT.P) GO TO 1
      X=X+1
    1 END DO
      RETURN
      END
      SUBROUTINE NBINOM(K,P,X)

```

```

C
C*****
C GENERATES A NEGATIVE BINOMIAL VARIATE ACCORDING TO THE SPECIFIED
C PARAMETERS: K,P.
C
C REFERENCE: NAYLOR, T. H., J. L. BALINTFY, D. S. BURDICK, AND
C             K. CHU. 1966.
C             COMPUTER SIMULATION TECHNIQUES.
C             PAGES 104-106.
C*****
C

```

```

      INTEGER X
      COMMON/R/ IX
      TR=1.0
      DO I=1,K
    10 R=RANO(IX)
      IF (R.EQ.0.0) GO TO 10
      TR=TR*R
      END DO
      X=ALOG(TR)/ALOG(1-P)
      RETURN
      END

```

```

      SUBROUTINE DISUNI(A,B,X)

```

```

C
C*****
C GENERATES A DISCRETE UNIFORM VARIATE FROM A TO B INCLUSIVE ACCORDING TO
C THE SPECIFIED PARAMETERS: A,B.
C*****
C

```

```

      INTEGER A,B,X
      COMMON/R/ IX
      R=RANO(IX)
      X=(B-A+1)*R+A
      RETURN
      END
      SUBROUTINE HRPAR(NTOTAL,NR,NU,NRC,NNRC,NUC,NNUC,NF,IHRPAR,DH)

```

```

C
C*****
C READS IN THE HOME RANGE MOVEMENT PARAMETERS VAR(X),VAR(Y), AND RHO
C OF THE BIVARIATE NORMAL DISTRIBUTION AND SETS THEM INTO PHR.
C*****
C

```

```

      REAL DH(2,3)
      COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3),
      1PC(1000,10)
      COMMON/R/ IX
      IF (IHRPAR.NE.0) GO TO 2
      READ(5,'(F7.2,1X,F7.1,2X,F5.3)')(PHR(1,J),J=1,3)
      IF (NTOTAL.EQ.1) GO TO 25
      DO J=1,3
      DO I=2,NTOTAL
      PHR(I,J)=PHR(1,J)
      END DO
      END DO
      GO TO 25
    2 IF (IHRPAR.NE.1) GO TO 8
      IF (NR.EQ.0) GO TO 11
      READ(5,'(F7.2,1X,F7.1,2X,F5.3)')(PHR(1,J),J=1,3)
      IF (NR.EQ.1) GO TO 11
      DO J=1,3
      DO I=2,NR
      PHR(I,J)=PHR(1,J)
      END DO
      END DO
    11 IF (NU.EQ.0) GO TO 12
      L=NR+1
      M=NR+NU
      READ(5,'(F7.2,1X,F7.1,2X,F5.3)')(PHR(L,J),J=1,3)
      IF (NU.EQ.1) GO TO 12
      L=L+1
      DO J=1,3
      DO I=L,M
      PHR(I,J)=PHR((L-1),J)
      END DO
      END DO
    12 IF (NRC.EQ.0) GO TO 13
      IF (NNRC.NE.0) GO TO 40
      READ(5,'(F7.3,1X,F7.3,1X,F7.3)')DH(1,1),DH(1,2),DH(1,3)
      GO TO 13
    40 L=NR+NU+1
      M=NR+NU+NNRC
      READ(5,'(F7.2,1X,F7.1,2X,F5.3)')(PHR(L,J),J=1,3)
      IF (NNRC.EQ.1) GO TO 13
      L=L+1
      DO J=1,3
      DO I=L,M
      PHR(I,J)=PHR((L-1),J)
      END DO
      END DO

```

```

13 IF (NUC.EQ.0) GO TO 14
   IF (NNUC.NE.0) GO TO 41
   READ (5, '(F7.3,1X,F7.3,1X,F7.3)') DH(2,1),DH(2,2),DH(2,3)
   GO TO 14
41 L=NR+NU+NNRC+1
   M=NR+NU+NNRC+NNUC
   READ (5, '(F7.2,1X,F7.1,2X,F5.3)') (PHR(L,J),J=1,3)
   IF (NNUC.EQ.1) GO TO 14
   L=L+1
   DO J=1,3
     DO I=L,M
       PHR(I,J)=PHR((L-1),J)
     END DO
   END DO
14 IF (NF.EQ.0) GO TO 25
   L=NR+NU+NNRC+NNUC+1
   M=NR+NU+NNRC+NNUC+NF
   READ (5, '(F7.2,1X,F7.1,2X,F5.3)') (PHR(L,J),J=1,3)
   IF (NF.EQ.1) GO TO 25
   L=L+1
   DO J=1,3
     DO I=L,M
       PHR(I,J)=PHR((L-1),J)
     END DO
   END DO
   GO TO 25
8 K=NR+NU
   IF (K.EQ.0) GO TO 32
   MEAN=47.0
   STD=20.0
   DO I=1,K
     READ (5, '(F7.2,1X,F7.1,2X,F5.3)') (PHR(I,J),J=1,3)
     a slight modification so that phr is generated each time
66 R1=RANNOR(IX)
     X1=(MEAN+(R1*STD))*2
     IF (R1.GT.2.5) GO TO 66
     IF (X1.LT.400.0) GO TO 66
     PHR(I,1)=X1
     PHR(I,2)=X1
     PHR(I,3)=0.000
C   WRITE (6, '(F10.2,1X,F10.2)') (PHR(I,J),J=1,2)
   END DO
32 IF (NRC.EQ.0) GO TO 33
   IF (NNRC.NE.0) GO TO 42
   READ (5, '(F7.2,1X,F7.1,1X,F5.3)') DH(1,1),DH(1,2),DH(1,3)
   GO TO 33
42 K=K+1
   KK=K+NNRC-1
   IF (KK.LT.K) GO TO 33
   READ (5, '(F7.2,1X,F7.1,2X,F5.3)') (PHR(K,J),J=1,3)
   KKK=K+1
   IF (KK.LT.KKK) GO TO 33
   DO J=1,3
     DO I=KKK,KK
       PHR(I,J)=PHR(K,J)
     END DO
   END DO
33 IF (NUC.EQ.0) GO TO 34
   IF (NNUC.NE.0) GO TO 43
   READ (5, '(F7.3,1X,F7.3,1X,F7.3)') DH(2,1),DH(2,2),DH(2,3)
   GO TO 34
43 KK=NR+NU+NNRC
   K=KK+1
   KK=K+NNUC-1
   IF (KK.LT.K) GO TO 34
   READ (5, '(F7.2,1X,F7.1,2X,F5.3)') (PHR(K,J),J=1,3)
   KKK=K+1

```

```

   IF (KK.LT.KKK) GO TO 34
   DO J=1,3
     DO I=KKK,KK
       PHR(I,J)=PHR(K,J)
     END DO
   END DO
34 IF (NF.EQ.0) GO TO 25
   KK=NR+NU+NNRC+NNUC
   K=KK+1
   KK=K+NF-1
   IF (KK.LT.K) GO TO 25
   DO I=K,KK
     READ (5, '(F7.2,1X,F7.1,2X,F5.3)') (PHR(I,J),J=1,3)
   END DO
25 RETURN
END
SUBROUTINE TROP (ITROP,TR,TU,TRC,NTRC,TUC,NTUC,TF,TW,NTOTAL,NTPER,D
1T)
C
C*****
C READS IN THE TRAP ACTIVATIONS AND SETS THEM INTO IOT.
C*****
C
   INTEGER TR,TU,TRC,TUC,TF,TW
   COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3),
1PC(1000,10)
   COMMON/R/ IX
   REAL DT(2,10)
   IF (ITROP.NE.0) GO TO 2
   M=TR+TU+NTRC+NTUC+TF+TW
   DO J=1,NTPER
     DO I=1,M
       IOT(I,J)=1
     END DO
   END DO
   GO TO 10
2 IF (ITROP.NE.1) GO TO 4
   READ (5, '(2011)') (IOT(1,J),J=1,NTPER)
   IF (NTOTAL.EQ.1) GO TO 10
   M=TR+TU+NTRC+NTUC+TF+TW
   DO J=1,NTPER
     DO I=2,M
       IOT(I,J)=IOT(1,J)
     END DO
   END DO
   GO TO 10
4 IF (TR.EQ.0) GO TO 11
   READ (5, '(2011)') (IOT(1,J),J=1,NTPER)
   IF (TR.EQ.1) GO TO 11
   DO J=1,NTPER
     DO I=2,TR
       IOT(I,J)=IOT(1,J)
     END DO
   END DO
11 IF (TU.EQ.0) GO TO 12
   L=TR+1
   M=TR+TU
   READ (5, '(2011)') (IOT(L,J),J=1,NTPER)
   IF (TU.EQ.1) GO TO 12
   L=L+1
   DO J=1,NTPER
     DO I=L,M
       IOT(I,J)=IOT((L-1),J)
     END DO
   END DO
12 IF (TRC.EQ.0) GO TO 13
   IF (NTRC.NE.0) GO TO 20

```

```

      READ(5,' (2011)') (DT(1,I),I=1,NTPER)
      GO TO 13
10  L=TR+TU+1
      M=TR+TU+NTRC
      READ(5,' (2011)') (IOT(L,J),J=1,NTPER)
      IF(NTRC.EQ.1) GO TO 13
      L=L+1
      DO J=1,NTPER
        DO I=L,M
          IOT(I,J)=IOT((L-1),J)
        END DO
      END DO
13  IF(TUC.EQ.0) GO TO 14
      IF(NTUC.NE.0) GO TO 21
      READ(5,' (2011)') (DT(2,I),I=1,NTPER)
      GO TO 14
21  L=TR+TU+NTRC+1
      M=TR+TU+NTRC+NTUC
      READ(5,' (2011)') (IOT(L,J),J=1,NTPER)
      IF(NTUC.EQ.1) GO TO 14
      L=L+1
      DO J=1,NTPER
        DO I=L,M
          IOT(I,J)=IOT((L-1),J)
        END DO
      END DO
14  IF(TF.EQ.0) GO TO 10
      L=TR+TU+NTRC+NTUC+1
      M=TR+TU+NTRC+NTUC+TF
      READ(5,' (2011)') (IOT(L,J),J=1,NTPER)
      IF(TF.EQ.1) GO TO 10
      L=L+1
      DO J=1,NTPER
        DO I=L,M
          IOT(I,J)=IOT((L-1),J)
        END DO
      END DO
10  RETURN
      END
      SUBROUTINE HRMOVN(I,C,NTOTAL,IUHR)
C
C*****
C  MOVES EACH ANIMAL IN ITS HOME RANGE ACCORDING TO THE BIVARIATE NORMAL
C  DISTRIBUTION WITH ITS SPECIFIC HOME RANGE MOVEMENT PARAMETERS.
C*****
C
      COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3),
1PC(1000,10)
      COMMON/R/ IX
      L=(4*I)-1
      K=L-1
      C1=C/2-C
      C2=C-C/2
      DO J=1,NTOTAL
        IF(IUHR.EQ.0) THEN
          CALL BIVNOR(AP(J,2),AP(J,3),PHR(J,1),PHR(J,2),PHR(J,3),T(J,K),T(J
1,L))
          IF(T(J,K).GE.C1.AND.T(J,K).LE.C2) THEN
            GO TO 13
          ELSE
            T(J,K)=T(J,K)
          END IF
13  IF(T(J,L).GE.C1.AND.T(J,L).LE.C2) THEN
            GO TO 18
          ELSE
            T(J,L)=T(J,L)
          END IF
      END DO

```

```

      ELSE IF(IUHR.EQ.1) THEN
        CALL UHR(AP(J,2),AP(J,3),PHR(J,1),PHR(J,2),T(J,K),T(J,L))
        IF(T(J,K).GE.C1.AND.T(J,K).LE.C2) THEN
          GO TO 14
        ELSE
          T(J,K)=T(J,K)
        END IF
14  IF(T(J,L).GE.C1.AND.T(J,L).LE.C2) THEN
          GO TO 18
        ELSE
          T(J,L)=T(J,L)
        END IF
      ELSE IF(IUHR.EQ.2) THEN
        CALL UDISTR(AP(J,2),AP(J,3),PHR(J,1),PHR(J,2),PHR(J,3),T(J,K),T(J
1,L))
        IF(T(J,K).GE.C1.AND.T(J,K).LE.C2) THEN
          GO TO 15
        ELSE
          T(J,K)=T(J,K)
        END IF
15  IF(T(J,L).GE.C1.AND.T(J,L).LE.C2) THEN
          GO TO 18
        ELSE
          T(J,L)=T(J,L)
        END IF
      ELSE IF(IUHR.EQ.3) THEN
        CALL BIVNOR(AP(J,2),AP(J,3),PHR(J,1),PHR(J,2),PHR(J,3),T(J,K),T(J
1,L))
        X1DIST=T(J,K)-AP(J,2)
        X2DIST=T(J,L)-AP(J,3)
        HR95X1=2*V1
        HR95X2=2*V2
        IF(ABS(X1DIST).GT.HR95X1.OR.ABS(X2DIST).GT.HR95X2) PC(J,I)=999.9
        IF(T(J,K).GE.C1.AND.T(J,K).LE.C2) THEN
          GO TO 16
        ELSE
          T(J,K)=T(J,K)
        END IF
16  IF(T(J,L).GE.C1.AND.T(J,L).LE.C2) THEN
          GO TO 18
        ELSE
          T(J,L)=T(J,L)
        END IF
      END IF
18  END DO
      RETURN
      END
      SUBROUTINE UHR(U1,U2,V1,V2,X1,X2)
C
C*****
C  MOVES EACH ANIMAL IN ITS HOME RANGE ACCORDING TO
C  THE UNIFORM DISTRIBUTION. THE RADIUS OF THE HOME RANGE
C  IS CONSIDERED EQUAL TO 2*STANDARD DEV OR 2*SQRT(V1).
C  THIS IS EQUIVALENT TO THE 95% CONTOUR AREA OF THE BIVARIATE
C  NORMAL UTILIZATION DISTRIBUTION. AREA CAN BE ELLIPTICAL OR
C  CIRCULAR. POINTS OUTSIDE THE ELLIPSE ARE DISCARDED AND NEW POINTS
C  CHOSEN.
C*****
C
      COMMON/R/ IX
      V1=SQRT(V1)
      V2=SQRT(V2)
      Z1=U1-(2*V1)
      Z2=U2-(2*V2)
10  X1=Z1+(4*V1)*RANO(IX)
      X2=Z2+(4*V2)*RANO(IX)
      SOLN=((X1-U1)**2)/(2*V1)**2+((X2-U2)**2)/(2*V2)**2

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      IF(SOLN.GT.1.0) GO TO 10
      RETURN
      END
      SUBROUTINE UDISTR(U1,U2,V1,V2,RHO,X1,X2)
C*****
C MOVES EACH ANIMAL IN ITS HOME RANGE ACCORDING TO A BIVARIATE U-SHAPED
C DISTRIBUTION, WHERE THE PROBABILITY OF OCCURENCE INCREASES AWAY FROM
C THE CENTER OF THE HOME RANGE. LIMITED TO A HOME RANGE OF + OR - 2
C STANDARD DEVIATIONS OR 95% OF THE BIVARIATE NORMAL DISTRIBUTION.
C*****
      COMMON/R/ IX
      HR95X1=2*SQRT(V1)
      HR95X2=2*SQRT(V2)
      10 CALL BIVNOR(U1,U2,V1,V2,RHO,X1,X2)
      X1DIST=X1-U1
      X2DIST=X2-U2
C-IF LOCATION OUTSIDE 95% AREA RETURN TO 10
      IF(ABS(X1DIST).GT.HR95X1.OR.ABS(X2DIST).GT.HR95X2) GO TO 10
      IF(X1DIST.GE.0) THEN
        X1=(HR95X1-X1DIST)+U1
      ELSE
        X1=(-1*HR95X1-X1DIST)+U1
      END IF
      IF(X2DIST.GE.0) THEN
        X2=(HR95X2-X2DIST)+U2
      ELSE
        X2=(-1*HR95X2-X2DIST)+U2
      END IF
      RETURN
      END

      SUBROUTINE RANVEC(VEC2,N)
C*****
C YIELDS A VECTOR, VEC2, OF RANDOM INTEGERS FROM 1 TO N, INCLUSIVE.
C*****
      INTEGER VEC1(1000),VEC2(1000)
      COMMON/R/ IX
      DO K=1,N
        VEC1(K)=K
      10 END DO
      M=N
      DO I=1,N
        INDEX=(M*RANO(IX))+1
        VEC2(I)=VEC1(INDEX)
        IF(I.EQ.N) GO TO 1
        NI=N-I
        DO J=1,NI
          IF(J.LT.INDEX) GO TO 2
          VEC1(J)=VEC1(J+1)
        2 END DO
        M=M-1
      1 END DO
      RETURN
      END
      REAL FUNCTION RANO(ISEED)
      INTEGER ISEED
C
C RAND IS THE PORTABLE RANDOM NUMBER GENERATOR OF L. SCHRAGE.
C
C THE GENERATOR IS FULL CYCLE, THAT IS, EVERY INTEGER FROM
C 1 TO 2**31 - 2 IS GENERATED EXACTLY ONCE IN THE CYCLE.
C IT IS COMPLETELY DESCRIBED IN TOMS 5(1979),132-138.
C

```

```

C THE FUNCTION STATEMENT IS
C
C REAL FUNCTION RAND(ISEED)
C
C WHERE
C
C ISEED IS A POSITIVE INTEGER VARIABLE WHICH SPECIFIES
C THE SEED TO THE RANDOM NUMBER GENERATOR. GIVEN THE
C INPUT SEED, RAND RETURNS A RANDOM NUMBER IN THE
C OPEN INTERVAL (0,1). ON OUTPUT THE SEED IS UPDATED.
C
C
C INTEGER A,B15,B16,FHI,K,LEFTLO,P,XHI,XALO
C REAL C
C FORTRAN ... FLOAT
C
C SET A = 7**5, B15 = 2**15, B16 = 2**16, P = 2**31 - 1, C = 1/P.
C
C DATA A/16807/, B15/32768/, B16/65536/, P/2147483647/,
C 1 C/4.656612875E-10/
C
C THERE ARE 8 STEPS IN RAND.
C
C 1. GET 15 HI ORDER BITS OF ISEED.
C 2. GET 16 LO BITS OF ISEED AND FORM LO PRODUCT.
C 3. GET 15 HI ORDER BITS OF LO PRODUCT.
C 4. FORM THE 31 HIGHEST BITS OF FULL PRODUCT.
C 5. GET OVERFLO PAST 31ST BIT OF FULL PRODUCT.
C 6. ASSEMBLE ALL THE PARTS AND PRESUBTRACT P.
C THE PARENTHESES ARE ESSENTIAL.
C 7. ADD P BACK IN IF NECESSARY.
C 8. MULTIPLY BY 1/(2**31 - 1).
C
C XHI = ISEED/B16
C XALO = (ISEED - XHI*B16)*A
C LEFTLO = XALO/B16
C FHI = XHI*A + LEFTLO
C K = FHI/B15
C ISEED = ((XALO - LEFTLO*B16) - P) + (FHI - K*B15)*B16 + K
C IF (ISEED.LT. 0) ISEED = ISEED + P
C RANO = C*FLOAT(ISEED)
C RETURN
C END

C A FUNCTION TO GENERATE NORMALLY DISTRIBUTED DEVIATES WITH 0
C MEAN AND UNIT VARIANCE: FROM NUMERICAL RECIPES (PRESS ET AL.
C 1986, CAMBRIDGE UNIV PRESS, P.203

      REAL FUNCTION RANNOR(ISEED)
      INTEGER ISEED
      DATA ISET/0/

      1 IF (ISET.EQ.0) THEN
        V1=2.*RANO(ISEED)-1.
        V2=2.*RANO(ISEED)-1.
        R=V1**2+V2**2
        IF (R.GE.1.) GO TO 1
        FAC=(-2.*ALOG(R)/R)**.5
        GSET=V1*FAC
        RANNOR=V2*FAC
        ISET=1
      ELSE
        RANNOR=GSET
        ISET=0
      END IF
      RETURN
      END

```



```

REAL FUNCTION NORM(ISEED)
INTEGER ISEED
PI=3.1415927
10 R1=RANO(ISEED)
IF(R1.EQ.0) GO TO 10
R2=RANO(ISEED)
A=(-2*ALOG(R1))**.5
B=2*PI*R2
NORM=A*COS(B)
RETURN
END

SUBROUTINE MINITAB(NTRAPS,NTOTAL,NTPER,OUT)
C
C*****
C SETS UP AN OUTPUT FILE CALLED MINIT.DAT FOR USE WITH MINITAB.
C OUTPUT CONSISTS OF TRAP LOCATIONS IN COLUMN 1(C1) AND C2, INITIAL
C ANIMAL LOCATIONS IN C3 & C4. EVERY 4 COLUMNS FOLLOWING THE C4
C REPRESENT A TRAPPING PERIOD(UP TO 4 PERIODS POSSIBLE OR 16 COLUMNS).
C C5 IS 1 IF THE ANIMAL IS CAUGHT AND ZERO OTHERWISE. C6 & C7
C ARE THE LOCATIONS OF THE ANIMALS FOR PERIOD 1. C8 IS 1 IF THE
C TRAP IS OCCUPIED AND 0 OTHERWISE. THIS PATTERN REPEATS FOR C9-C12,
C C13-C16, AND C17-C20. SEE MINITAB HANDBOOK FOR PLOTTING TECHNIQUES.
C NOTE: MAXIMUM 400 ANIMALS PLOTTED.
C*****
C
DIMENSION IT(500,4),M(4),MY(4),MX(4),MT(4),IA(400,4)
INTEGER OUT
COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3
1),PC(1000,10)
IF(NTPER.GT.4) THEN
NN=4
ELSE
NN=NTPER
END IF
IF(NTRAPS.GT.NTOTAL) THEN
NTT=NTRAPS
ELSE
NTT=NTOTAL
END IF
DO I=1,NTT
DO J=1,NN
M(J)=J*4
MY(J)=M(J)-1
MX(J)=MY(J)-1
MT(J)=MX(J)-1
IT(I,J)=0
IF(I.LE.NTOTAL) IA(I,J)=0
END DO
END DO
DO J=1,NN
DO I=1,NTT
IF(I.LE.NTOTAL) THEN
IF(T(I,MT(J)).NE.0) THEN
IA(I,J)=1
IT(I,MT(J)),J)=1
END IF
END IF
END DO
END DO
DO I=1,NTT
WRITE(13,'(4F6.1,4(I1,2F6.1,I1))',ERR=9)TP(I,2),TP(I,3),AP(I,2
1),AP(I,3),(IA(I,J),T(I,MX(J)),T(I,MY(J))),IT(I,J),J=1,4)
END DO
RETURN
9 WRITE(OUT,'(A)') ' ERROR-FORMAT MINITAB'

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```

WRITE(6,'(A)') ' ERROR-FORMAT MINITAB'
GO TO 10
END
SUBROUTINE XMATRIX(NAME,NTPER,ISIM,NTOTAL,FCAP)
C*****
C SETS UP OUTPUT FILE OF X-MATRIX FOR PROGRAM CAPTURE FOR POPULATION
C ESTIMATES.
C REFERENCE: WHITE, ET.AL. 1978. USER'S MANUAL FOR PROGRAM CAPTURE.
C UTAH STATE UNIV. PRESS. LOGAN, UT.
C*****
C
DIMENSION IXMAT(10)
CHARACTER NAME*25
COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3
1),PC(1000,10)
IF(ISIM.EQ.1) THEN
WRITE(6,'(A,A,A,A)') 'TITLE=',',',NAME,',',
END IF
WRITE(6,'(A,I2)') 'TASK READ CAPTURES X MATRIX OCCASIONS=',
1NTPER
IFCAP=IFIX(FCAP)
WRITE(6,'(A,I3,A,I4,1X,A)') 'DATA='WEB',ISIM,',',IFCAP,
1'CAUGHT''
IF(NTPER.LT.10) THEN
WRITE(6,'(A,I1,A)') 'FORMAT=''(A4,',NTPER,'F1.0)'''
ELSE
WRITE(6,'(A,I2,A)') 'FORMAT=''(A4,',NTPER,'F1.0)'''
END IF
WRITE(6,'(A)') 'READ INPUT DATA'
DO I=1,NTPER
IXMAT(I)=0
END DO
DO I=1,NTOTAL
DO J=1,NTPER
K=(4*J)-3
IF(T(I,K).NE.0) THEN
IXMAT(J)=1
JXMAT=1
END IF
END DO
IF(JXMAT.NE.0) THEN
WRITE(6,'(I4,<NTPER>I1)') I,(IXMAT(J),J=1,NTPER)
DO J=1,NTPER
IXMAT(J)=0
END DO
END IF
WRITE(13,'(I1)',(JXMAT))
JXMAT=0
END DO
WRITE(6,'(A)') 'TASK CLOSURE TEST'
WRITE(6,'(A)') 'TASK MODEL SELECTION'
WRITE(6,'(A)') 'TASK POPULATION ESTIMATE ALL'
RETURN
END
SUBROUTINE CAPXYRED(NTRAPS,ISIM,NAME,NTPER,NTOTAL,TU,G,FCAP)
C*****
C SETS UP XY REDUCED OUTPUT FILE FOR PROGRAM CAPTURE FOR POPULATION
C ESTIMATES.
C REFERENCE: WHITE, ET.AL. 1978. USER'S MANUAL FOR PROGRAM CAPTURE.
C UTAH STATE UNIV. PRESS. LOGAN, UT.
C*****
C
INTEGER TU,XYRED(10,3),GRID(500,2)
CHARACTER NAME*25
COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3

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1),PC(1000,10)
N=0
TREAL=FLOAT(TU)
ITS=IFIX(SQRT(TREAL))
DO I=ITS,1,-1
DO J=1,ITS
N=N+1
GRID(N,1)=I
GRID(N,2)=J
END DO
END DO
IF(ISIM.EQ.1)THEN
WRITE(15,'(A,A,A,A)')'TITLE=',',NAME,'''
END IF
WRITE(15,'(A,I2)')'TASK READ CAPTURES XY REDUCED OCCASIONS=',
1NTPER
IF(NTPER.LT.10) THEN
WRITE(15,'(A,I1,A)')'FORMAT=''(A4,',NTPER,'(F3.0,2F2.0))''
ELSE
WRITE(15,'(A,I2,A)')'FORMAT=''(A4,',NTPER,'(F3.0,2F2.0))''
END IF
IFCAP=IFIX(FCAP)
WRITE(15,'(A,I3,A,I3,A)')'DATA='WEB',ISIM,',',IFCAP,'CAPTURED''
WRITE(15,'(A)') 'READ INPUT DATA'
DO I=1,NTPER
DO J=1,2
XYRED(I,J)=0.0
END DO
END DO
DO I=1,NTOTAL
N=0
M=0
DO J=1,NTPER
K=(4*J)-3
IF(T(I,K).NE.0) THEN
M=1
N=N+1
JT=IFIX(T(I,K))
XYRED(N,1)=J
XYRED(N,2)=GRID(JT,1)
XYRED(N,3)=GRID(JT,2)
END IF
END DO
IF(M.EQ.0) GO TO 10
WRITE(15,'(I4,<NTPER>(I3,2I2))') I,(XYRED(J,1),XYRED(J,2),
1XYRED(J,3),J=1,N)
DO JJ=1,3
DO II=1,N
XYRED(II,JJ)=0
END DO
END DO
END DO
10
END DO
WRITE(15,'(A)')'TASK CLOSURE TEST'
WRITE(15,'(A)')'TASK MODEL SELECTION'
WRITE(15,'(A)')'TASK POPULATION ESTIMATE APPROPRIATE'
WRITE(15,'(A)')'TASK UNIFORM DENSITY TEST'
ITSP=IFIX(G/SQRT(FLOAT(TU)))
WRITE(15,'(A,I2,A)')'TASK DENSITY ESTIMATE APPROPRIATE INTERVAL
1=' ,ITSP,'METERS CONVERSION-10000'
WRITE(15,'(A)')'INNER GRID X=5-14 Y=5-14'
WRITE(15,'(A)')'MIDDLE GRID X=4-15 Y=4-15'
WRITE(15,'(A)')'2ND MIDDLE GRID X=3-17 Y=3-17'
WRITE(15,'(A)')'TOTAL GRID X=1-18 Y=1-18'
WRITE(15,'(A)')'END OF GRID DEFINITIONS'
RETURN
END
SUBROUTINE TRNSCT(ISIM,ITL,TSP,NTOTAL,NTPER,NAME,NSIMS,OUT,FCAP)

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C
C*****
C SETS UP OUTPUT FILE FOR DENSITY ESTIMATE ON PROGRAM TRANSECT.
C REFERENCE: LAAKE ET.AL. 1979. USER'S MANUAL FOR PROGRAM TRANSECT.
C UTAH STATE UNIV. PRESS. LOGAN, UT.
C*****
C
REAL RGAREA(20)
INTEGER IRING(20),ISAMSZ(100),KRING(20,10),OUT,NCP(10),U(10)
CHARACTER NAME*25,LINE*80,LXLL*80,LARR*80,COMMA*20
COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3
1),PC(1000,10)
IF(ISIM.EQ.1) THEN
DO I=1,ITL
RGAREA(I)=3.14159*(I*TSP)**2
END DO
ICOUNT=0
I2CNT=100
END IF
ICOUNT=ICOUNT+1
DO I=1,ITL
IRING(I)=0
DO J=1,NTPER
KRING(I,J)=0
NCP(J)=0
U(J)=0
END DO
END DO
ISAMSZ(ICOUNT)=0
MTP1=0
DO I=1,NTOTAL
DO J=1,NTPER
K=(4*J)-3
IF(T(I,K).NE.0) THEN
ISAMSZ(ICOUNT)=ISAMSZ(ICOUNT)+1
TDIST=SQRT((TP(T(I,K),2)**2)+(TP(T(I,K),3)**2))
TAREA=3.14159*(TDIST**2)
DO L=ITL,2,-1
IF(TAREA.GT.RGAREA(L-1).AND.TAREA.LE.RGAREA(L)) THEN
IRING(L)=IRING(L)+1
KRING(L,J)=KRING(L,J)+1
GO TO 906
END IF
END DO
IRING(1)=IRING(1)+1
KRING(1,J)=KRING(1,J)+1
GO TO 906
END IF
END DO
906
END DO
DO J=1,NTPER
DO I=1,ITL
U(J)=U(J)+KRING(I,J)
END DO
MTP1=MTP1+U(J)
END DO
WRITE(OUT,'(//,T20,A)') ' TRAPPING PERIODS'
WRITE(OUT,'(//,T14,<NTPER>(I2,5X))') (I,I=1,NTPER)
WRITE(OUT,'(//,T6,A)') ' RINGS'
DO I=1,ITL
WRITE(OUT,'(1X,T8,I2,5X,<NTPER>(I2,5X))') I,(KRING(I,J),J=1,NT
1PER)
END DO
WRITE(OUT,'(1X,A,7X,<NTPER>(I3,4X))') 'U(J)''S', (U(J),J=1,NTPER)
WRITE(OUT,'(1X,A,7X,I3)') 'M(T+1)=-',MTP1
WRITE(18,'(1X,A,7X,<NTPER>(I3,4X))') 'U(J)''S', (U(J),J=1,NTPER)
WRITE(18,'(1X,A,7X,I3)') 'M(T+1)=-',MTP1

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WRITE(OUT,'(1X,A,F5.0)') 'TOTAL NUMBER OF ANIMALS CAUGHT=' ,FCAP
R4=(.5*TSP)+(3*TSP)
R4SQ=R4*R4
NCAP=0
NLOC=0
DO I=1,NTOTAL
  RSQ=AP(I,2)**2+AP(I,3)**2
  IF(RSQ.LE.R4SQ) THEN
    NLOC=NLOC+1
    DO J=1,NTPER
      K=(4*J)-3
      IF(T(I,K).NE.0) THEN
        NCAP=NCAP+1
        NCP(J)=NCP(J)+1
        GO TO 99
      END IF
    END DO
  END IF
END DO
99 DO K=2,NTPER
  IF(NCP(K-1).LT.NLOC) THEN
    NCP(K)=NCP(K-1)+NCP(K)
  ELSE IF(NCP(K-1).EQ.NLOC) THEN
    NCP(K)=NCP(K-1)
  END IF
END DO
IF(NLOC.GE.1) THEN
  XLOC=FLOAT(NLOC)
  P1=FLOAT(NCAP)/XLOC
ELSE
  P1=0.0
  XLOC=1
END IF
WRITE(18,'(1X,A,I3)') 'SIMULATION # ',ISIM
DO J=1,NTPER
  WRITE(18,'(1X,A,I2,2X,F5.3)') 'PROB OF CAPT INNER 4 RINGS IN PERIOD '
1,J,(FLOAT(NCP(J))/XLOC)
  WRITE(18,'(2(1X,A,I3)')') 'NUMBER CAUGHT=' ,NCAP,'NUMBER LOCATED=' ,NLOC
END DO
WRITE(OUT,'(1X,A,I3)') 'NUMBER CAUGHT IN INNER 4 RINGS=' ,NCAP
WRITE(OUT,'(1X,A,I3)') 'NUMBER LOCATED IN INNER 4 RINGS=' ,NLOC
WRITE(OUT,'(1X,A,F5.3)') 'PROBABILITY OF CAPTURE IN INNER 4 RINGS
1=P1
IF(ISIM.EQ.1.OR.ISIM.EQ.101.OR.ISIM.EQ.201.OR.ISIM.EQ.301) THEN
  WRITE(16,'(A1,A25,A1)') '***,NAME,***
  WRITE(16,'(A)') '**DISTANCE MEASURED IN.SQ METERS.**'
  WRITE(16,'(A)') '**LINE LENGTH MEASURED IN.NO UNITS.**'
  WRITE(16,'(A)') '**AREA EXPRESSED IN.HECTARES.*10000.*'
  WRITE(16,'(A,1X,F6.0)') '**GRPD,PEST,NPOL** ,RGAREA(ITL)
  WRITE(16,'(A,/A,/A)') '2.','**FSER**','**EXPS**'
  DO KK=1,(ITL-1)
    COMMA(KK:KK)=' , '
  END DO
END IF
IFCAP=IFIX(FCAP)
WRITE(16,'(A10,I3,1X,I4,A9)') 'WEB SIM # ',ISIM,IFCAP,'CAPTURED'
JJ=0
DO J=1,ITL,10
  WRITE(LARR,'(10(F6.0,A1)')') (RGAREA(I),' , ',I=J,MIN(J+9,ITL))
  JJ=JJ+1
  IF(JJ.EQ.1) LARR(80:80)='S'
  IF(J+9.GE.ITL) LARR(((ITL-(J-1))*7):80)=' '
  WRITE(16,'(A)') LARR
END DO
  WRITE(16,'(20(I3,A1)')') (IRING(L),COMMA(L:L),L=1,ITL)
IF(ISIM.EQ.NSIMS.OR.ISIM.EQ.I2CNT) THEN
  I2CNT=I2CNT+100

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DO II=1,ICOUNT,26
  WRITE(LXLL,'(26A3)') ('.5,',I=II,MIN(II+25,ICOUNT))
  LXLL(80:80)='S'
  IF(II+25.GE.ICOUNT) THEN
    LXLL(((ICOUNT-(II-1))*3):80)=' '
  END IF
  WRITE(16,'(A80)') LXLL
END DO
DO II=1,ICOUNT,19
  WRITE(LINE,'(19(I3,A)')') (ISAMS2(I),' , ',I=II,MIN(II+18,ICOUNT))
  LINE(80:80)='S'
  IF(II+18.GE.ICOUNT) THEN
    LINE(((ICOUNT-(II-1))*4):80)=' '
  END IF
  WRITE(16,'(A)') LINE
END DO
ICOUNT=0
END IF
RETURN
END
SUBROUTINE ANLCN(NTOTAL,NTPER)
C
C*****
C PRINTS AN OUTPUT FILE WITH THE CENTER OF HOME RANGES AND LOCATIONS
C FOR UP TO 4 TRAPPING PERIODS, ALONG WITH INDICAION OF WHETHER OR
C NOT THE ANIMAL WAS CAPTURED AND WHICH TRAP CAPTURED THE ANIMAL.
C*****
C
  INTEGER KAT(4)
  CHARACTER NAME*40
  COMMON/A/AP(1000,3),PHR(1000,3),T(1000,40),IOT(500,10),TP(500,3
1),PC(1000,10)
  DO I=1,4
    KAT(J)=0
  END DO
  DO I=1,NTOTAL
    DO J=1,NTPER
      MT=(J*4)-1
      IF(T(I,MT).NE.0) KAT(J)=1
    END DO
    WRITE(17,ERR=99) AP(I,2),AP(I,3),T(I,2),T(I,3),KAT(1),T(I,4),T(I,6),
1T(I,7),KAT(2),T(I,8),T(I,10),T(I,11),KAT(3),T(I,12),T(I,14),
2T(I,15),KAT(4),T(I,16)
  END DO
999 RETURN
99 WRITE(6,'(A)') 'ERROR IN WRITING TO SUBR LOCATE'
GO TO 999
END

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