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Robustness of capture–recapture estimators to sample biases in a cyclic snowshoe hare population

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Summary

1. A Monte Carlo simulation model was used to determine estimator robustness to trap saturation and other sample biases typical of a cyclic snowshoe hare population.

2. Field studies showed that hare capture probability varied directly with the amount of nightly movement made by an individual. This relationship was simulated by using an individual-based model of individual hare movement and the trapping process.

3. All estimation models in program CAPTURE except the jackknife heterogeneity (M_h) estimator showed increasing negative bias with increasing hare abundance in computer simulations. The jackknife estimator was robust to biases caused by trap saturation, and showed an acceptable coefficient of variation.

4. The program CAPTURE model selection routine performed poorly by selecting estimation models of different bias for each simulated hare abundance.

5. We conclude that for closed populations the jackknife estimator (M_h) is the most robust to sampling variation in a cyclic snowshoe hare population. These results suggest that it is optimal to use one model rather than change models for populations which exhibit large changes in abundance.

Key-words: capture–recapture, Monte Carlo simulation, program CAPTURE, snowshoe hare, trap saturation bias.

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Introduction

One of the most common techniques in the study of small mammal populations is the estimation of abundance using capture–recapture methods. During the past 20 years a variety of estimation models have become available to biologists through micro-computer software packages such as program CAPTURE (Otis *et al.* 1978). The reason for continued theoretical attention to this subject is that most simple ratio population estimators, such as the Jolly–Seber estimator, display an unknown bias when unequal probabilities of capture exist within the population being trapped (Gilbert 1973).

There are many estimation models available and it is difficult for the field biologist to know which of the newer techniques is optimal for wild populations (Hallet *et al.* 1991; Carothers 1973). There are three main problems with current estimation methods. First, most theoretical simulation tests of capture–recapture experiments are difficult to apply to field experiments because capture probability distributions of wild animals are usually unknown (Carothers 1973). Secondly, data-based model selection routines lack power to pick unbiased models unless the population being trapped is large (Menkins & Anderson 1988; Hallet *et al.* 1991; Otis *et al.* 1978). Thirdly, few field data sets exist in which true population values are known that would allow empirical determination of estimator bias (Carothers 1973; Boulanger & Krebs 1994; Hallet *et al.* 1991).

The objective of this study was to determine optimal estimation models for capture–recapture data from populations that exhibit large changes in abundance. In our study of snowshoe hare *Lepus americanus* (Erxleben) populations, capture–recapture abundance estimates are used to calculate rates of increase of hares on trapping grids, and to compare and evaluate experimental treatments (Krebs *et al.* 1992). The cyclic nature of snowshoe hare populations creates many potential sample biases and provides an ideal test of estimator robustness to the variations present in many wild populations. Snowshoe hares exhibit unequal probabilities of capture (Krebs *et al.* 1986). This population also shows widespread changes in abundance from about 1 to 400 hares on a 60 ha trapping grid during a 10-year population cycle. Given that there are a fixed number of traps available to the population, the capture probability of an individual changes at higher hare abundance, becoming increasingly related to its home range position relative to trap sites and individual movement patterns. Consequently, both the capture probability and subsequent capture frequencies of individual hares in the trapping data can be substantially affected by changes in population abundance on the trapping grid. We define this type of sample bias *trap saturation bias*.

We evaluated capture–recapture estimators performance using an individual-based Monte Carlo simulation model to generate trapping data to test the robustness of estimation models found in program CAPTURE (Otis *et al.* 1978). Our model simulated hare movements, hare capture probability differences, and the trapping processes. By simulating hares at different abundances, we could determine which estimators showed the most consistent bias at all abundances and were therefore most robust to trap saturation bias.

No previous Monte Carlo simulation evaluations of CAPTURE estimators have simulated capture probability variation caused by the trapping procedure. One reason for this is that there has been little field research into the natural causes of capture probability variation (White *et al.* 1982; Carothers 1973). To aid in developing a realistic simulation model we first conducted a field study into sources of capture probability variation in a natural population of hares living on an island.

We also used trapping data from the Kluane project and other field observations of hares to define other parameters for the model. While the model was designed for snowshoe hares, we feel our results are applicable to any population which exhibits widespread changes in abundance.

EMPIRICAL STUDIES OF HARE MOVEMENT PATTERNS AND CAPTURE PROBABILITY VARIATION

We designed a study to determine the degree of variation in movement patterns between hares and resolve whether this affects capture probabilities. Trap saturation bias is related to hare movement patterns, trap encounter rate, and the abundance of hares on a trapping grid. Little empirical work has been conducted on the role of movement patterns and trap encounter rates in determining capture probability variation. Most simulation studies have assumed that animals exhibit similar movements and random trap encounter (Skalski & Robson 1992; Wilson 1983; Zarnoch 1969). However, it is more likely hares exhibit differences in movement patterns, and non-random trap encounter which may be an important cause of capture probability variation. The method in which hare movement and trap encounter is simulated should have significant effects on the capture frequencies generated by the simulation model and bias characteristics of estimators tested.

For this study we used the southern peninsula of Jacquot Island, located in Kluane Lake, 6 km north-east of Destruction Bay in the Yukon Territory of Canada. The closest point of land is the Talbot Arm, ≈ 4 km to the east.

We fenced off the southern peninsula from the rest of the island to assure complete closure within the study area.

The vegetation in this area is a mosaic of white spruce *Picea glauca* (Moench (Voss)), willow (*Salix* spp.), and birch *Betula glandulosa* (Michx) groves. The study was conducted from March to May 1992, prior to the emergence of summer vegetation, and prior to the first litter of female hares (Boulanger & Krebs 1994; Boulanger 1993).

The first objective of the field study was to compare movement patterns of hares. Adult radio-collared hares ($n = 15$) were tracked from 21.00 to 02.00 hours for 20 nights. We used a three tower null-peak triangulation system to allow evaluation of error associated with animal locations (Fig. 1). During a session, locations were taken on hares every 45 min. Only animals whose locations had a confidence limit of less that 0·1 ha (Lenth maximum likelihood estimator) were tracked (White & Garrot 1989). Movement distance indices were calculated by dividing the cumulative distance between successive radio-locations by the elapsed time of radio observations. This provides an index of animal movement distances scaled for the duration of time between fixes, and thus allows comparison between animals (Siniff & Jessen 1969). The limited scale of resolution with telemetry sampling prevented us from detecting small-scale movement patterns. For this reason the movement distance is best considered an index, rather than an absolute measure of the distance an animal covers in one trap night.

Our second objective was to measure the differences in capture probability between individual hares. We obtained an index of individual hare capture probability by intensively trapping the population of snowshoe hares on Jacquot Island. The capture probability of an individual was estimated by the number of times trapped divided by the number of trap nights (11). We used a grid of 120 traps spaced 55 m apart trapped for 11 nights. These traps were spaced uniformly across the entire 40-ha surface of the island. With this design the number of traps outnumbered hares by 4 to 1, and each hare had at least 6 traps in its home range (Boulanger 1993) (Fig. 1). We could therefore assume that sample bias was minimal allowing a valid index of probability of capture to be calculated.

Movement distances and capture probabilities of individual hares were positively correlated ($r = 0{\cdot}6$, $P = 0{\cdot}016$, $n = 15$) (Fig. 2). From these results it can be inferred that hares do not exhibit similar movements and random trap encounter as has been assumed in previous simulation studies (Skalski & Robson 1992; Wilson 1983; Zarnoch 1976). This relationship suggests a possible mechanistic relationship between individual biological differences between

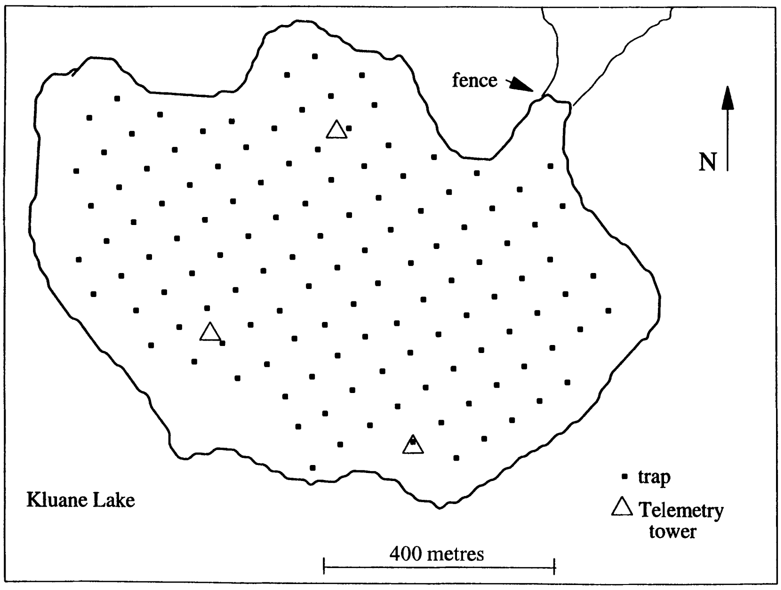


Fig. 1. A map of the Jacquot Island study site showing telemetry stations and live traps.

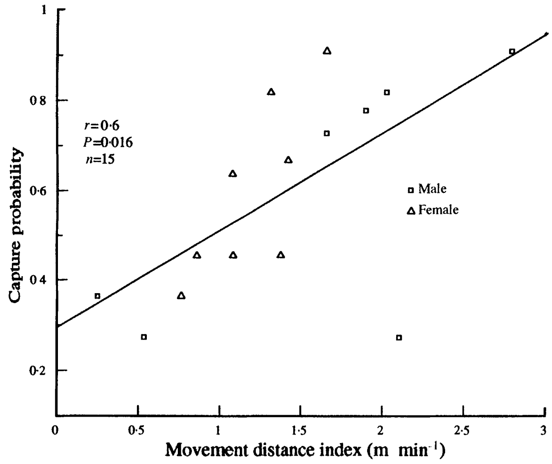


Fig. 2. Movement distance index of hares as a function empirical capture probabilities on Jacquot Island. Movement distance index is expressed as metres moved per minute ($n = 15$).

hares (movement distance), the sampling process (trap encounter), and subsequent capture probability variation reflected in the data. Consequently, we developed an individual-based movement–trap encounter model to simulate this relationship.

SIMULATION METHODS

General description of simulation model

The objective of our model was to create a realistic simulation of our trapping procedure in the field. On the Kluane grids a population is sampled for a series of five successive trap nights to obtain data for estimation of abundance with program CAPTURE. Each night a grid of traps is set, and then checked in the morning. The simulation model used to mimic this process is a modified version of a program produced by Zarnoch (1976) and later modified by Wilson (1983). The three basic submodels of the simulation model are: (i) random walk movement model; (ii) capture probability model; and (iii) trapping process model. The trapping process simulation model integrates the random walk movement model and the capture probability simulation model to produce simulated data. For this reason we will explain it first.

Trapping process model

A set pattern of traps mimicking a uniform 8 × 10 grid with 71 m trap spacing was employed for each simulation. At the beginning of a simulation animals are 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 then 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. If a hare's location is within the capture radius of a trap it may be trapped depending on its probability of capture. If the hares 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 of the five trap nights.

Random walk hare movement model

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. A correlated random walk model developed by Bovet & Benhamou (1988) and further refined by Benhamou (1989) was used to accomplish this objective. The random walk model was modified so that a hare's movements were controlled by a single parameter: sinuosity (S_b). Sinuosity (S_b) is the tendency of the animal to turn while travelling across a landscape. 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. By simulating a distribution of hare sinuosities,we could simulate differences in hare movement patterns. The details of the random walk model and the means by which we simplified it are given in Appendix 1.

Sinuosity (S_b) was set proportional to the observed home range size. The home range sizes for the hares were generated for each five trap night simulation as a normally distributed random variable ($\bar{x} = 7{\cdot}0 \pm 3{\cdot}5$ (SD) ha). No home ranges were smaller than 1 ha because this small size is rarely observed in the field. These parameter values are the mean and standard deviation of home range sizes of hares found in the Kluane area (Boutin 1984; Boulanger & Krebs 1994; Hik 1994). We assumed hares had a circular home range and that its tendency to turn or wander from its home range centre is proportional to its home range size. Clearly this is a simplification but it is adequate to describe an animal's basic central tendency and the area traversed within one trap night.

During each simulated trap night animals were moved 1000 m in 100 10-m time-steps. This is the mean movement distance of a snowshoe hare on the Kluane grids (Hik 1994). We assumed that what determines the area an animal traverses is not actual distance moved, but the straightness of the individual hare's 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' (Hik 1994). Therefore, an adequate simulation of areas covered in one trap night can be obtained by varying sinuosity alone and keeping the step length constant.

During the simulation hares are allowed to wander out of the grid area. It is important to note that their initial positions are on, or within 25 m 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 ha, even animals that had home ranges on the edge of the grid would traverse the grid area and encounter traps and could therefore be considered part of the trappable population. In reality, hares with home ranges farther than 25 m of the edge of the grid are only occasionally caught on the grid. Using this conservative distance minimizes variations caused by the particular distributions of hare home ranges in any particular simulation.

Capture probability variation model

The capture probability variation model assigned capture probabilities to individual hares in each simulation. The experiments on Jacquot Island suggested that differential movement patterns were a principle mechanism for variation in hare capture probabilities. In addition to this type of variation, it was also possible that individual hare capture probabilities changed as a function of prior trapping experience (*behaviour*) Also, some individuals had innate tendencies to be trapped independent of past experience and movement pattern (*heterogeneity*). Presence of predators, weather and seasonal vegetation changes could also cause *time* variation in capture probabilities. It is difficult to determine how much time, behaviour, and heterogeneity variation contribute to overall capture probability variation. For this reason we used two capture probability simulation models, one in which all hares had equal probability of capture (abbreviated M_0) and one in which capture probability was influenced by time, behaviour and heterogeneity (abbreviated M_{tbh}). In reality, the true underlying model is probably somewhere in the range between these two models.

No simulation program is needed to simulate capture probabilities when all capture probabilities are equal. To simulate variation of capture probabilities with time, behaviour and heterogeneity we used a version of K. Burnham's simulation model (Otis *et al.* 1978; Wilson 1983) which will be abbreviated as model M_{tbh}. The details of this model are given in Appendix 2.

CHOICE OF SIMULATION PARAMETERS

Abundances of hares

The main objective of this model was to simulate possible sampling biases at different hare abundances and capture probability levels. We found the abundances ranged from 1 to 2 to 400 hares on a 39·06 ha trapping grid for Kluane data from November 1985 to October 1992. We therefore chose to simulate hare abundances of 20, 50, 100, 200 and 400 on the trapping grids.

Trapping data from the Kluane projects was also analysed to determine the range of capture probabilities usually observed. We used data from trapping periods that occurred in the spring or late autumn, and had at least five successive trap nights. The probabilities were calculated using the formula:

$$\bar{p} = \frac{n}{tN} \qquad \text{eqn A}$$

In this formula, n is the total captured in a trapping period, t is the number of trapping periods, and N is the estimated population size. We used the M_h (jackknife) estimate for population size found in program CAPTURE (Otis *et al.* 1978) because previous empirical studies have shown it to be approximately unbiased with snowshoe hare populations (Boulanger & Krebs 1994). From these data we chose to simulate the mean capture probabilities of 0·23 and 0·35 found on most Kluane grids. We also simulated mean capture probability of 0·1 to determine estimator performance at the lowest observed mean capture probability level.

Capture radius, hare abundance and mean 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. However, both the population abundance and capture radius parameters effect the opportunity of a hare to be caught and subsequent capture probability. To adjust for this problem we used iteration in which capture radius was varied until mean capture probability input would approximately equal capture probability output as calculated in the formula described previously. We found the optimal capture radius for the model was 7 m for the 0·23 and 0·35, and 5 m for the 0·1 capture probability simulations.

Number of simulations run

In this study there were 45 different combinations of parameters simulated. More specifically, there were five hare abundances (20, 50, 100, 200, 400), three different mean capture probabilities (0·1, 0·23, 0·35) and two underlying capture probability models (M_0 and M_{tbh}). For each combination of parameters 1000 simulations were run. This was a sufficient number of simulations to allow for comparable results between treatments.

The model is written in FORTRAN. All programs were run on a SUN SPARC station. The FORTRAN base code for program CAPTURE was modified so that it would produce abridged data files for later analysis. A master driver file was written in a UNIX shell script to call programs, and keep track of simulations.

CAPTURE ESTIMATION MODELS EVALUATED

We used the data generated from the simulation model to evaluate the estimation models in program CAPTURE (Otis *et al.* 1978), which is one of the more commonly used population estimation computer packages. CAPTURE incorporates eight different estimation models each of which makes specific assumptions regarding the capture probability structure of the population. These models assume population closure (no births, deaths, emigration and immigration during sampling). The particular assumptions are broken down to capture probability variation by null (0) (all animals exhibit equal probability of capture), time (t) (temporal change in population capture probabilities only), behaviour (b) (capture probability change only after an animal is trapped the first time), and heterogeneity (h) (all animals have a constant, individual capture probability). For each model there is at least one statistical estimator of population size (except for model M_{tbh} which has no estimator). The CAPTURE models (with estimators in parenthesis) tested are; M_0 (Null), M_t (Darroch), M_t (Chao 1989), M_b (Zippin), M_h (jackknife), M_h (Chao 1991), M_{tb} (Burnham), M_{th} (Chao & Lee 1991), M_{bh} (Pollock), and M_{bh} (Pollock & Otto 1983). The subscript denotes the type of assumptions made by each model. Detailed descriptions for each estimator can be found in Otis *et al.* (1978) with the exception of more recent estimators in which a full reference is given in parentheses.

The premise for having eight different estimation models is that for any given set of data one of the models will most closely approximate the capture probability variations in the trapped population, and the estimator for this model will provide the least biased estimate of population size. CAPTURE uses a series of goodness-of-fit tests and a discriminant analysis to determine which model is most appropriate for a given set of data (Otis *et al.* 1978). We also test the model selection routine to see if it picks models of constant bias at all hare abundances.

INTERPRETING ESTIMATOR BIAS AND PRECISION

Bias

It is erroneous to assume that the results from any particular simulation reflect the actual bias that may be found in the field. Instead, these results should be used to compare models, and to determine what possible biases in estimates could result from the sampling biases simulated. Because the true population is known in these simulations, bias is calculated as:

$$PRB = \frac{E(\hat{N}) - N}{N} \times 100 \qquad \text{eqn B}$$

In this formula $E(\hat{N})$ is the mean estimate of population size from 1000 simulations and N is the true population value. Given the objectives of this study the criteria for appraisal of bias is as follows. First, an adequate model should exhibit constant bias as abundance increases which would infer that it is robust to trap saturation biases. Secondly, because edge effects were minimal (i.e. all hares had home range centres on, or within 25 m 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 a slight edge effect. If an estimator exhibits negative bias with this simulation, it probably will exhibit an even larger negative bias in the real world.

Precision

The precision of an estimator is the repeatability of its estimates from similar data sets. Precision is indexed by the coefficient of variation. The formula for coefficient of variation is:

$$CV = \frac{\theta}{E(\hat{N})} \times 100 \qquad \text{eqn C}$$

In this equation $E(\hat{N})$ is the mean estimated population number for the particular estimation model and is the mean standard deviation of $\hat{N}$. The degree of precision needed in estimates relates to the objectives of the particular study. In the case of most studies of population dynamics, estimates are used mainly for assessing general trends in populations. In this case, an estimator of fairly high precision is desirable. Pollock *et al.* (1990) suggest that a coefficient of variation of 20% or less is usually adequate for most capture–recapture studies.

Results

Estimators showed widely varying bias and precision characteristics as a function of abundance, capture probability model and mean population capture probability. All estimation models showed decreased estimates of population size when capture probabilities varied with time, behaviour and heterogeneity (M_{tbh} model) as compared to equal capture probabilities (M_0 model). Mean capture probability had varying effects on estimators. The results from the 0·1 capture probability were erratic with all models (except models M_{bh} (Pollock) and M_h (jackknife)) showing unacceptable coefficients of variation above 30%. The 0·1 capture probability level represents the extreme lower end of capture probabilities for the Kluane study, and as a result we will not focus discussion on these results. The 0·23 and 0·35 simulations produced similar results for all models at all abundance levels. Because the probability of 0·23 represents the usual mean capture probability found on Kluane grids it will be discussed in more detail.

The effect of abundance on bias of estimators was model specific. Few models were robust to changes in abundance and subsequent trap saturation bias. These results will be discussed in a model-specific fashion.

Heterogeneity model estimators

The heterogeneity estimators of Burnham & Overton (1978) and Chao (1989) displayed the least overall bias with both underlying models of capture probability (Figs 3a and 4a). They also showed a generally acceptable coefficient of variation with exception of the $N = 20$ simulations (Figs 3b and 4b).

The jackknife estimator (M_h) of Burnham & Overton (1978) showed a positive bias with the equal probability capture simulations (Fig. 3a) and a slightly negative bias (Fig. 4a) with the more complex M_{tbh} simulations. Unlike most estimators, it showed a slight increasing positive trend in bias with increasing abundance with the equal capture probability model. With the M_{tbh} model it showed virtually no change in bias with abundance.

The heterogeneity estimator, M_h of Chao (1989) was similar to the jackknife estimator in terms of general bias and precision. It did show sensitivity to change in abundance, with an increasing negative bias as abundance increased especially with the M_{tbh} capture probability model (Fig. 4a). It also showed a high coefficient of variation (35%) and population number was small ($N = 20$) when the underlying capture probability model was M_{tbh} (Fig. 4b). With the 0·1 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 abundances) with this simulation.

Null, behaviour, and model estimators

The null (M_0) and behaviour (M_b) model estimators performed similarly and will therefore be discussed together. Both models displayed a significant overall negative bias (–10 to –30%) and an increasing negative bias as abundance increased (Figs 3a and 4a) However, both showed a low coefficient of variation (M_0, 12%; M_b, 15%) with both capture probability models (Figs 3b and 4b).

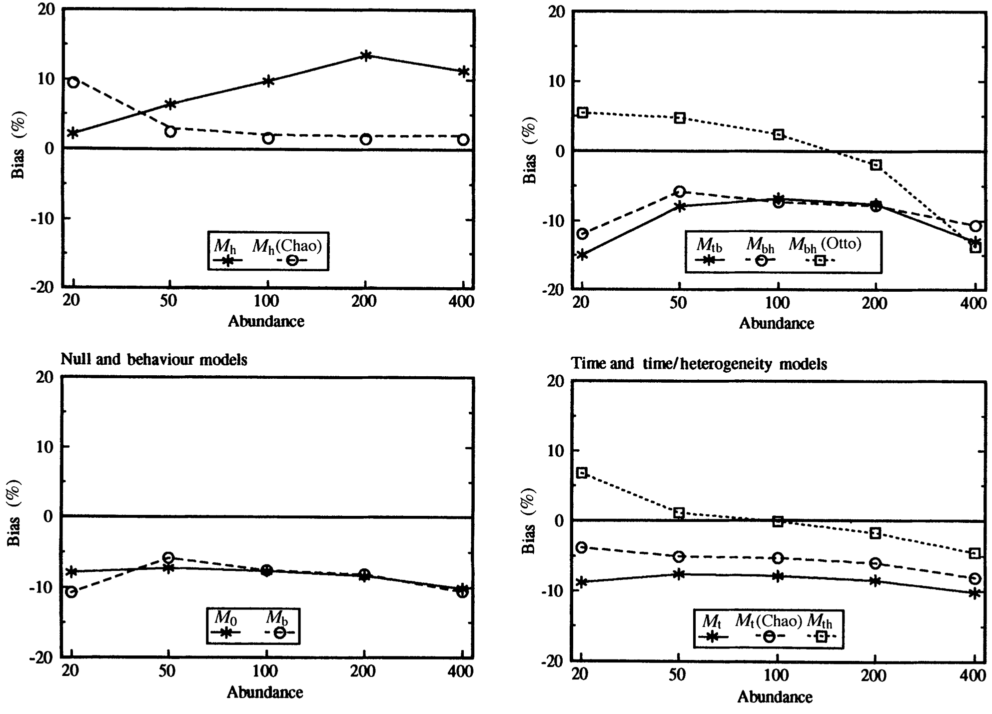
The time model estimators – M_t and M_t(Chao 1989) – showed a substantial negative bias that increased with abundance (Figs 3a and 4a). Each showed an acceptable coefficient of variation (Figs 3b and 4b).

Behaviour/heterogeneity model estimators

The behaviour/heterogeneity model estimators of Pollock (1974) (M_{bh}) and Pollock & Otto (1983) (M_{bh} (Pollock)) showed similar performance characteristics. The Pollock & Otto (1983) estimator showed an overall positive bias with the equal capture probability simulations (Fig. 3a), and a negative bias with the M_{tbh} simulations (Fig. 4a). The Pollock (1974) estimator showed a negative bias with both capture probability models. Both estimators showed an increasing negative bias as abundance increased.

The Pollock estimator showed a large coefficient of variation (25%) with both capture probability models

(a) Equal hare capture probabilities, mean $P = 0{\cdot}23$



(b) Equal hare capture probabilities, mean $P = 0{\cdot}23$

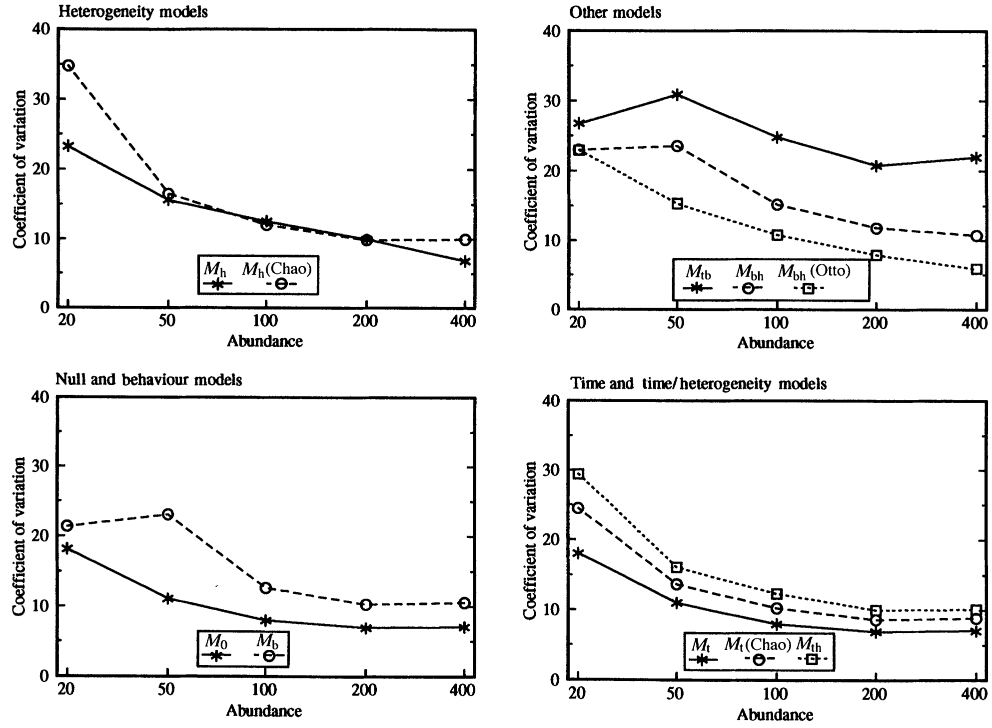


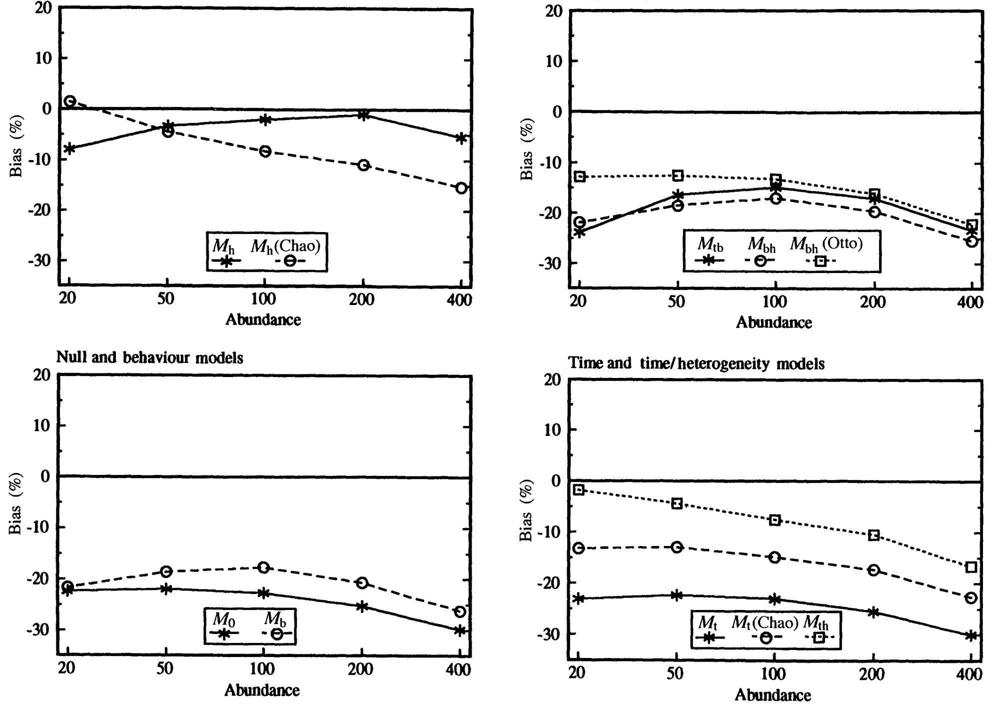
Fig. 3. The results from simulations in which all animals had equal probability of capture of 0·23 was simulated: (a) displays bias and (b) displays precision as reflected by coefficient of variation. Each line represents bias or CV of a specific estimation model and estimator as detailed on the figure.

(Figs 3b and 4b). 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 abundance is most noteworthy.

Time/behaviour model estimators

The model M_{tb} estimator showed the most erratic performance of any estimator as noted by the large coefficient of variation (30%) in all simulations (Figs 3b and 4b) It showed a negative bias that increased as abundance increased (Figs 3a and 4a).

(a) M_{tbh} capture probability model, mean P =0·23



(b) M_{tbh} capture probability model, mean P =0·23

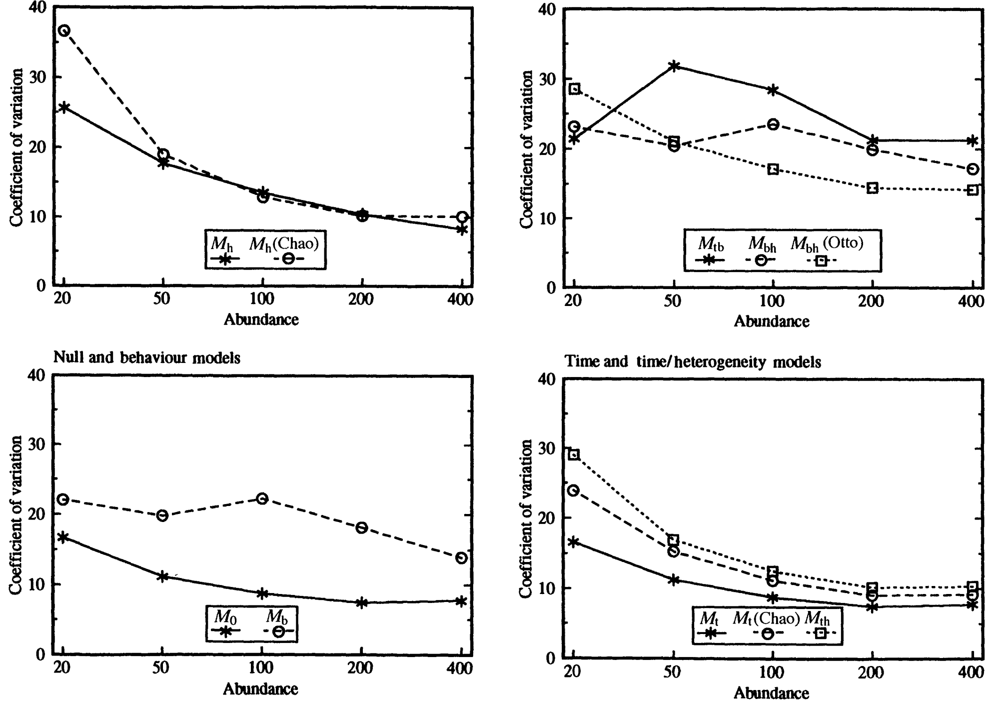


Fig. 4. The results from simulations in which model M_{tbh} was the underlying capture probability model. A mean capture probability of 0·23 was assigned to each animal. Each line represents bias or CV of a specific estimation model and estimator as detailed on the figure.

G. White (personal communication) commented that this estimator exhibits poor performance, especially when data do not conform to the underlying assumptions of the M_{tb} model.

Time/heterogeneity model estimators

The model M_{th} estimator was designed by Chao & Lee (1991) for data with low capture probabilities. It showed a roughly unbiased performance for data at low abundances (Figs 3a and 4a). However, as abundance increased it showed an increasing negative bias. Also, at lower abundances it showed a large coefficient of variation (27%) (Figs 3b and 4b). Overall, this estimator showed a mediocre performance due to increasing negative bias at higher abundances.

Program CAPTURE *model selection routine*

The program CAPTURE model selection routine picked different estimation models as a function of hare abundance simulated, and underlying capture probability model. Because models M_0 and M_h were chosen in the majority of the simulations they are displayed in Fig. 5.

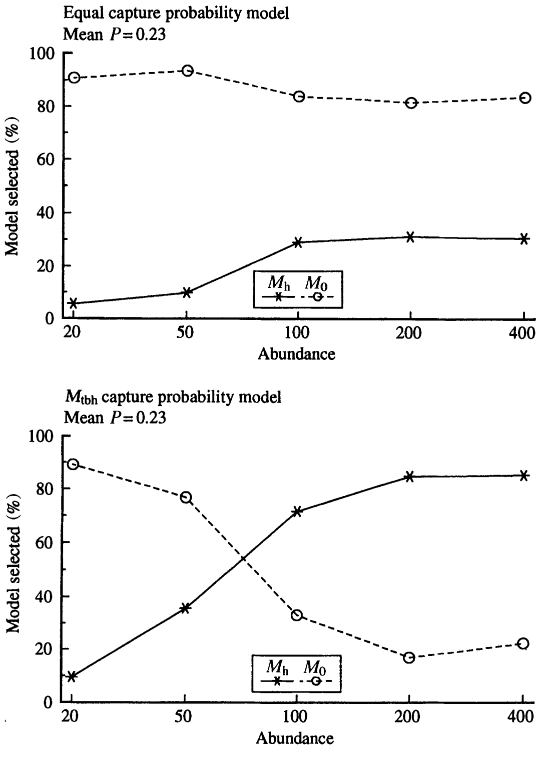
In general, the model selection routine picked the negatively biased model M_0 at lower abundances and the less biased model M_h at higher abundances. Estimators for models M_0 and M_h vary by $<$ 20% in terms of bias when confronted with identical data sets.

These results suggest that the program CAPTURE model selection routine picks models of different bias at different hare abundances.

Discussion

HETEROGENEITY ESTIMATORS

The jackknife (M_h) estimator showed the most reliable performance of all estimators tested. These results agree with Otis *et al.* (1978) who comment that the jackknife is the most robust of estimators to variation in capture probabilities. They also note that its performance is best in experiments in 'which many animals are caught a relatively large number of times'. Our results agree with these observations as the coefficient of variation of the jackknife estimator decreased substantially as abundance increased. Chao (1989) reported that the jackknife estimator shows a substantial negative bias when capture probabilities are low. However, it was one of the best estimators with the 0·1 capture probability simulations showing an even (at all abundances) 10% negative bias and one of the lowest coefficients of variation (mean = 15%) of any of the estimators. The characteristics of even bias with variation in abundance, and an approximately unbiased performance suggest this estimator is best for the stated objectives, especially at abundances greater than 20 hares.


Equal capture probability model
Mean $P = 0.23$

M_{tbh} capture probability model
Mean $P = 0.23$

Fig. 5. 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. In some cases, both models were chosen by the model selection routine for a set of data. Hence, some of the percentage frequencies add up to more than 100%.

The Chao (1989) M_h estimator was less reliable than the jackknife estimator, showing an increasing negative bias as abundance increased in all simulations. This estimator was developed because the jackknife heterogeneity estimator has been documented to underestimate population size when capture probabilities are low. With the 0·1 capture probability simulations (equal capture probability model) this estimator showed a decreasing positive bias as well as a very large coefficient of variation (greater than 27% for all hare abundances) with this simulation. Chao (1989) does report a large standard error with this estimator which is attributed to low capture probabilities in the data. However, our results suggest that this estimator is not an improvement over the jackknife estimator.

Other estimators

Most of the CAPTURE estimators (M_0, M_t, M_b) showed increasing negative bias with increasing abundance. The consistent negative bias of these models could be due to the presence of heterogeneity within the population. Otis *et al.* (1978) 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 estimators seemed to be the most negatively biased of all models in program CAPTURE.

The time model estimator of Chao (1989) was designed for use with data that have lower capture probabilities. Chao (1989) reports that the Darroch M_t estimator can show a significant negative bias with lower capture probabilities. Our results suggest that this model is an improvement from the traditional estimator, but it is still is not robust to biases caused by increasing abundance.

The more complex models (M_{tb}, M_{bh}, M_{th}) all showed increasing negative bias and higher coefficients of variations than the simpler older models. These results suggest that despite their complex structure, these models offer little improvement than older models with this type of simulated data. Furthermore, the complex structure results in a loss of estimate precision as reflected by the higher coefficient of variation of most estimators.

Program CAPTURE *model selection routine*

The model selection routine in CAPTURE showed high sensitivity to the population size being simulated. The actual shape of the curves in Fig. 5 could represent the extremes of model selection trends actually found in the field. The trends reflected in Fig. 5 can be explained in terms of power of the 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_{tbh} is the underlying model a larger 'effect size' or variation in capture probabilities is present and therefore the null model is rejected more often as sample size increases. The lack of power of the program CAPTURE model selection routine has been documented by Menkins & Anderson (1988) and Hallet *et al.* (1991). In these studies lack of power was related to mean capture probability of the population. No prior studies have related lack of power to changing abundance of animals in the population.

An optimal model(s) for estimation of abundance 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 abundances, as well as calculation of population rates of increase for it may pick models of different bias dependent on abundance of the population. These results suggest that it is a better strategy to use one robust estimator such as the jackknife that displays a consistent bias at different hare abundances than rely on the program CAPTURE model selection routine.

Conclusion

Estimators showed markedly different performance characteristics as a function of population abundance and underlying capture probability models. From the results of these simulations, the M_h jackknife estimator is the most robust to variations caused by differential movement patterns and increasing hare abundance. The program CAPTURE model selection routine lacked the power to select an estimator or estimators of consistent bias at different hare abundances.

Complex theoretical estimation models are being produced on a yearly basis, but few studies attempt to test these estimators in applied field situations. The results from this study suggest that these newer estimators offer little improvement over older methods. For example, estimators for models M_{tb}, M_{th} and M_{bh} showed little or no improvement over the older jackknife estimator with snowshoe hare populations. Furthermore, the lack of resolution with most trapping data limits the reliability in which model selection routines can discern differences in capture probability variation and pick appropriate models. For this reason, the utility of having eight different models will be minimal without further research in applicability of individual models and development of more powerful model selection routines.

Capture–recapture estimation models attempt to integrate theoretical statistics with the actual biology of animals. As a result, 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. 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.

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Appendix 1

RANDOM WALK MODEL OF BENHAMOU (1989) AND BOVET & BENHAMOU (1988)

In the original model of Benhamou (1989) an animal's spatial behaviour was controlled by two parameters: 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. The central tendency factor (k) determines how far an animal will on average travel from its home range centre and also varies from 0 to 1.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 equation for these parameters are:

$$\sigma_b = S_b\sqrt{P} \qquad \text{eqn 1}$$

$$\sigma_i = \sigma_\mathrm{b}\left(1 + k\frac{dD_i}{p}\right) \qquad \text{eqn 2}$$

$$D_{i+1} = \{(X_{i+1} - X_0)^2 + (Y_{i+1} - Y_0)^2\}^{1/2} \qquad \text{eqn 3}$$

$$dD_{i+1} = D_{i+1} - D_i \qquad \text{eqn 4}$$

$$\alpha_i = N(0, \sigma_i) \qquad \text{eqn 5}$$

$$\theta_{i+1} = \theta_i + \alpha_i \qquad \text{eqn 6}$$

$$X_{i+1} = X_i + P\cos\theta_{i+1} \qquad \text{eqn 7}$$

$$Y_{i+1} = Y_i + P\sin\theta_{i+1} \qquad \text{eqn 8}$$

The computational sequence in which a hare is moved will now be described. Numbers in parentheses pertain to particular equations being described. A hare is in its home range centre (X_0, Y_0) initially. It moves from its centre 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 (eqn 1). σ_i varies with the distance of the hare from its home range centre. It is determined by the central tendency (k), step length (P), and dD_i (eqn 2). The parameter dD_i is the change in the hares distance from its home range centre between time step i and $i+1$ (eqns 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 centre then this ratio is equal to 1, otherwise it is less than 1. In this way σ_i varies with each step the animal takes (eqn 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 (eqn 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 (eqn 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 centre, α_i will tend to increase (as σ_i increases) causing the animal to turn more frequently and not cross off the home range boundary. How quickly this happens is dependent on k, the animal's central tendency and sinuosity (S_b). Finally, the hare's new coordinates are determined using trigonometric functions (eqns 7 and 8). The process is repeated for each time step in the simulation.

The sources of variation in hare movement we 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 0·5, 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 m.

SINUOSITY AS A FUNCTION OF HOME RANGE SIZE

Using simulations Benhamou (1989) 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 0·95 probability density of an animals location from the centre. With this relation the home range area (HRA) could then be related to the standard deviation (L) of points from the home range centre by the following equation (for more details see Benhamou 1989):

$$HRA = 7{\cdot}5\pi\delta^2 \qquad \text{eqn 9}$$

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

$$\sigma = \frac{1{\cdot}92}{k \cdot S_b^2} \qquad \text{eqn 10}$$

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, we assumed k was constant at 0·5, and S_b was determined by the hares' home range size. We 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.

$$S_b = \frac{4{\cdot}27}{(HRA)^{1/4}} \qquad \text{eqn 11}$$

Appendix 2

CAPTURE PROBABILITY MODEL OF BURNHAM

No simulation program is needed to simulate capture probabilities when all capture probabilities are equal. To simulate capture probability variation with behaviour and heterogeneity we used a slightly modified version of K. Burnham's simulation model as used by Wilson (1983)

We 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.

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

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

$$p_{ij} = \frac{e^{\theta_{ij}}}{1 + e^{\theta_{ij}}} \qquad \text{eqn 14}$$

In equation 12, θ_{ij} is a capture probability for individual i on trapping occasion (or trap night) j. P 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 behaviourial 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.

For each individual hare (i) on each trap night (j) an effect (θ_{ij}) is generated by the above equations. 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 (eqn 14).

Each effect was generated from a beta distribution. For our simulation we used beta parameters a = 2 and b = 2 to simulate the heterogeneity effect. This produced a slightly centred distribution with mean 0·5 and variance 0·05. We 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 0·24 and variance 0·07. We chose these parameters to make the effect of trapping time centred, with occasional larger effects.