Comparison of capture–recapture estimators of snowshoe hare populations

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We used two island populations of snowshoe hares (*Lepus americanus*) in the Kluane Lake area of the Yukon Territory of Canada to evaluate capture–recapture estimators. These islands were intensively sampled, allowing us to enumerate the actual population size. Population size estimates were calculated using the programs CAPTURE and JOLLY, and estimators were compared for bias characteristics. Results from both islands suggest that the CAPTURE heterogeneity models M_h (jackknife), M_h (Chao), and M_{th} (time–heterogeneity) and the Jolly–Seber model were approximately unbiased. All other CAPTURE models displayed a negative bias. The CAPTURE model selection routine picked estimation models of different biases for each trapping period, an undesirable result. We conclude that it is best to use one robust estimator such as the M_h (jackknife) with snowshoe hare data.

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Nous avons utilisé deux populations insulaires de Lièvres d'Amérique (*Lepus americanus*) de la région de Kluane Lake, Yukon, Canada, pour évaluer les indices d'estimation capture–recapture. Les îles ont été fortement échantillonnées de façon à connaître la taille réelle de la population. Les estimations de la taille de la population ont été calculées au moyen des logiciels CAPTURE et JOLLY et les indices ont été comparés pour en évaluer la marge d'erreur. Les résultats obtenus dans les deux îles indiquent que les modèles d'hétérogénéité obtenus avec le logiciel CAPTURE, M_h (jackknife), M_h (Chao), M_{th} (temps–hétérogénéité) et le modèle Jolly–Seber ne comportent à peu près aucune marge d'erreur. Tous les autres modèles de CAPTURE donnent des sous-estimations. Le programme de sélection d'un modèle du logiciel CAPTURE a choisi des modèles d'estimations comportant des marges d'erreur différentes pour chaque période de capture, un résultat non souhaité. Il faut conclure qu'il est préférable d'utiliser un seul indice d'estimation robuste, tel M_h (jackknife), pour estimer les populations du Lièvre d'Amérique.

[Traduit par la Rédaction]

Introduction

The theoretical properties of capture–recapture population estimation models have been widely addressed in the literature (Otis et al. 1978; Menkins and Anderson 1988; Pollock et al. 1990; Chao 1989). However, few studies have tested the models available for population estimation in natural populations for which independent estimates of population size are available. As a result it has become difficult for biologists to determine which models produce unbiased estimates when applied to actual wild populations. White and Nichols (1992) suggested that more studies in which true parameter values are known are needed in order to develop valid estimation models.

The most popular estimation models are incorporated in the program CAPTURE (Otis et al. 1978), which is available as computer software. These models assume population closure (no births, deaths, emigration, and immigration during sampling). CAPTURE integrates 8 different estimation models, each of which makes specific assumptions regarding the capture-probability structure of the population. The particular assumptions are broken down to capture-probability variation by time (t), behaviour (b), and heterogeneity (h). The CAPTURE models are M_0, M_t, M_b, M_h, M_{tb}, M_{th}, M_{bh}, and M_{tbh}. All models have at least one estimator except model M_{tbh}, which has no estimator. The premise for having 8 different models is that for any given set of data one of the models will most closely approximate the capture-probability variations in the population being trapped, and the estimator for this model will provide the least biased estimate of population size.

We became interested in estimator performance when analyzing data from a population dynamics study (the Kluane Boreal Forest Ecosystem Project) of snowshoe hares (*Lepus americanus*) in the Yukon Territory of Canada (Krebs et al. 1992). In the Kluane project, various experimental treatments are compared using capture–recapture population estimates. Fundamental to the evaluation of treatments are unbiased population estimates. Unfortunately, it was difficult to determine which models produce unbiased estimates from Monte Carlo simulation evaluations of estimators found in the literature because the actual capture-probability distributions of hares or other animals are rarely known. Consequently, it was difficult to determine which simulation results actually applied to the snowshoe hare populations we were studying (Carothers 1973).

To determine estimator robustness to variations in capture probability caused by wild hare populations, we designed a study in which we could make population size estimates independent of the actual trapping data. To accomplish this objective we trapped entire island areas in which the trap coverage was even and continuous on all areas inhabited by hares. With this design every animal was at risk of capture to some degree, making the calculation of actual population at risk of capture feasible. Independent estimates of population size were acquired by a combination of radiotelemetry and intensive trapping. Trapping samples had minimal sampling error because the trapping grid covered the entire island surface, and each hare had at least five traps in its home range (Boulanger 1993). The rationale for this intensive sampling design was that if an estimator failed to perform well in this ideal situation its performance would be unreliable in a mainland trapping grid, where more sources of sampling error and bias are present.

Methods

Jacquot and Dezadeash islands in the Kluane area of the southern Yukon were used for these studies. The areas used for this study on the islands are large (48 and 40 ha) and support substantial hare populations, but these are still logistically possible to enumerate. By using two islands we 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 (61°20'N, 138°45'W) is located in Kluane Lake, 6 km northeast of Destruction Bay. The closest point of land is along the Talbot Arm, approximately 4 km to the east. Owing to the large size of this island (120 ha), only its southern peninsula (Fig. 1) was used for the study. The southern peninsula could be easily separated from the main part of the island by a fence (to ensure there was no immigration or emigration from the trapping area) and could be considered a separate island. This area is a mosaic of white spruce (*Picea glauca*), willow (*Salix* spp.), and bog birch (*Betula glandulosa*) groves. The main habitat areas are slightly elevated from the lake by 5- to 10-m bluffs. Access was by boat in summer and across the ice in winter.

A grid composed of 240 trap stations spaced 40 m apart across the southern peninsula of Jacquot Island was initially surveyed. This trap spacing allowed for the 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 m apart (Fig. 1). The data from this effort were used for estimator evaluation. A secondary smaller grid scheme was employed by Zimmerling (1993) in which 160 traps (40-m spacing) in a 10 × 15 uniform grid were used. The data were utilized for continuous enumeration of the population and estimator evaluation.

Dezadeash Island

Dezadeash Island (60°25'N, 137°3'W) is located approximately 70 km south of Haines Junction, Yukon. It lies approximately 800 m east of the western shore of Dezadeash Lake. The island consists of a mosaic of willow and open white spruce. The island has minimal topographic relief. Access was by canoe from the western shore of Dezadeash Lake.

A grid encompassing 75% of the island area was surveyed on Dezadeash Island. The northern end of the island consists of swampland in which summer hare habitation was minimal (this area was submerged in water, precluding hare use) and was not surveyed. One hundred traps were initially placed, 1 every 30 m, in various sections of the island to allow for an initial intensive sample of the population to be obtained for enumeration. After this initial period, a full-island grid of 100 traps spaced 55 m apart was trapped (Fig. 1).

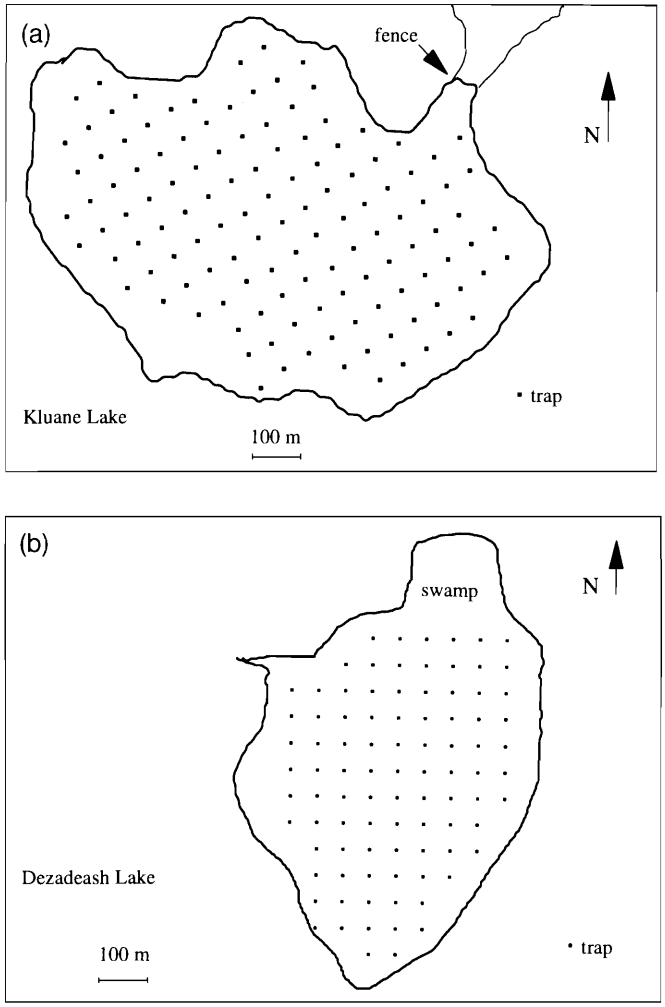

FIG. 1. (*a*) Jacquot Island (48 ha), with "full island" trap stations. Island areas not covered by trap stations are cliffs or rocky shoreline. Traps were spaced 55 m apart. A fence with traps in it controlled emigration from the northern part of this island. (*b*) Dezadeash Island (40 ha), with trap stations. The northern end was a swamp not inhabited by snowshoe hares and was not surveyed. The traps were spaced 55 m apart.

Trapping methods

Hares were tagged with metal and plastic orange ear tags to allow for visual confirmation of whether an animal was marked. On Jacquot Island, animals were also radio-collared for survival and movement monitoring. At the end of the summer field season, animals were again exposed to an intensive trapping effort to account for the fate of all hares. Traps were baited with alfalfa cubes and apples.

A trapping period consisted of 5 nights in which traps were set in the evening and checked the following morning. These 5 nights were interspersed over a 10-day period to avoid deleterious effects on the population (Boulanger 1993). Traps were set only in periods of stable weather conditions to minimize capture-probability variation and adverse effects on the population.

Data from each 5-day trapping period were used with the closed population estimators in the program CAPTURE (Otis et al. 1978). Data from each sampling period were also pooled for use with the Jolly–Seber estimator. The full open model implemented in the program JOLLY (Pollock et al. 1990) was used for these estimates.

Population enumeration

Enumeration of the trappable population was a primary objective of this study. This number is based on the number of adult hares 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 hares caught during that 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 we assumed that it had 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. The juvenile segment of the population was not included in calculations of population number.

This technique is similar to the minimum-number-known-alive estimator (MNA; Krebs 1966), which is negatively biased (Pollock et al. 1990) when capture probabilities are low. The intensive sampling effort maximized overall capture probabilities and minimize any negative bias of this method. It should also be noted that because of this study design, the enumeration in 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 in the population estimate.

On Jacquot Island we also calculated another estimate of population size using the subpopulation of radio-collared animals. The RADIO population estimate is calculated by estimating the capture probability

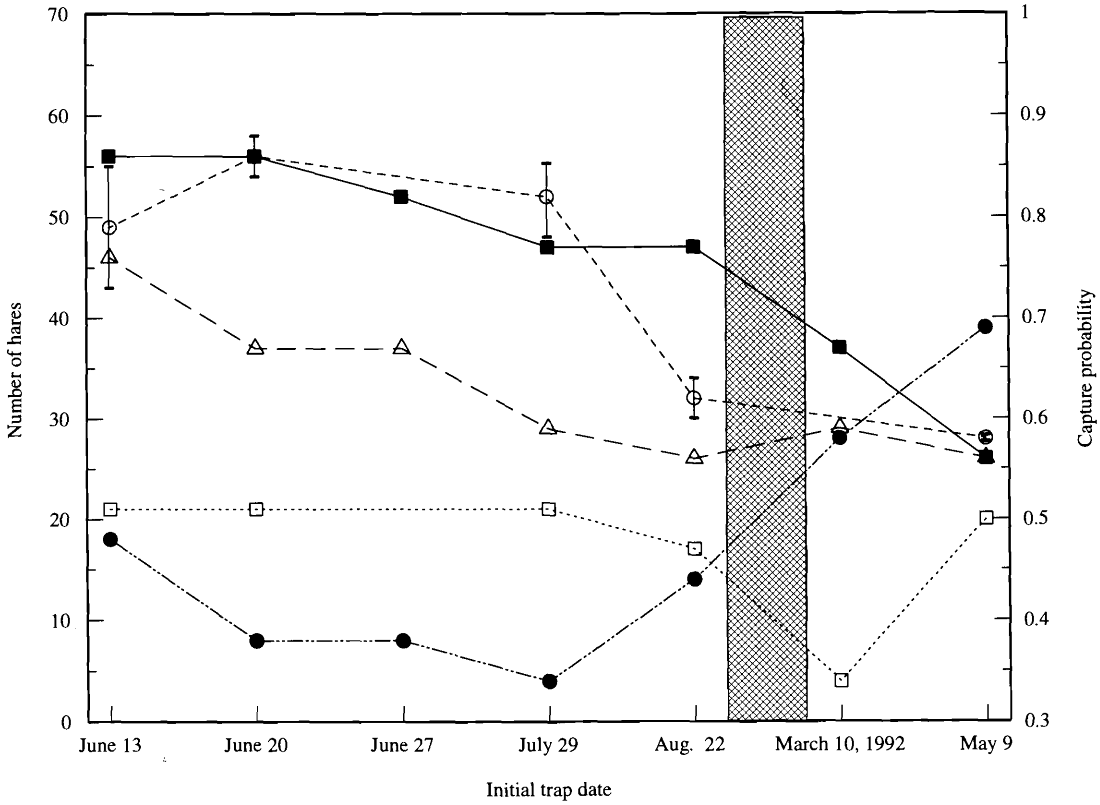

FIG. 2. Summary of the sample sizes on Jacquot Island during field seasons from June 13, 1991, to May 9, 1992. Note that the x axis denotes an ordering of samples, not an exact time scale. ■, enumerated N; ○, RADIO estimate; □, number of radio-collared hares; △, number of hares trapped per period; ●, mean nightly capture probability. The RADIO estimate has standard error bars. Mean nightly capture probabilities were calculated under model M_0 (Otis et al. 1978). Initial trapping dates were the first night of a 5-day trapping period. The shaded area represents the winter of 1991 – 1992 in which no sampling took place.

of the population as the proportion of the radio-collared population caught during a given trapping period. The estimate of population size is the total number of hares caught (with or without radio collars) divided by the estimated capture probability (see Hallet et al. 1991). This estimator is different from the enumeration estimate in that it uses an estimate of capture probability in estimating population size (instead of a count of animals captured). This estimator assumes that radio-collared animals exhibit behaviour similar to that of non-radio-collared animals. It assumes that animals which are captured and radio-collared exhibit behaviour similar to that of animals that have never been caught. The RADIO estimator is considered conservative with respect to the actual population number (Hallet et al. 1991).

Using the RADIO estimator allowed us to partially check for the consistency of bias associated with the enumeration estimate. If capture probabilities decrease over the course of the study, it would be expected that the enumeration estimate would show an increasing negative bias (Pollock et al. 1990). The RADIO estimator should be more robust to decreasing capture probabilities, since any change in capture probability should be reflected in the proportion of radio-collared animals captured (and the subsequent RADIO estimate of capture probability and population size). Therefore, by comparing these two estimates, we can partially determine the *consistency* of bias with either technique.

There is a chance that a portion of the hare population was untrappable and was never caught. We attempted to test this by marking trapped hares with large plastic ear tags to provide a secondary visual check of whether a hare had been caught. However, ear-tag loss and low sightability of hares precluded the effectiveness of this method. In the case of an untrappable segment, the enumerated and RADIO estimates could be considered to be a lower bound for the actual population number, and it would be expected that a valid estimator should match this number or exceed it.

Evaluation of population estimators

Owing 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. To simplify comparison between estimators we computed comparative bias, which is the estimated number subtracted from the enumerated number divided by the enumerated number. This was done for all estimators for each trapping period. Comparative bias scaled the bias of estimators during each period to the enumerated or base-line number of animals present and therefore simplified the display and interpretation of estimator bias. Because the enumerated estimate is considered to be a lower bound on population number, a good estimator should exhibit a zero to a positive comparative bias.

Results

Enumeration studies

Jacquot Island

An initial starting population of 56 adult hares was tagged on Jacquot Island. Throughout the field season there were 950 recaptures of individuals (Fig. 2). The full-island grid was sampled twice (trapping periods 2 and 4) and the slightly smaller grid area (which covered 70% of the island) three times (trapping periods 1, 3, and 5), owing to logistical constraints and to accommodate a simultaneous study by Zimmerling (1993). 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 adult hares were caught (Fig. 3). The average daily population capture

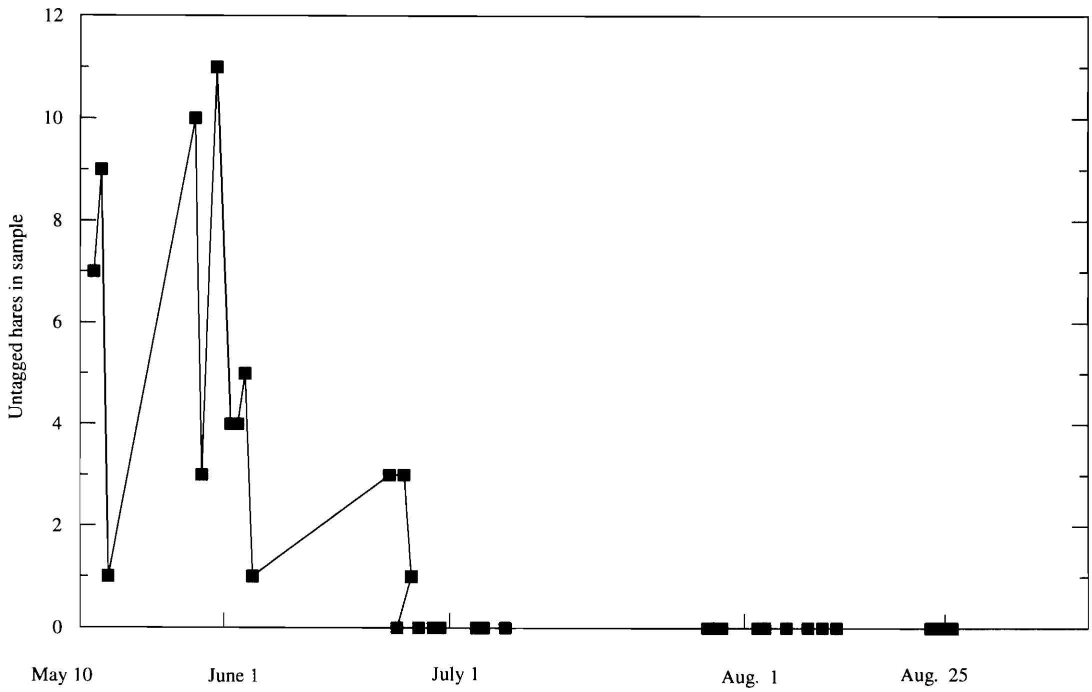

FIG. 3. Numbers of new hares in a sample on Jacquot Island during the 1991 field season. Each square represents a trapping effort.

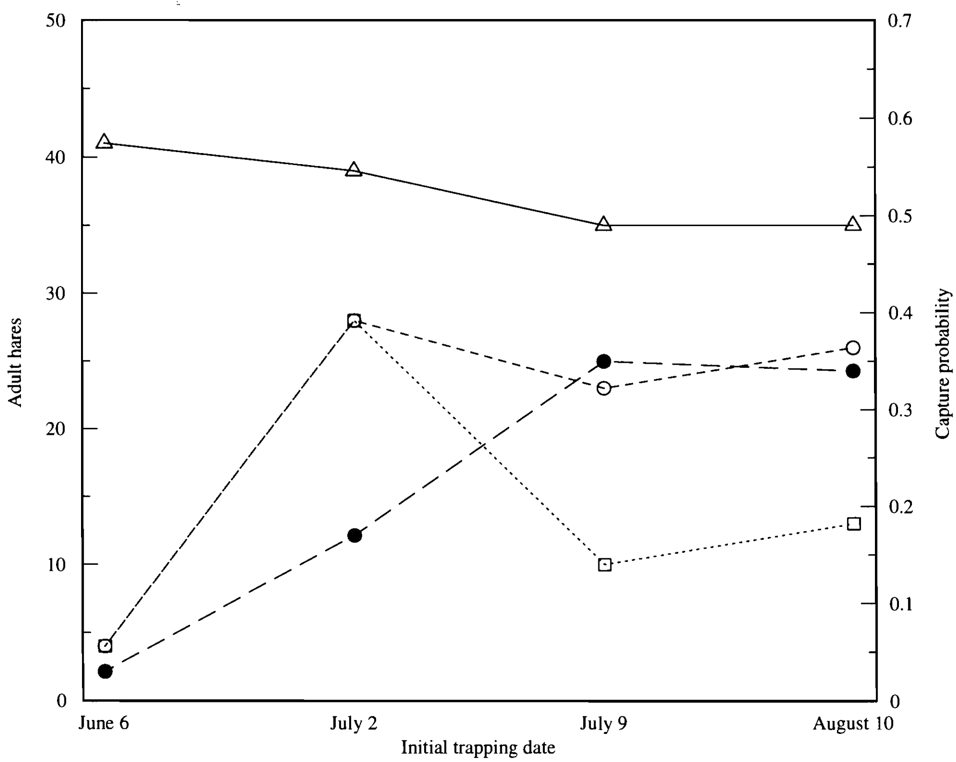

FIG. 4. Summary of sample sizes on Dezadeash Island during the 1991 field season. Note that the x axis denotes an ordering of samples, not an exact time scale. △, enumerated N; ○, number of hares trapped per period; □, number of untagged hares in the sample; ●, mean nightly capture probability. No RADIO estimate was possible, owing to a lack of radio collars. The initial trapping date was the first night of a trapping period. Mean nightly capture probabilities were calculated under model M_0 (Otis et al. 1978).

probability was 0.41 ± 0.05 (SD) (n = 5). No hares without orange ear tags were observed, but poor visibility during the summer months limited the effectiveness of this method.

Because this is an open population, births and deaths did occur. As a result, the enumerated adult population decreased as the summer progressed (Fig. 2). During the 1991 field season, 28-day survival rates of radio-collared hares on Jacquot Island averaged 0.94 (95% confidence limits 0.87–0.99; n = 47) evaluated by the Kaplan–Meir method (Pollock et al. 1989). The juvenile hare population increased during the 1991

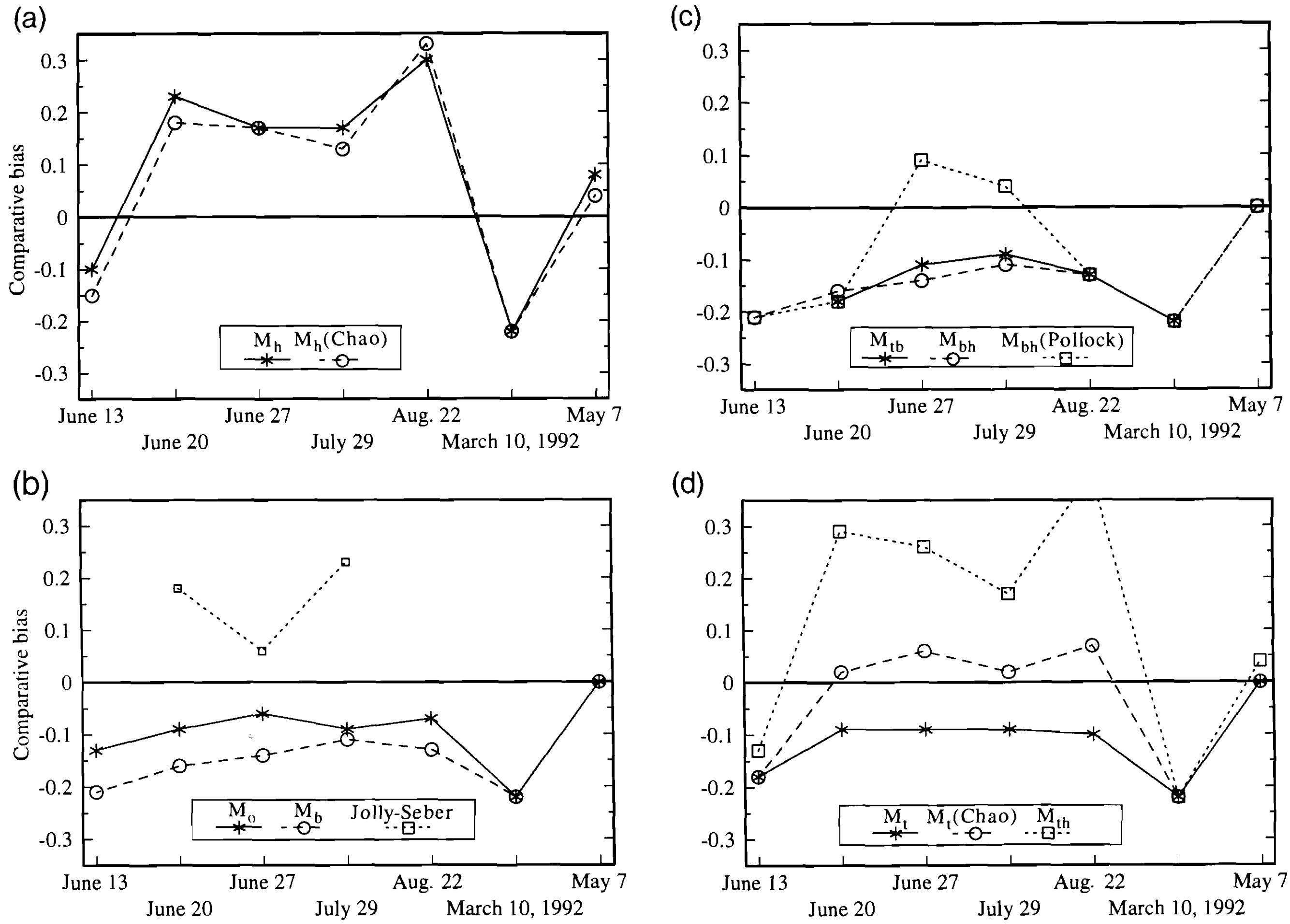

FIG. 5. Comparative bias of estimators according to trapping period on Jacquot Island from samples taken between June 13, 1991, and May 9, 1992. (*a*) Heterogeneity models. (*b*) Null, behaviour, and Jolly–Seber models. (*c*) Other models. (*d*) Time and time–heterogeneity models. Note that the *x* axis denotes an ordering of samples, not an exact time scale. Comparative bias is the estimated value subtracted from the enumerated value divided by the enumerated value.

field season, but this segment of the population was ignored in the estimation of adult population size.

Jacquot Island was also sampled in March and May 1992. During this time a starting population of 37 hares was captured 417 times. During the 1992 field season, mortality was high (the Kaplan–Meir survival rate was 0.76 per 28 days; 95% confidence limits 0.5–0.89; $n = 24$). The mean nightly capture probability was 0.63 ± 0.04 (SD) ($n = 2$) (Fig. 2). Substantial mortality occurred during April, and the population was reduced to 26 individuals.

Dezadeash Island

Trapping was conducted for four 5-day periods on Dezadeash Island during the 1991 field season (June–August) and 41 individual hares were enumerated. Unlike on Jacquot Island, new animals appeared in all four samples (Fig. 4). Possible reasons for differences in capture probabilities between the islands are discussed in Boulanger (1993). The mean nightly capture probability of the population was 0.22 ± 0.07 (SD) ($n = 4$). Radio collars were not used on the island, so an estimate of survivability, 0.92 (95% confidence limits 0.75–1.11), was gained from the Jolly–Seber model. At the end of the summer, five hares had disappeared and were not included in the enumerated population after the dates on which they were last trapped.

Comparison of RADIO *and enumeration estimates*

The RADIO estimates and the enumeration values of the Jacquot Island hare population were correlated ($r = 0.79$, $p = 0.1$, $n = 5$), and four-fifths of the enumeration values were within 1 standard error of the RADIO estimates (Fig. 2). From this we conclude that both estimators show similar bias characteristics.

Estimator performance

The CAPTURE models showed similar characteristics for both islands. In cases where more than one estimator exists for a model, the estimator has been put in parentheses following the model. On each island, models M_0, M_b, M_t (Darroch), M_t (Chao), M_{bh} (generalized removal), M_{bh} (Pollock), and M_{tb} showed a negative bias relative to the enumeration estimate. Models M_h (jackknife), M_h (Chao), and M_{th} showed a positive bias (Fig. 5 and Table 1). The CAPTURE model selection routine picked different models for each trapping occasion. The models picked by 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 for the first and last trapping periods are not possible) made the evaluation of this model difficult.

The precision of an estimator can be indexed by the standard deviation of the mean comparative bias (Table 1). This is similar to the straightness of the given estimator line in Fig. 5. In the case of Jacquot Island, models M_h (Chao), M_h (jackknife), and M_{th} showed the largest standard deviations.

The precision of estimators on Dezadeash Island 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 M_{bh}, M_h (Chao), and M_h (jackknife) 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 the confidence intervals was quite model dependent. The M_h (Chao) and M_{th} models all had large confidence intervals, which could make interpretation of these estimates difficult.

No estimator gave unbiased results when capture probability was below 0.1, which corresponds to 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).

TABLE 1. Mean comparative bias of estimators for Jacquot and Dezadeash islands for the 1991 and 1992 field seasons

Model	Comparative bias	SD	95% CI coverage In	95% CI coverage Out	Average CI width
Jacquot Island					
M_0	−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 (Chao)	0.06	0.19	6	0	29.6
M_t	−0.10	0.07	4	2	7.0
M_t (Chao)	−0.03	0.11	6	1	17.1
M_{bh}	−0.13	0.07	3	4	6.0
M_{bh} (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					
M_0	−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 (Chao)	0.08	0.61	4	0	81.7
M_t	−0.36	0.34	1	3	11.0
M_t (Chao)	−0.17	0.47	3	1	17.5
M_{bh}	−0.21	0.58	2	2	6.0
M_{bh} (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

NOTE: The 95% confidence interval coverage is the number of times the enumerated value was in or out of the estimator's confidence interval. The 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 were 4 for Dezadeash Island and 7 for Jacquot Island.

Discussion

Population closure

A key assumption of the island studies is that the hare population is completely closed and all emigration, immigration, deaths, 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 this evaluation of estimators. During the August trapping sessions juveniles filled 30% ($\bar{x}$ = 38/120; n = 5) of traps on Jacquot Island and 36.25% ($\bar{x}$ = 36.25/100; n = 5) of traps on Dezadeash Island. This slight trap saturation effect may 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.

A possible source of nonclosure was mortality of hares due to predation and other causes. Survival was high on Jacquot and Dezadeash islands during the summer of 1991, but during the 1992 field season, survival was low on Jacquot Island. The death of individuals was accounted for by constant adjustment of the enumerated population number. Trapping dates for estimate analyses were always set at short intervals to assure closure within trapping periods.

Validity of comparison with non-island trapping grids

The island studies could be considered a simplification of a more dynamic system found on mainland trapping grids. Because movement is constrained on the island, there may be differences in movement patterns and animal interactions, which could cause trap behaviour different from that which would occur in the mainland populations. One comparison of island and mainland hares is in their home-range sizes. If home-range sizes are similar it can be generally assumed that spatial use by hares is similar between islands and mainland populations. The mean home-range size of snowshoe hares on Jacquot Island was 7.16 ± 3.0 ha (SD) (n = 13) (Boulanger 1993), which is similar to that of mainland populations (Boutin 1984).

Determination of estimator bias

The evaluation of estimators in this study was somewhat difficult because of the small number of replicates. However, on both islands estimators showed similar bias characteristics, and even though sample sizes are small, inferences still can be made regarding optimal estimation models.

It is important to note the difference between actual estimator bias and comparative bias. Actual estimator bias or percent relative bias is the expected value ($E(\hat{N})$) of estimates subtracted from the true population number divided by the true number. The expected value of repeated estimates and true population number can only be calculated from repeated Monte Carlo simulation trials or artificial sampling situations (Edwards and Eberhardt 1967; Carothers 1973).

The similarity of population estimates between the RADIO and enumeration estimators suggests that each estimator displays similar bias characteristics. It also suggests that any negative bias of the enumeration estimate is probably not due to low capture probabilities of the trapped (and radio-collared) segment of the population, but might be due to an untrappable segment of the population.

The comparison of estimator bias is the most relevant result of the island studies. Estimator precision, which is the variance of the estimate around the true population value, can also be approximated. However, this attribute can also be addressed more powerfully with Monte Carlo simulation, where more replicates are possible (Boulanger 1993).

Nonheterogeneity estimators (M_0, M_t, M_b)

The nonheterogeneity estimators in the 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 nonheterogeneity class estimators when heterogeneity was present within the population. Hallet et al. (1991) reported similar results with a study of opossums and raccoons. It is important to note that the intensive sampling design in this study should have minimized heterogeneity of capture probabilities. However, even with this design heterogeneity was evident, and all the nonheterogeneity estimators displayed a negative bias. It can be inferred that these estimators have limited utility for snowshoe hare populations estimation especially if less ideal sampling designs are used. Further studies on the causes of heterogeneity of capture probabilities on these islands are presented in Boulanger (1993).

The jackknife estimator (M_h)

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 this study. Hallet et al. (1991) also found the jackknife to be the most unbiased of the CAPTURE estimators when used with data from raccoons and opossums. Overall, the jackknife displayed the best characteristics of all the estimators we evaluated.

Chao's M_h, M_t, and M_{th}

Models M_t (Chao) and M_h (Chao) were developed after simulation results suggested that the jackknife M_h and Darroch M_t estimators (Otis et al. 1978) showed negative biases when population capture probabilities were low. Simulation results suggest that the Chao estimators are best when used with low capture probabilities, but are biased when capture probabilities are high (Chao 1989). 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, this model is preferred only when capture probabilities are low.

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

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

CAPTURE model selection routine

The CAPTURE model selection routine picked negatively biased models for three-quarters and five-sevenths of the trapping periods on Dezadeash and Jacquot islands, respectively. The general trend in our results suggests that the heterogeneity class models were the least biased. However, heterogeneity models were picked only 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 Island 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 reflects the low power of the selection routine, as documented in simulation studies by Menkins and Anderson (1988) and Otis et al. (1978). Menkins and Anderson comment that unless the population exhibits high capture probabilities or is large, the model selection routine may not be able to detect a given pattern in capture probabilities and settle on the default M_0 model. For these reasons we suggest that it is better to always use one model of consistent bias than to rely on the CAPTURE model selection routine for typical snowshoe hare trapping data.

The Jolly–Seber model

The Jolly–Seber model displayed a bias comparable to that of many of the CAPTURE models. Most simulation results show a negative bias of this estimator when heterogeneity of capture probabilities is 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 0.68 for Jacquot Island and 0.57 for Dezadeash Island (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 0.5, Gilbert (1973) found that bias due to heterogeneity was minimal with the Jolly–Seber model. Unfortunately, in mainland studies average capture probabilities of snowshoe hares are frequently below 0.5 (Krebs et al. 1986), and unbiased performance of this model cannot be expected.

Conclusion

The objective of the island studies was to evaluate bias in estimation models with populations of known size. From this work, we 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 the program CAPTURE picked models of different bias for each trapping period on both islands. We consider it more useful for our studies to utilize the same estimator consistently, and of the closed population estimators we have found the heterogeneity models to be most accurate.

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Boulanger, J. 1993. Evaluation of capture–recapture estimators using a cyclic snowshoe hare population. M.Sc. thesis, The University of British Columbia, Vancouver.

Boutin, S. 1984. Home range and methods of estimating snowshoe hare densities. Acta Zool. Fenn. **171**: 275–278.

Carothers, A. 1973. The effects of unequal catchability on Jolly–Seber estimates. Biometrics, **29**: 79–100.

Chao, A. 1989. Estimating population size for sparse data in capture–recapture experiments. Biometrics, **45**: 419–428.

Edwards, W., and Eberhardt, L. 1967. Estimating cottontail abundance from livetrapping data. J. Wildl. Manage. **31**: 87–96.

Gilbert, R. 1973. Approximations of the bias in the Jolly–Seber capture–recapture model. Biometrics, **29**: 501–526.

Hallet, J., O'Connel, M.A., Sanders, G., and Seidensticker, J. 1991. Comparison of population estimators for medium-sized mammals. J. Wildl. Manage. **55**: 81–93.

Krebs, C.J. 1966. Demographic changes in a fluctuating population of *Microtus californicus*. Ecol. Monogr. **36**: 239–273.

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. 1986. Population biology of snowshoe hares. I. Demography of populations in the southern Yukon, 1976–1984. J. Anim. Ecol. **55**: 963–982.

Krebs, C.J., Boonstra, R., Boutin, S., Dale, S., Hannon, S., Martin, K., Sinclair, A.R.E., Smith, J.N.M., and Turkington, R. 1992. What drives the snowshoe hare cycle in Canada's Yukon? *In* Wildlife 2001: populations. *Edited by* D.M. McCullough and R. Barrett. Elsevier Science Publishing Co., Inc., pp. 886–896.

Menkins, G.E., and Anderson, S.H. 1988. Estimation of small mammal population size. Ecology, **69**: 1952–1959.

Otis, D., Burnham, K., White, G.C., and Anderrson, D. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. No. 62.

Pollock, K., Nichols, J., Brownie, C., and Hines, J. 1990. Statistical inference from capture–recapture experiments. Wildl. Monogr. No. 107.

Pollock, K.H., Winterstein, S., and Conroy, M. 1989. Estimation and analysis of survival distributions for radio-tagged animals. Biometrics, **45**: 99–109.

White, G., Anderson, D., Burnham, K., and Otis, D. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos Natl. Lab. Rep. LA-8787-NERP.

White, G.C., and Nichols, J. 1992. Introduction to the methods section. *In* Wildlife 2001: populations. *Edited by* D.R. McCullough and R.H. Barret. Elsevier Science Publishing Co., Inc., New York. pp. 13–15.

Zimmerling, T. 1993. A study of factors influencing a non-cyclic, island population of snowshoe hares. M.Sc. thesis, The University of British Columbia, Vancouver.