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SAMPLING DESIGN AND BIAS IN DNA-BASED CAPTURE–MARK–

RECAPTURE POPULATION AND DENSITY ESTIMATES OF GRIZZLY BEARS

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Abstract: Over a 3-year period, we assessed 2 sampling designs for estimating grizzly bear

(*Ursus arctos*) population size using DNA capture–mark–recapture methods on a

population of bears that included radiomarked individuals. We compared a large-scale

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design (with 8 × 8-km grid cells and sites moved for 4 sessions) and a small-scale design (5 × 5-km grid cells with sites not moved for 5 sessions) for closure violation, capture-probability variation, and estimate precision. We used joint telemetry/capture–mark–recapture (JTMR) analysis and traditional closure tests to analyze the capture–mark–recapture data with each design. A simulation study compared the performance of each design for robustness to heterogeneity bias caused by reduced capture probabilities of cubs. Our results suggested that the 5 × 5-km grid cell design was more precise and more robust to potential sample biases, but the risk of closure violation due to smaller overall grid size was greater. No design exhibited complete closure as estimated by JTMR. The results of simulation studies suggested that CAPTURE heterogeneity models are relatively robust to probable forms of capture-probability variation when capture probabilities are >0.2. Only the 5 × 5-km designs exhibited this capture-probability level suggesting that this design is preferred to ensure estimator robustness when population size is <100. The power of the CAPTURE model selection routine to detect capture probability variation was low regardless of sampling design used. Our study illustrated the trade-off between intensive sampling to ensure robustness and adequate precision of estimators while being extensive enough to avoid closure violation bias.

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Incorporating DNA genotyping with capture–mark–recapture methods has been used to estimate grizzly bear population sizes (Woods et al. 1999, Mowat and Strobeck 2000, Poole et al. 2001, Boulanger et al. 2002). The basic methodology involves hair-traps consisting of bait surrounded by a single strand of barbed wire. When bears investigate the hair-traps, their hair is snagged on the barbed wire allowing "capture" of their genetic identification. A systematic sampling grid of hair-traps is then repeatedly sampled to obtain capture–mark–recapture estimates. Although this technique shows promise in forested areas where bears are difficult to observe, optimal sampling design and estimator robustness have received little consideration. Our primary objectives were to compare 2 sampling designs in terms of capture probabilities, closure violation, estimation bias, and sampling efficiency.

Bears traverse in and out of grid areas during sampling, which violates the assumption of geographic closure in most studies that use capture–mark–recapture or related methods (Smallwood and Schonewald 1996, Miller et al. 1997). In this case, naïve estimates from capture–mark–recapture correspond to the "superpopulation" (called N^* by White [1996]) if movement is random across grid boundaries (Kendall 1999). The superpopulation of bears is defined as the population of bears that inhabit the sampling grid and surrounding area (as opposed to the grid area alone). While the superpopulation estimate represents the number of animals that traverse an area, the estimate is compromised by the undefined sampling area and therefore cannot be used to estimate density. The estimation of density is essential for comparing different sampling areas and is a principal objective of most studies.

Capture-probability variation in grizzly bears is potentially due to closure violation (Boulanger and McLellan 2001), differences in trap encounter rates between bears (Boulanger et al. 2004), age- and sex-based vulnerability to hair-trap sampling (Woods et al. 1999), and temporal variation in capture probabilities (Poole et al. 2001). Among the potential causes of capture probability variation, several are related to females and their offspring. First, the small size of cubs (bears <1 yr-of-age) in relation to barbed wire height at hair-traps may lead to under sampling these bears (Woods et al. 1999). Because bears cannot be aged via DNA, we cannot directly parameterize this source of bias. This potential source of bias may be significant given that cubs can represent >22% of the bear population being sampled (Craighead et al. 1974, McLellan 1989). Second, females with cubs exhibit restricted movements compared to other segments of the population (Mace and Waller 1997), potentially leading to reduced rates of capture. Third, females with young travel together and thus their captures are not independent. We used the observed capture probabilities with Monte Carlo simulation trials to determine relative gains in estimator performance with different sampling intensities.

We emphasized the relationship between closure and capture-probability variation in relation to the design of capture–mark–recapture projects. Given fixed resources, researchers are faced with the trade-off of making sampling grids large with sparse hair-trap coverage to potentially minimize closure violation or making grids small with intensive sampling to detect and model capture-probability bias. We used both intensive small-scale (many hair-traps to increase recapture probabilities) and larger-scale designs

(fewer hair-traps but larger grid to minimize closure violation), and we therefore presented

a case study for the comparison of designs.

METHODS

Study Design and Field Methods

We conducted our study in the Upper Columbia River drainage of British

Columbia, Canada. In 1996, we sampled a square grid consisting of 64 8 × 8-km cells for

4 10-day sessions. We moved hair-traps within each cell after each session (Woods et al.

1999). Within each cell, 1 hair-trap was placed each session in good grizzly bear habitat

as judged by the study team. Hair-traps need to be accessible by helicopter or the ground.

This large-scale design had the advantage of covering a large area and allowed a new

location of hair-traps for each sample session. However, some female bears, particularly

those with cubs, may not have had a chance of encountering a hair-trap with the larger cell

sizes. To compare with the large-scale design, we used a small-scale design with 5 × 5-km

cells and fixed hair-trap sites for each sample session in 1997 and 1998. In 1997, we

sampled a small-scale grid of 76 5 × 5-km cells for 5 sessions, each lasting 7–10 days. A

hair-trap was fixed in 1 location within each cell for all sessions. In 1998, we sampled

another small-scale grid of 94 5 × 5-km cells for 5 sessions. As with 1997, hair-traps were

not moved within grid cells. The shape of the grids in 1997 and 1998 was partially defined

by barriers to movement such as lakes, highways, and mountains to minimize population-

closure violation. The small-scale design had the advantage of reduced cost, which

allowed the addition of a fifth sampling session and potential higher capture probabilities

due to increased spatial trap coverage. However, smaller cells lead to a smaller overall

grid size and increased risk of closure violation. The 1997 and 1998 grids overlapped the

northeastern and southwestern sections of the 1996 grid, respectively. Details regarding

the study area, field, and genetic methods can be found in Woods et al. (1999), Paetkau

(2003), and Apps et al (2004).

Estimation of Radiomarked Bear Capture Probabilities and Movements

We used radiomarked bears to index movements across grid boundaries. Grizzly

bears were captured in foot snares or culvert traps distributed throughout the study area.

We accessed traps by road and helicopter. We darted additional bears from a helicopter in

old wildfire burns where bears concentrate to eat huckleberries (*Vaccinium*

membranacium) in late summer (McLellan and Hovey 2001). The sample sizes of

radiomarked bears were 15 (5 F, 10 M) in 1996, 11 (7 F, 4 M) in 1997, and 9 (3 F, 6 M) in

1998. We located radiomarked bears on a weekly schedule throughout the study area.

Radiomarked bears that were never located within 10 km of the sampling area were not

included in radiotelemetry analyses.

We used a JTMR model developed by Powell et al. (2000) to estimate movement

rates of bears on and off the grid and to compare capture probabilities of radiomarked

bears (p_{radio}) with non-radiomarked bears (p_{DNA}). Parameters of the JTMR model are

capture probability (p_{radio}, p_{DNA}), movement probability (emigration from grid [ψ_e],

immigration to grid [ψ_i]), and true survival (*S*). Because grizzly bear annual survival rates

are usually >0.90 (McLellan et al. 1999) and sampling only occurred for approximately 40

days in the spring season, we assumed survival to equal 1.0 for the duration of each

sampling effort.

To assess whether radiomarked bears exhibited different hair-trap capture probabilities, we compared models that constrained capture probabilities to be equal between radiomarked and non-radiomarked bears to unequal models. In addition, we assessed time-specific formulations of each model for relative fit. Models were constructed using program MSSURVIVRT (Powell et al. 2000) in collaboration with J. D. Nichols and J. E. Hines (U.S. Biological Survey, Patuxtent Wildlife Research Center, Maryland, USA).

We pooled sexes for analyses due to low sample sizes of radiomarked bears. We used sample size-adjusted Akaike Information Criterion (AIC_c) model selection (Burnham and Anderson 1998) to determine which models were most supported by the data. Models with the lowest AIC_c values were considered the most supported by the data, but those with ΔAIC_c values <2 were also considered. We used model-averaged parameter estimates to allow inference from multiple models based upon Akaike weights (Burnham and Anderson 1998).

Geographic Closure and Sampling Design

We used statistical tests designed to detect closure violation in program CAPTURE (Otis et al. 1978) to initially screen the data for potential closure violation. We then used the test of Stanley and Burnham (1999) to assess whether closure violation was due to temporary or permanent bear movement using goodness-of-fit tests of various constrained Jolly Seber (JS) models. Permanent movement refers only to the duration of the capture–mark–recapture project. In contrast, temporary movement refers to bears moving in and out of the grid during ≥2 sessions. The exact models that we used in the test of Stanley

and Burnham (1998) were the fully open JS model, a recruitment but not mortality model (NM), a mortality but not recruitment model (NR), and a closed model with no mortality or recruitment (M_t), which is analogous to the M_t model in program CAPTURE. We compared model fit to the data using likelihood ratio tests (Additions: NR vs. JS, M_t vs. NM; Losses: NM vs. JS, M_t vs. NR). If all tests were rejected except NR versus JS, then permanent movement from the grid is suggested; whereas, if all tests except M_t versus NR and NM versus JS were rejected, then movement into the grid is suggested. If temporary movement in or out of the grid occurred, then all tests would be rejected. The NM versus JS and NR versus JS tests were then broken down into session-specific components to explore session-specific closure-violation events (Stanley and Burnham 1999).

Capture Probability Variation and Sampling Design

Data-based Tests.—We initially used the program CAPTURE model-selection routine to screen the data for capture-probability variation. In addition, we conducted simulations to evaluate estimator robustness to likely forms of capture bias and to evaluate the power of program CAPTURE model-selection tests.

Simulation Trials.—A focus of our simulations was to determine if increased capture probabilities resulting from the small-scale design enhanced the performance of estimators when confronted with age-specific capture probabilities. We estimated simulation parameters for the 2 designs from the capture–mark–recapture data. We used a true population size of 100 bears with an average capture probability of 0.15 sampled for 4 sessions to emulate typical data from the large-scale design. We used a true population of 50 bears with a mean capture probability of 0.22 sampled for 5 sessions to emulate the

small-scale design. We based mean capture probabilities for each design upon the results

of our study and the Central Purcell Mountain project, which also used a 5 × 5-km cell size

design (with an associated capture probability level of 0.26 [M_h Chao]; Strom et al. 1999).

Because age cannot be estimated from DNA data, we used a variety of methods to

determine likely age-specific capture probabilities. First, we used capture frequencies of

cubs of radiomarked females to empirically estimate cub capture probabilities.

Radiomarked female bears were considered vulnerable to sampling if ≥1 telemetry location

was on the grid during the study or the bear was captured at a hair-trap. Capture of a cub

was determined if a radiomarked female bear known to have cubs was captured at the same

hair-trap as another bear that shared at least 1 allele at all loci sampled (Woods et al.

1999). Using these data, we estimated cub binomial capture probabilities using an

intercept-only logistic regression model in SAS PROC GENMOD (SAS Institute 1997)

with individual cubs treated as the sample unit. We estimated other simulation parameters

using the hypothesized differences among age and sex classes as described in Table 1.

We further customized simulation trials to investigate potential biases caused by

non-independent captures of females and cubs and reduced capture probabilities of cubs.

Family groups consisting of a female with 2 cubs were simulated with fixed capture

probabilities for adult females and a range of capture-probability levels for cubs (Table 1).

Cubs could only be captured if the mother was captured, so that the capture probability of

a cub was the product of the mother's capture probability and the conditional probability

that a cub was captured given capture of the mother. At 1 extreme, every time a female

was captured the offspring were also captured (conditional capture probability of 1), so

that cub capture probabilities were the same as the mother ($p = 0.17$ for the large-scale

design and $p = 0.25$ for the small-scale design). At the other extreme, offspring were not

captured when the female was captured (conditional capture probability of 0). Note that

these simulations differ from the simulation modules in program CAPTURE that assume

independence of captured animals.

We suggest that the best combination of study design and population estimator

should exhibit reasonable performance across all potential ranges of cub capture

probability. We evaluated estimator performance using percent relative bias, precision as

indexed by coefficient of variation (CV), and confidence interval coverage. Bias levels of

±10%, CV levels ≤20%, and confidence interval coverage of >85% were considered

acceptable. We modified program CAPTURE to produce abridged data files for

population estimates (Boulanger and Krebs 1996). We used Visual Basic[©] to program

simulations and SAS (SAS Institute 1997) statistical software for analysis of simulated

data sets. We conducted 2,000 simulation trials for each combination of cub capture

probability and study design simulated.

Superpopulation and Density Estimates

We produced superpopulation estimates using program CAPTURE. We selected

appropriate models and estimators based upon results of capture-probability tests and

simulation trial findings. Superpopulation estimates were multiplied by the proportion of

sampling occasions that radiomarked bears were on the sampling grid (White and Shenk

2001) to obtain estimates of the average number of bears on the sampling grid. This

estimate of average number of bears on the grid assumes that capture-probability variation

caused by closure violation (Kendall 1999) is accounted for by scaling of estimates by the proportion of locations of radiomarked bears on the sampling grid. This estimator is not affected by any differences in capture probabilities between radiomarked and DNA bears. The estimate of the average number of bears on the grid was divided by the grid area to obtain estimates of density. Both the CAPTURE superpopulation estimate and the proportion of radiomarked bears on the grid estimate have error. Therefore, we used the delta method (Seber 1982) to estimate combined variances under the assumption that correlation between population estimates and the proportion of time on the grid was zero. We calculated log-based, confidence-interval estimates for Ave N estimates using formulas presented in White et al. (2002).

Comment [JWM1]: What is Ave N. Average superpopulation size?

RESULTS

We identified 122 individual grizzly bears (54 F, 59 M, 9 of unknown sex) in DNA samples from 1996 to 1998. Fifty-four (25 F, 29 M) bears were identified in 1996, 41 (24 F, 12 M, 5 of unknown sex) in 1997, and 39 (13 F, 22 M, 4 of unknown sex) in 1998.

Estimation of Radiomarked Bear Capture Probabilities and Movements

Models that suggested capture probabilities of radiomarked bears were different from DNA capture probabilities were most supported by the data for 1996 and 1997, as indicated by the lowest AIC_c score (Table 2). In both years, ΔAIC_c values for competing models were >3.82, suggesting strong support for the most supported models. For 1998, models that assumed different capture probabilities for radiomarked bears and non-radiomarked bears, and a model that assumed equal probabilities of radiomarked and non-radiomarked bears had similar AIC_c values (Table 2). Model-averaged estimates suggest

that radiomarked bears had reduced recapture probabilities compared to DNA-captured

bears in 1996 and 1997 (Fig. 1). In 1998, the radiomarked bear capture probabilities were

slightly larger than DNA-captured bears.

The JTMR model estimates suggested that the 1997 design had slightly lower

emigration and immigration rates than in 1996 and 1998 (Fig. 2). The 1996 large-scale

design had the highest immigration rate suggesting that if a radiomarked bear left the grid,

it had a high probability of returning, indicating high fidelity to the grid area. In all years,

immigration rates were higher than emigration rates, suggesting attraction of bears to the

grid area or non-random distributions of radiomarked bears relative to the grid area.

Geographic Closure and Sampling Design

Violation of population closure was not detected for 1996 ($Z = 1.41$, $P = 0.921$),

1997 ($Z = 1.92$, $P = 0.103$), or 1998 ($Z = -0.19$, $P = 0.164$) by the program CAPTURE

closure test. This test is mainly sensitive to net movement events in early or later sampling

periods and failure to detect closure violation with this test does not prove that closure

violation did not occur (Otis et al. 1978).

Violation of population closure was detected for 1996 ($\chi^2 = 15.2$, df = 4, $P =$

0.004), 1997 ($\chi^2 = 52.8$, df = 5, $P < 0.001$), and 1998 ($\chi^2 = 22.3$, df = 5, $P < 0.001$) by the

closure test of Stanley and Burnham (1999). In terms of the subcomponent tests, M_t versus

NR and M_t versus NM were rejected for the 1996 and 1998 data at $P < 0.001$. For the

1997 data, all subcomponent tests were rejected. The general pattern of rejection in these

tests suggests that the majority of closure violation was caused by temporary rather than

permanent (for the duration of the sampling project) movement from grid areas. This test

will reject the null hypothesis of no closure violation at greater than nominal rates in the

presence of heterogeneity; therefore, results should be interpreted cautiously (Stanley and

Burnham 1999).

Capture Probability Variation and Sampling Design

The program CAPTURE model selection goodness-of-fit tests did not detect any

forms of capture-probability variation in the 1996 and 1997 data, and model M_o was

chosen as the appropriate estimation model for both years. Heterogeneity variation was

suggested in Test 1 ($\chi^2 = 6.17$, df $= 1$, $P = 0.170$), and time variation was detected ($\chi^2 =$

14.3, df $= 4$, $P = 0.006$) in the 1998 dataset; thus, M_t was chosen as the most appropriate

model. Mean capture probabilities were 0.16 (M_h Chao) for 1996, 0.2 (M_h Chao) for 1997,

and 0.12 (M_t Chao) for 1998. The capture probabilities in 1998 were reduced due to

violation of closure.

Empirical Analysis of Capture Probabilities of Females with Cubs.—In 1996, 4

radiomarked female bears with a total of 7 cubs were monitored. Of these, 1 female with 2

cubs was DNA captured twice with another bear with whom she shared at least 1 allele at

all 15 loci sampled, suggesting her cub was also caught. In 1997, no females with cubs

were monitored. In 1998, 2 female bears with a total of 3 cubs were monitored with no

documented capture of cubs. Given sparse sample sizes, we pooled 1996 and 1998 leading

to a capture-probability estimate of 0.05 (95% CI: 0.01 to 0.17) from the intercept-only

logistic regression model. Given the uncertainty in this parameter, we also simulated a

range of values for the proportion of cubs sampled (Table 1).

Simulation of Age-specific Capture Probabilities and Family-group Bias.—The

degree of bias caused by family groups was sensitive to assumptions made about cub

capture probability and capture-probability levels associated with each sampling design

(Fig. 3). If cub capture probability was zero, then all estimators exhibited negative bias

and less than nominal confidence interval coverage, since the effective population size

being sampled did not include cubs and was 21.5% smaller. The M_h (Chao) estimator,

which was designed for sparse data (Chao 1989), displayed the best confidence interval

coverage of 94 and 80% with the large- and small-scale sampling designs, respectively,

when zero cubs were caught. If cub capture probability was low (the most likely scenario

with cub capture probabilities of 0.01–0.05), then the non-heterogeneity estimators

exhibited negative biases of –10 to –30%, while the heterogeneity estimators exhibited

more acceptable biases of –7 to 10% with both designs. Only the M_h (Chao) estimator

exhibited acceptable levels of bias with the large-scale design when cub capture

probability was low. If cub capture probability was higher (>0.05), then the bias of most

estimators was acceptable for both designs except for the M_h (Chao) estimator that

exhibited biases of > 10% with the large-scale design.

Coefficients of variation for all estimators were high for the large-scale design but

decreased substantially with the small-scale design. Confidence-interval coverage was

reasonable for most estimators for the large-scale design; however, this was offset by low

precision for most of the estimators. Confidence-interval coverage was acceptable for the

heterogeneity estimators with the small-scale design as long as the cub capture probability

was <0.15. Confidence-interval coverage was close to nominal levels for the M_h Chao

estimator with both designs; however, this estimator was the least precise. Overall, the

best combination of estimators and sampling design for the most likely range of cub

capture probabilities was the small-scale design and the heterogeneity estimators that

displayed moderate bias (approx −10 to 10% if cub capture probability was >0), acceptable

levels of precision (CV < 20% for the jackknife estimator), and near nominal confidence-

interval coverage (>85%).

We also simulated the non-independent capture of yearlings with attendant females

(in addition to non-independent capture of cubs). For these simulations, yearlings were

always captured when an attendant female was captured, a scenario of extreme non-

independence of captures. The degree of bias did not change for estimators; however,

precision decreased for both designs with estimators exhibiting CV levels 5–10% higher

than values in Fig. 3. In addition, confidence-interval coverage was reduced as a function

of increasing cub capture probability, with most estimators exhibiting confidence-interval

coverage levels that were approximately 10% lower than Fig. 3. The M_h (Chao) estimator

displayed the best confidence-interval coverage when confronted with non-independent

captures with coverage levels between 75 and 85% for both designs simulated.

We ran simulations (Table 1) to test the power of the CAPTURE model-selection

routine to detect heterogeneity. The CAPTURE model-selection routine exhibited

relatively low power to detect heterogeneity variation with either design. The M_h model

was only selected for 10% of the large-scale and 4% of the small-scale simulations.

Exploratory simulations were run in which the population of bears was increased to 200

for both designs to determine if power increased if larger populations were sampled. In

this case, the M_h model was chosen in 30 and 22% of the small- and large-scale

simulations, respectively.

CAPTURE Superpopulation Estimates

Simulation results suggested the M_h Chao model exhibited the best performance in

terms of confidence-interval coverage and bias levels when confronted with likely cub

capture probability levels (approx 0.05); therefore, this model is most appropriate for

estimating population size. A large degree of time variation (bears caught per session [n_j]

= 7, 19, 14, 11, 5) was evident in the 1998 data. Further simulations suggested that the

most appropriate estimator in this case was M_t (Chao), due to positive bias with the M_h

estimators (with time variation) and poor performance of the M_{th} estimator, which was

potentially due to poor sample coverage (Chao and Jeng 1992). Therefore, the appropriate

models and estimators were M_h (Chao) for 1996 and 1997, and M_t (Chao) for the 1998

data. These results suggest a slight gain in precision with the 1997 small-scale design over

the 1996 large-scale design grid.

Closure Adjustment of the Superpopulation Estimates

The correction for closure violations based on the proportion of radiomarked bears

on the grid suggests that superpopulation estimates range from 36 to 15% greater than

average *N* on grid estimates (Table 3). The precision of the proportion of radiomarked

bears on the sampling grid was low when compared to the precision of capture–mark–

recapture estimates. Densities can be derived by dividing the average *N* (Table 3) by the

area of each sampling grid (1996: 4,096 km^2, 1997: 1,900 km^2, 1998: 2,350 km^2). The

resulting density estimates and corresponding confidence intervals are 19 (13 to 38)

bears/1,000 km^2 for 1996, 25 (20 to 41) for 1997, and 25 (16 to 53) for 1998.

      The sex ratio of radiomarked bears should also be considered when interpreting the

closure-corrected population estimates (Table 4). More males were present in grid areas

than females for all years except 1997, which might have reduced the 1997 estimate of grid

occupancy compared to other years. However, sex-specific estimates of proportion-on-

grid for females also suggested that the 1997 grid was the most closed. The proportion-on-

grid estimate for males suggested that the 1997 grid was roughly similar to the 1996 grid in

terms of the proportion of time radiomarked bears were on the grid. Therefore, the ranking

of grids for relative closure violation was partially robust to differences in sex ratios. The

sex ratio of DNA captures also suggested that the actual ratio of males to females on grids

(M/F ratios; 1996: 29/25, 1997: 12/24, 1998: 22/13) was similar to the ratio of

radiomarked bears in Table 4, suggesting that correction of estimates due to the sex ratio of

radiomarked bears was not warranted.

DISCUSSION

      Our study illustrates some of the main challenges confronting the use of DNA-

based capture–mark–recapture methods to achieve reliable population estimates. First,

increased sample intensity and subsequent higher capture probabilities with the small-scale

grid boosts estimator robustness to heterogeneity and increases precision of estimates (Fig.

3). However, the smaller size of grid areas increases risk of closure violation bias, reducing

capture probability (Kendall 1999, Boulanger and McLellan 2001), and, therefore,

potentially negating the advantages of smaller cell size if the grid is not topographically

closed. The radiotelemetry-based movement analyses results suggest that the 1997 small-

scale grid met the closure assumption better than the larger 1996 large-scale grid design,

an effect likely due to greater topographic closure. For example, analysis of the capture–

mark–recapture and radiotelemetry data from this study (Apps et al. 2004) suggests that

the northern edge of the 1996 grid was composed of high quality habitat as shown by the

concentration of bear captures in this area. The 1997 grid boundary was moved north to

partially accommodate this area of higher bear density, while the southern boundary was at

the Trans-Canada Highway. Both of these modifications improved topographic closure.

In contrast, the 1998 small-scale grid was not topographically closed, and JTMR analysis

suggested closure was severely violated, substantially reducing capture probabilities. To

minimize closure violation, grid placement with respect to topographic barriers and areas

of high bear density may be more important than grid size alone (Boulanger and McLellan

2001). However, since initial bear density and distribution is difficult to determine,

readjusting sampling designs in subsequent years may be necessary.

Cubs of the Year Heterogeneity Bias

The results of our study illustrate the possible effects of low cub capture

probabilities on population estimates. The actual proportion of cubs that are captured is

difficult to estimate. Given this uncertainty, we believe estimators that are robust in terms

of point (percent relative bias) and variance estimates (confidence interval coverage) to

varying levels of cub capture probability are most appropriate. All estimators displayed

increasing estimates as cub capture probability increased. However, only the M_h Chao

model displayed reasonable confidence-interval coverage even when estimates were biased (e.g., high cub capture probabilities in Fig. 3).

One argument is that cubs should be ignored in capture–mark–recapture estimates, since they most likely form a small proportion of the sampled population due to low capture probabilities. A possible strategy would be to use non-heterogeneity estimators that are less likely to account for heterogeneity bias caused by reduced cub capture probabilities. Our results suggest that this is a potentially risky approach for a variety of reasons. First, some cubs are likely captured and, therefore, are part of the sampled population as suggested by multiple captures of a cub from a radiomarked female in our study. Therefore, any estimate will most likely include some representation of cubs and will potentially be a positively biased representation of the population without cubs included. For example, in our simulations, we used a realistic 21.5% proportion of cubs in the population (McLellan 1989; Table 1). Most estimators however, exhibited biases of less than –21.5% (Fig. 3), suggesting an overall positive bias if estimates were considered not to include cubs. Second, many other forms of heterogeneity variation exist that were not considered in our simulations due to closure violation (Boulanger and McLellan 2001), past live-capture history (Fig. 1), and age/sex-specific capture probabilities. These other forms of heterogeneity will also cause negative bias of both point and variance estimates of non-heterogeneity estimators, as suggested by the results of our simulations (Fig. 3), leading to a potentially dangerous "biased-but-apparently-precise" estimate. The penalty for use of heterogeneity estimators, such as M_h (Chao) that are designed for data with lower capture probabilities (Chao 1989), is reduced precision of estimates; however, a

larger confidence interval is probably the most indicative of certainty in estimates, given the uncertainty in cub capture probabilities.

Non-independence of captures of yearlings and cubs with attendant females causes a decrease in precision and confidence-interval coverage with most estimators. This problem cannot be parameterized given that age cannot be identified from DNA data, which makes determining the relationship between closely related individuals in the DNA dataset difficult. For example, mother and attendant young are suspected if bears share at least 1 allele at all loci sampled; however, the actual relationship between bears could be a mother–cub, mother–yearling, or mother–older independent offspring. As with cub heterogeneity bias, the M_h (Chao) heterogeneity estimator is the most robust to non-independence of captures but also displays lower levels of precision than other estimators.

Monte Carlo simulations suggested that the CAPTURE model-selection routine lacked power to detect heterogeneity capture-probability variation. The low power of the CAPTURE model-selection routine has been documented extensively by other simulation studies (Otis et al. 1978, Boulanger and Krebs 1996, Stanley and Burnham 1998). The small-scale grid design showed greater power than the large-scale design; however, the small-scale grid was still compromised by the lower number of bears present in the sampling area

Heterogeneity variation caused by cubs in population estimates has not been considered in previous studies that have attempted to estimate grizzly bear population size (Mowat and Strobeck 2000, Poole et al. 2001, Boulanger et al. 2002). Mowat and Strobeck (2000) conducted simulation tests of estimators to explore robustness to

heterogeneity bias; however, the parameterization of heterogeneity simulations were not

tied to the capture–mark–recapture data or potentially important aspects of bear biology in

the sampled population. This makes determining the applicability of these results difficult.

Potential methods, such as installing a second wire closer to the ground, could be

used to increase cub capture probabilities and potentially mitigate cub heterogeneity bias.

In addition, the use of stable isotopes in hairs to identify nursing cubs (Hobson et al. 2000)

might also allow partial identification of cubs in the dataset. If this method is successful,

then age-stratified analyses using the Huggins (1991) or Pledger (2000) heterogeneity

models in program MARK (White and Burnham 1999) will be possible, therefore

eliminating any bias due to cubs. Another method would be to estimate the population of

independent bears (Miller et al. 1997) by eliminating all potential parents and dependent

offspring from the dataset that share at least 1 allele at all loci sampled. However, this

method would result in a negatively biased estimate of the population of independent bears

since parents and older independent offspring, except father and sons, would also be

eliminated from the data set. Until these methods are developed and verified, we suggest

that the general guidelines from our simulations be used when considering appropriate

population estimators for grizzly bear populations.

Closure violation

The program CAPTURE closure test displayed low power to detect closure-

violation bias as demonstrated by the difference between superpopulation and average N

estimates in Table 3. One assumption made when radiotelemtry is used to index closure

violation is that radiomarked individuals represent a random sample of the population of

bears that could potentially encounter traps during the time of sampling. We distributed and accessed trapping sites using a helicopter to ensure thorough coverage of our study area; however, the high immigration rates of bears in all years into the sampling grid area suggests that most radiomarked bears exhibited relatively high fidelity to the sampling grid. This result suggests that the distribution of radiomarked bears may have been biased toward the grid area. However, the fidelity of the radiomarked bears to the grid may also reflect our effort to locate the grid so that it was topographically closed as much as possible. A larger issue with our study was low numbers of radiomarked bears and subsequent imprecise estimates of the proportion of radiomarked bears on the grid (Table 3) that led to imprecise estimates of the average number of bears on the sampling grid. Increasing the sample size of radiomarked bears would mitigate this issue.

Other methods to estimate population density from DNA-based capture–mark–recapture projects, such as the core-extrapolation method of Boulanger and McLellan (2001), could not be used with our data because of the extremely uneven density of bears in the study area. For example, the town of Golden was located near the center of the 1996 study grid, and, consequently, this area had lower densities than other areas. The obvious dependence of bear densities on habitat and human conditions limits the ability of managers to interpret and extrapolate grid-based density estimates. As a result, a resource selection function-based analysis (Boyce and McDonald 1999), providing a habitat-based spatial interpolation of estimated densities, was conducted by Apps et al. (2004).

MANAGEMENT IMPLICATIONS

A major challenge of capture–mark–recapture estimation of grizzly bear populations is meeting the assumption of population closure. The concept of superpopulation provides a way to interpret estimates when closure is violated. However, this and other studies (Boulanger et al. 2002, 2004) suggest that the degree of closure-violation bias is strongly influenced by local topography and habitat. Therefore, extreme attention to closure in study design must be undertaken to ensure reliable estimates. Increasing grid size will not significantly offset closure violation in comparison with grid placement designed to maximize topographic closure. Results of this and other studies (Boulanger and McLellan 2001) suggest that the program CAPTURE closure test has limited power to detect closure violation with sample sizes typical of bear studies. Therefore, the use of alternative tests to detect closure violation (Stanley and Burnham 1999, Boulanger and McLellan 2001), as well as the use of radiomarked bears to assess movement, should be considered.

Study designs resulting in capture probability levels >0.2 and population sizes >50 must be used to ensure reliable results. The robustness of estimators to factors such as family group bias and levels of precision climb dramatically once the capture-probability level is >0.2. Of the 7 studies reviewed by Boulanger et al (2002), only designs with 5 × 5-km and 7 × 7-km grid cell sizes have achieved this capture-probability level. If populations are much larger than 100 (e.g., 200 bears), designs with larger grid cell sizes and reduced capture probabilities may be used. Recent likelihood-based heterogeneity models (Pledger 2000) in program MARK should also allow greater flexibility in the

modeling of heterogeneity variation. Boulanger et al. (2002) demonstrated how datasets

from different studies can potentially be pooled in program MARK to enhance estimate

precision. The pooling approach requires standardization of study designs making it less

applicable to our study. In addition, further simulation testing of likelihood-based

heterogeneity estimators and accompanying information-theoretic model selection is

needed to determine the overall performance of this newer method of analysis (Stanley

1998, Dorazio and Royle 2003).

Given the low power of the CAPTURE model-selection routine, selection of

appropriate estimation models should be based on simulations that incorporate the biology

of bears, combined with results of some of the capture–mark–recapture projects with larger

sample sizes and higher capture probabilities. We suggest that researchers use the

simulation model parameters in Table 1 and simulation modules such as those found in

CAPTURE and MARK to explore particular biases and levels of precision with their study

designs.

Ours and other studies suggest that obtaining precise and unbiased estimates of

population size and density for grizzly bears using DNA capture–mark–recapture methods

requires extremely careful attention to sampling design. An alternative to estimation of

population size that is potentially more robust to sampling issues is the estimation of trend

through repeated sampling of study areas. For example, the Pradel model (Pradel 1996) in

program MARK estimates population rate of change and is more robust to heterogeneity of

capture probabilities such as cub bias and closure violation (Franklin 2002, Hines and

Nichols 2002, Nichols and Hines 2002, Schwarz 2001, Williams et al. 2002). From a

manager's perspective, the main disadvantage of this approach is that it requires a long-term perspective toward the management of bears, given that at least 3 yearly sampling sessions are needed to obtain estimates of relative survival and population trend. However, due to their long life span and subsequent time lags in population response to perturbation, rigorous management of bears requires a long-term perspective (Anderson et al. 1995, Thompson et al. 1998).

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Table 1: Parameters used for age- and sex-bias simulations of grizzly bears. The

population size (N) and mean capture probabilities ($\bar{p}$) used for each design were

estimated from field results. Percent composition of each age and sex class is from

McLellan (1989). The expected number of bears of each age and sex class in the

population was calculated as $E(N) = N \times$ % composition/100. The proportion of each

cohort snagged relative to adult males (P_{snag}) was hypothesized upon bear height relative

to barb wire and trap encounter rates. Also presented are the capture probability of each

age and sex cohort (P_{cohort}) and the expected number of each cohort captured per sampling

session ($E(n_j) = E(N)\, p_{cohort}$). The value of $\bar{p}$ for each simulation treatment was estimated

as $\sum_{j=1}^{k} E(n_j) \Big/ N$, where k is the number of age and sex cohorts (4). For cubs, yearlings, and

adult females, P_{cohort} was the product of p_{snag} and p_{cohort} for adult males. For adult males,

P_{cohort} was solved iteratively so that $\bar{p}$ equaled the desired level (e.g., 0.15 for the large-

scale grid).

Age	Sex	% composition	$E(N)$	p_{snag}	p_{cohort}	$E(n_j)$
Large-scale: 8 × 8-km grid cell size ($N = 100$, $\bar{p} = 0.15$)						
Cubs	males and females	21.5	22	0.10	0.05 (0–0.17)[a]	0.47
Yearlings	males and females	17.5	18	0.75	0.17	2.86
Adult	females	30.5	30	0.75	0.17	5.04
Adult	males	30.5	30	1.00	0.22	6.72
Small-scale: 5 × 5-km grid cell size ($N = 50$, $\bar{p} = 0.22$)						
cubs	males and females	21.5	11	0.10	0.05 (0–0.25)	0.33

yearlings	males and females	17.5	9	0.75	0.25	1.98
adult	females	30.5	15	0.75	0.25	3.71
adult	males	30.5	15	1.00	0.33	4.95

[a]Range of values simulated given uncertainty in capture probabilities of cubs.

Table 2: Model selection results for joint telemetry/capture–mark–recapture analysis of grizzly bears in the Upper Columbia River drainage, British Columbia, Canada, 1996–1998. "Radiomarked p" represents whether a model was constrained to estimate capture probabilities for radiomarked bears and DNA bears ("yes") or whether capture probabilities were pooled ("no"). Log likelihood (Log (Λ)), the number of parameters (K), Akaike's Information Criteria corrected for sample size (AIC_c), ΔAIC_c, and Akaike weights (w_i) for each model are given.

Time	Specific p		Radiomarked p	Log (Λ)	K	AIC_c	ΔAIC_c	w_i
	S	Ψ						
1996								
no	no	no	yes	−21.75	4	56.31	0	0.85
no	no	no	no	−24.78	3	60.13	3.82	0.13
no	no	yes	no	−24.07	5	63.22	6.91	0.03
no	yes	yes	no	−22.88	8	80.82	24.51	0.00
no	no	yes	yes	−35.56	9	90.91	34.6	0.00
no	yes	yes	yes	−25.37	17	91.32	35.01	0.00
1997								
no	no	no	yes	−30.53	4	74.05	0	0.87
no	no	no	no	−33.73	3	78.15	4.1	0.11
no	no	yes	yes	−27.12	9	82.19	8.14	0.01
no	no	yes	no	−33.03	5	83.79	9.74	0.01
no	yes	yes	no	−28.14	8	108.1	34.05	0.00
no	yes	yes	yes	−28.6	17	119.4	45.35	0.00

Comment [JWM2]: You need to explain these 3 headings.

1998								
no	no	no	no	−33.03	3	76.86	0	0.47
no	no	no	yes	−31.87	4	76.87	0.01	0.47
no	no	yes	no	−31.64	5	81.24	4.38	0.05
no	no	yes	yes	−30.68	9	89.87	13.01	0.00
no	yes	yes	no	−26.33	8	106.4	29.54	0.00
no	yes	yes	yes	−28.87	17	122.8	45.94	0.00

Table 3: Estimates of superpopulation and average number of grizzly bears on the sampling grid based upon proportion of radio locations on the grid in the Upper Columbia River drainage, British Columbia, Canada 1996–1998.

	Naïve (superpopulation)[a]			Proportion radio locations on grid		Average N on grid		
Estimator	Estimate (CI)	SE	CV	Estimate	SE	Estimate (CI)	SE	CV
1996 (Large-scale design)								
M_h (jackknife)	103 (85 to 132)	11.9	12%	0.71	0.34	73 (50 to 143)	35.91	49%
M_h (Chao)	108 (78 to 177)	23.8	22%	0.71	0.34	77 (51 to 155)	40.31	53%
M_t (Chao)	90 (70 to 137)	16.2	18%	0.71	0.34	64 (46 to 130)	32.60	51%
1997 (Small-scale design)								
M_h (jackknife)	65 (52 to 92)	10	15%	0.85	0.25	55 (42 to 90)	18.60	34%
M_h (Chao)	55 (48 to 107)	9.5	17%	0.85	0.25	47 (37 to 79)	16.16	35%
M_t (Chao)	63 (45 to 86)	13.8	22%	0.85	0.25	54 (40 to 92)	19.87	37%
1998 (Small-scale design)								
M_h (jackknife)	94 (74 to 127)	13.5	14%	0.64	0.31	60 (39 to 117)	30.30	50%
M_h (Chao)	130 (71 to 301)	52.8	32%	0.64	0.31	83 (47 to 183)	52.50	63%
M_t (Chao)	92 (71 to 301)	29.8	16%	0.64	0.31	59 (37 to 125)	34.23	58%

[a]Most appropriate model in italics

Table 4: Sex-specific proportion of radiomarked grizzly bears on sampling grids on the

Upper Columbia River drainage, British Columbia, Canada 1996–1998.

Year	Females			Males		
	Proportion on grid	SE	*n*	Proportion on grid	SE	*n*
1996	0.9	0.22	5	0.63	0.35	10
1997	1	0	7	0.6	0.28	4
1998	0.86	0.23	3	0.53	0.32	6

List of Figures

Fig. 1. Model-averaged estimates of recapture rate for DNA bears and radiomarked bears

from joint telemetry/capture–mark–recapture analysis (Table 2) for the Upper Columbia

Grizzly Bear Study, British Columbia, Canada, 1996–1998. Error bars represent 95%

confidence intervals of estimates.

Fig. 2. Model-averaged estimates of emigration and immigration from grid areas from the

joint telemetry/capture–mark–recapture analysis for the Upper Columbia Grizzly Bear

Study, British Columbia, 1996–1998. Error bars represent 95% confidence intervals.

Fig. 3. Family-group bias simulation results. CAPTURE models shown are: M_h (Chao);

(square), M_h (jackknife); circle, M_0 (triangle) and M_t (Chao) (diamond). Percent relative

bias, coefficient of variation, and confidence-interval coverage are shown for the large-

and small-scale designs. The dashed vertical line indicates estimated cub capture

probability levels as listed in Table 1.