SOURCES OF HETEROGENEITY BIAS WHEN DNA MARK-RECAPTURE SAMPLING METHODS ARE APPLIED TO GRIZZLY BEAR (*URSUS ARCTOS*) POPULATIONS

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One of the challenges in estimating grizzly bear (*Ursus arctos*) population size using DNA methods is heterogeneity of capture probabilities. This study developed general tools to explore heterogeneity variation using data from a DNA mark-recapture project in which a proportion of the bear population had GPS collars. The Huggins closed population mark-recapture model was used to determine if capture probability was influenced by sex or collar status. In addition, trap encounter rates were estimated by comparing the closest distance from traps where hair was snagged of bears that were captured, with bears for which we had radiolocations but were not captured. Results of the Huggins analysis suggested that sex, distance of bear DNA capture from grid edge, and whether a bear was radiocollared potentially affected capture probabilities. The encounter rate analysis estimated that 63% of bears that encountered traps were snagged, and that males encountered more traps than females. The following conclusions arise from this study. First, the distance of DNA capture of bears relative to the grid edge should be modeled as an individual covariate to ensure robust estimates of superpopulation size when closure violation is suspected. Second, sampling should be intensive to minimize heterogeneity and to ensure all bears encounter traps. Finally, estimators that are robust to heterogeneity variation should be used, given the various sources of heterogeneity variation.

Key words: DNA genotyping, grizzly bear, Huggins closed captures model, mark-recapture population estimation, program MARK

Estimation of population size using mark-recapture methods has been challenged by heterogeneity of capture probabilities due to biological differences between individuals. Most simpler estimators display negatively biased population estimates and associated variance estimates in the presence of heterogeneity. Various estimators have been developed that are robust to unequal capture probabilities (Otis et al. 1978) and therefore unbiased estimates are still possible; however, these estimators are often less precise than simpler models (Chao 1989). In addition, most of these estimators provide no insight into the biological causes of heterogeneity variation. Information about the causes of heterogeneity variation is essential to the continued development of sampling designs that minimize heterogeneity variation.

We became interested in heterogeneity variation while using DNA methods to estimate grizzly bear population size. DNA identification of grizzly bears (*Ursus arctos*) from hair (Mowat and Strobeck 2000; Poole et al. 2001; Woods et al. 1999) has been used in many studies to provide estimates of bear population size. The basic technique, pioneered by Woods et al. (1999), involves a systematic grid of bait sites surrounded by barbed wire (termed hair traps) that snag hair when bears visit the sites, allowing genetic identification of individuals. Mark-recapture estimates of population size are then generated from repeated samplings of hair-trap sampling grids. Given the recent introduction of this technique, there has been little investigation into the efficiency of hair traps to sample bears and the biological causes of unequal capture probabilities in bear populations. This information is essential to the continued development of DNA mark-recapture sampling procedures and to ensure researchers adequately can assess the utility of this approach.

It is probable that bears exhibit individual capture probabilities based on sex, age, home range size, recent capture for collaring, and other biological attributes. However, it is difficult

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to separate each potential factor influencing capture probabilities from DNA data alone. In particular, an essential study design question is whether most of the variation in capture probabilities is due simply to bears encountering traps at different rates (due to different home range sizes and movement rates) or whether different physical (age and bear height), behavioral (females with cubs), or other biological factors influence the probability of a bear being captured.

We examined differences in capture probabilities based on sex, age, and recent live capture (for collaring) history of bears. We attempted to separate the influence of trap encounter from other biological causes of capture probability variation. We developed a method to estimate the efficiency of hair traps using data from GPS collared bears collected during a DNA inventory project in the Foothills Model Forest in Alberta. We illustrate the use of information theoretic model selection (Burnham and Anderson 1998) as a method of evaluating biologically based hypotheses regarding capture probabilities and encounter rates of grizzly bears. Although this manuscript focuses on grizzly bears, the general techniques used to investigate heterogeneity should be applicable to studies of other species where biologically-caused variation of capture probabilities is suspected.

METHODS AND MATERIALS

Field sampling methods.—An ongoing study, the Foothills Model Forest Grizzly Bear Study, is being conducted on the eastern slopes of the Canadian Rocky Mountains (Nielsen et al. 2002). In 1999, a DNA mark-recapture project was conducted by Mowat et al. (2004) in a 5,350 km^2 study area. For this project, a single hair trap was placed in a 9×9 km grid cell for three 14-day sampling sessions. The hair trap was moved to a new location (>1 km) for each sampling session. Sixty-four 9×9 km cells were sampled in a contiguous sampling grid. Fish oil and cow blood were used to attract bears to hair traps and each hair trap was surrounded by a barbed wire fence to snag hair (Mowat and Strobeck 2000; Poole et al. 2001; Woods et al. 1999). Once collected, hair was genotyped using methods described in Woods et al. (1999) and Mowat and Strobeck (2000). Paetkau (2003) provides a detailed assessment of screening procedures and error rates associated with genotyping.

Bears were captured for collaring purposes within 16 predefined watersheds or bear management units. The goal of the collaring effort was to radiocollar at least 1 bear in each of these watersheds during the spring capture period. Bears were captured using helicopter darting and Aldrich foot-snare capture methods. Before and during the DNA study, bears were captured and fitted with GPS collars (Televilt, Sweden, and Advance Telemetry Systems, Isanti, Minnesota) that were programmed to acquire a location from satellites every 4 h. The locations were stored in the collar and downloaded remotely on a monthly basis. Of the 19 bears captured, 12 provided enough data to interface with the DNA sampling effort.

For the mark-recapture analysis, the term DNA bears refers to bears that were identified only using the DNA hair traps. GPS bears were those that were fitted with GPS collars, a proportion of which were sampled using DNA hair traps.

Huggins analysis of collar status and sex of bear.—The identifiable sources of capture probability variation in this data set were sex of bear and collar status. Bears were grouped according to these classes and the relative degree of difference due to each factor was evaluated using the Huggins closed model (Huggins 1991) in Program MARK (White and Burnham 1999). The Huggins model estimates capture probability (p) and recapture rate (c). Recapture rate in the context of closed models refers to the capture probability conditional on initial capture and is used to model behavioral response to trapping. Grizzly bears often were captured at multiple hair traps during the course of DNA sampling, and the mean location of capture was used to index the home range center of captured bears.

Bears traverse in and out of grid areas during sampling, therefore violating the assumption of geographic closure. The distance of the mean location of capture to the edge of the sampling grid was modeled as a capture probability individual covariate in MARK, because closure violation directly affects estimates of capture probability (Boulanger and McLellan 2001; Kendall 1999). More specifically, if closure is violated, then it would be expected that capture probability would increase and reach an asymptote or increase indefinitely as a function of the distance from where a bear was captured relative to the grid edge. This effect is due to lower trap encounter rate of edge bears that presumably only spent a proportion of time on the sampling grid. Most GPS bears were captured and collared on the DNA sampling grid and potentially were resident bears, whereas bears caught exclusively in DNA sets (DNA bears) potentially were resident or edge bears (Fig. 1). Therefore, a prime objective of model building was to determine if DNA bear capture probabilities were reduced due to lessened trap encounter of edge bears in the DNA sample. Polynomial and log-transformed distance from edge covariate terms were introduced into the model to allow a full range of potential curve shapes to be tested using an approach similar to the fitting of curves to line transect data (Boulanger and McLellan 2001; Buckland et al. 1993).

Models were evaluated using the sample-size-corrected Akaike information criterion (AIC$_c$) index of model fit. The model with the lowest AIC$_c$ score was considered the most parsimonious, thus optimizing the tradeoff between bias and precision (Burnham and Anderson 1998). The difference between any given model and the most supported (ΔAIC$_c$) was used to evaluate the relative fit of models when their AIC$_c$ scores were close. In general, any model with an ΔAIC$_c$ score of ≤ 2 was most supported by the data. Model-averaging of estimates using AIC$_c$ weights (w_i) was used to confront model selection uncertainty (Burnham and Anderson 1998).

Population estimates produced from each Huggins model allowed a test of the sensitivity of population estimates to assumptions about heterogeneity in the population of bears being sampled. These estimates did not include marked bears of unknown sex; therefore, they only can be used to interpret the relative differences in population estimates from different Huggins models. Program CAPTURE (Otis et al. 1978) also was used to provide population estimates for comparison with Huggins model results. Mowat et al. (2004) provides estimates of the entire grizzly bear population.

Encounter rate analysis.—GPS collars were programmed to collect locations every 4 h during the course of DNA sampling, thereby allowing a reasonably detailed description of bear movement paths during sampling. These data were used to construct a data set of the closest distance of bears from active hair traps for bears captured at hair traps and bears not captured at hair traps for each sampling session. Data initially were screened to determine the greatest distance from hair traps for bears that were captured. The data set was then truncated at the distance that included 90% of bear captures to allow direct comparison of the distribution of distances for captured and non-captured bears. It is possible for a bear to be captured at >1 hair trap/sample session using DNA mark-recapture methods. To increase sample size, all bear captures, including bears caught at multiple hair traps per session, were used for this analysis.

Theoretically, the closer proximity of a bear to a hair trap, the higher the probability of it being captured. The actual slope and shape of this curve, therefore, allows an approximation of the efficiency and attractiveness of the hair trap. One important issue is that each GPS point is only a partial description of a bear's movement trajectory and only gives a relative indication of how close a bear came to a hair trap. However, this form of bias will be present for both captured and noncaptured bears; therefore, comparison of the distribution of distances for captured and noncaptured bears still gives an indication of the efficiency of hair traps.

Logistic regression analysis was conducted to test for a relationship between distance from hair trap and probability of being snagged. Higher order polynomial and log-transformed distance variables were used to test for different potential shapes of the distance from hair traps and capture probability curve. Sex and age of bear also were entered into the logistic analysis to determine if the curve shape varied as a function of these classes and covariates. The y-intercept (at 0 distance) estimated the probability of a hair trap capturing a bear if the hair trap was encountered if the assumption of equal bias in closest distance as a measure of encounter rate between noncaptured and captured bears was met.

AIC_c or sample size corrected quasi Akaike information criterion ($QAIC_c$) model selection was used to select the most supported mark-recapture models. Because multiple observations of bears were used in this analysis, there was a possibility of non-independence of binomial trials and hence overdispersion. A repeated measures generalized estimating equation model (Crowder 1995; Liang and Zeger 1986; Ziegler and Ulrike 1998) was used to estimate correlations between successive observations of the same bear for the most supported model and adjust variances. An exchangeable correlation matrix structure in which an individual bear was the sample unit also was used to provide an estimate of overdispersion. An exchangeable correlation matrix was used because it could accommodate nonuniform timing of capture events and working correlation matrices of different sizes (Ziegler and Ulrike 1998). If the overdispersion parameter was much greater than 1, then $QAIC_c$ rather than AIC_c methods were used to select models (Burnham and Anderson 1998). The number of parameters (K) used for calculation of $QAIC_c$ was increased by 1 to account for the estimation of the overdispersion parameter (Anderson and Burnham 2002). Analyses were conducted using SAS PROC GENMOD (SAS Institute Inc. 2000).

RESULTS

Forty-one different grizzly bears were identified over 3 DNA sampling sessions. The number of bears captured in the 3rd session ($n = 10$) decreased due to snow and poor weather as compared to the 1st and 2nd sessions ($n = 19$ and 22, respectively). Thirty-two bears were caught once, 8 caught twice, and 1 captured 3 times. Of the bears identified, sex was determined for 37 (24 F, 13 M) (Mowat et al. 2004).

Huggins analysis.—Time-specific models that pooled capture probabilities for all groups for session 3 (in which capture success was reduced by snow) were more supported than time-specific or pooled session models (Table 1). Therefore, the time-specific model formulation, in which capture probabilities were set equal for all groups for session 3, was used in the majority of the analyses (with group-specific parameterizations for sessions 1 and 2). The most supported model (Table 1; Model 1) had capture probability estimates for GPS and DNA bears, and sexes, and capture probability of DNA bears varying
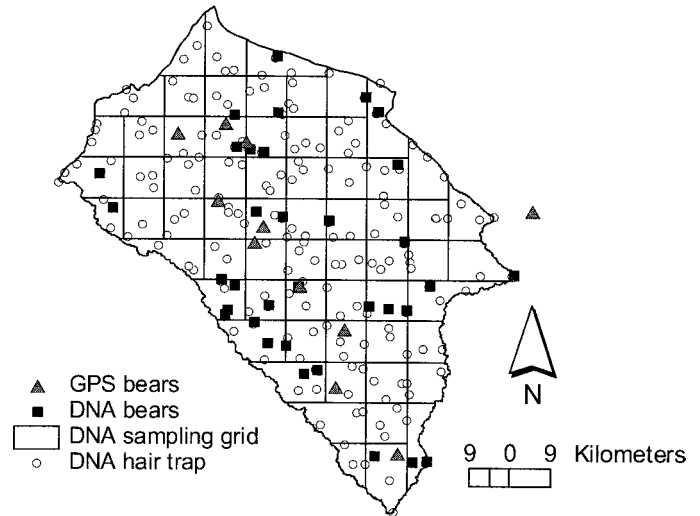

FIG. 1.—Map of the Foothills Model Forest study area, Alberta, Canada, where grizzly bears were studied in 1999. Each grid cell is 9×9 km. Each circle is a hair trap, which was placed in each grid cell for 1 sample session. Mean capture locations for bears only sampled using DNA methods are indicated by black boxes and initial capture location (for collaring) for GPS collared bears are indicated by gray triangles.

as a function of distance of capture from grid edge as a quadratic relationship. Models that considered group-specific capture probabilities or capture probabilities to vary as a function of distance from the sampling grid edge differed from constant models (Models 16–17) by at least 6.39 AIC_c units.

The models with distance-from-edge covariates were removed from the data set allowing capture probability estimates from the non-covariate models to be model-averaged. Model-averaged estimates without distance-from-edge represent the average capture probability of each sex and radiocollar status group. Model-averaged estimates suggested that males with collars exhibited the greatest capture probabilities and DNA females had the lowest capture probabilities. Capture probability estimates were 0.59 (*C.I.* = 0.21–0.82) for GPS males, 0.42 (0.16–0.74) for GPS females, 0.27 (0.07–0.63) for DNA males, and 0.13 (0.04–0.35) for DNA females.

Observation of distance from edge curves suggested that capture probability increased as distance from edge increased for DNA bears. GPS bears were captured further into the sampling grid than DNA bears as reflected by mean distances from grid edge for each group (mean for GPS bears = 13.1 km, 95% *C.I.* = 8.3–17.9, $n = 14$; mean for DNA bears = 7.5 km, 95% *C.I.* = 4.8–10.2, $n = 27$), and therefore their capture probabilities were less influenced by the distance of capture from grid edge, as suggested by the most supported AIC_c model.

Population estimates from the Huggins models that incorporated heterogeneity (i.e., Model 1) exhibited greater estimates and standard errors than models that did not incorporate heterogeneity (Models 16–18). The model-averaged population estimate using AIC_c weights from all models was 96 ± 45.3 (*SE*) bears. In comparison, population estimates (with unknown-sex bears excluded) from models M_{th}, M_h (Chao estimator), M_t (Chao estimator), and M_t (Darroch

TABLE 1.—AIC$_c$ model selection results for Huggins closed-model analysis, showing Akaike information criteria, corrected for sample size (AIC_c), difference in AIC$_c$ values between the ith model and the model with the lowest AIC$_c$ value (ΔAIC_c), Akaike weights (w_i), number of parameters (K), deviance, and population estimates ($\hat{N}$) and standard error of population estimates ($S.E.$ ($\hat{N}$)). Covariates are denoted as ld (log-transformed distance from edge) and d (untransformed distance from edge). A dot (.) refers to a constant model in which all groups were pooled.

No.	Model	Time variation	AIC_c	ΔAIC_c	w_i	K	Deviance	$\hat{N}$	SE ($\hat{N}$)
1	GPS−DNA+SEX+(DNA+ld ld^2)	t_{1-2}, t_3	124.39	0.00	0.25	6	111.6	104	46.0
2	GPS−DNA+(DNA+ld ld^2)	t_{1-2}, t_3	125.34	0.95	0.16	5	114.8	98	40.4
3	GPS−DNA+(DNA+ld ld^2 ld^3)	t_{1-2}, t_3	125.51	1.11	0.14	6	112.7	106	46.5
4	GPS−DNA+Sex	t_{1-2}, t_3	126.42	2.03	0.09	5	115.9	97	41.5
5	GPS−DNA	t_{1-2}, t_3	126.47	2.07	0.09	3	120.3	85	30.7
6	GPS−DNA+(DNA+d d^2)	t_{1-2}, t_3	126.88	2.48	0.07	5	116.3	94	37.7
7	GPS−DNA+d d^2	t_{1-2}, t_3	127.72	3.33	0.05	5	117.2	92	35.8
8	(GPS−DNA X Sex)+ d d^2	t_{1-2}, t_3	128.55	4.16	0.03	7	113.5	102	45.6
9	Sex	t_{1-2}, t_3	129.42	5.02	0.02	3	123.2	79	26.6
10	GPS−DNA+(GPS+ld ld^2)	t_{1-2}, t_3	129.53	5.14	0.02	5	118.9	87	32.8
11	GPS−DNA+d d^2 d^3	t_{1-2}, t_3	129.69	5.29	0.02	6	116.9	93	36.4
12	GPS−DNA X d d^2 d^3	t_{1-2}, t_3	129.90	5.51	0.02	7	114.8	98	40.8
13	(.)+ d d^2	t_{1-2}, t_3	130.20	5.81	0.01	4	121.8	81	28.3
14	(GPS−DNA X Sex)+ ld ld^2	t_{1-2}, t_3	130.44	6.05	0.01	7	115.4	98	42.2
15	(GPS−DNA) X Sex	t_1, t_2, t_3	130.79	6.39	0.01	12	103.8	92	53.4
16	(.)	t_{1-2}, t_3	131.03	6.64	0.01	2	126.9	72	20.7
17	(.)	t_1, t_2, t_3	132.26	7.86	0.00	3	126.0	71	20.4

estimator) in program CAPTURE were 89 ± 42, 95 ± 30, 71 ± 17 and 69 ± 14 bears, respectively.

Encounter rate analysis.—Thirty one hair trap captures of bears with GPS collars occurred during the course of DNA sampling. Initial screening revealed that 90% of captures occurred when the bear's closest location was within 4 kilometers of the hair trap; therefore, bear locations >4 km were deleted from the analysis. This screening retained 195 locations in which bears were within 4 km of the bait stations. Of these locations, 29 (14.8%) resulted in bears being captured at the hair traps.

An estimate of overdispersion of 1.53 was obtained from the generalized estimating equation model (Model 1 in Table 2), suggesting moderate overdispersion. Thus, QAIC$_c$ methods were used for model selection. The relationship between distance from hair trap and bear capture probability was best described with log-transformed closest distance predictor variables (Table 2). Models with various polynomial forms of the log-transformed predictor variable also were supported. Models that considered bear-specific relationships between distance from hair trap and capture probability were substantially less supported.

The logistic curve from the quadratic model suggested that the capture probability was reduced to <0.05 at closest locations >1.69 km (Fig. 2). The y intercept for this model was 0.49 ± 0.51 *SE* (*C.I.* = 0.26–0.72). Model-averaging using QAIC$_c$ weights (with sex and age pooled) was used to produce an estimate for the y intercept estimate of capture probability of 0.63 ± 0.76, given encounter of a hair trap. This estimate considered all models in the analysis and is, therefore, more robust. The mean number of occasions in which the closest location was within 1.69 km of the hair traps was 10.4 (*C.I.* = 3.9–16.9, $n = 5$) for males and 5.3 (2.3–8.3, $n = 7$), for females, suggesting that males encountered more traps than

females. One adult male bear came within 1.69 km of 17 hair traps but was never captured.

DISCUSSION

The results of this study suggest that heterogeneity of capture probabilities can be influenced by sex of animal, recent capture history, and location of capture at hair traps relative to the sampling grid edge (when population closure is violated). Results from this study also illustrate how program MARK can be used for rigorous analysis of biological causes of capture probability variation when compared with more general tests for capture probability variation in program CAPTURE.

Comparison with other studies.—One issue that should be considered when interpreting the results of this study is the design of sampling. Compared to other DNA studies (Boulanger et al. 2002; Poole et al. 2001; Woods et al. 1999), the grid cell size (9 × 9) from this study is large and the number of sessions conducted (3) was low. For example, Poole et al. (2001) conducted a grizzly bear DNA mark-recapture study with a 9 × 9 km grid cell size in the Prophet River area of British Columbia, Canada, where they sampled for 5 sessions. Therefore, 5 rather than 3 hair traps were placed in each 9 × 9 cell during the course of the study, which increased the coverage of the study area and probably reduced the degree of heterogeneity by allowing more traps to be available to bears with different home range sizes and trap encounter rates. Boulanger and McLellan (2001) conducted a similar Huggins model analysis with the data set from Prophet River, British Columbia and found that models that considered sex-specific capture rates were not supported by the data, further suggesting that sex-specific capture rates found in this study could be an artifact of the study design. However, Boulanger and McLellan (2001) found that distance of capture from the grid edge influenced bear capture probability. In addition, Poole et al.

Table 2.—Results of encounter analysis model selection, showing sample size corrected quasi Akaike information criteria ($QAIC_c$), the difference in $QAIC_c$ values between the ith model and the model with the lowest $QAIC_c$ value ($\Delta QAIC_c$), Akaike weights (w_i), number of parameters (K), log- likelihood (Log L). Covariates are denoted as ld (log-transformed closest distance to hair trap) and d (untransformed closest distance to hair trap).

No.	Model[A]	$QAIC_c$	$\Delta QAIC_c$	w_i	K	Log L
1	ld	70.61	0.00	0.22	3	−49.32
2	ld ld^2	70.96	0.35	0.18	4	−48.00
3	ld, ld^3	71.36	0.75	0.15	4	−48.30
4	ld, ld^2, ld^3	72.18	1.58	0.10	5	−47.32
5	sex, ld	72.19	1.59	0.10	4	−48.94
6	dist dist^2	72.30	1.69	0.09	4	−49.02
7	dist	72.54	1.93	0.08	3	−50.80
8	age, ld	72.69	2.09	0.08	4	−49.32
9	dist, dist dist^3	72.72	2.12	0.08	5	−47.73
10	age sex ld	73.99	3.38	0.04	5	−48.70
11	intercept only	81.76	11.16	0.00	2	−59.44

FIG. 2.—Probability of capture as a function of closest observed distance to bait sites as estimated from GPS collared bears. Each bait site was surrounded by barbed wire to obtain DNA hair from grizzly bears in the Foothills Models Forest Study area, Alberta, Canada in 1999. Estimated points (from Model 1 in Table 3) are shown as diamonds to describe the distribution of distances used to fit the logistic model. Confidence intervals (95%) are shown on either side of the predicted line.

(2001) documented different distances moved between captures for sexes of bears, further suggesting differential trap encounter rates. Most other DNA studies (Boulanger et al. 2002) have used at least 4 sampling sessions and grid designs with 8 × 8 km grid cell sizes, which potentially minimizes sex-specific differences in encounter rates by allowing all bears some opportunity to be sampled during each sampling session.

The greater capture probabilities of GPS bears relative to DNA bears contradicts findings of the Upper Columbia River Bear Study in British Columbia (Boulanger et al. 2004; Woods et al. 1999) where collared bears exhibited lower capture probabilities in 2 of 3 years of the study. However, this difference is most likely explained by the fact that GPS bears in our study were composed of resident bears, whereas DNA bears were composed of resident and edge bears. In the case of the Upper Columbia study, radiocollared bears primarily were resident bears, suggesting that reduced capture probabilities of radiocollared bears might have been due to collared bears avoiding DNA hair traps (Boulanger et al. 2004).

The results of this study further demonstrate the interaction of closure violation and capture probability variation as discussed in Boulanger and McLellan (2001). Kendall (1999) suggested that closed models will give an unbiased estimate of the superpopulation if the type of movement across grid boundaries is temporary and random and other closed model assumptions are met. Other forms of movement across grid boundaries that could potentially bias superpopulation estimates from closed models—as described by Kendall (1999)—are permanent (1 entry, 1 exit), Markovian, temporary, emigration only, and immigration only. In reality, all these forms of movement might exist and no mark-recapture data-based test can distinguish or test for dominant forms of movement. Our method of modeling capture probabilities of bears as a function of distance captured from grid (Boulanger and McLellan 2001) directly estimates capture probability bias caused by closure violation. Therefore, our approach should be robust to any form of movement, providing more reliable
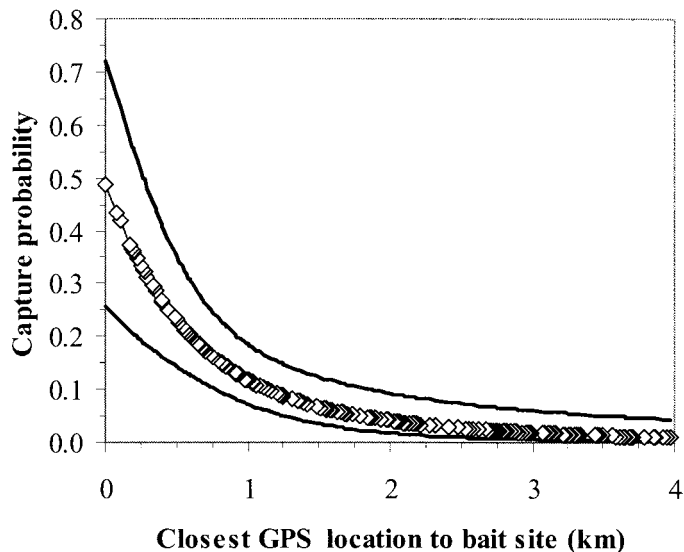
superpopulation estimates than standard closed population models. This general technique should be applicable to a wide variety of species.

Encounter rate analysis.—The analysis of encounter rates make a series of assumptions that should be considered when interpreting the results. First, it is assumed that the closest GPS location to the hair trap is a reasonable indicator of whether a trap was encountered. If this assumption is violated equally for captures compared to noncaptures, then the y intercept should estimate the probability of capture, if the bear encounters the trap. In reality, it is difficult to determine when a bear actually is attracted to a hair trap. Therefore, we feel our approach is the most parsimonious given the main objectives of the analysis.

Investigation of trap encounter rates suggests that DNA sets were not entirely efficient, with an estimated 37% of bears encountering the hair trap not having hair captured by it. This analysis also suggests that sex influences heterogeneity of capture probabilities due to differential trap encounter rates. Models with bear-specific response curves were less supported; however, this might have been due to low sample sizes and subsequent low power to discern bear-specific response curves. Bears might show specific responses to hair traps, as demonstrated by the adult male of 14 years, which came within 1.69 km of 17 hair traps but was never captured. There are many plausible biological explanations for this behavior such as an association of capture and/or handling experience with hair traps, or preoccupation with the breeding season and subsequent lack of interest in hair traps. Given the limited sample sizes of this study, it is difficult to determine if a substantial proportion of bears exhibit trap aversion as strong as this bear,

or if this bear is truly untrappable, or just exhibits a very low capture probability. These indirect observations further support the conclusion that heterogeneity of capture probabilities due to bear-specific behavior exists, and that general differences in capture probabilities cannot be solely explained by trap encounter.

The pooling of multiple capture events of individuals at hair traps within a sampling session potentially reduces heterogeneity by pooling multiple captures of some individuals to 1 capture/sampling session. For example, a male caught many times during each sample session will have the same session-based capture history as a female caught only once during each session. However, heterogeneity still is introduced if some individuals do not encounter any traps for the majority of sampling sessions. The results of the encounter analysis suggest that bears are not necessarily attracted to bait stations from large distances from the bait station. Given this finding, sparse trap coverage may not give certain individuals the opportunity to be captured, such as females with cubs that have small home range areas. In this case, most estimators of population size will exhibit a negative bias, because a segment of the population is not identifiable. In addition, the precision of estimates will be lowered if a segment of the population exhibits extremely low capture probabilities, as in this study in which coefficients of variation for population estimates are in the range of 50%.

Research Implications.—This study illustrates new methods to detect and model heterogeneity variation that should be generally useful to biologists conducting mark-recapture studies on species other than bears. Heterogeneity variation can be modeled using covariates with the Huggins model in this analysis; however, this approach assumes all dominant forms of heterogeneity are identifiable. If unidentifiable forms of heterogeneity, such as age variation, exist in the data set, then CAPTURE models such as the Chao heterogeneity estimators (Chao 1989; Chao and Jeng 1992), jackknife estimator (Burnham and Overton 1979), or mixture models of Pledger (2000) can be used with the data. In general, all heterogeneity models require larger sample sizes in the form of marked animals and recapture rates of marked animals to exhibit acceptable levels of precision. However, they will give a less-biased indication of population size and associated variance than non-heterogeneity estimators such as the Darroch M_t estimator or the Huggins estimator with no covariates (Table 1, Model 17). In this case, these models are biased both in terms of population estimates and variance that potentially creates a ''biased but apparently precise'' scenario (White et al. 1982) that is highly undesirable if the estimates are to be used for management.

In terms of study design, the results of this study further support the general conclusion that at least 4 sessions and grid cell sizes of 8 × 8 km or less are needed to ensure robust and precise performance of mark-recapture estimators (Boulanger et al. 2002). The 8 × 8 km cell size roughly corresponds to the home range size of an adult female grizzly bear (Woods et al. 1999). In British Columbia, population estimates with co-efficients of variation of less than 20% have been obtained using more intensive sampling regimes (Boulanger et al. 2002; Poole et al 2001).

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