Management and Conservation Article

Use of Occupancy Models to Estimate the Influence of Previous Live Captures on DNA-Based Detection Probabilities of Grizzly Bears

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ABSTRACT Large carnivores potentially change their behavior following physical capture, becoming less responsive to the attractants that resulted in their capture, which can bias population estimates where the change in behavior is not appropriately modeled. We applied occupancy models to efficiently estimate and compare detection probabilities of previously collared grizzly bears (*Ursus arctos*) with bears captured at DNA hair-snag sites that were not previously collared. We found that previously captured bears had lower detection probabilities, although their detection probabilities were still >0, implying that they were still visible to be sampled via the DNA hair-snag grid, which was able to detect finer differences in capture probabilities of previously collared bears compared with Huggins closed-captures population models. To obtain relatively unbiased population estimates for DNA surveys, heterogeneity caused by previous live capture should be accounted for in the population estimator. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):589–595; 2008)

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Use of hair-snag DNA sampling to estimate grizzly bear (*Ursus arctos*) populations has resulted in vastly improved population estimates in Canada and the United States (Woods et al. 1999, Poole et al. 2001, Boulanger et al. 2002). However, often live capture of carnivores has also occurred in these areas using leg-snaring techniques that are similar to hair-snag bait sites used to sample DNA. Physical capture uses bait (rotten meat) that resembles the smell of scent-lures used in DNA sites and both likely have human odors. Therefore, physical trauma experienced during live capture and human scent associated with each technique might make bears less likely to enter DNA hair-snag sites. Bears are not physically captured in DNA sites, and therefore, we refer to probability of obtaining DNA from a bear at a hair-snag site as a detection probability rather than a capture probability. In theory, reduced detection probabilities of previously live-captured bears will cause little bias in mark–recapture results because estimation models allow detection probability variation if appropriate estimators robust to heterogeneity are used for analysis of the data (Burnham and Overton 1979, Pledger 2000). However, if a substantial segment of previously collared bears displays zero detection probability, then these bears are effectively invisible to DNA sampling and resulting estimates will be biased.

A challenge in exploring the effect of past live capture on current DNA detection probabilities is that often live-capture events occurred years before the DNA project began. Often, it is unknown whether bears that were live captured are alive and still on the DNA-sampling grid. The question becomes how to treat bears that were previously live captured but not detected in DNA samples. One potential method is to only include bears that are currently radiocollared. For example, Boulanger et al. (2004*a*, *b*) found that DNA detection probabilities of bears with active collars during sampling were equal or slightly reduced compared with other bears. However, sample sizes in these studies were limited to bears with active collars resulting in reduced sample sizes and lower test power. Alternatively, open models can potentially be used to account for survival or movement from grids for animals captured alive in previous years. However, open models, such as the Cormack Jolly Seber model, do not allow within-year estimation of capture probabilities such as is done with closed-captures population estimation models. Robust design models allow estimation of within-year capture probabilities and survival rates between yearly sessions. However, we only conducted multiple within-year sessions for 1 year for each study area, thereby minimizing advantages of survival estimation from this method.

We present a method using occupancy models in Program MARK to efficiently compare detection probabilities of previously live-captured animals that may have died or otherwise left the area with those detected only using DNA mark–recapture or traditional mark–recapture methods (White and Burnham 1999, MacKenzie et al. 2002). We suggest that this approach is applicable to any species in which multiple types of encounters are used to estimate population parameters. We use data from 2 DNA mark–recapture estimation projects conducted in the Foothills of

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Alberta (Boulanger et al. 2005*a*, *b*). Our fundamental question was whether these bears had reduced detection probabilities or, in the extreme, were undetectable using DNA hair snags at bait stations.

STUDY AREA

In spring of 2004, we sampled a DNA hair-snag grid of 180 7 × 7-km cells (8,820 km^2) in Alberta Grizzly Bear Management Area 3 between Hinton and Highway 11 in western Alberta. In 2005, we sampled a DNA hair-snag grid with 173 7 × 7-km cells (8,477 km^2) in Alberta Grizzly Bear Management Area 4 between Calgary and Highways 1 and 11 (Alberta Grizzly Bear Recovery Team 2005). These areas were defined as genetically based subunits using Program STRUCTURE by Proctor (2004), thereby maximizing applicability of estimates to the overall population and minimizing closure violation (Pritchard et al. 2000, Proctor et al. 2002). In each year, we conducted sampling for 4 occasions with bait sites moved between occasions to ensure adequate coverage of bear habitats within the study area. We identified 44 bears in 2004 and the resulting population estimate was 53 (SE = 8.3, 95% CI = 44–80) bears. We identified 41 individual bears in 2005, and the resulting population estimate was 47 (SE = 3.99, 95% CI = 44–60; Boulanger et al. 2005*a*, *b*; Boulanger et al. 2006).

In both the 2004 and 2005 DNA mark–recapture projects the actual number of bears with Global Positioning System (GPS) collars during sampling was low ($n = 8$ and 9 for 2004 and 2005, respectively). However, 32 bears had been historically collared in the study areas but were not carrying working radiocollars during DNA sampling (Table 1; Fig. 1).

METHODS

We applied occupancy models to estimate probability of detection for DNA and radiocollared bears (p) and probability that radiocollared bears were present on the sampling grid during DNA sampling (Ψ). Occupancy models estimate detection probability in an analogous fashion to Huggins closed-captures population size-estimation models except that occupancy of the sample unit (sites in most scenarios, bears in our study) rather than population size of sample units is estimated (Huggins 1989, 1991; MacKenzie et al. 2002; MacKenzie et al. 2004). A key distinction between occupancy and closed-captures population-estimation models is that undetected sample units (i.e., 0000 encounter histories) are included in the encounter history for occupancy models, whereas closed-captures models only use sample units that are detected at least once.

Our data set contained information about bears potentially on the grid but not captured (the zero capture-frequency group in Fig. 1) as well as information about occupancy and detection probability of bears that were previously collared (bears with >0 detection frequency that were previously collared in Fig. 1). Conceptually, each bear that had been collared in years previous to DNA sampling had a probability of occupancy (Ψ) on the sampling grid, and therefore, encounter histories of bears not captured in DNA sampling could be parameterized using occupancy models. For example, if we did not detect a previously collared bear on the sampling grid (i.e., a detection frequency of zero or a 0000 detection history) then it was either not present or was present and not detected. In terms of occupancy model parameters, probabilities of each event would be $\Psi(1 - p_1)(1 - p_2)(1 - p_3)(1 - p_4)$, or $\Psi \prod_{j=1}^{4}(1 - p_j)$, if we did not detect the bear, but it was present on the grid; or $(1 - \Psi)$, if the bear was not present on the grid, leading to an overall probability of the 0000 encounter history of $\Psi \prod_{j=1}^{4}(1 - p_j) + (1 - \Psi)$, where j corresponds to a sampling session (MacKenzie et al. 2004). Probability of an encounter history of a bear captured in the first session only (i.e., 1000) would be $\Psi p_1 \prod_{j=2}^{4}(1 - p_j)$. We parameterized each encounter history for previously collared bears in terms of occupancy models by using the same approach as the 0000 or 1000 encounter histories. We also incorporated bears that were monitored on the grid during DNA sampling and bears captured using DNA methods (including bears that were not previously collared) into this analysis by fixing Ψ at 1 (as described later) for this group because occupancy was certain. The occupancy-model analysis, therefore, used information from bears with detection frequencies of 0–4 in Figure 1 as well as information from bears that were not previously collared but that we detected on the DNA grid to model influence of covariates on detection probability and occupancy. Parameterization of the encounter history for closed models is similar to occupancy models, except that Ψ is not modeled, and therefore, closed models do not include bears with a zero detection frequency (Fig. 1), resulting in less power to estimate differences in detection probabilities between collared bears.

We conducted our analysis using the occupancy models currently available in Program MARK. We used detection histories from the 2004 and 2005 DNA surveys to model detection and occupancy rates of bears. Bears that had been previously monitored on the area but that we did not detect in DNA projects received a 0000 detection history. We divided bears into groups based on the year last monitored (i.e., yr since bear was last known to be alive and on DNA survey grids). Bears that were currently being monitored (using radiotelemetry or GPS methods) or bears detected in DNA hair snags were both assigned into the zero-years-since-last-monitored group. We assigned previously live-captured bears to a group according to the year they were last monitored up to 5 years previous, which resulted in 6 unique groups in the Program MARK occupancy-model analysis. We first constrained Ψ to have no within-year (occasion-based) variation, meaning that the bear population was demographically and geographically closed during the DNA survey. We then used the design matrix in Program MARK and a log-link (e^{β}) to model estimates of Ψ as an exponentially decreasing function for each group in the analysis, which allowed us to estimate probability of occupancy or presence of bears that we did not know whether they still existed on the DNA survey grids (White et al. 2002). We gave bears in the zero group a zero in the

Table 1. Collared grizzly bears possibly on the 2004 and 2005 DNA grids by year last monitored. Captured refers to capture in hair-snag traps employed during DNA sampling. Data are from live-capture and DNA-capture projects in Alberta Grizzly Bear Management Areas 3 and 4, Alberta, Canada.

	Collared-bear DNA detections							
	2004 DNA grid				2005 DNA grid			
	Total bears		Detected		Total bears		Detected	
Yr last monitored	M	F	M	F	M	F	M	F
1999	1	1	0	0	0	0	0	0
2000	2	1	0	0	0	0	0	0
2001	2	3	1	1	0	0	0	0
2002	1	4	1	3	0	0	0	0
2003	7	7	4	3	0	0	0	0
2004	1	7	0	3	1	2	0	0
2005					0	9	0	7

design matrix, which resulted in a $\beta \times 0$ term of zero and a resulting estimate of $\Psi = 1$ because $e^0 = 1$ because we were certain of presence of these bears on the grid. We successively constrained other groups with design matrix values 1 to 5, which modeled an exponential decline in the estimated Ψ and, thus, probability of presence of bears with unknown occupancy status. We also tested year-specific and quadratic declines in Ψ to test a full range of potential declines in Ψ.

We modeled detection probabilities (p) using a logit-link. We entered as individual covariates sex of bear, year of DNA study, years since last live capture, last live capture in snare (binary), last live capture with helicopter darting (binary), and total number of live captures. We were particularly interested in the effect of snares on bear detection probabilities given the similarity of this type of capture to DNA hair-snag sampling. In particular, we hypothesized that female bears that had been snared would be least likely to be detected in hair snags given that females are most difficult to physically recapture after previous snaring. For this reason, we specified a priori models that assumed snare-specific and sex-specific capture probabilities of bears that were previously snared. It was likely that undefined heterogeneity because of factors such as age were present in the data set that could potentially bias occupancy estimates (Mackenzie et al. 2002, Boulanger et al. 2004*b*). We modeled heterogeneity that could not be explained by identifiable factors (i.e., sex) using a mixture-model approach (Pledger 2000). Mixture models use a mixture of ≥ 2 detection probabilities to model heterogeneity of one detection probability, which allows modeling of multipoint distributions that may arise from heterogeneity of detection probabilities (Pledger 2000). For example, overall detection probability for an encounter history where a mixture of A distributions is used is $\sum_{i=1}^{A} \pi_i \ \theta_i^v \ (1 - \theta_i)^{t-v}$, where v equals number of detections of the animal for t occasions, π_i

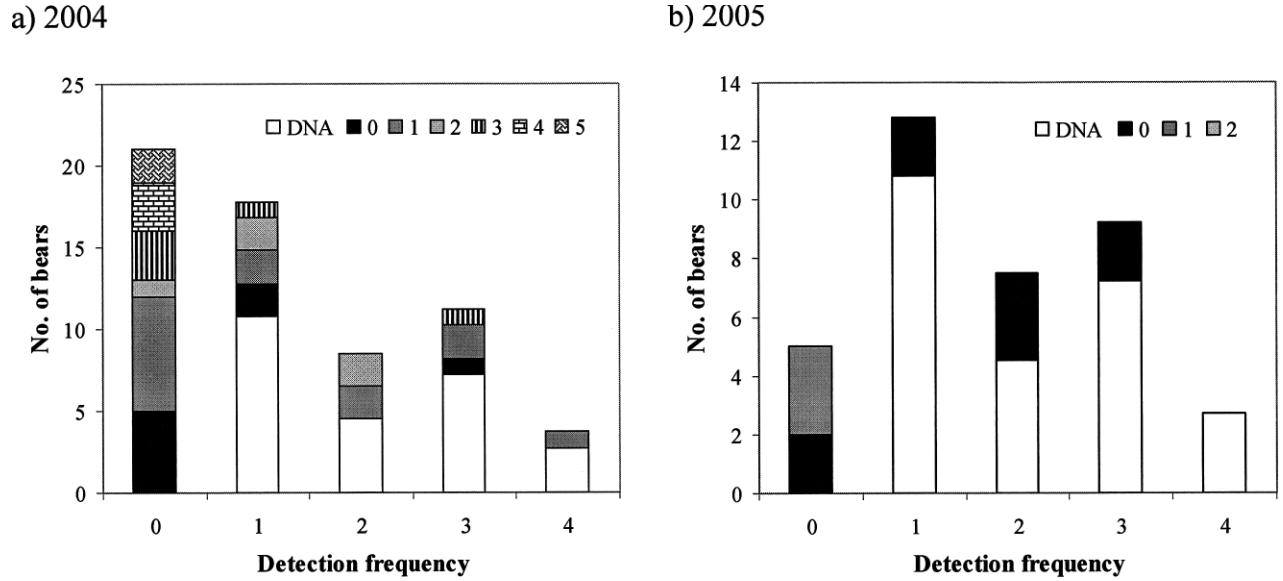

Figure 1. Detection frequencies (no. of DNA sampling sessions in which a grizzly bear was detected) of DNA bears (bears that were not previously collared that were detected in hair snags) and previously collared bears as categorized by years since last monitored on DNA grids and year of DNA survey for Alberta Grizzly Bear Management Areas 3 and 4, Alberta, Canada, May–August 2004 and 2005. For example, the zero group corresponds to collared bears that were monitored during DNA sampling; a one corresponds to collared bears that were last monitored 1 year previous to DNA sampling. Occupancy models use information for all the bears, whereas closed models only include bears with detection frequencies that are >0.

is probability the animal has detection probability θ_i, with the sum of the $\pi_i = 1$. Thus, for $A = 2$, $\pi_2 = 1 - \pi_1$. From Carothers (1973), we estimated mean detection probability (based on 2 mixture distributions) as $\overline{\theta} = \pi_1\ \theta_1 + (1-\pi_1)\ \theta_2$. We estimated variance of $\overline{\theta}$ using the delta method (Seber 1982) as:

$$\begin{aligned}\mathrm{var}(\overline{\theta}) = {} & 2\mathrm{cov}(\pi, \theta_1)(\theta_1 - \theta_2) \\ & + \ 2\mathrm{cov}(\pi, \theta_2)(1 - \pi)(\theta_1 - \theta_2) \\ & + 2\mathrm{cov}(\theta_1, \theta_2)\pi(1 - \pi) + \mathrm{var}(\pi)(\theta_1 - \theta_2)^2 \\ & + \mathrm{var}(\theta_1)\,\pi^2 + \mathrm{var}(\theta_2)(\pi - 1)^2\end{aligned}$$

We then transformed variances to the logit scale to estimate confidence intervals for $\overline{\theta}$ (White et al. 2002).

We also analyzed the data using Huggins (Huggins 1989, 1991) closed models in Program MARK to determine if the same differences in capture probabilities detected by occupancy models could also be detected using closed models. We used the same covariates as the occupancy analysis; however, we only included the radiocollared bears that we detected in DNA sampling (bears with detection frequency >0 in Fig. 1).

We performed model selection using the Akaike's Information Criterion corrected for small sample size (AIC_c). The model with the lowest AIC_c value was the most parsimonious model of the models evaluated to explain the observed data (Burnham and Anderson 1998). We used change in AIC_c (ΔAIC_c) values to compute Akaike weights (w_i) to evaluate relative importance of each of the candidate models (Burnham and Anderson 1998).

RESULTS

We detected 85 bears using DNA methods in the 2004 and 2005 studies. Of the 85 bears we detected, 23 were currently or had been previously collared. We did not detect with DNA sampling 26 bears that were currently or previously collared. Mean age of collared bears at last capture was 9.06 (SD = 5.1, $n = 33$) for females and 6.92 (SD = 5.1, $n = 14$) for males.

Occupancy model-selection results suggested that detection probability was influenced by sample occasion (1–4), year (2004 or 2005) of DNA survey, previous capture type (helidart or snare), and an interaction between sex of bear and whether a bear was previously snared (Table 2, model 1). In addition, support of mixture heterogeneity models suggested that undefined heterogeneity was present in the data set. Models that included years since last live capture (*yrscap*) or total captures were less supported (Table 2, model 7). Of the most interest was detection probability variation induced by previous capture method. The minimum AIC_c model that included snare, dart, and sex × snare variables was 10.9 units better than the equivalent mixture model lacking those covariates, demonstrating the importance of those variables in modeling detection probabilities.

On average, detection probabilities were 1.6 times higher in 2005 than 2004. We were most interested in the lower values in detection probabilities, so we focused our interpretation on 2004. We found detection probabilities decreased as a function of previous live capture, especially for females that had been snared; however, confidence intervals were above zero (Fig. 2). Bears that had been previously helidarted had detection probabilities between DNA bears and snared bears (Fig. 2).

A model with an exponential decline in occupancy (Table 2, model 12) was most supported by the data compared with more complex models (Table 2, models 15–16). Probability of presence (occupancy) decreased as a function of years since the bear was last monitored (Fig. 3). Probability of presence was <0.5 for bears last monitored ≥3 years before DNA sampling.

Results from the Huggins model closed-captures analysis suggested that it was possible to detect effect of snaring on detection probabilities as shown by support for a model with year-specific, occasion-specific, and snare-specific detection probabilities (Table 3, model 1). However, models with lowered detection probabilities of bears that were helidarted or lower detection probabilities of females that had been snared were not as supported. For example, an equivalent form of the most supported occupancy model (Table 2, model 1) was less supported with the closed-model analysis (Table 3, model 5) by 3.06 AIC_c units. As with the occupancy model data set, mixture models with undefined heterogeneity were most supported.

DISCUSSION

Our fundamental objective was to determine whether previously captured bears displayed low or zero detection probabilities such that they would appear invisible to DNA sampling and, therefore, cause bias in population estimates. Results from both analyses suggest collared bears were visible for the Alberta projects we analyzed. However, collared bears displayed lower detection probabilities, although point estimates and confidence intervals of detection probabilities were >0, which suggests that the number of collared bears not detected in the DNA surveys could be explained by sampling variation as opposed to there being a segment of impossible-to-detect bears. The similarities between physical capture sites and DNA sampling sites (smell of capture bait and DNA scent lures and the likely presence of human odors at each) are likely responsible for the reduced DNA-detection probability of previously physically captured bears.

The main advantage of occupancy models for exploration of bear detection probabilities is that occupancy models use the full amount of information available from multiple data sources. That is, in occupancy models, probability that a previously captured bear is present on the DNA grid is modeled, which is not possible with the Huggins closed-captures model. The DNA data set allows precise estimation of detection and occupancy probabilities for the segment of bears that were detected in DNA sampling. Unlike closed models, occupancy models include information on the segment of bears that were potentially on the grid during sampling but not detected (through entering bears with detection frequencies of zero in Fig. 1 in the encounter history). As shown in the comparison of occupancy and

Table 2. Akaike's Information Criterion corrected for small sample size (AIC_c) model-selection results for occupancy-estimation models applied to grizzly bear live-capture and DNA hair-snag data from projects in Alberta, Canada, May–August 2004 and 2005. Time-specific models are models that allowed detection probability to vary for each sample session. Covariates included *dnayr* (yr sampling conducted), *dart* (previous darting for live capture), *snare* (previous snaring for live capture), *sex*, *yrscap* (yr since last live-capture event), *total captures* (total no. of previous live captures), and *LM* (yr since last monitored on the sampling grid). The AIC_c, difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (ΔAIC_c), Akaike weights (w_i), number of parameters (K), and model deviance are presented.

No.	Detection probability	Occupancy	AIC_c	ΔAIC_c	w_i	K	Deviance
1	π(.)[a] $\theta_{1\&2}$(time-specific + *dnayr* + *dart* + *snare* + *sex* × *snare*)	*LM*	530.9	0.00	0.281	11	506.2
2	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *snare*)	*LM*	532.7	1.75	0.117	9	512.9
3	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *dart* + *snare*)	*LM*	532.7	1.76	0.117	10	510.5
4	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *dart* + *snare* + *sex* × *snare* + *sex* × *dart*)	*LM*	532.8	1.88	0.110	12	505.6
5	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *dart* + *snare* + *sex* × *snare* + *total captures*)	*LM*	532.9	2.03	0.102	12	505.8
6	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *snare* + *sex* × *snare*)	*LM*	533.3	2.43	0.083	10	511.1
7	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *snare* + *yrscap*)	*LM*	533.8	2.85	0.068	10	511.6
8	π(.) $\theta_{1\&2}$(*dnayr* + *dart* + *snare*)	*LM*	534.5	3.60	0.046	7	519.4
9	*p*(time-specific + *dnayr* + *dart* + *snare* + *sex* × *snare*)	*LM*	535.3	4.40	0.031	9	515.5
10	*p*(time-specific + *dnayr* + *dart* + *snare*)	*LM*	535.4	4.49	0.030	8	518.0
11	*p*(time-specific + *dnayr* + *dart* + *snare* + *sex*)	*LM*	537.5	6.63	0.010	9	517.8
12	*p*(*dnayr* + *dart* + *snare* + *sex*)	*LM*	540.8	9.88	0.002	6	528.0
13	π(.) $\theta_{1\&2}$(time-specific + *dnayr*)	*LM*	541.8	10.90	0.001	8	524.4
14	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *dart*)	*LM*	542.3	11.40	0.001	9	522.5
15	*p*(*dnayr* + *dart* + *snare* + *sex*)	*LM* × *sex*	543.0	12.13	0.001	7	528.0
16	*p*(*dnayr* + *dart* +*snare* + *sex*)	$LM + LM^2$	543.1	12.14	0.001	7	528.0
17	*p*(.)	*LM*	555.4	24.50	0.000	2	551.3
18	*p*(.)	*LM* + *dnayr*	557.4	26.53	0.000	3	551.2
19	*p*(.)	year-specific	558.3	27.41	0.000	7	543.2

[a] (.) indicates the parameter was constant.

closed models, this additional information allowed occupancy models to detect finer-scale variation in detection probabilities, such as the effect of helidarting on detection probabilities and reduced detection probabilities for females that have been snared. Conveniently, occurrence of bears known to be previously on the sampling grid can be modeled using the Ψ parameter even though DNA sampling did not occur in years before the project. The occupancy model in this context is similar to an open model in that it is not assuming that all bears that were previously on the grid are present. However, unlike open models, occupancy of previously collared bears is estimated with a minimal number of parameters, thereby, increasing the power of the analysis to detect differences in detection probabilities. Occupancy or presence in this context is analogous to apparent survival or the product of true survival rate and emigration rate of bears from the grid.

Lower detection probabilities of collared bears constitute heterogeneity variation, which is common in bear DNA mark–recapture data sets. Multiple empirical and simulation studies have shown that bias in estimates is minimal in the presence of heterogeneity variation if appropriate methods are used to analyze the data (Otis et al. 1978, Pledger 2000, Boulanger et al. 2002, Boulanger et al. 2004*a*). However,

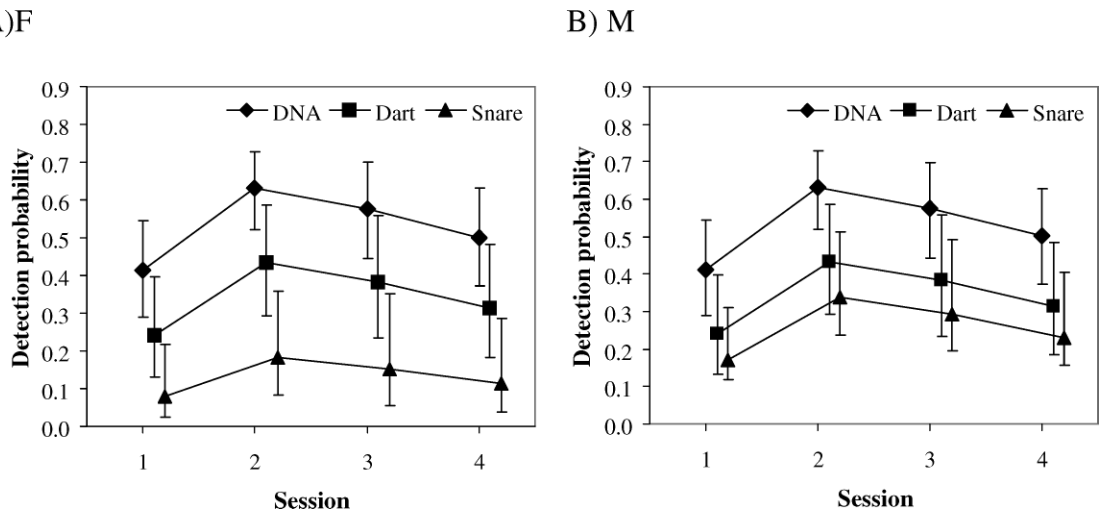

Figure 2. Estimated grizzly bear detection probabilities by previous capture method for DNA efforts in 2004, Alberta Grizzly Bear Management Areas 3 and 4, Alberta, Canada, May–August 2004 and 2005. Estimates are for A) females and B) males across sampling occasions. Estimates are shown from the minimum Akaike's Information Criterion corrected for small sample size (AIC_c) occupancy model (Table 2). Error bars are 95% confidence intervals on predictions.

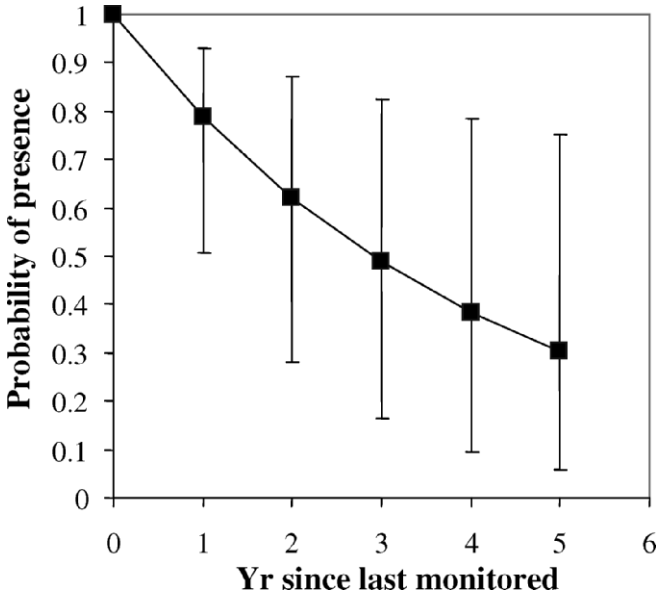

Figure 3. Probability of grizzly bear occupancy as a function of years since last monitored (and known to be alive) from occupancy-model analysis, Management Areas 3 and 4, Alberta, Canada, May–August 2004 and 2005. Estimates are from the minimum from the minimum Akaike's Information Criterion corrected for small sample size model. Error bars are 95% confidence intervals on predictions.

sampling should be intensive enough so that bears have multiple chances to be detected during sampling to ensure adequate performance of heterogeneity estimators (Boulanger et al. 2006). Detection probabilities in the Alberta projects we used were relatively high (i.e., $P = 0.33$ and 0.52 for 2004 and 2005 grids, respectively; Boulanger et al. 2005*a*, *b*; Boulanger et al. 2006). If detection probabilities were lower, it would become more probable that bears with relatively low detection probabilities (i.e., F that had been previously snared) would become less visible to hair-snag sites leading to potential bias.

Our approach using occupancy models shares the same set of assumptions as the Huggins closed-population estimators. Namely, it assumes that the sampling grid is closed to movement during sampling. Given the similarity of occupancy and closed-captures models, MacKenzie et al. (2006) suggest that violation of closure does not bias estimates of occupancy if movement is random across grid boundaries (Kendall 1999). Heterogeneity of occupancy probabilities will not bias occupancy estimates but may cause variance of occupancy probability to be inflated. Heterogeneity in detection probability will negatively bias occupancy probabilities (MacKenzie et al. 2006). We used mixture models and covariates to effectively model heterogeneity variation, thereby, minimizing this source of bias. Another assumption of occupancy estimators is independence between detections of sample units. In our case the assumption is translated to independence between detected bears. This assumption is probably met for most of the population given that the degree in which bears associate is minimal (Stenhouse et al. 2005). One exception would be family groups that are more likely to be detected together (Boulanger et al. 2004*a*). Violation of the assumption of independence between detected bears would result in overdispersion of multinomial variances and underestimates of occupancy variance in an analogous manner to underestimation of variance of population size in closed models. Currently, there is no method demonstrated to estimate overdispersion reliably for closed-population models or occupancy-estimation models that include individual covariates.

Our approach is potentially useful for species other than grizzly bears and for detection methods other than DNA sampling. For example, methods have been proposed that use both live-capture and mark–recapture methods or use mark–recapture methods to analyze live-capture data (Powell et al. 2000, Amstrup et al. 2001, Brongo et al. 2005). In some cases, these methods assume that previous live capture does not affect subsequent detection rates. Occupancy models provide an efficient and powerful method to test this assumption using data from currently and previously marked animals.

MANAGEMENT IMPLICATIONS

We found that previous physical capture of individual grizzly bears reduces their detection probability with subsequent DNA hair-snagging surveys. Consequently, studies relying on physical capture for radiocollaring may be biasing

Table 3. Akaike's Information Criterion corrected for small sample size (AIC_c) model selection results for Huggins closed-captures population models applied to grizzly bear DNA hair-snag data from projects in Alberta Grizzly Bear Management Areas 3 and 4, Alberta, Canada, May–August 2004 and 2005. Time-specific models are models that allowed detection probability to vary for each sample session. Covariates included *dnayr* (yr sampling conducted), *dart* (previous darting for live capture), *snare* (previous snaring for live capture), *yrscap* (yr since last live-capture event), and *sex* of bear. The AIC_c, difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (ΔAIC_c), Akaike weights (w_i), number of parameters (K), and model deviance are presented.

No.	Model	AIC_c	ΔAIC_c	w_i	K	Deviance
1	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *snare*)	446.7	0.00	0.329	8	430.2
2	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *snare* + *sex* × *snare*)	447.8	1.12	0.187	9	429.2
3	π(.) $\theta_{1\&2}$(time-specific + *dnayr*)	448.4	1.72	0.139	7	434.0
4	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *dart* + *snare*)	448.4	1.78	0.135	9	429.9
5	π(.) $\theta_{1\&2}$(time-specific + *dnayr* + *snare* + *dart* + *sex* × *snare*)	449.7	3.06	0.071	10	429.1
6	π(.) $\theta_{1\&2}$(time-specific + *dnayr* +*dart*)	450.4	3.70	0.052	8	433.9
7	π(.) $\theta_{1\&2}$(time-specific + *dnayr* +*snare*+ *dart* + *sex* × *snare* + *sex* × *dart*)	450.4	3.73	0.051	11	427.6
8	π(.) $\theta_{1\&2}$ time-specific + *dnayr* + *snare* + *dart* + *sex* × *snare* + *yrscap*)	451.8	5.14	0.025	11	429.0
9	π(.) $\theta_{1\&2}$(*dnayr* + *dart* + *snare*)	453.8	7.15	0.009	6	441.6
10	p(time-specific + *dnayr* + *snare* + *dart* + *sex* × *snare*)	456.3	9.67	0.003	8	439.9

subsequent population estimates obtained with DNA hair snagging unless the additional individual heterogeneity from previous capture is included in the population-estimation analysis. It is also essential that studies are designed to ensure multiple encounters of bears with DNA sites to, therefore, maximize detection probabilities. In addition, researchers should attempt to minimize similarities between live capture and DNA hair snags by using different baits and minimizing human scent when setting up DNA hair-snag stations. Finally, the supplementation of genotypes obtained from hair snags with genotypes obtained from other sampling methods (such as rub trees) can potentially reduce biases caused by hair-snag sampling alone (Boulanger et al. 2008).

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