

Evaluation of Rules to Distinguish Unique Female Grizzly Bears With Cubs in Yellowstone

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ABSTRACT The United States Fish and Wildlife Service uses counts of unduplicated female grizzly bears (*Ursus arctos*) with cubs-of-the-year to establish limits of sustainable mortality in the Greater Yellowstone Ecosystem, USA. Sightings are clustered into observations of unique bears based on an empirically derived rule set. The method has never been tested or verified. To evaluate the rule set, we used data from radiocollared females obtained during 1975–2004 to simulate populations under varying densities, distributions, and sighting frequencies. We tested individual rules and rule-set performance, using custom software to apply the rule-set and cluster sightings. Results indicated most rules were violated to some degree, and rule-based clustering consistently underestimated the minimum number of females and total population size derived from a nonparametric estimator (Chao2). We conclude that the current rule set returns conservative estimates, but with minor improvements, counts of unduplicated females-with-cubs can serve as a reasonable index of population size useful for establishing annual mortality limits. For the Yellowstone population, the index is more practical and cost-effective than capture-mark-recapture using either DNA hair snagging or aerial surveys with radiomarked bears. The method has useful application in other ecosystems, but we recommend rules used to distinguish unique females be adapted to local conditions and tested. (JOURNAL OF WILDLIFE MANAGEMENT 72(2):543–554; 2008)

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The Yellowstone grizzly bear (*Ursus arctos*) was listed as a threatened species in 1975 under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service [USFWS] 1975). The USFWS Recovery Plan invoked counts of females with cubs-of-the-year (hereafter FCOY) to estimate minimum population size, quantify bear distribution, and establish annual mortality limits (USFWS 1993). In 1995, several environmental and conservation organizations challenged the adequacy of the Grizzly Bear Recovery Plan. The challenge focused partly on counts of FCOY, the method for measuring numbers of FCOY (including variability associated with observer effort), and use of counts of FCOY as a measurable criterion of adequate habitat management. In the United States District Court's final decision, Judge P. L. Friedman held that "the rational reasons for monitoring methods incorporated in plan was not shown" (*Fund for Animals vs. Babbitt*, Federal Register 903 F. Supplement 96 D.D.C. 1995:96).

Counts of unduplicated females and their use as an index of population size have been criticized (Craighead et al. 1995, Mattson 1997). Craighead et al. (1995:447–448) stated "it is our contention that annual numbers of unduplicated adult females with cubs is unproven as an index of trend. But even if it had been proven, its use in the Recovery Plan as the basis for projecting population size raises the issue, once again of what constitutes 'unduplicated.'" Craighead et al. (1995:452) also stated that "we conclude that IGBST [Interagency Grizzly Bear Study

Team] census methods were insufficiently rigorous to provide a reliable index of population size and trend. The likelihood of errors in the 'unduplicated' counts is too great, as is the probability that methodological bias has rendered the counts useless as an index of population size or trend, even if all counted females were, in fact, unduplicated."

The paper referenced in the 1993 Recovery Plan as Knight and Blanchard (1993) was subsequently published as Knight et al. (1995). The criticism of these counts by Craighead et al. (1995) came prior to the publication of Knight et al. (1995). The views of Craighead et al. (1995) were premised on the fact that the rule set used to determine "what constitutes unduplicated" was untested. Knight et al. (1995) presented the rule set used to distinguish sightings of unique FCOY from repeated observations of the same FCOY. Females with cubs-of-the-year were judged to be unique based primarily on 3 criteria: 1) distance between sightings, 2) family group descriptions, and 3) dates of sightings.

The minimum distance for 2 groups to be considered distinct, based on standard diameter of annual ranges (radiomarked FCOY, 1 May–31 Aug, 1975–1987), was 30 km (Harrison 1958, Blanchard and Knight 1991). Knight et al. (1995) used this 30-km rule to discriminate sightings of unique FCOY from repeat sightings of the same female. Other factors distinguished FCOY groups within 30 km. The Grand Canyon of the Yellowstone was considered a natural barrier and paved highways were considered impediments to travel. Litter size also distinguished FCOY under the assumption that cubs were correctly counted and Knight et al. (1995) only included observations from the air where

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bears were in the open and easily observed. Ground observers watched family groups long enough to ensure all cubs were seen; observers reported any doubt. Finally, Knight et al. (1995) referenced a time-separation criterion but did not provide specific rules for its application.

During the past decade, other jurisdictions have employed the Knight et al. (1995) technique (Herrero 2005, Brodie and Gibeau 2007, Ordiz et al. 2007) and various scientists have focused on counts of FCOY to improve the methodology. We use the notation of Keating et al. (2002), who summarized those efforts. The minimum number of FCOY present each year was estimated as the number of FCOY actually seen (\hat{N}_{Obs}). Because Knight et al. (1995) were inherently conservative, and because not all FCOY were seen in any given year, \hat{N}_{Obs} underestimated true number of FCOY (i.e., N). Consequently, this estimate of \hat{N}_{Obs} helped ensure allowable mortality limits were conservative but precluded calculation of valid confidence intervals. Efforts to calculate statistically sound estimates of N have focused on both parametric and nonparametric approaches (Eberhardt and Knight 1996, Boyce et al. 2001, Keating et al. 2002, Cherry et al. 2007). These methods addressed issues of statistically valid confidence intervals about estimates of N , heterogeneity in sighting probabilities, and variation in observer effort. The Chao2 (\hat{N}_{Chao2}) estimator is the recommended method currently used in the Greater Yellowstone Ecosystem (GYE; Chao 1989, Cherry et al. 2007). Implicit in all these approaches is the underlying assumption that all individuals were correctly identified. Misidentifications do occur, but their consequences have not been thoroughly investigated.

Our objective was to evaluate the rule set of Knight et al. (1995) to determine if the rules resulted in correct identification of unique FCOY and to ascertain consequences of any errors on the estimators \hat{N}_{Obs} and \hat{N}_{Chao2} .

STUDY AREA

Our study area encompassed the GYE, which included Yellowstone and Grand Teton National Parks, 6 adjacent national forests, and state and private lands in portions of Montana, Wyoming, and Idaho, USA. The GYE, a high-elevation plateau with 14 mountain ranges $>2,130$ m, contains the headwaters of 3 major continental-scale rivers. Summers were short with average annual precipitation (50.8 cm) falling mostly as snow. Vegetation transitioned from low-elevation grasslands through conifer forests at mid-elevation, reaching alpine tundra around 2,900 m. Detailed descriptions of the geography, climate, and vegetation appear in Knight and Eberhardt (1985), Blanchard and Knight (1991), Mattson et al. (1991), and Schwartz et al. (2006c).

METHODS

Data

We used 2 datasets in our analyses. Our telemetry dataset contained relocations of collared FCOY in the GYE from 1976 to 2003. Our unduplicated FCOY database contained verified observations from qualified personnel, ecosystem

wide, of FCOY collected from 1997 to 2006. Qualified observers were generally agency staff with a history of experience in the ecosystem. Occasionally, we accepted sightings from nonagency people, but we only used those sightings if confirmed by a qualified agency observer (i.e., picture, video, tracks).

We used the telemetry database to evaluate the validity of each rule and to test the accuracy of the integrated rule set. Methods used to capture and instrument bears were given in Blanchard (1985) and Schwartz et al. (2006c). Trapping efforts in the GYE have focused on marking a representative sample of bears throughout the ecosystem (Schwartz et al. 2006c). Crews typically trapped a site until an adult female was captured, then moved to a new location. Bears were radiolocated using aircraft at approximately 7–14-day intervals from mid-April through late November. We only used observations through 31 August, the cut-off date used by Knight et al. (1995). Because the rule set only addressed FCOY, we excluded records when a collared female was known to have lost her litter. On average, grizzly bears were sighted during approximately 10% of aerial relocations (West 2001, 2002), but we included all relocation records regardless of whether the bear was seen. We assumed litter size did not change for relocations when the bear was not sighted if litter size remained constant between visual sightings; we adjusted cub litter size when known losses occurred. All relocations were georeferenced.

Testing Individual Rules

Using the telemetry dataset, we generated a database that contained the time (days) and distance (km) between all possible pairs of points for each bear. We filtered this dataset to include only comparisons within a given year for the same bear. Using these data, we generated a frequency distribution, mean, and standard error. We examined this distribution to evaluate how often the 30-km rule was violated.

Knight et al. (1995) referenced a time-distance rule (e.g., 25 km to separate 2 families seen on successive days) but did not define it explicitly. Presumably Knight et al. (1995) surmised that FCOY are only capable of moving some maximum distance on any given day, and if the time between locations is short enough (e.g., 1 day) and the distance between them great enough, one can presume the observations are of different bears. This subjective time-distance criterion has been applied in 2 ways. The IGBST considered sightings of females with identical litter sizes distinct if 1) distance between the pair was approximately ≥ 10 km and < 2 days apart, or 2) if 3 locations were ≤ 3 days apart and distance between earliest and latest was ≥ 20 km. The assumption here is that bears do not typically move ≥ 20 km in 2 days. To evaluate these 2 cases, we took the same bear database and filtered it to include only those paired comparisons where time between locations was < 5 days. To evaluate distance moved among days, we constructed standard box plots. We fit a gamma distribution to the distances using the method of maximum likelihood to

estimate scale and shape parameters and we used a quantile–quantile plot to evaluate model fit.

The Knight et al. (1995) rule set assumes that if 2 observations of FCOY were <30 km apart and a female with a smaller litter was observed after a female with a larger litter, then the 2 sightings were of the same female unless other information distinguishes them as unique (e.g., both radiocollared, both seen on the same day in different areas, or larger litter seen after the smaller litter). Without additional information, the rule set assumes sightings were of the same family group and that litter size declined due to loss of ≥ 1 cub.

Because declines in litter size are a function of cub survival, we evaluated probability that litter size would decline based upon time between sightings using estimates of cub survival for grizzly bears in the GYE (Schwartz et al. 2006d). The best-supported model of Schwartz et al. (2006d) estimated cub survival at 0.64 (95% CI = 0.44–0.78) for the 224-day active period. Using the unduplicated FCOY database, we calculated probability a female would have a litter size of L_t at time t given a litter size of L_0 at time of initial sighting using the zero-truncated binomial probability (Johnson et al. 1993:135),

$$P_1(L_t) = \binom{L_0}{L_t} \frac{(S^t)^{L_t} (1 - S^t)^{L_0 - L_t}}{1 - (1 - S^t)^{L_0}}$$

where L_0 = litter size at the first sighting, L_t = litter size at time t (t = time in days between sightings), S = daily probability of survival (0.998), and $P_1(L_t)$ is the zero-truncated probability of observing litter size L_t , given that observations came from the same bear. We use the zero-truncated distribution because a female that loses all her cubs is no longer available for resighting under the Knight et al. (1995) rule set. Consequently, data do not contain sightings of zero-cub litters.

We calculated $P_1(L_t)$ for all pairs of sightings (L_0, L_t) for each $L_0 = 3, 2, \text{ or } 1$. For example, assume we observed 2 FCOY within 30 km of each other, the first with a 2-cub litter on 1 May and a second with a 1-cub litter 20 days later. The $P_1(L_t)$ of this 2-cub litter remaining at 2 or declining to a 1-cub litter in 20 days was 0.924 and 0.076, respectively. Summing $P_1(L_t)$ over all records for each L_0 (3, 2, or 1) provided expected number of litters from the database. We compared these expected frequencies to observed sighting frequencies using a Pearson statistic for testing a specified multinomial distribution (Agresti 2002).

Total litter loss makes a FCOY unavailable for subsequent recapture. The inability to recapture a 0-cub litter could skew resight distributions and, thereby, bias the Chao2 estimator. We evaluated probability that a litter would decline to zero using the unduplicated FCOY database and the formula

$$P_2(L_t) = \binom{L_0}{L_t} (S^t)^{L_t} (1 - S^t)^{L_0 - L_t},$$

which reduces to $P_2(L_t) = (1 - S^t)^{L_0}$ when $L_t = 0$ (i.e., total litter loss). We estimated expected number of 0-cub litters

for each litter size category (3, 2, or 1) by summing over all observations where $L_0 = 3, 2, \text{ or } 1$. Consequences to the Chao2 estimator occur when recapture events are missed for a female because she is no longer available for recapture under the Knight et al. (1995) rule set once her litter size goes to zero. The Chao2 estimator is given by Wilson and Collins (1992) as

$$\hat{N}_{\text{Chao2}} = m + \frac{f_1^2 - f_1}{2(f_2 + 1)} \quad (1)$$

where m is the number of individual animals captured, and f_1 and f_2 are the number seen exactly 1 and 2 times, respectively. Distributions of f_1, f_2 , and $>f_2$ (no. seen >2 times) can shift, depending on which female is resighted. Not recapturing a female with zero cubs could affect the Chao2 estimator in 3 ways. For example, assume the observed ratio of $f_1:f_2:>f_2$ for 6 females with $L_0 = 1$ is 2:2:2. If any 1 of these 6 females had equal probability of being seen one more time, the ratio could shift to 1:3:2 (f_1 F seen again), 2:1:3 (f_2 F seen again), or 2:2:2 ($>f_2$ F seen again). Decreasing f_1 and increasing f_2 reduces the estimate of \hat{N}_{Chao2} , whereas increasing f_1 and decreasing f_2 increases the estimate of \hat{N}_{Chao2} . Adding another observation to the class $>f_2$ does not change the estimate. To assess potential error associated with no recaptures of 0-cub litters, we compared observed sighting frequencies from the unduplicated FCOY database to calculated changes in the Chao2 correction factor [i.e., $f_1^2 - f_1/2(f_2 + 1)$, eq 1] by randomly assigning resighted FCOY with 0-cub litters based on expected frequencies.

We queried the telemetry database for individual females adjacent to the Grand Canyon of the Yellowstone and within 30 km of it. We visually inspected each bear's relocations to determine if any animal was observed on both sides of the canyon, a violation of this rule.

We visually inspected the telemetry database for each female-year to ascertain if any major highways were crossed. We excluded bears with <2 relocations in any given year.

Evaluating the Integrated Rule Set

Computer program to differentiate FCOY.—We contracted to have a computer program developed that simulated the manual procedure used to distinguish unique FCOY for repeated observations of the same FCOY. Using this program, we performed 7 tests among all possible pairs of observations. These tests addressed distance between sightings, velocity of movements, comparison of litter size, same-day sighting, Grand Canyon of the Yellowstone, time–distance movement, and marks (collared bears located via telemetry were treated as unique). To cluster observations, the program categorized the comparison for each rule as 1) strong join (good evidence for pair to be clustered), 2) weak join (pair could be clustered but evidence weak), 3) weak break (pair probably not from same bear but evidence weak), 4) equivocal test (no reason to join or split pair based on this test), 5) hard join (pair must be clustered, same marked bear), or 6) hard break (pair cannot be clustered,

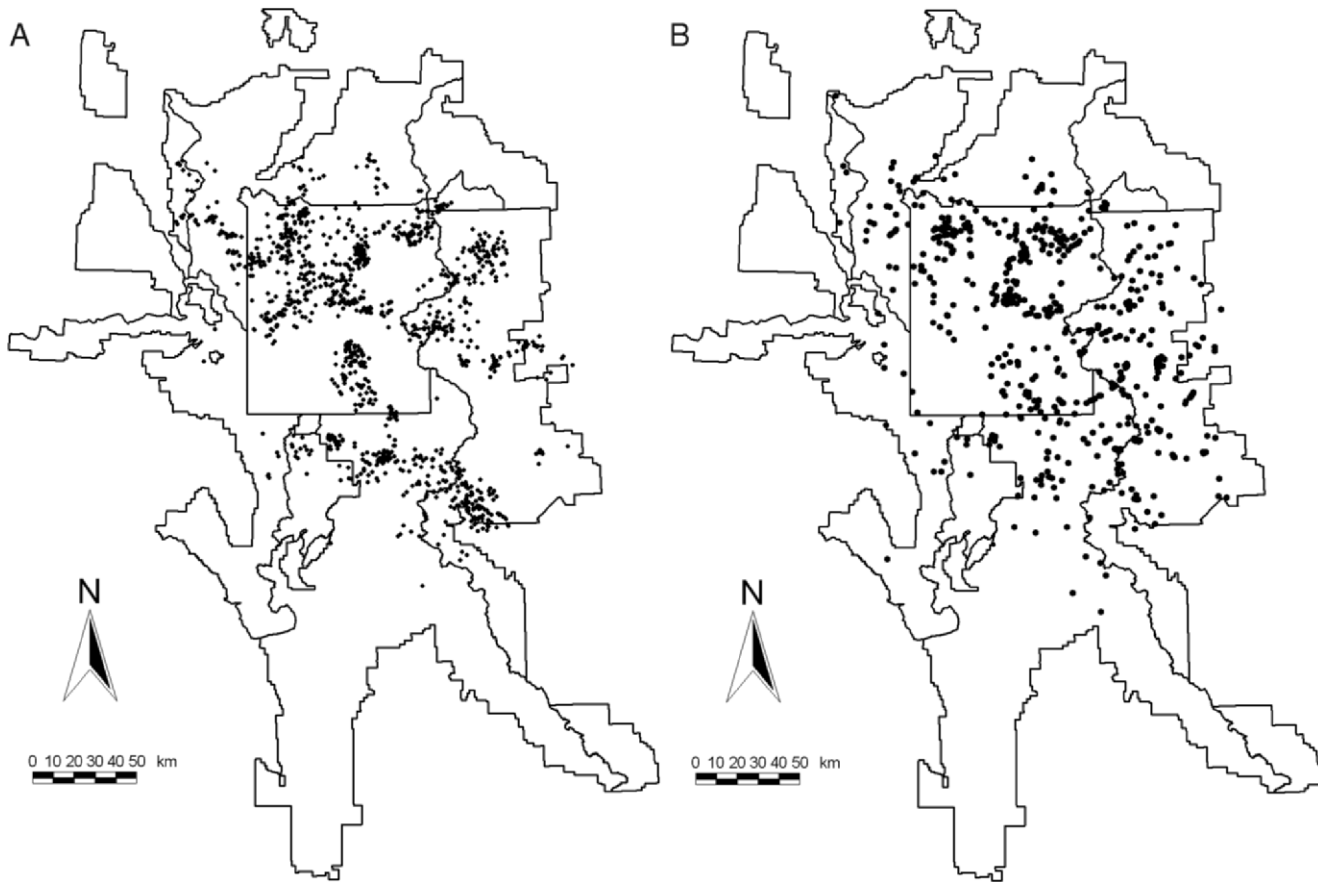


Figure 1. Distribution of telemetry fixes from 86 unique female grizzly bears with cubs-of-the-year, representing 115 bear-years of data (A), and annual locations of initial sightings of unique females with cubs from the unduplicated female database (B). All data are for the Greater Yellowstone Ecosystem, USA, 1976–2003.

different marked bears). We then assigned each pair a score for the 7 tests based on the following algorithm:

Threshold score

$$= ([strong\ joins \times 0.90] + [weak\ joins \times 0.75] \\ + [weak\ breaks \times 0.25] + [equivocal \times 0.10]) \\ \div (count[strong\ joins + weak\ joins \\ + weak\ breaks + equivocal])$$

Weights assigned to each category in the above equation were subjective and iterated until threshold scores resulted in correctly clustered sightings based on known clusters contained in test data sets. For testing, we developed a dataset specifically to evaluate the program's ability to accurately cluster individual sightings into known clusters. Additionally, we randomly inspected a small number of simulated datasets by visually clustering the raw sightings to determine whether the algorithm faithfully replicated the results achieved via manual clustering.

Construction of dataset.—Our telemetry dataset contained 115 FCOY-years (FCOY-yr = telemetry data for 1 FCOY for 1 yr) of data from 86 unique females. Bears in this dataset were not uniformly distributed across the GYE (Fig. 1A), and there were gaps on the landscape with known distribution of FCOY not containing a bear home range on

our dataset (Fig. 1B). To address the inconsistency between home ranges on our dataset and known distributions, we artificially constructed a dataset that contained 127 unique FCOY by randomly selecting 41 FCOY-years, the number necessary to populate the vacant area, moving them spatially into areas within the polygon that were unpopulated, and assigning them a new identification number. This procedure effectively created a more uniform distribution of FCOY across the 27,000-km² polygon and distributed our telemetry sample in a fashion comparable to known distribution of FCOY in the GYE (Figs. 1B, 2). We used this artificial dataset to test the integrated rule set. We recognize that telemetry data collected for FCOY in the sample were not from the same year. However, female bears colonize the home range of their mother, so it is possible for ≥ 2 FCOY to live in the same geographic area at the same time (Glenn and Miller 1980, Blanchard and Knight 1991, Schwartz et al. 2003).

We used the above database to test the integrated rule set with our program. We developed a separate routine that allowed us to specify number of unique females (identified by bear telemetry no.), total number of sightings, and number of random datasets generated. For example, we may have chosen to build 500 replicate datasets each containing 30 recorded sightings of 15 unique females. During each

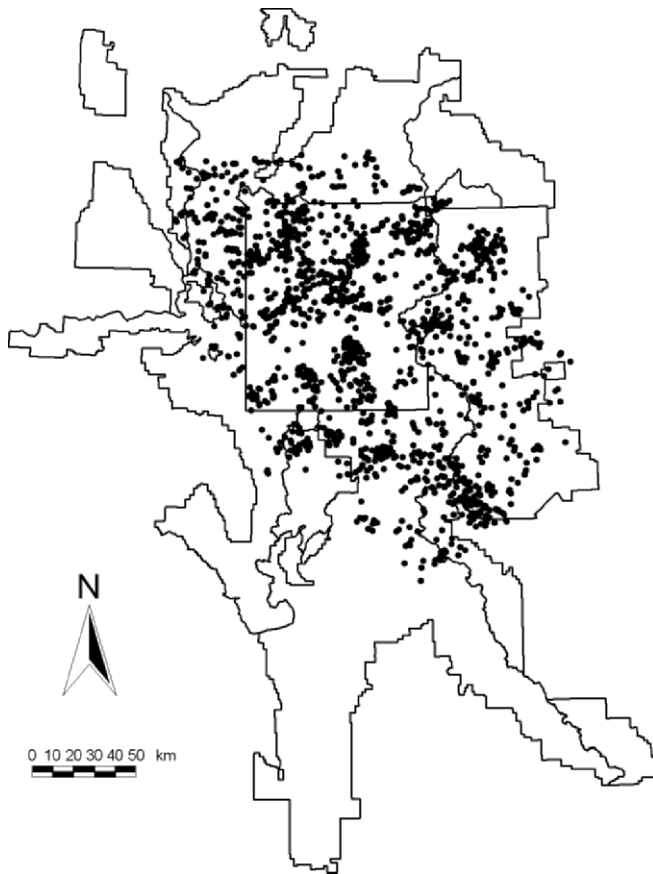


Figure 2. Distribution of telemetry fixes from 86 unique female grizzly bears with cubs-of-the-year (FCOY), representing 115 FCOY-years of data, plus 41 FCOY-years of data that we randomly chose and moved to fill in areas in the ecosystem where no data existed, resulting in a coverage with 127 quasi-unique bears with 156 bear-years of data. All data are for the Greater Yellowstone Ecosystem, USA, 1976–2003.

replicate, the program first randomly selected 15 unique females from the telemetry dataset without replacement and one random record for each female. Only one year was chosen for any female with multiple years of data. Remaining records from these 15 unique females were then put into a separate sub-file. From this sub-file, we randomly chose without replacement the remaining sightings, ignoring bear identification until the dataset contained 30 observations. We selected records without replacement to prevent duplicating sightings for the same bear in the same area on the same day. Although we knew the identification of each bear from its telemetry record, we treated individuals as unidentified (no known marks) in all simulations. We then ran each randomly generated dataset through the program, and we compared output (clustered result) to truth. Truth was the known identification number of the collared bear and clustering of her telemetry observations. We did not include known marks as part of rule-set testing, so our simulations did not test bears identified via telemetry, in keeping with Keating et al. (2002) where marked FCOY observed with the aid of telemetry were excluded from statistical estimates of \hat{N}_{Chao2} because such sightings were nonrandom.

Density and distribution of bears on the landscape would

affect rule-set performance. For example, a low-density population widely scattered over a large area would result in few bears living within 30 km of each other. Under such a scenario, the 30-km rule would work consistently well. The opposite would be true for a high-density population living in a small area, particularly if multiple females produced cubs in the same area. Using the telemetry database we varied the number of unique females drawn from the dataset to simulate varying bear densities on the landscape. Density of interior grizzly bear populations in North America, without access to salmon, varies from around 5 bears to 35 bears per 1,000 km², although a few estimates go as high as 80 (Schwartz et al. 2003, table 26.9). Current density in the GYE is probably around 14–16 bears per 1,000 km², assuming there are somewhere between 500–600 bears (IGBST 2006) and occupied range is around 37,000 km² (Schwartz et al. 2006b). Using data on reproduction and survival from the GYE, we used the PopTools extension in Excel to run Monte Carlo iterations to estimate the proportion of adult females in the GYE population (Hood 2004, Haroldson et al. 2006, Schwartz et al. 2006a, d). We ran 10,000 iterations for each of 2 possible mean independent female survival rates (0.922 and 0.950) and 2 possible mean independent male survival rates (0.874 and 0.823) to estimate expected proportion of reproductive (≥ 4 yr of age) females in the population under a stable age distribution. We used PopTools to convert life-table formats into Leslie matrix formats and took age-class proportions from the eigenvector (i.e., stable age distribution) associated with each iteration. From these simulations we estimated variation about the ratio of adult females (age ≥ 4 yr) in the total population. Estimates did not include temporal variation in rates. Results using the high (0.273) and low (0.277) survival rates were quite similar with the same estimate of variance (0.00017). Because the adult female population comprised about 27–28% of the total population in the GYE and because about 28.9% of these females are accompanied by cubs in any given year, we assumed FCOYs comprised about 8% of the total population (0.275×0.289 ; Interagency Grizzly Bear Study Team 2006). Therefore, for a population density ranging from 5 bears to 35 bears per 1,000 km², FCOY density would range from 0.4 FCOY to 2.8 FCOY per 1,000 km². Area of the minimum convex polygon associated with distribution of females in our telemetry dataset was 27,062 km². Applying a density of 0.4–2.8 FCOY per 1,000 km² equated to a FCOY population in the polygon ranging from about 11 to 76 unique females. We did not consider issues of sightability, but previous analyses suggest that we observed radiocollared FCOY independent of radiotracking flights approximately 51.8% of the time (95% CI = 44–59%; Cherry et al. 2007).

We ran 500 simulations at each population level. Earlier testing suggested that estimated error about the number of modeled clusters stabilized around 200 simulations. Keating et al. (2002) recommended that the ratio of number of sightings to number of unique females (n/N) should be ≥ 2

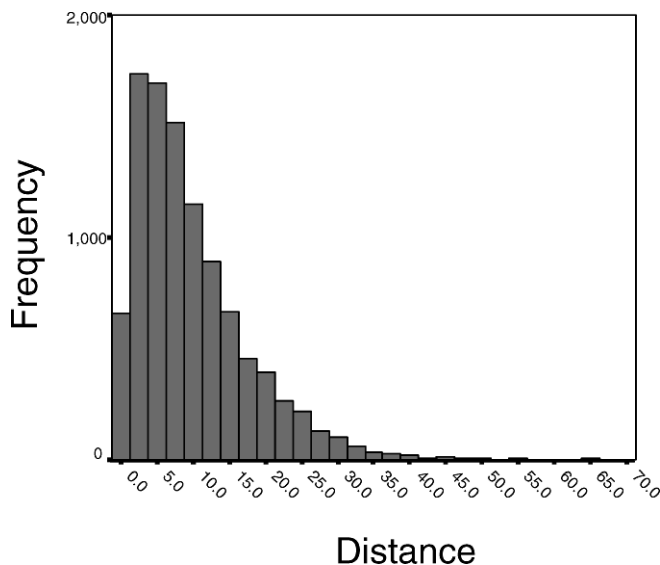


Figure 3. Linear distance (km) between pairs of radio relocations for the same radiomarked female grizzly bear with cubs-of-the-year. All data are for the Greater Yellowstone Ecosystem, USA, 1976–2003.

to narrow confidence intervals around the nonparametric estimators they tested and suggested it was a reasonable and achievable goal, based on estimates of N for 1996–2000. Because this ratio has been met in most years and because other studies have focused on this ratio and its relationship with estimates of uncertainty, we ran simulations varying population level (known no. of unique FCOY) from 10 to 100, keeping $n/N = 2$ (Keating et al. 2002, Cherry et al. 2007).

Chao2 estimates.—Based on extensive simulations, Cherry et al. (2007) recommended the Chao2 estimator as the preferred estimator of the total number of FCOY (\hat{N}_{Chao2} ; Chao 1989). For each simulation, we therefore tallied number of clusters, and number of clusters comprised of 1 or 2 sightings, and calculated \hat{N}_{Chao2} (eq 1). We then compared \hat{N}_{Chao2} estimates based on known sighting frequencies from the telemetry sample with those we obtained from the program.

We evaluated the impact of sample frequency relative to program results for the number of unique females observed. We compared simulations varying n from $n/N = 1$ to $n/N = 4$ for populations of 40 and 80 unique FCOY, with 500 simulations for each population size.

Gaming the 30-km rule.—We used the program and varied the 30-km rule in 5-km increments from 30 km to 10 km to evaluate effect of this distance criterion in combination with other rules tested. We set number of unique females at 80 for each series of simulations ($n = 500$ iterations) and $n/N = 2$.

RESULTS

Our telemetry dataset contained 1,319 relocation records from 86 adult FCOY. Most females were only sampled one year, but some were sampled in multiple years (2–4 yr), resulting in a sample of 115 FCOY-years. Number of

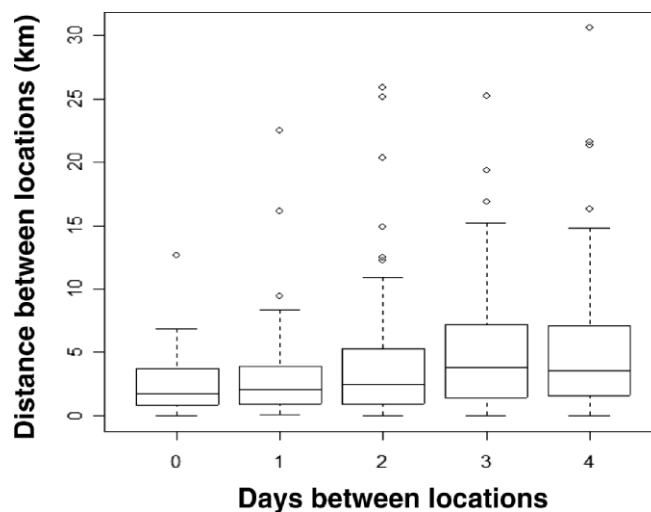


Figure 4. Side-by-side box plots of distance between paired telemetry locations for the same female grizzly bear accompanied by cubs-of-the-year ranging from 0 days to 4 days apart. Data are for female grizzlies with cubs-of-the-year in the Greater Yellowstone Ecosystem, USA, 1976–2003.

telemetry fixes per FCOY-year (den emergence through 31 Aug) varied from 1 to 39 ($\bar{x} = 11.5$).

Testing Individual Rules

There were 10,056 distances generated among pairs of relocations from the same bears in the same year. Mean distance was 9.7 km (SE = 0.08) with minimum and maximum distances of 0 km and 79 km, respectively. The 30-km rule was violated by 239 paired distances (2.4%) for 13 bears that exceeded 30 km (Fig. 3). All were from female bears that had a history of conflict with humans and had been transported from the conflict site to another location in the ecosystem.

Time between locations was <5 days for 415 distance observations from 64 bears. Number of distance observations associated with each interval varied from 32 to 138, and number of unique bears varied from 21 to 41. Box plots of distributions were right-skewed with some observations that could reasonably be called unusual (Fig. 4). Overall, there were 13 distances >15 km, 8 distances >20 km, 4 distances >25 km, and only one distance >30 km. Standard interpretation for the upper whisker of a box plot is that it is a cut-point for determination of potential unusual values. Our cut-points were 6.9, 8.3, 10.9, 15.8, and 15.2 for 0–4 days between pairs of locations, respectively, suggesting that observations >15 km are unusual. Thus, observations >15 km and <5 days apart most likely came from different bears.

A quantile–quantile plot indicated that our fitted gamma distribution was reasonable, with the exception of the maximum value of 30.6 km. The 96th percentile of the estimated gamma distribution is 15 km, suggesting that for any given pair of locations from the same bear <5 days apart, a distance ≥ 15 km is unusual. The analysis indicated application of the time–distance rule was reasonable, and only 2 paired-comparisons exceeded the 10-km threshold. Likewise for distances 2 days apart, only 3 could be identified as extreme outliers.

Table 1. Mean probability and standard deviation of observing a grizzly bear litter of size L_t given initial litter size of L_0 . We calculated probabilities excluding (zero-truncated, P_1) and including (P_2) $L_t=0$. Observed values represent the number of observations documented from the unduplicated female-with-cubs database for the Greater Yellowstone Ecosystem, USA, 1997–2006. We calculated expected values based on the appropriate P .

Litter size		P_2		P_1 zero-truncated		No.		Zero-truncated no. (exp)
L_0	L_1	\bar{x}	SD	\bar{x}	SD	Obs	Exp	
3	3	0.833	0.114	0.833	0.114	103	109.93	109.99
3	2	0.151	0.096	0.151	0.096	24	19.97	19.99
3	1	0.015	0.019	0.015	0.019	5	2.01	2.01
3	0	0.001	0.001			0	0.09	
2	2	0.901	0.079	0.905	0.074	365	359.65	361.08
2	1	0.094	0.073	0.095	0.074	34	37.57	37.92
2	0	0.004	0.007			0	1.78	
1	1	0.949	0.037	1.00		150	142.34	
1	0	0.051	0.037			0	7.66	

The unduplicated FCOY database from 1997 to 2006 contained 1,049 observations of FCOY separated into 368 unduplicated females. There were 131 unique females observed exactly one time and 237 observed >1 time. For unique females seen >1 time, there were 681 paired comparisons. Of these, 132, 399, and 150 were from females first seen with a 3-cub, 2-cub, and 1-cub litters, respectively. For 132 females initially observed with a 3-cub litter, 103, 24, and 5 were subsequently sighted with 3-cub, 2-cub, and 1-cub litters, respectively. No litter that started with 3 cubs declined to 2 cubs and then to 1 with repeated sightings. Of 399 observations where initial litter size was 2, 365 and 34 were subsequently sighted with 2-cub and 1-cub litters, respectively. Mean time between first and subsequent sightings was 27.9 days (SD = 22.7) with a range of 1 day to 109 days. Data were not normally distributed (i.e., long right-hand tail) with 25%, 50%, and 75% of resightings occurring ≤ 9 days, 24 days, and 40 days after the initial sighting, respectively.

The zero-truncated probability [$P_1(L_t)$] that a female would have a litter size of L_t at time t , given a litter size of L_0 at first sighting, varied with litter size at L_0 (Table 1). Observed sighting distribution for litters starting at 3 cubs was not statistically different from the expected distribution ($\chi^2 = 5.679$, 3 df, $P = 0.872$); the same was true for 2-cub litters ($\chi^2 = 0.448$, 2 df, $P = 0.201$), suggesting this rule was reasonable.

The probability [$P_2(L_t)$] of observing $L_t=0$ increased with decreasing litter size but was always quite small (Table 1). Of the 375 unique females observed 21.1%, 52.3%, and 26.9% were initially observed with 3-cub, 2-cub, or 1-cub litters, respectively. Weighting the probability of observing females with 3-cub, 2-cub, or 1-cub litters by their occurrence in the database suggests that probability of observing any female with litter size $L_t=0$ was about 0.016, which suggests that if we could identify females without litters, we should have resighted one in about every 62 (1/0.016) sightings.

From 1997 to 2006, mean (range) for n , m , and n/\hat{N} was 105.6 (54–148), 36.8 (29–49), and 2.79 (1.54–4.52), respectively. Mean sighting frequencies for f_1 , f_2 , or $>f_2$ were 13.1, 10.6, and 13.1, respectively. If this expected

recapture is apportioned to sighting frequency observed over the 10 years of the FCOY database, then we could expect an additional sighting of f_1 , f_2 , or $>f_2$ would be added somewhere between 0.87 (54×0.016) and 2.37 (148×0.016) times in any given year.

Consequences of additional sightings to frequency distributions vary with frequency of unique female resighted. The Chao2 equation uses distribution of f_1 s and f_2 s to adjust m for bears never seen. Adding a resight to an f_1 shifts it to an f_2 , thereby increasing the denominator and reducing correction to m . Adding a resight to an f_2 shifts it to $>f_2$, reducing the denominator and increasing correction to m . Adding a resight $>f_2$ has no effect on the Chao2 estimate. Using mean sighting frequencies observed over the past 10 years and assuming equal probability of any unique female being resighted one more time, one would expect the correction factor to Chao2 to be biased low, high, or not change about 35.6%, 28.8%, and 35.6% of the time, respectively, suggesting that on average, the consequences of no recaptures of 0-cub litters tends to bias estimates low.

There were 37 FCOY-years from 25 females in the telemetry dataset with 486 locations adjacent to or within 30 km of the Grand Canyon of the Yellowstone. One of the 37 FCOY-years (2.7%) had radiolocations on both sides of the canyon. One location was approximately 2.5 km east of the lower falls, but the remaining points ($n=6$) were west of the canyon but north of this point; the closest location was approximately 4.8 km across the canyon on the west side. If sighted on both sides as an unmarked female, this bear would have been incorrectly classified as 2 unique females.

We had 109 FCOY-years of telemetry data to ascertain major highway crossings. Of these, 36 (33.0%) crossed one major highway, 9 (8.3%) bisected >1 major highway, and 64 (58.7%) did not bisect a major highway. To our knowledge the highway crossing rule was not applied by itself to distinguish unique FCOY prior to 1997 and was not used at all after 1996.

Evaluating the Integrated Rule Set

Our computer program mimicked the manual process used to cluster sightings of unique FCOY and performed correctly in preliminary tests. The small number ($n=36$)

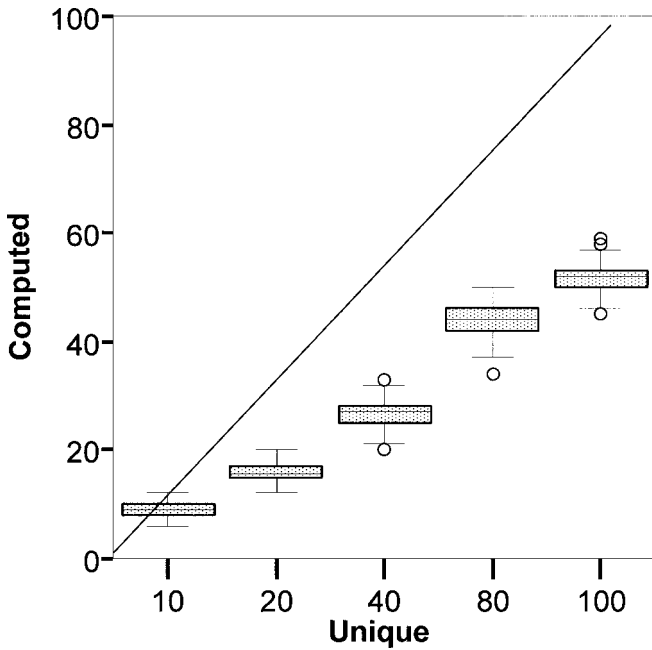


Figure 5. Side-by-side box plots of the computed number of unique female grizzly bears with cubs-of-the-year (FCOY) using the Knight et al. (1995) rule set to distinguish among telemetry locations for radiocollared FCOY sampled over a population size ranging from 10 to 100 unique bears. For each number of unique FCOY, we ran 500 simulations with the total number of sightings equal to twice the number of unique FCOY. The black line depicts the expected relationship in the absence of bias. Data are for FCOY in the Greater Yellowstone Ecosystem, USA, 1976–2003.

of randomly generated datasets we visually inspected contained the correct number of clusters when compared to manual clustering. In some cases, individual sightings were clustered differently by the program compared to manual clustering, typically when litter size declined. The manual procedure clustered litters of similar size if there were >1 clusters <30 km apart (similar litter size was the subjective criterion we used to cluster), whereas the program used distance as its first criterion for clustering and would occasionally cluster a 3-cub litter with a 1-cub litter if the 1-cub litter was closer in distance than an adjacent 2-cub litter, which in most cases changed frequency sightings for $>f_2$ and did not impact m or \hat{N}_{Chao2} .

Our simulations indicated an increasing tendency for the integrated rule set to return negatively biased results as

population size increased (Fig. 5). As we increased number of unique FCOY from 10 to 100, application of the Knight et al. (1995) rule set returned values 12–48% lower than the true number of unique FCOY. Once the number of unique FCOY exceeded 10, the maximum number returned from 500 simulations never reached or exceeded the true number of females in the simulation (Table 2).

Chao2 estimates.—Frequency of sightings (f_1 and f_2) comparing known number of unique FCOY to program estimates showed a shift from f_1 s toward more f_2 s as number of unique FCOY increased (Table 2). Consequently, \hat{N}_{Chao2} derived from sighting frequencies using the rule set always underestimated both the known minimum number simulated (m known) and \hat{N}_{Chao2} derived from known sighting frequencies of sampled bears (Fig. 6). Percentage increase in \hat{N}_{Chao2} using modeled sighting frequencies above the modeled number of unique FCOY (m modeled) declined as the known number increased from 10 to 100 (17–4%, $\bar{x} \pm \text{SD} = 9.25 \pm 5.35\%$), resulting in nearly parallel lines when we graphed the two (Fig. 6). Percentage increase in \hat{N}_{Chao2} above the known number of unique FCOY (m known) was (22–30%, $\bar{x} \pm \text{SD} = 25.57 \pm 2.30\%$), resulting in an increasing estimate of \hat{N}_{Chao2} as the known minimum number sampled increased (Fig. 6).

Varying n/N from 1 to 4 for known populations of unique FCOY of 40 or 80 indicated that as n/N increased, negative bias in the rule set decreased (Fig. 7). As with previous runs, as N increased from 40 to 80, so did negative bias.

Gaming the 30-km rule.—Incrementally changing the 30-km rule to smaller distances without adjusting other rules reduced negative bias (Fig. 8). With a model population of $N = 80$ FCOY, the number of unique FCOY identified by the rule set was unbiased when the rule was set to a value between distance 11 km and 12 km.

DISCUSSION

Our simulations clearly suggest that the rule set of Knight et al. (1995) inherently underestimates known number of unique FCOY, and that this negative bias increases with increasing population size. Additionally, every rule of Knight et al. (1995) we tested was violated to some degree. We are not surprised by these outcomes. The pertinent questions that must be asked are how often do the rules fail, and what are the consequences of these failures?

Table 2. Results of simulations of known numbers of unique female grizzly bears and the mean modeled estimates (\bar{m}) using the Knight et al. (1995) rule-set test. Sighting frequencies (f_1, f_2) represent number of unique individuals (\bar{x} and SE) seen exactly 1 or 2 times, respectively. Data are for female grizzlies with cubs-of-the-year in the Greater Yellowstone Ecosystem, USA, 1976–2003.

Unique (n)	Modeled				f_1		f_2		f_1		f_2	
	\bar{m}	SD	Min.	Max.	Unique		Modeled		Unique		Modeled	
					\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
10	8.84	1.01	6	12	4.02	1.07	3.04	1.30	3.31	1.48	2.66	1.44
20	15.59	1.41	12	20	8.21	1.48	4.21	1.73	6.48	2.13	4.61	1.87
40	26.70	2.05	20	33	16.64	1.99	5.50	2.11	12.82	2.89	6.95	2.34
80	44.07	2.40	34	50	33.45	2.75	6.28	2.33	25.51	3.93	9.17	2.70
100	51.55	2.40	45	59	42.07	3.15	6.53	2.37	31.26	4.45	9.78	2.83

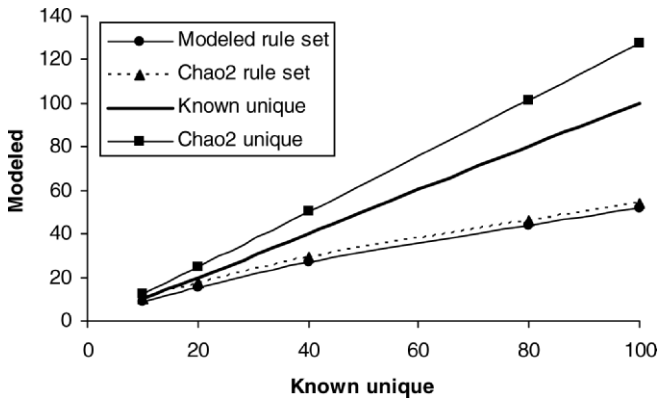


Figure 6. Results of a model simulating the Knight et al. (1995) rule set used to distinguish unique female grizzly bears with cubs-of-the-year from repeat sightings of the same female. The number of known females varied from 10 to 100, with $n = 500$ iterations per number. The heavy black line represents truth (known unique = modeled), whereas lines below it indicate a negative bias. We derived estimates of \hat{N}_{Chao2} using sighting frequencies in combination with the minimum number of unique bears estimated or known to be in the sample. Data are for female grizzlies with cubs-of-the-year in the Greater Yellowstone Ecosystem, USA, 1976–2003.

As stated in the 1993 Recovery Plan, “the purpose of this number is to demonstrate that a known minimum number of adult females are alive to reproduce and offset existing mortality in the ecosystem” (USFWS 1993:20). Mortality thresholds in the 1993 Recovery Plan were based on \hat{N}_{Obs} derived from this rule set. Our results indicate that \hat{N}_{Obs} is conservative relative to actual numbers of FCOY in the population. Consequently, mortality thresholds established using \hat{N}_{Obs} are also conservative.

Anderson (2001) provided compelling arguments against using crude indices (e.g., relative abundance) to estimate abundance, although Engeman (2003) presented an alternative view. In a response to Engeman (2003), Anderson (2003) provided an example to support his argument. Index value (C), parameter of interest (N), and detection probability (p) are related as $C = Np$; solving for parameter of interest, we have $N = C/p$. If an empirical estimate of detection probability were available (\hat{p}), then the parameter

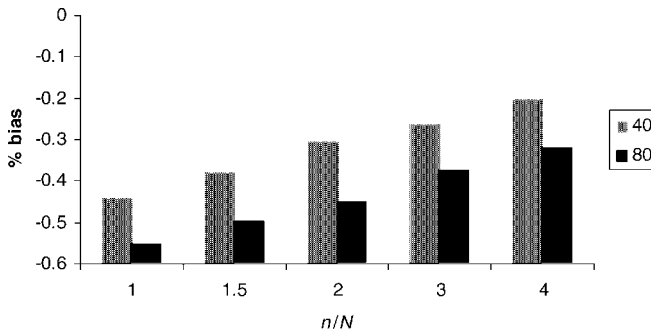


Figure 7. Percent bias in the number of unique female grizzly bears with cubs-of-the-year derived from the rule set of Knight et al. (1995) when known number of unique females (N) in the simulations was 40 or 80 and number of locations (n) varied between $n = N$ and $n = 4N$. Results represent the mean of 500 simulations for each combination of n/N and N . Data are for female grizzlies with cubs-of-the-year in the Greater Yellowstone Ecosystem, USA, 1976–2003.

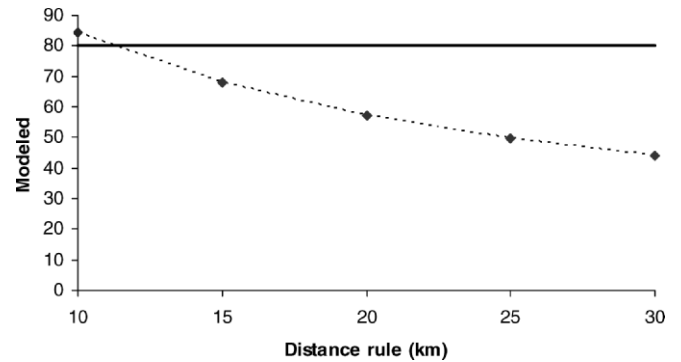


Figure 8. Number of unique female grizzly bears with cubs-of-the-year derived from the Knight et al. (1995) rule set (modeled) compared with the known number of unique females (80, solid black line) as a function of the threshold value used for the distance rule. Error bars (not shown) did not overlap 80. Data are for female grizzlies with cubs-of-the-year in the Greater Yellowstone Ecosystem, USA, 1976–2003.

could be estimated simply as $\hat{N} = C/\hat{p}$. Anderson (2003) argued that many factors ultimately affect detection probability including observer effects, environment effects, and species of interest. Anderson (2003) further argued that it is the empirical estimate of detection probability that allows the incomplete count (index value) to have meaning and allow a rigorous interpretation.

Early criticism of using \hat{N}_{Obs} to estimate population size and establish sustainable mortality limits focused on biases in detection probability associated with variable survey effort and sighting heterogeneity (Mattson 1997). These concerns were valid, and efforts were undertaken to estimate total number of FCOY using methods that were not affected by variation in search effort and sightability (Boyce et al. 2001, Keating et al. 2002, Cherry et al. 2007), thereby taking into account changes in detection probability as recommended by Anderson (2001, 2003) and allowing for a more rigorous interpretation of \hat{N} . Our evaluations suggest that even after making such a correction, \hat{N}_{Chao2} is biased low relative to the known number of unique FCOY selected for each simulation (i.e., $\hat{N}_{\text{Chao2}} < \text{FCOY}_{\text{simulated}}$) and N .

At this point, one might ask whether \hat{N}_{Chao2} is a useful index of population size or trend if it is biased. First, are there better alternative methods? The short answer is no. The IGBST investigated capture–mark–recapture estimators using observation flights and radiomarked bears as an alternative but found that resighting frequencies were so low that confidence intervals around \hat{N} were extremely large (Miller et al. 1997; Schwartz 1999, 2000). The IGBST also investigated the potential of capture–mark–recapture using hair snags but concluded it is too expensive to implement on an annual basis (Woods et al. 1999, Boulanger et al. 2002). The cost of one population estimate for the Northern Continental Divide Ecosystem, Montana, which is approximately the same size as the GYE, was US\$3.5–5 million and lag between sampling and a resulting population estimate was 3 years (Federal Register 2007). We are unaware of other estimators that are cost-effective and reliable that might be used on an annual basis to estimate

population size and set mortality thresholds. Second, what is a reasonable estimate? The main purpose of \hat{N}_{Chao2} is to establish an estimate of population size against which to set mortality limits. For threatened and endangered species, such estimates must ensure that the population will remain stable or increase, or alternatively, mortality limits must be conservative relative to population size to minimize potential for overexploitation. An index that is inherently conservative (underestimates N) accomplishes this. Grizzly bears were listed as threatened in 1975 and the goal of recovery among other things was to ensure that population increased. During the time \hat{N}_{Obs} was used to establish mortality thresholds, independent data from radiocollared bears indicated that population trajectory was positive (Harris et al. 2006). Third, trend (λ) derived from the Chao2 estimates of annual number of FCOY is similar to the population trend derived from vital rates obtained from radiomarked individuals in the GYE (Harris et al. 2006, 2007; IGBST 2006). The close match between these 2 independent datasets increases our confidence that counts of FCOY have tracked population change. The fact that counts are likely influenced by environmental variation and negatively biased at high population size may affect our ability to detect subtle changes in trend (Harris et al. 2007), but counts appear useful as an independent measure of λ uncoupled from the telemetry sample. However, because negative bias in \hat{N}_{Chao2} increases with increasing population size, if populations continue to increase, the estimate of λ will likely be biased low. For a decreasing population, the rate of decline might be underestimated but Harris et al. (2007) make recommendations for dealing with these subtle changes.

Since the rule set was established, improved methods have been developed to adjust \hat{N}_{Obs} to account for effort and sighting heterogeneity, and the recommended estimate is based on \hat{N}_{Chao2} (Keating et al. 2002, Cherry et al. 2007). But estimates of total FCOY (i.e., \hat{N}_{Chao2}) are premised on the rule set correctly separating repeat sightings of the same female from observations of different females. Our results indicate this is not always the case. As discussed above, when application of \hat{N}_{Chao2} is put into context (used to set mortality limits), the index underestimates known number of unique females. Consequently, mortality limits are likely set low relative to true population size.

Based on our results, and assuming a relatively constant mortality rate over time, one would anticipate that established mortality limits could eventually be exceeded, not because the number of bears dying is not sustainable, but simply because the estimate of population size was much less than true population size. Indeed, this is likely what happened in the GYE in 2004 and 2005, when total female mortality was exceeded using \hat{N}_{Obs} and the recovery criteria established under the 1993 Recovery Plan (Haroldson 2006).

A conservative index of population size can be a double-edged sword. A conservative estimate minimizes potential for overexploiting small populations, but there also may be

consequences to having false triggers of exceeding conservative mortality limits. A contrasting future scenario may be that some bears should be removed from the population because of nuisance or depredation issues but such actions are not undertaken because mortality limits have been exceeded.

Finally, we recognize our tests of the rules and the program simulations of all the rules are only approximate. Data we used were not specifically collected for such a test. For example, to obtain a dataset with an adequate number of unique females we were forced to use multiple years of data from radiomarked FCOY and assume that this distribution was reflective of what might have been the case in any given year. Although this is a reasonable assumption, it may not be entirely accurate. Second, one rule that we did not test in our simulations was the same day sighting rule. This rule assumes (and we believe correctly) that bears seen on the same day some distance apart over a short period of time are distinct. About 30% (range 18–50%) of all unique females identified annually from 1997 to 2006 were first observed on moth sites (Bjornlie and Haroldson 2007). Nearly all FCOY at moth sights are observed during aerial observation flights. Many are seen on the same day and we would argue that because of the time and distance between sightings they are unique. Our telemetry database undersampled FCOY at moth sites and, consequently, they were not part of our simulations. Therefore, our simulations likely overestimated bias in the rule set.

MANAGEMENT IMPLICATIONS

Our evaluations and program simulations suggest that the most influential rule used in distinguishing repeat observations of the same female from those of a different female is the 30-km rule. However, we do not recommend simply adjusting the distance downward from 30 km to maximize truth. Clearly, all rules operate in concert and the results we present here demand a more comprehensive approach to distinguish repeat sightings of the same bear from sightings of unique bears.

Rather than adjusting individual rules in an attempt to approximate truth, we recommend that the IGBST, in collaboration with other experts, take a comprehensive approach to improving the rule set. Such an approach might include a Bayesian framework that estimates conditional probability that any pair of sightings, given all the rules, came from the same bear. Such an approach might require collecting additional empirical information on FCOY, with a trapping protocol that was unbiased relative to the questions being addressed. In the meantime, we argue that using the existing method is inherently conservative and should not result in mortality limits that allow population decline.

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LITERATURE CITED

- Agresti, A. 2002. *Categorical data analysis*. Second edition. John Wiley and Sons, Hoboken, New Jersey, USA.
- Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* 29:1294–1297.
- Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. *Wildlife Society Bulletin* 31:288–291.
- Bjornlie, D., and M. A. Haroldson. 2007. Grizzly bear use of insect aggregation sites documented from aerial telemetry and observations. Pages 24–26 in C. C. Schwartz, M. A. Haroldson, and K. West, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2006*. U.S. Geological Survey, Bozeman, Montana, USA.
- Blanchard, B. 1985. Field techniques used in the study of grizzly bears. Interagency Grizzly Bear Study Team Report, Bozeman, Montana, USA.
- Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. *Biological Conservation* 58:41–67.
- Boulanger, J., G. C. White, B. N. McLellan, J. G. Woods, M. F. Proctor, and S. Himmer. 2002. A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia. *Ursus* 13:137–152.
- Boyce, M., B. M. Blanchard, R. R. Knight, and C. Servheen. 2001. Population viability for grizzly bears: a critical review. *International Association of Bear Research and Management Monograph Series No. 4*, Knoxville, Tennessee, USA.
- Brodie, J. F., and M. L. Gibeau. 2007. Brown bear population trends from demographic and monitoring-based estimators. *Ursus* 18:136–143.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. *Biometrics* 45:427–438.
- Cherry, S., G. C. White, K. A. Keating, M. A. Haroldson, and C. C. Schwartz. 2007. Evaluating estimators of the number of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Journal of Agricultural, Biological, and Environmental Statistics* 12:195–215.
- Craighead, J. J., J. S. Sumner, and J. A. Mitchell. 1995. *The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959–1992*. Island Press, Washington, D.C., USA.
- Eberhardt, L. L., and R. R. Knight. 1996. How many grizzlies in Yellowstone? *Journal of Wildlife Management* 60:416–421.
- Engeman, R. M. 2003. More on the need to get the basics right: population indices. *Wildlife Society Bulletin* 31:286–287.
- Federal Register. 2007. Grizzly bears: Yellowstone distinct population. Notice of petition findings; final rule. Federal Register, Thursday, March 29, 2007. Part II. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.
- Glenn, L. P., and L. E. Miller. 1980. Seasonal movements of an Alaska Peninsula brown bear population. *International Conference on Bear Research and Management* 4:307–312.
- Haroldson, M. A. 2006. Grizzly bear mortality. Pages 25–30 in C. C. Schwartz, M. A. Haroldson, and K. West, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2005*. U.S. Geological Survey, Bozeman, Montana, USA.
- Haroldson, M. A., C. C. Schwartz, and G. C. White. 2006. Survival of independent grizzly bear in the Greater Yellowstone Ecosystem, 1983–2001. Pages 33–43 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. *Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem*. *Wildlife Monographs* 161.
- Harris, R. B., C. C. Schwartz, M. A. Haroldson, and G. C. White. 2006. Trajectory of the Yellowstone grizzly bear population under alternative survival rates. Pages 44–56 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. *Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem*. *Wildlife Monographs* 161.
- Harris, R. B., G. C. White, C. C. Schwartz, and M. A. Haroldson. 2007. Population growth of Yellowstone grizzly bears: uncertainty and future monitoring. *Ursus* 18:167–177.
- Harrison, J. L. 1958. Range of movement of some Malayan rats. *Journal of Mammalogy* 38:190–206.
- Herrero, S., editor. 2005. *Biology, demography, ecology and management of grizzly bears in and around Banff National Park and Kananaskis Country: the final report of the Eastern Slopes grizzly bear project*. Faculty of Environmental Design, University of Calgary, Alberta, Canada.
- Hood, G. M. 2004. PopTools. PopTools version 2.6.2. <<http://www/cse.csiro.au/poptool/>>. Accessed 30 Sep 2006.
- Interagency Grizzly Bear Study Team [IGBST]. 2006. Reassessing methods to estimate population size and sustainable mortality limits for the Yellowstone grizzly bear: workshop document supplement. U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, USA.
- Johnson, N. L., S. Kotz, and A. W. Kemp. 1993. *Univariate discrete distributions*. Second edition. John Wiley & Sons, New York, New York, USA.
- Keating, K. A., C. C. Schwartz, M. A. Haroldson, and D. Moody. 2002. Estimating numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Ursus* 13:161–174.
- Knight, R. R., and B. M. Blanchard. 1993. Can the status of the Yellowstone grizzly bear population be determined by counting females with cubs-of-the-year? Interagency Grizzly Bear Study Team, Bozeman, Montana, USA.
- Knight, R. R., B. M. Blanchard, and L. L. Eberhardt. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. *Wildlife Society Bulletin* 23:245–248.
- Knight, R. R., and L. L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology* 66:323–334.
- Mattson, D. J. 1997. Sustainable grizzly bear mortality calculations from counts of females with cubs-of-the-year: an evaluation. *Biological Conservation* 81:103–111.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69: 1619–1629.
- Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. Barnes, Jr., R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resighting techniques. *Wildlife Monographs* 133.
- Ordiz, A., J. Naves, A. Fernández, D. Huber, P. Kaczensky, Y. Mertzanis, A. Mustoni, S. Palazón, P. Quenette, G. Rauer, and C. Rodríguez. 2007. Distance-based criteria to identify minimum number of brown bear females with cubs in Europe. *Ursus* 18:157–166.
- Schwartz, C. C. 1999. Evaluation of a capture-mark-recapture estimator to determine grizzly bear numbers and density in the Greater Yellowstone Area. Pages 13–20 in C. C. Schwartz and M. A. Haroldson, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 1998*. U.S. Geological Survey, Bozeman, Montana, USA.
- Schwartz, C. C. 2000. Evaluation of a capture-mark-recapture estimator to determine grizzly bear numbers and density in the Greater Yellowstone Area. Pages 15–18 in C. C. Schwartz and M. A. Haroldson, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency*

- Grizzly Bear Study Team, 1999. U.S. Geological Survey, Bozeman, Montana, USA.
- Schwartz, C. C., M. A. Haroldson, and S. Cherry. 2006a. Reproductive performance of grizzly bears in the Greater Yellowstone Ecosystem, 1983–2002. Pages 18–24 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. Temporal, spatial and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Schwartz, C. C., M. A. Haroldson, K. A. Gunther, and D. Moody. 2006b. Distribution of grizzly bears in the Greater Yellowstone Ecosystem in 2004. *Ursus* 17:63–66.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2006c. Study area and methods for collecting and analyzing demographic data on grizzly bears in the Greater Yellowstone Ecosystem. Pages 9–17 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. Temporal, spatial and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2006d. Survival of cub and yearling grizzly bears in the Greater Yellowstone Ecosystem, 1983–2001. Pages 25–32 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly bear. Pages 556–586 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America: biology, management, and conservation*. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- U.S. Fish and Wildlife Service [USFWS]. 1975. Amendment listing the grizzly bear of the 48 conterminous United States as a threatened species. *Federal Register* 40:31734–31736.
- U.S. Fish and Wildlife Service [USFWS]. 1993. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- West, K. 2001. Telemetry relocation flights. Pages 20–23 in C. C. Schwartz and M. A. Haroldson, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2000*. U.S. Geological Survey, Bozeman, Montana, USA.
- West, K. 2002. Telemetry relocation flights. Pages 21–22 in C. C. Schwartz and M. A. Haroldson, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2001*. U.S. Geological Survey, Bozeman, Montana, USA.
- Wilson, R. M., and M. F. Collins. 1992. Capture–recapture estimation with samples of size one using frequency data. *Biometrika* 79:543–553.
- Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free ranging black and brown bears. *Wildlife Society Bulletin* 27:616–627.

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