

Reassessing Methods to Estimate Population Size and Sustainable Mortality
Limits for the Yellowstone Grizzly Bear
Workshop Document Supplement¹¹
19-21 June, 2006

The information contained in this supplement is the result of a Workshop held at the AMK Ranch in Grand Teton National Park, 19-21 June, 2006. The purpose of this workshop was to address concerns and issues raised during the professional peer review of the original Workshop Document (Interagency Grizzly Bear Study Team 2005). We do not address all comments expressed during the public review period as those have been addressed elsewhere (NEED REFERENCE FROM CHRIS).

Items addressed here focus on 2 issues: (1) the wide variation about the original method proposed to index population size using annual estimates of females with cubs of the year as derived from the Chao₂ estimator ($FCOY_{Chao2}$), and (2) the uncertainty about the estimate of independent females, independent males, and dependent young in the population.

Professional peer reviewers expressed concern about the wide swings in the index of population size using annual counts derived from estimates of $FCOY_{Chao2}$ and the use of a constant in the denominator when extrapolating $FCOY_{Chao2}$ to an index of independent females, males, and dependent young. In the original Workshop Document, the group rejected using a “running average” over multiple years because of “possible unknown statistical biases” (IGBST 2005:25) but rather chose to smooth the mortality limit provided to managers “to dampen variability and provide managers with inter-annual stability in the threshold” consequently “allowable mortality limits will be based on a 3-year running average” derived from the annual index of population size (IGBST 2005:7-8).

We anticipated that the normal process variation associated with grizzly bear reproduction in the Greater Yellowstone Ecosystem (GYE) would result in wide swings in counts of $FCOY$ and the resultant $FCOY_{Chao2}$ estimate (see Schwartz et al. 2006a:20, Figure 6). Female bears tend to produce cub litters in the year following a year with highly abundant naturally occurring autumn foods. Hence using a constant in the denominator to extrapolate $FCOY_{Chao2}$ to index independent females, cubs and yearlings, and males failed to remove this process variation.

After considerable discussion, the group concluded that it was more appropriate to use all the data and the information-theoretic model selection methods (Burnham and Anderson 2002) to select the best model. We considered both linear and quadratic models and model averaging of the $FCOY_{Chao2}$. This approach brings the value in the numerator (estimated number of $FCOY$) in line with the mean estimate used in the

Comment [c1]: Chris is there a formal document we can cite here?

¹¹ This document is the product of team work. Participants from the original workshops contributed to its production. Please cite as follows: Interagency Grizzly Bear Study Team. 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, Montana, USA.

denominator (transition probabilities) based on previous work (IGBST 2005:60-65). The method and its application are presented in the following sections.

ESTIMATION OF NUMBER AND TREND FOR FEMALES WITH CUBS OF THE YEAR

The Chao₂ estimator (Chao 1989, Keating et al. 2002, Cherry et al. 2007) is used annually to estimate the number of females with cubs of the year ($\text{FCOY}_{\text{Chao2}}$) for year i ($\hat{N}_i$). The trend in this segment of the population and its rate of change (λ) can also be estimated from these annual estimates. Annual estimates of $\text{FCOY}_{\text{Chao2}}$ can vary because of sampling error associated with the annual estimates, and because of pulsed or synchronized reproductive output by a segment of the female population. Consequently, using each annual estimate independently each year can result in wide swings in the estimate of total population size, producing results that may be inconsistent with expected changes in true population size. This procedure was criticized during professional peer review. Therefore, we investigated methods to smooth these potential swings.

Comment [c2]: Note, CCS changed the original notation provided by GCW from FemCOY to $\text{FCOY}_{\text{Chao2}}$ to be consistent with the text above. Gary, will you be sure you still feel comfortable with the notations.

METHODS

Estimation of Rate of Population Change (λ) and the Number of Females with Cubs of the Year.

The natural logarithm of $\text{FCOY}_{\text{Chao2}}$ [$\log(\hat{N}_i)$] can be fit with a linear model of year (y_i) to estimate the number of $\text{FCOY}_{\text{Chao2}}$ and λ as:

$$\log(\hat{N}_i) = \beta_0 + \beta_1 y_i + \varepsilon_i,$$

so that the population size of $\text{FCOY}_{\text{Chao2}}$ at time zero is estimated as $\hat{N}_0 = \exp(\hat{\beta}_0)$ and the rate of population change is estimated as $\hat{\lambda} = \exp(\hat{\beta}_1)$, giving $\hat{N}_i = \hat{N}_0 \hat{\lambda}^{y_i}$. Confidence intervals on λ can be estimated as the exponential of the confidence bounds on β_1 , providing an asymmetric confidence bound.

Changes in the numbers of FCOY are representative of the rate of change of the entire population, but with additional process variation coming from the proportion of the female population that has cubs of the year (COY). Thus, random noise of $\hat{N}_i$ is coming from both sampling variation from the Chao₂ estimator and the proportion of the population with COY. When we assume a reasonably stable age and sex structure for the total population, the model provides an estimate of λ , which represents the rate of change of the entire population, and a modeled estimate of FCOY for the current year. When we fit the linear relationship, we are assuming the standard assumptions of least squares regression.

Estimation of Change Through Time.

A quadratic regression is used to detect a change in λ through time. Thus, we fit the model

Comment [c3]: Note, CCS changed the original notation of FemCOY to $\text{FCOY}_{\text{Chao2}}$ to be consistent with the text above.

$$\log(N_i) = \beta_0 + \beta_1 y_i + \beta_2 y_i^2 + \varepsilon_i,$$

and the estimate of β_2 provides an estimate of the change in λ through time. We expect that the estimate of β_2 will become negative as the population reaches carrying capacity, so that λ approaches 1. This approach considers a leveling off of FCOY as the population reaches carrying capacity, thus preventing overestimation of FCOY as population size stabilizes at or near carrying capacity. Information-theoretic model selection methods (Burnham and Anderson 2002) are used to select between the linear and quadratic models, and hence to detect changes in λ and $\hat{N}_i$ as additional data are collected. Model averaging of the population of FCOY_{Chao2} is used to estimate population sizes through time, and thus smooth the variation of the Chao₂ estimates. AIC_c weights (Burnham and Anderson 2002) are used to weight the estimates from the linear and quadratic models to produce our best estimate of the current number of FCOY.

RESULTS

Data for the period 1983–2005 (Table 1) were used to estimate the rate of population change (Figure 1). The parameter estimates and AIC_c weights for the linear and quadratic models (Table 2) suggest that only the linear model was needed to model changes in the FCOY_{Chao2} population during this period. The estimate of $\hat{\lambda} = 1.0479$ with 95% confidence interval 1.031 to 1.065, and was quite close to the independent estimates of Harris et al. (2006) using data from radiocollared bears (point estimates 1.04 and 1.07). The estimated quadratic effect (-0.00071104, SE = 0.00133) was not significant ($P = 0.600$), with 79% of the AIC_c weight associated with the linear model. Thus, we concluded that the linear model was the best approximating model for the data, but still produced the model averaged estimates (Figure 1). As shown in Figure 1, the effect of the quadratic term was negligible in that a nearly exponentially increasing function was estimated.

Sensitivity to Detect Major Change

To assess the ability of our proposed model selection to detect a decline in λ or $\hat{N}_i$, we added 2 hypothetical years of data for 2006 and 2007, with 2006 equal to 0.9 times the 2005 estimate and 2007 equal to 0.9 times the 2006 estimates. In other words, we assumed that λ was equal to 0.9 for 2006 and 2007. The resulting quadratic model had an AIC_c weight of 0.67847 with the estimated quadratic effect equal to -0.00278 (SE = 0.00120) and significantly differing from zero ($P = 0.0302$). Thus, should such a decline have occurred, our model selection would have suggested that an important decline in λ and $\hat{N}_i$ had occurred.

DISCUSSION

The FCOY is the critical segment of the population driving reproduction. Thus, we appropriately use all the data to estimate the number of FCOY each year and the rate of change of this segment as a measure of the rate of change of the entire population.

Comment [c4]: Group, I think we might want to explore this more fully. A 10% decline in 2 consecutive years may not be as realistic as smaller declines over many years. I think we may also want to look at rates of decline in the 2-5% range over several years to determine just how many years are necessary for the quadratic model to assume the majority of the weight. My concern centers around slight declines that do not force the fit to assume an asymptotic plane (K) with the consequence of overestimating the number of FCOY for several years before the quadratic model pulls the line down. We don't want to create paper bears where real ones do not exist with the potential for overharvest. Your thoughts?

Chuck – maybe you want to label this section as sensitivity to detect major (i.e., important) declines – which is what the $\lambda = 0.9$ is meant to be. It wouldn't be difficult to conduct more simulations – the issue is just how much process variance should be included in the estimates, i.e., how much year-to-year noise should be used to contaminate the change in lambda. The results will completely depend on this process variance assumption. GCW

Both reproductive effort and mortality of the entire population are driven by the performance of the FCOY segment.

MANAGEMENT RECOMMENDATIONS

We propose using the linear and quadratic models as described above to estimate changes in λ and the predicted numbers of FCOY. The results will then be used in calculations to estimate the number of independent (aged ≥ 2 years) females, independent males, and dependent young following procedures outlined in the Workshop Document (Interagency Grizzly Bear Study Team 2005). We recommend this new method replace the older method proposed in the Workshop Document where we recommended using the annual estimate of FCOY_{Chao2}. The new method addresses the issue of normal process variation and associated swings in annual counts of FCOY. Details of how the methods will be applied to calculate the index of independent females, males, and dependent young are shown in the next section where we focus on uncertainty and provide confidence intervals around these indices.

The estimated λ and associated confidence interval demonstrate the healthy increase in the FCOY_{Chao2} numbers, and hence the total population. The proposed set of models will also allow managers to detect a decline in λ , and thus recognize when the population is approaching carrying capacity. We recommend this method of estimating λ be used as an independent measure of population trajectory that can be compared to estimates derived from data using radiocollared bears as recommended in the Workshop Document (IGBST 2005:42-44).

Table 1. Observations of females with cubs of the year (FCOY) in the Greater Yellowstone Ecosystem 1983–2005, where m is the number of unique individuals observed after n samples and f_j is the number of individuals observed either 1 or 2 times. Annual estimates of FCOY

Year	n^a	m^a	Sighting frequency		Chao ₂ Estimate	
			f_1	f_2	Annual	Modeled
1983	12	10	8	2	19.33	18.46238
1984	40	17	7	3	22.25	19.40793
1984	17	8	5	0	18.00	20.39578
1986	82	24	7	5	27.50	21.42746
1987	20	12	7	3	17.25	22.50457
1988	36	17	7	4	21.20	23.62873
1989	28	14	7	5	17.50	24.80158
1990	49	22	7	6	25.00	26.02483
1991	62	24	11	3	37.75	27.30021
1992	37	23	15	5	40.50	28.62948
1993	30	18	8	8	21.11	30.01446
1994	29	18	9	7	22.50	31.45699
1995	25	17	13	2	43.00	32.95893
1996	45	28	15	10	37.55	34.52222
1997	65	29	13	7	38.75	36.14879
1998	75	33	11	13	36.93	37.84063

Comment [c5]: Note: I replaced the original table 1 from Gary's document with this table. It contains the data he used plus the information we have to submit to make the observation of FCOY available.

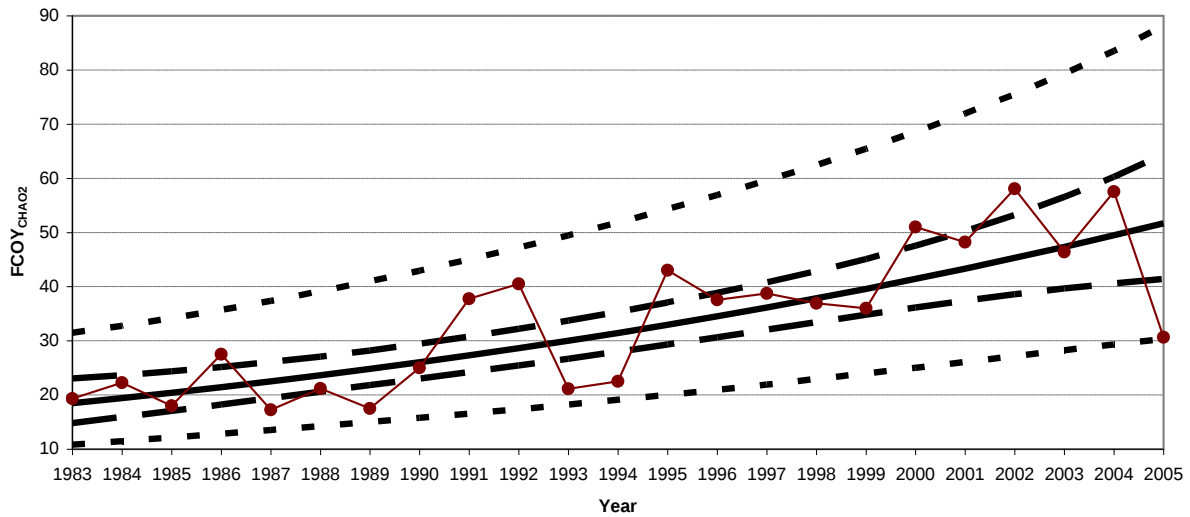
1999	96	30	9	5	36.00	39.59974
2000	76	34	18	8	51.00	41.42819
2001	84	39	16	12	48.23	43.32803
2002	145	49	17	14	58.07	45.30139
2003	54	35	19	14	46.40	47.35039
2004	202	48	15	10	57.55	49.47720
2005	86	29	6	8	30.67	51.68401

^aNote, values in this table differ slightly from those presented by Keating et al. (2002) because we included females throughout the Greater Yellowstone Ecosystem. Only observations made without the benefit of radiotelemetry are included.

Table 2. Estimates and model selection results from fitting the $\text{FCOY}_{\text{Chao2}}$ population estimates from the Chao₂ model for the period 1983–2005.

Model	Parameter	Estimate	Standard Error	<i>t</i> value	Pr(> <i>t</i>)
Linear	β_0	2.88051	0.10628	27.10	<0.0001
	β_1	0.04679	0.00775	6.04	<0.0001
	SSE	1.27685			
	AIC _c	-59.2320			
	AIC _c weight	0.78870			
Quadratic	β_0	2.80941	0.17165	16.37	<0.0001
	β_1	0.06386	0.03295	1.94	0.0669
	β_2	-0.00071104	0.00133	-0.53	0.5997
	SSE	1.25895			
	AIC _c	-56.5978			
	AIC _c weight	0.21130			

Figure 1. Model-averaged estimates of the estimated number of $\text{FCOY}_{\text{Chao2}}$ for the period 1983–2005, where the linear and quadratic models of $\log(\text{FCOY}_{\text{Chao2}})$ were fitted. The inner set of dashed lines represent a 95% confidence interval on the predicted population size, whereas the outer set of dashed lines represents a 95% confidence interval for the individual population estimates.



ESTABLISHING CONFIDENCE INTERVALS AROUND ESTIMATES OF INDEPENDENT FEMALES, MALES, AND DEPENDENT YOUNG

The second issue raised during professional peer review of the Workshop Document (Interagency Grizzly Bear Study Team 2005) was the need to display uncertainty around the estimates of independent females, independent males, and dependent young. Here we detail methods used and present confidence intervals around those estimates.

METHODS

We estimated the uncertainty around the indices using a formula derived from the delta method (Seber 1982:7) with the covariances of the various inputs assumed to be zero. For estimates of the form

$$\hat{\theta} = \frac{\hat{\beta}_1 \hat{\beta}_2}{\hat{\beta}_3 \hat{\beta}_4},$$

the estimated variance of the estimate can be approximated by

$$\text{var}(\hat{\theta}) = \hat{\theta}^2 \sum_{i=1}^4 \text{CV}(\hat{\beta}_i)^2,$$

where $\text{var}(\hat{\theta})$ is the estimated variance of the index $\hat{\theta}$ (independent females, independent males, or dependent young), and $\sum (\text{CV}^2)$ is the sum of the squared coefficients of variation used in the calculations of each estimate.

The coefficient of variation for the ratio of females 4 years and older in the population of females 2 years and older was derived using back-transformed logit normal distributions to model the 3 survival parameters: cub survival, yearling survival and adult (age 2+) survival; m_x was modeled with a beta distribution using the parameters α and β for each distribution so as to reproduce, as nearly as possible, the mean and 95% confidence limits about the mean, as reported in the monograph (Schwartz et al. 2006c). We used the PopTools extension on Excel to run Monte Carlo iterations from all 4 distributions simultaneously, each time. We ran 10,000 iterations for each of the 2 possible mean adult survival rates (0.922 and 0.950) to generate the expected relationship between the number of 2+ and 4+ females when stable age distribution was achieved. We used PopTools to convert the life-table format in the Leslie matrix format, and took age ratios from the eigenvector (i.e., stable age distribution) associated with each iteration. Variation about the ratio of “adult females (age 4+)” to “independent females” (age 2+) was derived from these simulations (Table 3). These estimates did not include temporal variation in rates. We used the mean estimate for the C data set to estimate the number of 2+ females in the population. This value is slightly different from the original value used in the Workshop Document (0.773). We used the C estimate over the AD estimate because it was more conservative.

Formatted: Lowered by 16 pt

Formatted: Centered

Formatted: Lowered by 3 pt

Formatted: Left

Comment [c6]: Rich, I lifted this out of your report, but rearranged some of the text to address age ratio but not lambda. Please read this section carefully to ensure it is accurate and correct. Thanks.

Comment [c7]: This need to be agreed upon by the group.

Table 3. Mean, variance, and upper and lower 95% confidence limits around the ratio (4+females/2+females) when mean vital rates during 1983-2002 varied randomly. Line AD was when adult survival was estimated assuming all females with unresolved fates died at last contact, line C was when adult survival was estimated censoring unresolved females (as in Haroldson et al. 2006). This ratio provides a way to estimate the number of females older than yearling based on an estimate of the number of 4+ females.

	Mean	Variance	Lower CL	Upper CL
AD	0.7842	0.0010	0.7265	0.8549
C	0.7935	0.0010	0.7412	0.8631

PLACE HOLDER FOR METHODS USED BY RICH TO ESTIMATE SEX RATIO AND A TABLE OF RESULTS.

Estimates of variation for transition probabilities were presented in the Workshop Document (Interagency Grizzly Bear Study Team 2005: Appendix C, page 62, Table 6). Estimates of variation for litter size and cub survival can be found in Schwartz et al. (2006a:19) and (Schwartz et al. 2006b:27), respectively.

RESULTS

We used the indices of abundance based on $FCOY_{Chao2}$ derived from model averaged estimates as described above (Table 1). Data from counts of FCOY used to generate the annual Chao₂ estimate are provided in Table 1.

Using this formula, we generated 95% confidence intervals around the estimate of independent females (Table 4), independent males (Table 5) and dependent young (Table 6).

Table 4. Model average estimate of $FCOY_{Chao2}$, the derived estimate of independent females (age ≥ 2 year old), the estimated variance, and the 95% Confidence interval about the estimate. Data are based on observations of females with cubs of the year in the Greater Yellowstone Ecosystem, 1983–2005.

Year	Model Averaged	$\hat{N}_i$ 2+ females	Estimated Variance	95% Confidence Interval	
				Lower	Upper
1983	18.46238	80.57	51.67497	66.48	94.66
1984	19.40793	84.63	57.02948	69.83	99.43
1984	20.39578	88.94	62.92516	73.39	104.49
1986	21.42746	93.44	69.40783	77.11	109.77
1987	22.50457	98.14	76.5274	80.99	115.28
1988	23.62873	103.04	84.33814	85.04	121.04
1989	24.80158	108.15	92.89896	89.26	127.04
1990	26.02483	113.49	102.2737	93.66	133.31
1991	27.30021	119.05	112.5316	98.26	139.84
1992	28.62948	124.84	123.7473	103.04	146.65
1993	30.01446	130.88	136.0015	108.03	153.74
1994	31.45699	137.17	149.3813	113.22	161.13
1995	32.95893	143.72	163.9804	118.62	168.82
1996	34.52222	150.54	179.8996	124.25	176.83
1997	36.14879	157.63	197.2473	130.11	185.16
1998	37.84063	165.01	216.1398	136.20	193.83
1999	39.59974	172.68	236.7019	142.53	202.84
2000	41.42819	180.66	259.0674	149.11	212.20
2001	43.32803	188.94	283.3791	155.95	221.93
2002	45.30139	197.55	309.7903	163.05	232.04
2003	47.35039	206.48	338.4642	170.42	242.54
2004	49.47720	215.75	369.5753	178.08	253.43
2005	51.68401	225.38	403.3095	186.02	264.74

Table 5. PLACE HOLDER FOR TABLE 6. I NEED ESTIMATES OF VARIANCE ON THE RATIO OF 2+ FEMALES:2+MALES FROM RICH

Year	$\hat{N}_i$ 2+ males	Estimated Variance	95% Confidence Interval	
			Lower	Upper
1983				
1984				
1984				
1986				
1987				
1988				
1989				
1990				
1991				
1992				
1993				
1994				
1995				
1996				
1997				
1998				
1999				
2000				
2001				
2002				
2003				
2004				
2005				

Table 6. Model average estimate of $FCOY_{Chao2}$, the derived estimate of dependent young (cubs and yearlings), the estimated variance, and the 95% Confidence interval about the estimate. Data are based on observations of females with cubs of the year in the Greater Yellowstone Ecosystem, 1983–2005.

Year	$\hat{N}_i$ dependent young	Estimated Variance	95% Confidence Interval	
			Lower	Upper
1983				
1984	63.70	78.28811	46.35	81.04
1984	66.95	86.40133	48.73	85.17
1986	70.34	95.32405	51.20	89.48
1987	73.89	105.1256	53.79	93.98
1988	77.58	115.8812	56.49	98.68
1989	81.44	127.6726	59.30	103.59
1990	85.47	140.5885	62.23	108.71
1991	89.67	154.7247	65.29	114.05
1992	94.05	170.1849	68.48	119.62
1993	98.61	187.0808	71.80	125.42
1994	103.36	205.5333	75.26	131.46
1995	108.31	225.6721	78.86	137.75
1996	113.46	247.6372	82.61	144.30
1997	118.82	271.5788	86.52	151.12
1998	124.39	297.6582	90.58	158.21
1999	130.19	326.0487	94.80	165.58
2000	136.21	356.9355	99.19	173.24
2001	142.48	390.5172	103.75	181.21
2002	148.98	427.0063	108.48	189.49
2003	155.74	466.6295	113.40	198.08
2004	162.75	509.629	118.51	207.00
2005	170.03	556.2632	123.81	216.26

DISCUSSION

DO WE NEED SOME DISCUSSION HERE?

MANAGEMENT RECOMMENDATIONS

We recommend mean values to estimate the number of independent females, independent males, and dependent young presented here be used to establish sustainable mortality limits as originally proposed in the Workshop Document (Interagency Grizzly Bear Study Team 2005). Methods to estimate unknown and unreported mortality remain unchanged. We recommend the demographic objective originally proposed in the Workshop Document (Interagency Grizzly Bear Study Team 2005:44–45) of 48 $FCOY_{Chao2}$ remains the same, however we recommend using the predicted number based on model averaging. As before we recommend a biology and monitoring review should

Comment [c8]: Note to the working group. Recall that we recommended the value of 48 but indicated if the lower 80% one-tailed bound declined below 48 for 2 consecutive years it required a management review. We further recommended if the lower 80% one-tailed bound dropped below 48 agencies should attempt to limit female mortality the following year. I recommend we drop the second half of this recommendation. A lot of people were confused about the lower 80% bench mark. See the text I added after this note. I think this is easier to understand. Your thoughts?

this estimate decline below 48 for any 2 consecutive years. We also recommend the management agencies attempt to limit female mortality if this estimate drops below 48 in any given year.

SUPPLEMENTAL DATA

Nearly all the information used in the Workshop Document (Interagency Grizzly Bear Study Team 2005) is available in the public domain. Mortality information, including date of death, sex, age, certainty of death, if the bear was marked or not, and location are published annually in the study team annual reports. The status of marked bears is also published in the annual reports. This information can be used to assess reporting rates. This information can be freely accessed via the internet at the following address: <http://nrmssc.usgs.gov/research/igbst-home.htm> Data to calculate population size using methods described in the workshop are available in the Tables provided by Keating et al. (2002), and we have updated and included them here (Table 1). Estimates of sustainable mortality and limits recommended in the Workshop Document can be found in the Wildlife Monograph (Schwartz et al. 2006c). The raw data used to generate those estimates are in the Monograph. All results of Harris et al. (2006), where estimates of population growth were derived, can be duplicated from raw data available in the other chapters of the Monograph. Raw data to calculate the transition probabilities have been included here (Table 7).

Table 7. Data used to calculate transition probabilities presented in Appendix C of the original Workshop Document. Data are presented as an inp file format compatible with Program MARK.

/	*	38	*/	YT00000000000000000000	-1	12	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	;		
/	*	43	*/	CYTC00000000000000000000	-1	6	7	8	9	0	0	0	0	0	0	0	0	0	0	0	0	0	;		
/	*	50	*/	YNCY00000000000000000000	-1	9	10	11	12	0	0	0	0	0	0	0	0	0	0	0	0	0	;		
/	*	59	*/	NCYC00000000000000000000	-1	5	6	7	8	0	0	0	0	0	0	0	0	0	0	0	0	0	;		
/	*	67	*/	ONN00000000000000000000	-1	0	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	;		
/	*	72	*/	000CY00000000000000000000	-1	0	0	9	10	0	0	0	0	0	0	0	0	0	0	0	0	0	;		
/	*	79	*/	000CYYTNY0000000000000000	-1	0	0	0	12	13	14	15	16	17	0	0	0	0	0	0	0	0	0	;	
/	*	79	*/	*0000000000YTYC0000000000	-1	0	0	0	0	0	0	0	0	19	20	21	22	0	0	0	0	0	0	;	
/	*	83	*/	000CY00000000000000000000	-1	0	0	0	18	19	0	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	86	*/	OYTNO00000000000000000000	-1	0	14	15	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	104	*/	000CYTCYTCYT00000000000000	-1	0	0	4	5	6	7	8	9	10	11	12	0	0	0	0	0	0	0	;	
/	*	106	*/	OCTNN00000000000000000000	-1	0	8	9	10	11	0	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	106	*/	*0000000000OYNN0000000000	-1	0	0	0	0	0	0	0	0	0	18	19	0	0	0	0	0	0	0	;	
/	*	109	*/	ONN00000000000000000000	-1	0	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	109	*/	*0000NC00000000000000000000	-1	0	0	0	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	116	*/	00TC00000000000000000000	-1	0	0	11	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	117	*/	*000000CY0000000000000000	-1	0	0	0	0	6	7	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	118	*/	000NNCY00000000000000000000	-1	0	0	3	4	5	6	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	124	*/	000NCY00000000000000000000	-1	0	0	6	7	8	0	0	0	0	0	0	0	0	0	0	0	0	0	;	
/	*	125	*/	*000NNNNCYTNCNNC0000000000	-1	0	0	0	3	4	5	6	7	8	9	10	11	12	13	14	0	0	0	0	;
/	*	126	*/	*0000TCYT000000000000000000	-1	0	0	0	15	16	17	18	0	0	0	0	0	0	0	0	0	0	0	0	;
/	*	128	*/	*00000NNN0000000000000000000	-1	0	0	0	0	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	;
/	*	128	*/	*00000000000000000000CNC000	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	14	15	16	0	0	;	
/	*	132	*/	*0000000000000000000000CY	-1	0	0	0																	

```

/* 154 */ 000000NN0000000000000000 -1 0 0 0 0 0 0 0 3 4 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ;
/* 161 */ 000000CYN0000000000000000 -1 0 0 0 0 0 0 15 16 17 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ;
/* 162 */ 000000CY000000000000000000 -1 0 0 0 0 0 0 14 15 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ;
/* 163 */ 000000NN000000000000000000 -1 0 0 0 0 0 0 4 5 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ;
/* 163 */ 0000000000CY00000000000000 -1 0 0 0 0 0 0 0 0 0 0 8 9 0 0 0 0 0 0 0 0 0 0 0 ;
/* 165 */ 000000NC000000000000000000 -1 0 0 0 0 0 0 0 11 12 0 0 0 0 0 0 0 0 0 0 0 0 0 ;
/* 166 */ 000000NC000000000000000000 -1 0 0 0 0 0 0 0 6 7 0 0 0 0 0 0 0 0 0 0 0 0 0 ;
/* 166 */ 00000000000000000000NNN0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 17 18 19 0 ;
/* 169 */ 000000NNNN0000000000000000 -1 0 0 0 0 0 0 0 3 4 5 6 0 0 0 0 0 0 0 0 0 0 0 ;
/* 179 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 6 7 8 0 0 0 0 0 0 0 ;
/* 179 */ 000000000000000000000000CYT -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 12 13 14 ;
/* 182 */ 000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 3 4 5 6 7 0 0 0 0 0 0 0 ;
/* 188 */ 000000000000000000000000CY -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 14 15 ;
/* 189 */ 0000000000YTC00000000000000 -1 0 0 0 0 0 0 0 0 0 10 11 12 0 0 0 0 0 0 0 0 0 0 0 ;
/* 189 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 14 15 16 0 0 0 0 0 0 0 0 ;
/* 190 */ 0000000000NN0000000000000000 -1 0 0 0 0 0 0 0 0 0 6 7 0 0 0 0 0 0 0 0 0 0 0 0 ;
/* 193 */ 0000000000NNN0000000000000000 -1 0 0 0 0 0 0 0 0 0 5 6 7 0 0 0 0 0 0 0 0 0 0 0 ;
/* 193 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 15 16 17 ;
/* 196 */ 0000000000TNC0000000000000000 -1 0 0 0 0 0 0 0 0 0 0 7 8 9 0 0 0 0 0 0 0 0 0 0 ;
/* 196 */ 000000000000000000000000NNNC -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 15 16 17 18 ;
/* 197 */ 0000000000NC0000000000000000 -1 0 0 0 0 0 0 0 0 0 0 8 9 0 0 0 0 0 0 0 0 0 0 0 ;
/* 205 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 8 9 10 11 0 0 0 0 0 0 0 0 0 ;
/* 205 */ 000000000000000000000000YT000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 13 14 0 0 0 0 0 0 0 ;
/* 210 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 10 11 12 13 0 0 0 0 0 0 0 0 ;
/* 213 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 7 8 9 10 11 ;
/* 214 */ 00000000000000000000NNNCN00000 -1 0 0 0 0 0 0 0 0 0 0 0 0 3 4 5 6 7 0 0 0 0 0 ;
/* 214 */ 00000000000000000000000000NN -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 10 11 ;
/* 217 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 9 10 0 0 0 0 0 0 0 0 0 0 ;
/* 237 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 13 14 0 0 0 0 0 0 0 ;
/* 242 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 13 14 15 16 0 0 0 0 0 0 0 ;
/* 246 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 7 8 9 0 0 0 0 0 0 0 ;
/* 249 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 7 8 9 0 0 0 0 0 0 0 ;
/* 254 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 6 7 8 0 0 0 0 0 0 0 ;
/* 258 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 8 9 10 0 0 0 0 0 0 0 ;
/* 264 */ 00000000000000000000NNCNC00000 -1 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 7 8 0 0 0 0 0 ;
/* 265 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 7 8 0 0 0 0 0 0 0 0 ;
/* 267 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 0 0 0 0 0 0 0 ;
/* 267 */ 00000000000000000000000000NCYN -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 8 9 10 11 ;
/* 270 */ 00000000000000000000000000YTC00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 6 7 8 0 0 0 ;
/* 271 */ 00000000000000000000000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 0 0 0 0 0 ;
/* 276 */ 00000000000000000000NNN000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 6 7 8 0 0 0 0 0 0 ;
/* 279 */ 00000000000000000000NNC000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 3 4 5 0 0 0 0 0 ;
/* 284 */ 00000000000000000000CNC000000 -1 0 0 0 0 0 0 0 0 0 0 0 0 5 6 7 0 0 0 0 0 ;
/* 289 */ 00000000000000000000NNNC0000 -1 0 0 0 0 0 0 0 0 0 0 0 0 3 4 5 6 0 0 0 ;
/* 295 */ 00000000000000000000NNCCYTC -1 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 7 8 9 10 ;
/* 296 */ 00000000000000000000NNC00000 -1 0 0 0 0 0 0 0 0 0 0 0 0 3 4 5 0 0 0 0 ;
/* 298 */ 00000000000000000000NNCY000 -1 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 7 0 0 0 ;
/* 303 */ 000000000000000000000000CYT -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 10 11 12 ;
/* 305 */ 000000000000000000000000NN00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 3 4 0 0 ;
/* 308 */ 000000000000000000000000YCYC00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 7 8 9 10 0 0 ;
/* 311 */ 000000000000000000000000CY0000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 17 18 0 0 0 0 ;
/* 311 */ 000000000000000000000000NN0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 20 21 0 ;
/* 315 */ 000000000000000000000000NN00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 3 4 0 0 0 ;
/* 316 */ 00000000000000000000000000NCY000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 3 4 5 0 0 0 ;
/* 321 */ 000000000000000000000000NNC000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 6 7 8 0 0 0 ;
/* 325 */ 00000000000000000000000000NCY00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 3 4 5 0 0 ;
/* 327 */ 00000000000000000000000000NCY00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 5 6 7 0 0 ;
/* 342 */ 00000000000000000000000000NC000 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 8 9 0 0 0 ;
/* 346 */ 00000000000000000000000000NCCY0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 7 0 ;
/* 349 */ 00000000000000000000000000NNNCN -1 0 0 0 0 0 0 0 0 0 0 0 0 0 5 6 7 8 9 ;
/* 351 */ 00000000000000000000000000NCN0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 10 11 12 0 ;
/* 358 */ 00000000000000000000000000NC00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 0 0 ;
/* 360 */ 00000000000000000000000000NNC0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 0 ;
/* 366 */ 00000000000000000000000000NC00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 5 6 0 0 ;
/* 367 */ 00000000000000000000000000NNNN -1 0 0 0 0 0 0 0 0 0 0 0 0 0 6 7 8 9 ;
/* 370 */ 00000000000000000000000000NN00 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 16 17 0 0 ;
/* 384 */ 00000000000000000000000000CY -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 6 7 ;
/* 386 */ 00000000000000000000000000CY0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 6 7 0 ;
/* 395 */ 00000000000000000000000000NN0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 3 4 0 ;
/* 399 */ 00000000000000000000000000NNN -1 0 0 0 0 0 0 0 0 0 0 0 0 0 5 6 7 ;
/* 402 */ 00000000000000000000000000NNN -1 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 ;

```


LITERATURE CITED

- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd edition. Springer-Verlag, New York.
- 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 numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Journal of Agricultural, Biological, and Environmental Statistics*. Submitted.
- Haroldson, M. A., C. C. Schwartz, and G. C. White. 2006. Survival of independent grizzly bear in the Greater Yellowstone Ecosystem, 1983–2001. Pages 33–42 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.
- Interagency Grizzly Bear Study Team. 2005. *Reassessing methods to estimate population size and sustainable mortality limits for the Yellowstone grizzly bear*. Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana, USA.
- Keating, K. A., C. S. 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.
- Schwartz, C.C., M.A. Haroldson, and S. Cherry. 2006a. Reproductive performance of grizzly bears in the greater Yellowstone ecosystem, 1983-2001. pp. 18–24 in Schwartz, C.C., M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. 2006. *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. 2006b. Survival of cub and yearling grizzly bears in the greater Yellowstone ecosystem, 1983-2001. pp. 25–31 in Schwartz, C.C., M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. 2006. *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, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006c. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Macmillian Publishing Company, Incorporated, New York, New York, USA. 654pp.