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Estimating reproductive rates for female bears: Proportions versus transition probabilities

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Abstract: Estimating reproductive rate is an important element in understanding the demographic status of any bear population. These rates have been traditionally estimated by marking a sample of individuals with radiocollars and tracking them for the life of the transmitter. Rates of reproduction have been estimated in various ways, but all essentially calculate a ratio of female cubs produced by the number of females in the sample. Inherent in these calculations is the assumption that the sample is representative of the female population at large. We compare methods used to estimate reproductive rate, comparing the proportion of females in various reproductive states estimated from capture data with a method that estimates transition probabilities and stable state conditions. The latter is unaffected by capture heterogeneity among reproductive states. We use examples from 2 study areas (Greater Yellowstone Ecosystem [Wyoming, Montana, Idaho] and Kenai Peninsula, Alaska), with grizzly (*Ursus arctos*) and black (*Ursus americanus*) bears. We discuss the effect of capture heterogeneity and concluded that reproductive rates are more accurately estimated using transition probabilities and stable state conditions if studies are short in duration, capture heterogeneity is evident, or individual bears in the sample are not recollared during the study.

Key words: black bear, grizzly bear, reproductive rates, transition probabilities, *Ursus americanus*, *Ursus arctos*

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Estimating reproductive rates for bear populations has largely been accomplished by radiocollaring a sample of females and documenting age at first reproduction, litter size, interbirth intervals of individuals or population averages, or simply the ratio of the total number of cubs produced to the total number of years all females were monitored. Implicit is that the sample is representative of the population of interest. If the capture protocol is biased, with a disproportional number of females in different reproductive states (alone, with cubs, with yearlings, with older offspring) marked relative to the actual population, parameter estimates will be biased.

With both ground-based trapping and helicopter captures, potential biases exist due to heterogeneity of capture probabilities for certain age–sex classes of bears (Miller et al. 1997). For example, adult females with cubs may tend to be underrepresented in samples because of their secretive nature (Miller et al. 1987, 1997). At best, the reconstructed population composition for various bear species based on field observations and capture records is an approximation.

Many researchers attempt to overcome capture bias by marking and tracking individual bears over multiple years, potentially dampening capture bias, but not eliminating it. Also, the expected life of radio transmitters may be short (2–3 years) compared to the reproductive interval (>3 years), or censoring (premature collar loss) may differ among various classes.

Reproductive rate typically expressed as female cubs/female/year has been estimated several ways. McLellan (1989) discussed 3 methods to estimate cub production in grizzly bears (*Ursus arctos*). The simplest (method 1) was the total number of cubs observed divided by the total number of bear-years required to produce them. This method gave more weight to females that were tracked longer. The

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sample unit was bear-years. The second method, also used by Eberhardt (1995), gave equal weight to each bear regardless of how many litters were recorded. Reproductive rate was calculated for each female as total cubs produced divided by the number of years she was sampled. A mean of these rates gave equal weight to the female regardless of how long she was monitored. Thus, the sample unit was the female. Methods 1 and 2 provide nearly identical values, but the confidence intervals are larger for method 2 because sample size is smaller. For the third method (McLellan 1989, Hovey and McLellan 1996), litter size was divided by interbirth interval for each female and expressed as a mean of these rates. This method required that females remain in the sample long enough to observe complete intervals or that additional assumptions be made when dealing with incomplete intervals. Estimates of interbirth could be biased low when excluding females with reproductive cycles longer than the period for which they were monitored (Schoen and Beier 1990, McLellan 1994), but Garshelis et al. (1998) provided a method to deal with right censoring. By definition, interbirth interval only estimates reproductive rate for multiparous females; consequently, the statistic is not directly comparable with the first 2 methods.

The first 2 methods estimate reproductive rate using ratios derived from a captured sample of bears. Both use all information regarding the reproductive state of females from time of capture. If capture bias results in an increase in one class of females that is disproportionate to their occurrence in the population, the resulting ratio is biased. For example, in some areas, females with new cubs are less likely to be captured because of behavioral characteristics that (1) reduce movements, (2) keep them in more remote areas (i.e., they stay at higher elevations in spring), or (3) cause them to use heavy cover (Miller et al. 1987, 1997). Hence, the number of females with cubs or the number of cubs produced by these females during the study returns a biased estimate for the proportion of females reproducing and reproductive rate. Even if captures continue over multiple years, the number of new bears entering the sample would be biased in a similar fashion. Marking all bears in a study area over multiple years and maintaining them in the sample would decrease such bias, but only if earlier years of data were excluded from the estimate. Because sample size for most bear studies is small, this approach is typically not followed.

Transition probabilities are the probability that an individual in a current state will transition to a different state or remain in the same state after a given time interval. Estimates of transition probabilities are not affected by bias in the state structure of the initial captures of the radiomarked sample; they are conditional on the current state. Hence sample sizes do not have to be proportional to the actual frequencies of females in each reproductive state in the population. Consequently, estimates are unbiased by this discordance in the frequency of reproductive states (hereafter referred to as states) in the sample compared to the population.

Adult female bears transition to various states depending on their reproductive status. We consider the transition from one state to another to occur during winter when females are denning. For example, a female without cubs in year t can transition to with cubs or remain without cubs in year $t + 1$. Similarly, a female with cubs in year t can transition the following year to a female with yearlings (successfully kept her litter), a female without cubs (lost her litter and did not breed), or remain a female with cubs (lost her litter and rebred). Bear species, length of maternal care, and interbirth interval determine the number of possible transitions. Typically, North American and Asian brown bears have extended maternal care and retain offspring for 2.3 years (i.e., 3-year interbirth interval), although some may keep their offspring longer (Garshelis et al. 2005). Black bears (*Ursus americanus*) and many European brown bears typically retain offspring for 1.3 years.

Transition probabilities represent the likelihood that an individual in the current state will transition to a specific subsequent state during 1 time interval. If one is interested in the proportion of the population in each state over time, it is necessary to estimate the stable state condition. For example, a simple reproductive strategy could involve an animal that typically produces offspring annually. On average, if a female has offspring in year t, there is a 0.9 probability she will have offspring in year $t + 1$. Some females do not produce; females without offspring are expected to produce offspring with a probability of 0.5 the following year. It follows that a female with offspring in year t has a 0.1 probability she will not produce offspring in year $t + 1$ ($1 - 0.9 = 0.1$). Similarly a female with no young in year t has a 0.5 probability she will not have young in year $t + 1$ ($1 - 0.5 = 0.5$). Using these values, we can predict the probability that a female will have young the following year and in subsequent years from year t. Assume a female in year t (t_0) is with offspring, then:

$$t_0 = [1 \quad 0]$$

The probability of this female also having offspring in year t+1 ($t_{(1)}$) can be predicted as:

$$t_1 = t_0 P = [1 \quad 0] \begin{bmatrix} 0.9 & 0.1 \\ 0.5 & 0.5 \end{bmatrix} = [0.9 \quad 0.1]$$

Thus there is a 90% chance she will have offspring the next year. Her reproductive status in year t+2 (t_2) can likewise be predicted as follows:

$$t_2 = t_1 P = t_0 P^2 = [1 \quad 0] \begin{bmatrix} 0.9 & 0.1 \\ 0.5 & 0.5 \end{bmatrix}^2 = [0.86 \quad 0.14]$$

After many iterations, the predicted values eventually reach an asymptotic or stable state distribution which for this example would be 0.833 and 0.167, respectively. Consequently, in this example, we would expect the population to have about 83% of the females with young and 17% without young over the long term. These stable state probabilities assume the transition probabilities are constant across time. This is a major assumption of the method we present because both time and age affect stable state values. This same assumption is inherent in the other methods discussed when data are pooled across years. Estimates of the average stable state probabilities result in average stable state probabilities.

Our objectives were to use transition probabilities to estimate reproductive rates in bears and contrast those results to traditional estimates derived from proportions of females in each state estimated from capture data (method 1 and 2 above). We do not focus on method 3, which uses interbirth interval to estimate reproductive rate in multiparous females. We provide examples using telemetry datasets for the Yellowstone grizzly bear and the Kenai Peninsula black bear.

Methods

Study areas and data

Yellowstone grizzly bears. Our Yellowstone study area encompassed the Greater Yellowstone Ecosystem (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. The GYE, a high elevation plateau with 14 mountain ranges above 2,130 m, contains the headwaters of 3 major continental-scale rivers. Summers are short, and average annual precipitation (50.8 cm) falls mostly as snow. Vegetation transitions 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 Blanchard and Knight (1991), Mattson et al. (1991), and Schwartz et al. (2006a).

We used data (1983–2003) collected for long-term demographic studies of the Yellowstone grizzly bear. Bears were captured in culvert traps or Aldrich leghold snares in both front- (road access) and backcountry (no road access) settings. We excluded data for bears $<$3 years of age, nuisance-trapped animals, and those with incomplete counts of litter size. Not all data for individual bears were in a continuous time series. In some cases their time series was interrupted and started again $>$1 year later because the individual lost its collar (or the collar ceased to function) and the individual was recaptured and recollared later.

Kenai Peninsula black bears. The Alaska study area was located in south-central Alaska on the Kenai Peninsula. The area was a glaciated plain with a relief of 15–100 m that was dotted with numerous lakes. Summers were short, with annual precipitation (mean 48 cm) evenly distributed through the year. Vegetation was typical northern coniferous forests.

We used data collected from a demographics study of black bears living in middle-aged (1947 burn) and recent (1969 burn) burned forests. Bears were captured using helicopters or barrel traps or were immobilized in winter dens. We used the reported reproductive histories (Schwartz and Franzmann 1991:Appendices D and E) and included all records for female bears $\geq$3 years of age. Years of data collection spanned 1978–1987 for the 1947 burn, whereas the data spanned 1982–1987 for the 1969 burn. Details of study areas and methods of capture have been previously reported (Schwartz and Franzmann 1991).

Analytical methods

We used visual observations of radiocollared females shortly after den emergence to determine

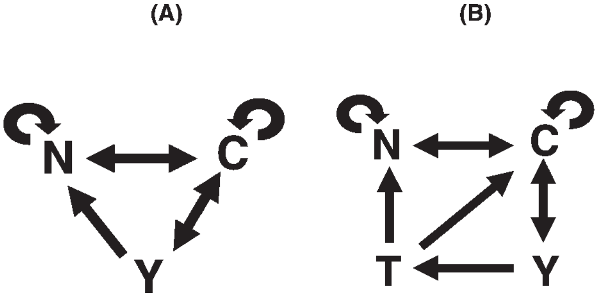

Fig. 1. Biologically possible transitions for reproductively active female bears weaning offspring as yearlings (A) or as 2-year olds (B). Arrows indicate possible transitions. States are for females alone (N), with cubs (C), yearlings (Y), or 2-year olds (T).

their reproductive state each year. To estimate transition rates, ≥ 2 consecutive years of observations were required. We used the multi-state model (Brownie et al. 1993) that assumes Markovian transitions in the software package Program MARK (White and Burnham 1999) to estimate transition rates. This model estimates the probability of transitioning among states, apparent survival rates, and recapture rates. We set survival and recapture rates = 1 in the model because only bears that transitioned (known to survive) and were recaptured (observed both years) were used in the analysis. We used the information-theoretic approach (Burnham and Anderson 2002) and Akaike's information criterion adjusted for small sample size (AIC_c) for model selection. We assumed 3 states for black bears and 4 states for grizzly bears (Fig. 1), generating 9 and 16 possible transition probabilities, respectively. However, 2 and 6 of these transitions are not biologically possible for black and grizzly bears, respectively (Table 1, Fig. 1). We assumed the probability of transitioning from N to Y, and Y to Y were zero for both species, and N to T, C to T, T to Y, and T to T were zero for grizzly bears, where states N = lone female, C = female with cubs-of-the-year, Y = female with yearlings, and T = female with 2-year olds. Further, the sum of transitions for each state (row) must equal 1, so only 4 and 6 transitions were estimated for black and grizzly bears, respectively; the remainder were obtained by subtraction (Table 1). For our estimation procedure, all transitions to N were obtained by subtraction (N to N, C to N, Y to N, and T to N).

To illustrate the utility of the method, we fit models assuming a constant time and age effect and models including age as an individual covariate. Time-specific models of the transition probabilities were not considered because of the limited amount of data available across all years of observations. For models with constant transition probabilities across time and no age covariate, transition probabilities were estimated directly from the multinomial distributions. We used this approach to verify the estimates from Program MARK.

Table 1. Transition probabilities estimated with the multi-state model for grizzly bears in the Greater Yellowstone Ecosystem and black bears on the Kenai Peninsula, Alaska, where N = lone female, C = female with cubs-of-the-year, Y = female with yearlings, and T = female with 2-year olds.

Current state	Transfer to state N	C	Y	T
N	subtraction	estimated	zero	zero
C	subtraction	estimated	estimated	zero
Y	subtraction	estimated	zero	estimated
T	subtraction	estimated	zero	zero

For models with age as a covariate, we included age of the female at the start of each transition in multistate models using the logit-link function. We considered models with each transition fit with its own intercept and linear age, and models with each transition fit with its own intercept, age, and age^2 effects. We included a quadratic function of age to explore the effect of reproductive maturation and senescence on model fit. A quadratic function provides a means of identifying the age at maximum reproduction. Based on these results, additional post hoc, reduced models were considered where results from the age and age^2 models suggested terms to remove that did not contribute to the fit of the model to the data.

To illustrate the effect of age on estimates, we constructed stable age distributions (SAD) for the Yellowstone grizzly bear using a Leslie matrix, setting cub and yearling survival at 0.64 and 0.82, respectively (Schwartz et al. 2006b) and adult survival at 0.92 (Haroldson et al. 2006). Since recruitment rate affects SAD, we also varied the m_x schedule from 0.25 to 0.40 in increments of 0.05 (converting each m_x to the appropriate F_x for use in Leslie matrices). We used these 4 SADs to approximate age structure in the population and estimated the proportion of bears in each state using the age-specific model.

To estimate the asymptotic proportion of the population in each state, assuming transition probabilities were constant across time and age, the vector [1, 0, 0, 0] was multiplied times the matrix of transition probabilities, with the multiplication repeated on the result, 50 times. The variance–covariance matrix of the resulting vector was obtained numerically with the delta method (Seber 1982).

We compared the proportion of bears in each stable state derived via transition probabilities to actual states from captured bears, which we refer to here as the capture state. Because not all bears are captured in the spring, some can change to a different state in a given year (i.e., wean offspring prior to capture). Because it is not possible to determine this, we used the current state of the individual at time of capture. We included bears as part of the capture state sample when first captured or recaptured but not wearing a functional transmitter. Capture state for bears first captured at age 3 were kept at the N state when they turned 4 regardless of the actual state at age 4. Hence, a bear with transitions N to N or N to C from age 3 to 4 had a capture state of N when the proportion in the capture state was calculated. We did this because the bear, even though not sexually mature (i.e., without cubs-of-the-year) at age 3, was first captured at this age. Hence, our capture state reflected the actual state when a bear was captured.

We also estimated the proportion of bears in each state from all years of study (i.e., the sampled distribution), which we refer to here as the all state. We excluded bears that were 3 years of age from the all state sample because they do not produce cubs. Essentially we tallied all bears observed in each state over the life of the study. The proportion in each state was simply the number in each state divided by the sum in every state. This provided an estimate of reproductive rate equivalent to method 1, when the proportion in the C state was multiplied by the mean litter size of female cubs. We used bootstrapping (Efron and Gong 1983) to estimate the 95% confidence interval for proportions in various states estimated. We calculated 1,000 bootstrap estimates in Microsoft Excel (Microsoft, Redmond, Washington, USA) using program PopTools add-in (G.M. Hood, 2004, PopTools version 2.6.2. http://www.cse.csiro.au/poptools). We used the 2.5% and 97.5% percentiles of the distribution as the 95% confidence interval.

Data for estimating transitions required that for any individual to be part of the analysis, $\geq$1 transition must have been observed, which in our case meant for 2 or more consecutive years. Any bear lost from the sample the same year of capture was excluded from the dataset. For direct estimates of proportions, this is not necessary as only the current state must be known. Here we chose to use the same dataset for illustration, so the proportions in the all state and capture state reflect bears that transitioned at least once unless they entered the data set at age 3. In a few cases 3-year-old bears only had 1 transition from age 3 to 4, but we included their state at age 4 when calculating the proportion in each reproductive state.

We estimated fecundity by multiplying the proportion of bears in the C state derived with the transition times mean litter size (female cubs only). We estimated the uncertainty associated with these estimates with the delta method.

Results

Yellowstone grizzly bears

We had radiocollar data from 106 unique females that contained 222 transitions. Of these 222 transitions, 120, 59, 29, and 14 started in the N, C, Y, and T states, respectively. Model estimates and model selection results (Table 2) suggested that age was an important predictor of transition probabilities. Estimates of the 6 transition probabilities for the intercept-only model were used to estimate the probability of transitioning to the N state (Table 3). The estimated proportions of the population that would exist in each state (Fig. 2*a*) assuming that transition probabilities were constant across time and age were 0.322, 0.289, 0.230, and 0.159 for the N, C, Y, and T states, respectively. Using the same dataset, excluding 17 observations of 3-year-old females, and estimating the proportions directly from the all state data returned estimates of 0.441, 0.305, 0.180, and 0.074, for the N, C, Y, and T states, respectively. The proportions from the trap state were 0.660, 0.226, 0.085, and 0.028 for the N, C, Y, and T states, respectively. The confidence interval for the N and T states computed with transition probabilities differed from these proportions estimated directly from the trap state.

The transition functions for the Yellowstone grizzly bear using the best model as determined by AIC_c selection (Table 2) suggested that 0.797 (Table 3) of females in the C state can be expected to transition to the Y state, and 0.034 will transition

Table 2. Results of model selection conducted in Program MARK for the 3 models considered a priori (bottom 3 models) and the 3 additional models (top 3 models) considered post priori to estimate 6 transition probabilities for Yellowstone grizzly bears, 1983–2003. N = lone female, C = female with cubs-of-the-year, Y = female with yearlings, and T = female with 2-year olds.

Model[a]	AICc	ΔAICc	AIC_c weights	Number parameters	Deviance
Age (Y to C, Y to T) x Transitions x Age^2 (N to C)	303.38	0	0.632	10	282.34
Age x Transitions x Age^2 for N to C, Y to C, and Y to T	305.60	2.22	0.208	12	280.11
Age x Transitions + N to C Age^2	306.21	2.83	0.154	13	278.46
Age x Transitions x Age^2	314.22	10.83	0.003	18	274.85
Constant	314.49	11.10	0.002	6	302.10
Age x Transitions	316.00	12.61	0.001	12	290.55

[a] Transitions were N to C, C to C, C to Y, Y to C, Y to T, and T to C. All transitions to the N state (N to N, C to N, Y to N, and T to N) were estimated by difference and are not in models.

back to the C state (Fig. 3*a*). By difference, 0.169 bears in the C state are expected to transition back to the N state. Likewise, about 0.643 of females in the T state can be expected to transition back to the C state, whereas by difference, 0.357 can be expected to transition back to the N state. Quadratic effects for age (Fig. 3*b*) also suggest that females are more likely to transition from the N state to the C state as age increased, peaking between 10 and 15 years (thus defining the prime reproductive ages), then declining with old age. The model predicted that 12.6% of 3-year-old females would transition to the C state at age 4. Previous work using methods proposed by Garshelis et al. (1998) estimated 9.8% (SD 4.6) of 3-year-old females produced litters at age 4 (Schwartz et al. 2006c), but the confidence intervals were quite large, indicating the 2 estimates are not statistically different. Comparisons at age 5 and above are inappropriate because some females age 4 and older can lose litters and transition back to the C or N states, precluding direct comparisons.

The estimated proportion of bears in the 4 states was relatively invariant to changes in SAD derived from the 4 m_x schedules. For example the proportion of females in the N state was estimated as 0.449, 0.452, 0.456, and 0.460 when m_x was set at 0.20, 0.30, 0.35, and 0.40, respectively. With age-specific transition probabilities, changes in m_x (and hence SAD) had little affect on changes in the proportions in various reproductive states. However, for populations where SAD is never reached because of very different year-to-year fluctuations in survival, stable states would never be reached. Under such a scenario, the estimated proportion of bears in each state would fluctuate under the age-specific model depending on the number or proportion of females in prime reproductive age classes (i.e., the area under the N to C curve in Fig. 3*b*).

Table 3. Matrix of transition probability estimates derived from the likelihood analysis of the constant model, where N = lone female, C = female with cubs-of-the-year, Y = female with yearlings, and T = female with 2-year olds. Estimates to the N state were derived by difference. Data from the Yellowstone grizzly bear, 1983–2003.

	Transfer to state			
Current state	N	C	Y	T
N	0.525	0.475	0	0
C	0.169	0.034	0.797	0
Y	0.207	0.103	0	0.690
T	0.357	0.643	0	0

Kenai Peninsula black bears

We had radiocollar data from 21 and 12 unique females from the 1947 and 1969 burn areas, respectively. The combined data sets contained 115 transitions, with 33, 48, and 34 starting in the N, C, and Y states, respectively. Models fit with and without group (1947 versus 1969 burn areas) as a covariate (Table 4) indicated group was not significant based on a likelihood ratio test comparing the model with group (1947 versus 1969 burns) and transition to the model only containing transition ($P = 0.366$). Additional models were constructed where groups were combined. Similar to the grizzly bear results, model estimates and model selection (Table 4) suggested that age was an important predictor of transition probabilities. Estimates of the 4 transition probabilities for the intercept-only model were used to estimate the probability of transitioning to the N state (Table 5). The estimated proportions of the population in each stable state (Fig. 2*b*) were 0.283, 0.366, and 0.351 for the N, C, and Y states,

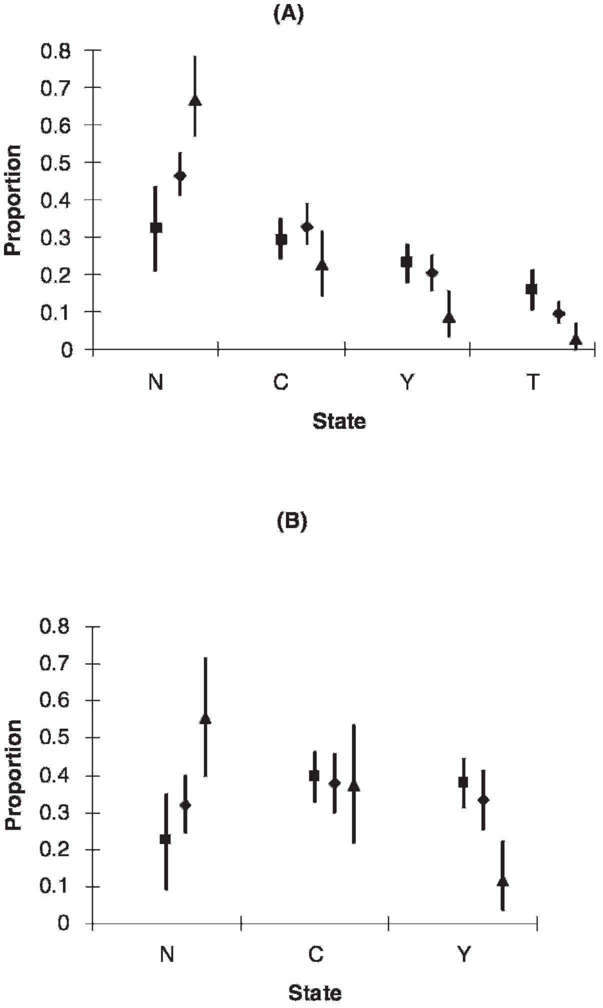

Fig. 2. States of female grizzly (A) and black bears (B) based upon the asymptotic stable state (box), their state when first captured (trap state, triangle), or for the duration of the study (all state, diamond). Transitions included bears from age 3, whereas the all state and trap state excluded this non-breeding age when directly calculating the proportion in each state, where N = lone female, C = female with cubs-of-the-year, Y = female with yearlings, and T = female with 2-year olds.

respectively. Using the same data, excluding 12 observations of 3-year-old females and estimating the proportions directly from the all state data returned estimates of 0.310, 0.368, and 0.323, for the N, C, and Y states, respectively. The proportions from the trap state were 0.538, 0.359, and 0.103, for the N, C, and Y states, respectively. The confidence interval for the N and Y states computed with transition probabilities differed from the proportions derived from the trap state.

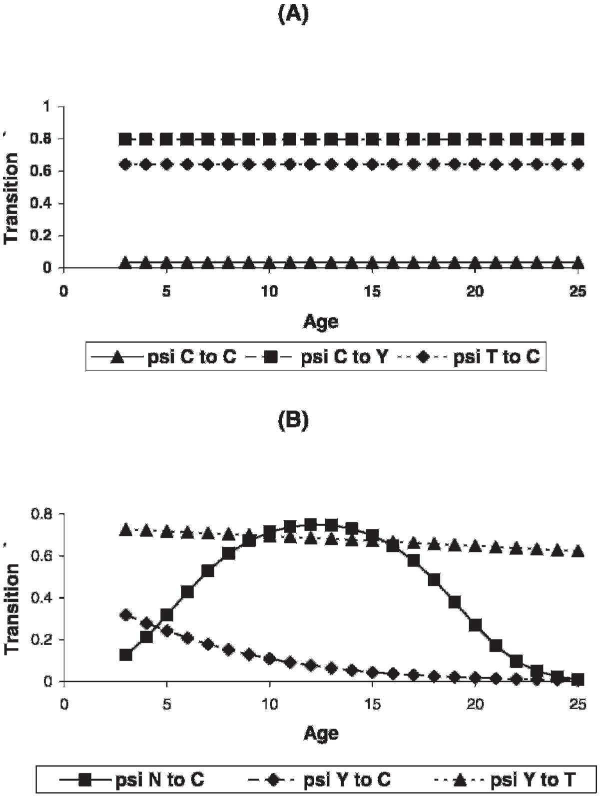

Fig. 3. Top model (Table 2, Age[Y to C, Y to T] x Transitions x Age^2[N to C]) describing transition probabilities (psi) for female grizzly bears for states N (alone), C (with cubs-of-the-year), Y (with yearlings), and T (with 2-year-old offspring). Transitions without age as a covariate are shown in A, whereas transitions with age (Y to C and Y to T) or age^2 (N to C) are shown in B. Data are for grizzly bears from the Greater Yellowstone Ecosystem, 1983–2003.

Discussion

The method we demonstrate to estimate the stable state for female bears in various reproductive classes is not affected by bias in the initial captures of the radiomarked sample, but does assume transition probabilities are constant across time, as do any of the methods in which data are pooled across time. And although the sample obtained over the duration of the study may not be proportional to the actual frequencies of the states in the population, estimates are unbiased by this discrepancy. Estimates of precision (Fig. 2) reflect sample sizes available to estimate each transition. Thus our method relaxes a critical assumption of other methods while still producing unbiased estimates of stable state probabilities from biased samples of the population

Table 4. Results of model selection conducted in Program MARK for the 4 models considered a priori and the 3 additional models considered post priori to estimate 4 transition probabilities for black bears on the Kenai Peninsula, Alaska, 1978–1987. A priori models considered were: transition, transition x group, transition x age, and transition x age x age^2 where N, C, and Y were lone females, females with cubs, or yearlings, respectively.

Model[a]	AIC$_c$	ΔAIC$_c$	AICc weight	Number parameters	Deviance
Transition x (age+age^2)	92.37	0	0.993	7	77.32
Transition x age	103.67	11.30	0.004	8	86.31
Transition x (age+age^2) from N and Y only	103.90	11.52	0.003	8	86.54
Transition x age from N and Y only	107.21	14.84	0.0006	6	94.43
Constant	112.78	20.41	0.000	4	104.42
C-group x transition	115.15	22.78	0.000	6	102.37
Group x transition	117.47	25.10	0	8	100.11

[a] Transitions were N to C, C to C, C to Y, and Y to C. All transitions to the N state (N to N, C to N and Y to N) were estimated by difference and therefore are not in models.

because transitions are conditioned on a female's initial state.

Studies of bear demographics are carried out over multiple years. New animals are captured and the extent to which any individual remains in the sample is contingent on radiocollar life or loss, recapture frequency, and the interval individuals may be censored from the sample. All of these factors affect the composition of the marked sample relative to the true distribution in the population. Both examples we provide here were long-term studies. For the Yellowstone grizzly, bears were captured in barrel traps or foot snares and entered and left the sample contingent on capture, collar life (including premature shedding), and recapture rates. For the Kenai example, bears were captured with barrel traps and helicopters. Once female black bears were part of the sample, they were maintained in the sample by recollaring during the denning season. But even with a long sample period and repeated collaring, the estimated proportion of females in the trap state differed from the estimate derived from the transitions. Direct estimates of proportions for both examples differ from the stable state estimates, suggesting a bias in the capture state frequencies (Fig. 2). Estimates of the proportion of each class captured suggested that the most likely state to be sampled was the N state, when the female is not encumbered by offspring.

Table 5. Matrix of transition probability estimates derived from the likelihood analysis of the constant model where N, C, and Y were lone females, females with cubs, or yearlings, respectively. Estimates to the N state were derived by difference. Data from the black bear on the Kenai Peninsula, Alaska, 1978–1987.

	Transfer to state		
Current state	N	C	Y
N	0.515	0.485	0
C	0.021	0.021	0.958
Y	0.264	0.736	0

The data also suggest that the stable state for females with dependent young older than cubs is likely to be undersampled, or possibly misclassified. For black bears that wean offspring as yearlings, this discrepancy is apparent in the trapped sample (Fig. 2). However, because captures can occur over the entire non-denning season, the bias is likely a result of weaning prior to capture. A female with yearlings in the spring that is captured in late summer after weaning would be classified in the N state. The same issue exists for grizzly bears with 2-year-old offspring or for those that wean yearlings. There is some indication that a portion of Yellowstone grizzly females wean offspring as yearlings (Blanchard and Knight 1991, Craighead et al. 1995). Both datasets suggest heterogeneity in capture probability among reproductive classes of bears. By misclassifying a female in the T state in the spring to an N state in the fall after weaning, our estimate for the transition from Y to T would be underestimated and the transition from Y to N overestimated. However, in either case if this female transitions back to the C state the next year (T to C or N to C), the transition to the C state would be accurately estimated, returning the necessary statistic for estimating reproductive rate. This misclassification would create some parameter heterogeneity, and hence the possible need to consider a variance correction factor.

Differences in estimated stable state using the transition probabilities versus the proportions derived from the all state data differed between the 2 study areas. These differences are likely the result of the different methods used to sample bears in the population. On the Kenai Peninsula, once a female bear was captured, it was kept in the study by constant recollaring in the den. And although the trap state was biased toward the N state, bears remained in the sample over the duration of the study, thus dampening capture bias. Hence the all state proportions were similar to the stable state condition, and as a consequence, estimates derived from both methods were nearly identical. Bears in the Yellowstone sample were captured with barrel traps or foot snares and females remained in the sample only if they were captured multiple times, so state estimates derived with transitions were not identical to those derived from proportions using the all state data, although the 95% confidence intervals overlapped. These results suggest that capture bias and its effect on obtaining an unbiased estimate of the proportion of females in each state is dampened the longer individual females remain in the sample.

Interestingly, the all state and stable state estimates (Fig. 2) tended to converge at the C state for both examples. This is likely the result of radiocollar life, which is generally 2–3 years. Hence, bears in the N state are likely to transition to the C state when part of the sample. This is reassuring, since previously some studies have relied on direct estimates of the proportion in the C state.

Reproductive rate has been calculated as a ratio of total cubs produced/total bear or bear-years sampled. Total cubs produced is derived from observations of females with cubs-of-the-year. As such, this estimate is unbiased by heterogeneity in capture rates associated with reproductive status. The sample comes entirely from females with cubs (C state). However, the denominator used in the ratio can be biased as we suggest here. Consequently, the estimate of reproductive rate is likely biased as well. Using the Yellowstone data as an example, our estimate of females with cubs in the population was 0.289, 0.226, and 0.305 based on stable, trap, and all state, respectively. Estimated litter size is 2.04 (Schwartz et al. 2006c). Assuming a 50:50 sex ratio, female cubs/litter equals 1.02. Estimates of fecundity (95% CI) are 0.295 (0.248–0.341), 0.231 (0.149–0.312), and 0.312 (0.259–0.365) using the stable, trap, and all state estimates, respectively. Although the 3 estimates are not statistically different, the mean estimate for the trap state is much lower than the estimate derived for the stable state and the all state.

The transitions from C to C and C to N may be informative when assessing sexually selective infanticide (SSI). SSI theory suggests that infanticidal males kill unrelated cubs to gain breeding opportunity with the mother (Hrdy 1979). SSI has been evaluated for the most part by looking at cub survival rates and comparing them to changes in male abundance (Swenson et al. 1997, 2001; Miller et al. 2003; McLellan 2005). However, one component of the theory suggests that the female should rebreed in the same year. If this is the case, one would expect females that lose cubs (in C state) to transition to the C state rather than to the N state. The Yellowstone dataset suggests that about 5 times as many females in the C state transitioned back to the N state than the C state (0.169/0.034), suggesting SSI is not a significant factor in the Yellowstone. The usefulness of these transitions to assess SSI can only be determined by comparing data from several studies, especially with areas where SSI has been suggested (Swenson et al. 1997, 2001).

The estimates of the proportions of each population in each reproductive state, which we used for illustration, are based on models where transitions did not vary with age. However, the minimum $\mathrm{AIC_c}$ models for both our examples included age as a predictor. For the Yellowstone grizzly bears, the N to C transition varied considerably with age and defined prime reproductive ages as 10–15 years old. We computed stable state compositions of the population based on the model without age effects because incorporating age into these calculations requires considerably more information. That is, to incorporate age to determine the proportion of the population in each state requires that age-specific survival rates and transitions be included.

We feel the assumption of SAD is reasonable for bear populations. Annual survival of female bears is generally high, especially for prime-aged individuals. For example, survival estimates for adult female grizzly bears from 12 study areas across North America ranged from 0.89–0.96 (Schwartz et al. 2003a). None had an adequate sample to estimate age-specific survival rates. Most mortality in independent female bears (no longer dependent upon the female) is directly linked to humans (McLellan et al. 1999, Johnson et al. 2004, Haroldson et al. 2006). One would anticipate reduced survival in physically senescent females. However, even in areas without legal hunting of bears, documenting reduced survival rates in old females is very difficult. First, the number in the population is small relative to prime age classes, and second, many die because of humans before natural mortality occurs. The Yellowstone ecosystem provides a good example. From a sample of 323 radiocollared bears spanning 19 years, 0 and 5 natural mortalities were recorded for independent females and males, respectively (Haroldson et al. 2006). However, Johnson et al. (2004) found that a quadratic function of age was significant in their survival model for this population. A quadratic of age is J-shaped, suggesting reduced survival in young and old animals. But, Johnson et al. (2004) included dependent young (yearlings) that had a lower survival (Schwartz et al. 2006b) than independent bears (Haroldson et al. 2006). When similar data were analyzed excluding dependent young, no age affect was detected. The oldest bear in the Haroldson et al. (2006) sample was 28, and 98% of their sample was comprised of bears ≤20 years of age. One would not expect to observe reduced survival due to physical senescence in a sample comprised of bears of these ages as one would not expect physical senescence to begin prior to reproductive senescence, which occurs around age 28 (Schwartz et al. 2003b).

Capture heterogeneity among age classes of parous females can bias both the proportions and transition estimators. However, we are unaware of published literature suggesting age-specific capture bias independent of reproductive state. Capture heterogeneity between nulliparous and parous females could also bias the transition estimates. Because we started our transitions at age 3, we included females prior to first reproduction. These nulliparous females can only transition from the N state to either the C or N state, and about 90% are expected to transition to the N state for the Yellowstone grizzly example. Consequently, the assumption that sample bias among states does not affect estimates of transitions from the current state may not be correct in this case. The stable age distribution (30 age classes) calculated for this population using estimates of reproduction and survival (IGBST 2005) suggests that approximately 5–8% of independent females (age ≥3) are 3-year-old individuals. Our transition database contained 17 of 222 (7.7%) records where the female's first transition started at age 3, suggesting that the proportion of nulliparous females in the sample approximated what would have been expected in the population assuming a stable age distribution.

In the examples we provide, the comparative statistics between estimates of stable state transitions and estimates derived using direct estimation of the proportions suggest that bear biologists should consider calculating the proportion of females in various reproductive states and reproductive rates using both approaches to determine if capture bias is present in their dataset. Denning and repeated helicopter capture can help minimize bias, especially in long-term studies, but the extent and consequences of bias can only be determined by comparing the statistics calculated with each method. Additionally, unlike the method that uses interbirth interval to estimate reproductive rate (McLellan 1989), which requires keeping females collared through a complete reproductive cycle, the method we propose only requires observing a transition over 1 year. Since radiocollar life, mortality, or censoring often result in observation lengths for individual females that are less than an interbirth interval, these incomplete records still provide data when using transition probabilities.

Study objectives determine sampling design. But often, data collected under one sampling protocol are subsequently used to estimate additional parameters not considered when the design was developed. For example, a habitat study may require a large sample of individuals because n = number of individual bears. Consequently, rather than collar the same individual repeatedly, efforts are made to mark different individuals over the duration of the study. Using data collected under this design to directly estimate reproductive rate would clearly contain a capture bias. We encourage the use of this technique, especially if the study is short in duration and there is little chance of maintaining captured females in the sample over the duration of the study.

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