

CALCULATING AVERAGE AGE OF FIRST REPRODUCTION FREE OF THE BIASES PREVALENT IN BEAR STUDIES

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Abstract: The average age of first reproduction appears to be a useful index of habitat quality for bear populations. However, the conventional method for calculating this age, using only bears whose first litters were observed, gives a low-biased estimate. This bias is a consequence of losing bears approaching their cub-producing years due to death, lost radio contact, or removal of radiocollar. Late-maturing bears are more likely than early-maturing bears to be lost before they produce a litter; thus, if they are not included in the sample, the estimate becomes biased low. We propose a method that generates virtually unbiased estimates of the mean and median ages of primiparity using data from bears that did not produce cubs as well as from those that did. First, we calculate the proportion of females that produced a first litter among all nulliparous females monitored at each age; these proportions are weighted by the proportion of females in the population that are available to have a first litter at each age. This procedure is analogous to the estimation of survivorship based on radio-days of monitoring. We tested our method using data from radiocollared black bears (*Ursus americanus*) in Minnesota and Massachusetts and found that the conventional method underestimated both the mean and median ages of first reproduction by 0.2–0.5 years. Our approach produced an estimate of the expected age of first reproduction free of the effects of study-related shortcomings and independent of mortality. This estimate is more appropriate for cross-population comparisons, as well as for population modeling.

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An individual's reproductive output is a function of 3 factors: age of primiparity, litter size, and interval between litters. Each of these parameters can be defined either in terms of all births or just births of surviving offspring; thus, each may be considered with or without the influence of mortality of dependent young. Also, each parameter can vary within and across populations in response to environmental conditions (habitat, weather, population density, etc.).

For bears, the age of first reproduction appears to be the most sensitive of the 3 reproductive parameters to environmental conditions (Garshelis 1994, Noyce and Garshelis 1994). Thus, estimation of this parameter is critical for comparisons among populations, comparisons among time periods within a population, and for population modeling.

An individual's age of first reproduction may be ascertained in a number of ways, including direct observation during regular monitoring (e.g., at den sites or shortly after den emergence), the spacing of annuli in teeth (Coy and Garshelis 1992, Carrel 1994), size and color of nipples (LeCount 1986, Garshelis et al. 1988, Kasworm and Manley 1988), and characteristics of reproductive tracts (i.e., corpora lutea and placental scars). Each of these methods, though, is prone to some error. Nevertheless, the greatest error may not be in data col-

lection, but in generating a useful statistic (i.e., for population comparisons or projections) from the data.

Ages of first reproduction have been reported as the proportion of bears that had their first cubs at various ages, or more commonly, the mean of these ages weighted by the number of bears that produced cubs at each age. Both of these approaches, however, may yield biased estimates because of bears that died or were otherwise lost from the study (e.g., collar failed, dropped off, or removed by investigator) before reaching primiparity. The bias arises because the group of bears lost from the sample tend to be those that would have produced cubs at a later age than those that were actually observed producing cubs during the study. For example, a bear that would have had its first cubs at 7 years old would more likely be killed or excluded from the sample because the study terminated before it produced its first litter than a bear that reached primiparity at age 4. The estimate of the average age of first reproduction is biased low by the omission of bears that reach primiparity at older ages. This bias may be large in areas where bears are heavily hunted and have a high chance of being killed before producing cubs or in studies of short duration where data collection may end before late-producing individuals have a chance to produce their first litter.

This bias is rectified by simply including all bears, whether or not they had cubs, in the calculation of age of first reproduction. However, we are unaware of other researchers who have done this. In this paper we explain a procedure for calculating a virtually unbiased estimate of the average age of first reproduction and demonstrate its use with data collected from 2 populations of black bears: one heavily hunted (Minnesota) and one lightly hunted which lost many individuals for other reasons (Massachusetts). We show that the analyses for comparing 2 such populations are exactly analogous to the analyses developed for comparing mortality rates (Pollock et al. 1989). For mortality, radiomarked animals are monitored until they die or are lost from the sample; animals whose radios fail, who disperse to some unknown location, or who disappear for other reasons are censored after they are lost, but are counted in the total radio-days of monitoring until that time. Similarly, in calculating the average age of first reproduction, animals are counted until they either have their first cubs or are lost from the sample and censored from further analysis.

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METHODS

Calculation of Mean and Median Age of Primiparity

Our method for calculating the mean age of primiparity is a 4-step process. To demonstrate, we follow a hypothetical example (Table 1).

Step 1.—We begin by calculating the percent of previously nulliparous females in each age class that gave birth to their first cubs (or first surviving cubs). In the example (Table 1, column A), the minimum age of first reproduction was 3, and 5 of 25 3-year-olds (20%) had litters; of the remaining 20 bears that did not produce at 3 years of age, 10 (50%) produced at 4, and the remainder (10 of 10; 100%) produced their first litters at 5.

Step 2.—Based on the results of Step 1, we calculate the percent of females in the total population that were available to have a first litter at each age. In the example (Table 1, column B), all females were available to have their first litter at 3 (100%); 5 of 25 did so, thus 20 females, or 80% of the original cohort, remained available

to have a first litter at 4; 10 of these 20 did so, leaving 10 females, or 40% of the original cohort available to have a first litter at 5.

Step 3.—We multiply the percent of the population available to have a first litter at each age by the percent, within each age, that produced cubs. In the example, 100% (Table 1, column B) multiplied by 20% (column A) equals 20% (column C), which is the percent of females in the population that had their first litter at 3 years old. For 4-year-olds we multiply 80% available by 50% that produced to get 40% of the population that produced a first litter at age 4. And for 5-year-olds we multiply 40% available by 100% that produced to get 40% of the population first giving birth at age 5. These sum to 100% (unless the oldest nulliparous females in the sample had not yet produced).

Step 4.—The mean age of first reproduction is calculated by multiplying the percent of the population that produced first litters at each age (calculated in Step 3) by the corresponding age, and summing these. In the example: $(20\% \times 3 \text{ yr}) + (40\% \times 4 \text{ yr}) + (40\% \times 5 \text{ yr}) = 4.2$ years old (column D).

The conventional estimate of the age of first reproduction, using the same hypothetical data, would be derived by simply averaging five 3-year-olds, ten 4-year-olds, and ten 5-year-olds, which also equals 4.2 years. The correspondence between the conventional method and our method in this example is not a coincidence; it occurs because no bears were lost from the sample. The conventional method is a shortcut for estimating the mean age of first reproduction for the case where all animals that reached reproductive age were monitored until they had their first litter. The procedure becomes biased, however, when animals are lost from the sample after reaching the minimum age of primiparity but before producing cubs.

Bias in the conventional method is shown in our second example, where mortality is added (Table 1). The percent of females in each class that produced a litter is the same as in the first example (i.e., 20% at age 3, 50% at age 4, and 100% at age 5), but because some bears were lost from the sample, the number of bears monitored in each age class was reduced. Specifically, of the 20 females that did not have cubs at age 3, 6 died, leaving only 14 that were alive and had not yet had cubs at age 4; of the 7 females that did not produce at 4 years old, 3 more died, leaving only 4 nulliparous 5-year-old females. Using our procedure, the mean age of first reproduction remains the same, as it should, since the only change was in deaths, not in reproductive rates within each age. The conventional method, however, yields an

Table 1. Calculation of mean and median ages of primiparity using hypothetical data without and with mortality (or other sample loss) between age classes.

Age (yr)	Number of nulliparous females available to produce	Number producing	Number of nulliparous females lost before next age	% of nulliparous females producing (A)	% of females in population available to produce (B)	% of females in population producing (C)	Age weighted % of population producing (D)
No mortality							
3	25	5	0	20	100	20	0.6
4	20	10	0	50	80	40	1.6
5	10	10	–	100	40	40	2.0
Sum		25				100	4.2
Mean age		4.2 ^a					4.2 ^b
Median age		4.25 ^c				4.25 ^d	
With mortality							
3	25	5	6	20	100	20	0.6
4	14	7	3	50	80	40	1.6
5	4	4	–	100	40	40	2.0
Sum		16				100	4.2
Mean age		3.9 ^a					4.2 ^b
Median age		3.93 ^c				4.25 ^d	

^a Conventional estimate of mean age of primiparity.

^b Our estimate of mean age of primiparity.

^c Estimate of the median age of primiparity based only on those that produced, using Sokal and Rohlf's (1969) procedure.

^d Our estimate of the median, derived by finding the age at which 50% of the females had produced cubs.

estimate (3.9 yr) that is biased low by the loss of these 9 bears.

These losses have a similar effect on the median age of primiparity. Again, our estimate includes data on bears that did not produce before they were lost from the sample. We calculate the median using the percent of females in the population that had their first litter at each age. In the example (Table 1, column C), 20% had their first litter at 3 and 40% had their first litter at 4; thus, 20% of females >3 but <4 years old had produced cubs, and 60% between the ages of 4 and 5 had produced cubs. The median represents the age at which 50% of the population would have produced. A simple answer would be 4.0 years old, since bears produce cubs at only 1 time of year, essentially on their own birthday. However, as shown by Sokal and Rohlf (1969), this estimate does not consider that whereas 4 is the median age class, 40% of the bears produced their first litter after age 4 but only 20% produced before age 4. Sokal and Rohlf (1969) presented an alternate calculation of the median that is influenced by the position of the middle value within the median age class. If an equal percent had cubs above and below age 4, then the median would equal 4.0. However, in our example, the distribution is skewed and the median falls 3/4 of the

way into the 4-year-old age class. Although the female at this position is still 4.0 years old, we can derive a more meaningful statistic by assuming that only the middle female among the 4-year-old group is exactly 4.0 years old, and the others decline or increase incrementally and linearly as we move toward the 3- and 5-year-old classes, respectively. On a regression line connecting 20% that had cubs by the time they were 3.5 years of age (exactly between the 3- and 4-year-olds) and 60% that produced by 4.5 years, the median bear, at the 50% mark, would be 4.25 years old. The median age of first reproduction based only on the frequency distribution of ages of bears that produced (Table 1, third column) would be the same as that calculated using all bears that reached reproductive age (Table 1, column C) if there were no losses. As with the mean, however, the median declines and becomes biased low if bears were lost from the sample (Table 1).

Criteria for Inclusion in Sample

In practice, individuals of reproductive age are not only lost from the sample being monitored but are also added. For example, researchers may catch and radiocollar animals older than the minimum age of reproduction, but might determine, from nipple characteristics, weight, or

patterns of cementum annulation, that some of these had not yet had cubs; thus, the age of first reproduction could be ascertained for these bears when they produced cubs at some later time. To maintain an unbiased estimate, though, these individuals should be included only if there were no other bears of the same age with earlier but unknown ages of primiparity.

The process for determining which bears should be included or excluded from the sample is best explained with another hypothetical group of bears with a minimum age of reproduction of 3 years old (Table 2). The first 2 bears in this group are clearly included in the sample, as they have been monitored since at least the minimum age of first reproduction (the first one as a cub, the second since age 3). Using our method the next 2 bears are also included, even though they never produced during the study period. The other bears require more consideration. Bear 5 had first surviving cubs at age 4, although it might have had nonsurviving cubs at 3; bear 6 had its first cubs at 3; bear 7 apparently nursed cubs for awhile, as indicated by its dark nipples (Garshelis et al. 1988), but none survived since no cubs or yearlings were present when it was 4 years old; bear 8 had light-colored nipples at 4, indicating no births before the observed litter at 5. Thus the age of first reproduction was known (with a fair degree of certainty) for only 2 of 4 bears caught first as 4-year olds (bears 6 and 8); the other 2 may have produced nonsurviving cubs at age 3. If we include the known ones and exclude the others, we bias our sample toward bears that did not produce cubs at 3 years old. So as not to introduce this bias, the entire group of bears that were

captured initially as 4-year olds must be excluded. Only when considering the age of first production of surviving cubs can this group of bears be included, because that information is known for 3 of these bears, and the absence of surviving cubs known for the other (bear 7).

Among females captured initially as 5-year olds, there were individuals with both unknown ages of first cub production and unknown ages of production of first surviving cubs (Table 2). Bear 9 had cubs when caught as a 5-year old, but could have had a previous surviving litter at 3 (or nonsurviving litters at 3 or 4). Bear 10 may have had cubs at 3, but assuming that they could not have been reared successfully in <1 year, its first surviving litter must have been at 4 since it had yearlings at 5. Bear 11 had dark nipples indicating a previous litter, possibly as a 3-year old (which could have survived) or as a 4-year old (which must not have survived, since there were no yearlings with her at 5). Bear 12 had light nipples, so its first potentially surviving cubs were those observed when it was 6 years old; however, because the bear died, that litter may not have survived. Due to these uncertainties, this whole group (bears 9–12) must be omitted from the analysis of age of production of first cubs and of first surviving cubs. Omitting this group, but not the group caught initially as 4-year olds (when considering the age of production of first surviving cubs), would not introduce a bias as long as no relationship existed between capture proneness and reproductive history.

The spacing of annuli in teeth of captured bears may provide more definitive documentation of surviving litters but not nonsurviving litters (Coy and Garshelis 1992,

Table 2. Reproductive characteristics of a hypothetical group of 12 bears monitored to assess age of first reproduction; ambiguous evidence for first reproduction necessitates exclusion of most of these data.

ID	Age (yr) when first monitored	Evidence of first reproduction	Age at production of	
			First cubs	First surviving cubs
1	0	Cubs at 4 yrs, yearlings at 5	4	4
2	3	Cubs at 7 yrs, yearlings at 8	7	7
3	3	None through age 7, died at 7	>7	>7
4	3	None, died at 5	>5	>5
5	4	Cubs at 4 yrs, yearlings at 5	3 or 4	4
6	4	Yearlings at 4 yrs	3	3
7	4	Dark nipples at 4 yrs, but no cubs or yearlings at 4	3?	>4
8	4	Light nipples at 4 yrs, cubs at 5, yearlings at 6	5	5
9	5	Cubs at 5 yrs, yearlings at 6	≤5	3 or 5
10	5	Yearlings at 5 yrs	3 or 4	4
11	5	Dark nipples at 5 yrs, but no cubs or yearlings at 5	3 or 4	≥3
12	5	Light nipples at 5 yrs, cubs at 6, died at 6	6	6?

Carrel 1994) than data on the presence or absence of cubs and yearlings and observations of nipple characteristics. Annular patterns may be difficult to interpret in some cases, but unless such ambiguity is related to the age of first cub production, exclusion of ambiguous cases would not bias the sample. Thus, if teeth were available for the hypothetical sample (Table 2), all bears could theoretically be included in the calculation of the average age of first production of a surviving litter.

Using teeth to reconstruct reproductive histories, the only remaining enigmatic individual would be bear 3. This bear never had cubs and died at 7 years old. If she had not died and eventually had cubs, her age of first cub production would have been the oldest in the study. Just as other bears that died before producing a surviving litter (e.g., bears 4 and 7), bear 3 could be included as not having a surviving litter at 3–7 years old and then censored (removed from the data set) at age 7. However, in censoring bears that never produced surviving cubs but who lived past the age that all other bears had their first litter, the sample becomes biased toward animals that produced cubs at younger ages; it is this bias that we are trying to avoid by including records of bears that did not have cubs at young ages. To avoid this bias, we could assume that bear 3 would have produced its first surviving cubs at 8, which would yield a minimum estimate of the average age of first reproduction that would still be higher than the estimate generated with this bear excluded.

Application of Procedure

We applied our procedure to data collected on black bears in northcentral Minnesota (see Noyce and Garshelis [1994] for description of study area) and western Massachusetts (see Fuller 1993) during 1981–96. Bears were radiocollared either as yearlings in the den with their mothers or when captured at an older age. We determined the age of bears that were not initially marked as cubs or yearlings by counting cementum annuli on an extracted premolar (Willey 1974).

We immobilized radiocollared females in dens each March to assess reproduction and eartag cubs. We checked these females in dens the following year to determine cub survival; surviving cubs should have been present as yearlings. We categorized litters with ≥ 1 yearling in the den as surviving and 0 yearlings as nonsurviving. We never reobserved, among trapped or harvested animals, a bear tagged as a cub that was not present with its mother as a yearling. Generally, if a mother died before denning (i.e., in the fall hunt), litter survival was unknown; however, in a few cases we were able to confirm litter survival if we observed the mother

and cubs together in the fall just before her death, captured ≥ 1 cub shortly after her death, captured an animal from the orphaned litter at a later date, or obtained ear tags from a hunter who killed one of the orphans.

For females first collared at < 3 years old, age of first reproduction was determined directly from observations at dens. For bears first captured and collared as 3-year olds, the minimum cub-bearing age observed in this study, we assessed whether they did or did not have cubs by lactation, nipple color and size, visual observations and den visits; if a 3-year old did not have cubs when captured and had small (< 1 cm), pink nipples, we categorized it as having not produced a litter. For bears initially captured at > 3 years old, production of surviving litters was assessed from nipple characteristics as well as the pattern of annuli in an extracted tooth (Coy and Garshelis 1992). For some we observed litter production and survival from den visits, which we later corroborated as the first surviving litter by obtaining and examining another tooth. Although we included bears caught initially at ≥ 3 years old in the analysis of the age of first production of a surviving litter, we did not include them in the analysis of the age of first reproduction because nonsurviving litters were not detectable from the pattern of cementum annuli.

We grouped data by study area (Minnesota or Massachusetts) and separately analyzed age of first reproduction and age of first production of a surviving litter. We used PROC LIFETEST (SAS Inst., Inc. 1996) to compare ages of primiparity between groups. This procedure was designed to compare survival curves but it can be adapted to ages of first reproduction, since both mortality and first litter production can occur only once in an animal's life. Each record consisted of an animal identification number, its age (in whole years) when it produced a litter or was lost from further observation, a field to indicate whether the age represented cub production or censorship due to loss, and a field identifying groups for comparison. We used different sets of data for first litters and first surviving litters.

PROC LIFETEST (SAS Inst., Inc. 1996) calculates the average (and standard error) time that an event occurred. For mortality data this would represent the average life-span but for our purposes this is the average age of primiparity. The procedure also generates survival curves, representing the rate of decline in the proportion of animals of a cohort remaining (i.e., that did not yet die) through time (starting at 1.0 at time 0, and declining toward 0). For our data these curves represent the declining proportion of animals that had not yet produced their first litter (corresponding to the proportion of females in

the population available to produce, Table 1, column B). PROC LIFETEST uses these age-specific values to test for differences between populations using nonparametric Wilcoxon and log-rank tests (Lee 1992).

Using PROC LIFETEST we found that animals who did not produce cubs through an age older than the oldest observed age of primiparity were censored not at the age that they were lost (or the study ended), but at the age of the oldest known age of primiparity. For example, a 7-year-old Massachusetts bear whose tooth indicated that it had not yet produced a surviving litter would have been censored by PROC LIFETEST at age 6, the maximum age of primiparity observed among other Massachusetts bears. We did not concur with this treatment of the data. Instead, we assumed that this bear would have produced at age 8 (i.e., we entered it in the data set as having produced at 8).

RESULTS

Age of primiparity was directly observed for 32 bears in northcentral Minnesota and 19 bears in western Massachusetts (Table 3). We monitored another 29 bears in Minnesota who reached ≥ 3 years old but were lost from the sample before producing their first cubs and 5 such bears in Massachusetts. Mean age of primiparity for Minnesota bears was 5.0 years using our method (i.e., using all available data), but only 4.6 years using the conventional method (i.e., including only those bears that produced cubs). Median ages of primiparity using all bears versus just those that produced cubs differed by about the same amount (0.3 yr, Table 3). The median was less than the mean because it was not affected by the long tail of the distribution (i.e., the single bear that first gave birth at 10 years old). Mean age of primiparity in Massachusetts was 3.7 years using our method and 3.5 years using the conventional method; again the medians differed by about the same amount (0.2 yr, Table 3). Ages of primiparity were significantly younger in Massachusetts than in Minnesota (log-rank and Wilcoxon tests, $P < 0.0001$).

Age of production of a first surviving litter was directly observed for 34 Minnesota bears and 15 Massachusetts bears. Teeth provided an additional 26 records of the age of production of first surviving litters in Minnesota and another 13 records in Massachusetts (Table 4). Based only on these bears, the mean and median ages of first production of a surviving litter were 4.8 and 4.7 years, respectively, in Minnesota and 4.6 and 4.4 years, respectively, in Massachusetts (i.e., a difference of 0.2–0.3 yr). However, 33 bears were lost from the sample in Minne-

sota and 21 were lost in Massachusetts before they produced surviving cubs but after reaching the age that other bears had surviving cubs. Including these in the calculation, the mean and median ages rose to 5.0 and 4.8 years, respectively, in Minnesota and 5.1 and 4.9 years, respectively, in Massachusetts (i.e., a difference of only 0.1 yr between areas). Whereas age of primiparity was younger in Massachusetts than in Minnesota, cub survival for first litters in Massachusetts was low; thus, the ages of first production of surviving litters were similar in the 2 states ($P > 0.7$). This conclusion would have been the same using the conventional estimate of age of first reproduction, although the similarity between the 2 areas was more obvious using the unbiased estimate (Table 4).

DISCUSSION

Several authors compared the ages of first reproduction of bears from different areas and related differences to nutrition (Beecham 1980, Alt 1989, Beck 1991, Schwartz and Franzmann 1991, Garshelis 1994, McLaughlin et al. 1994, Miller 1994). However, these comparisons may have been misleading, as these studies all estimated average ages of primiparity by the conventional approach. Two studies, though, attempted to adjust for the inherent negative bias resulting from the loss of older-age, nulliparous bears. Schwartz and Franzmann (1991) and Miller (1994) assumed that females that had reached the mean age of first reproduction but died before having cubs would have produced a litter the next year. This assumption improves the estimate of the average age of primiparity, but the estimate still tends to be biased low because some bears that were assumed to produce cubs the next year really would have produced 2 or more years later. To illustrate this, consider again our hypothetical example that includes mortality (Table 1). If the 6 bears that died between age 3 and 4 are tallied as having cubs at 4 (i.e., total = 13 producing cubs at 4), and the 3 that died between age 4 and 5 are tallied as having cubs at 5 (i.e., total = 7 producing at 5), the calculated mean age would be 4.08 years, still less than the 4.2 years derived using our method. Only if all mortality occurred just prior to the oldest possible age of primiparity (just before age 5 in our example) would this procedure of adding 1 year to bears that died before they produced cubs yield the correct estimate. If we had applied this correction procedure to the actual data from our study (Table 3), mean ages of first cub production would have increased (from 4.6 to 4.8 years in Minnesota and from 3.5 to 3.6 years in Massachusetts), but still would have been biased low,

Table 3. Production of first litters directly observed among radiocollared black bears in northcentral Minnesota and western Massachusetts, 1981–96, showing calculation of mean and median ages of primiparity and other statistics^a.

Age (yr)	Number of nulliparous females available to produce	Number producing	% of nulliparous females producing (A)	% of females in population available to produce (B)	% of females in population producing (C)	Age weighted by % of population producing (D)
Minnesota						
3	61	2	3.3	100.0	3.3	0.10
4	37	16	43.2	96.7	41.8	1.67
5	17	11	64.7 ^a	54.9 ^a	35.5 ^a	1.77 ^a
6	3	1	33.3	19.4	6.5	0.39
7	2	1	50.0	12.9	6.5	0.45
8	1	0	0	6.5	0	0
9	1	0	0	6.5	0	0
10	1	1	100.0	6.5	6.5	0.65
Sum		32			100 ^b	5.03
Mean age		4.62 ^c				5.03 ^d
Median age		4.38 ^e			4.64 ^f	
Massachusetts						
3	24	13	54.2	100.0	54.2	1.63
4	6	3	50.0	45.8	22.9	0.92
5	3	3	100.0	22.9	22.9	1.14
Sum		19			100 ^b	3.69
Mean age		3.47 ^c				3.69 ^d
Median age		3.23 ^e			3.42 ^f	

^a Raw data are shown in second and third columns. Calculated statistics are shown in columns lettered A–D. Procedure for calculating these statistics are demonstrated using 5-year olds in Minnesota: (A) 11/17 = 64.7% of 5-year-olds that had not previously had cubs produced a litter; (B) 96.7% of females had not produced a litter at 3 years old, and 100% - 43.2% = 56.8% of these had not produced at age 4, so 56.8% of 96.7% = 54.9% of females in the population were available to produce a first litter at age 5; (C) 64.7% of 54.9% = 35.5% of the population produced first cubs at 5 years old; (D) 35.5% × 5 years = 1.77, the percent of the population producing weighted by the respective age.

^b Column should total 100%.

^c Conventional estimate of mean age of primiparity.

^d Our estimate of mean age of primiparity. Age for Minnesota females was significantly greater than in Massachusetts ($P < 0.0001$).

^e Estimate of the median based only on those that produced, using Sokal and Rohlf's (1969) procedure.

^f Our estimate of the median derived by interpolating the age at which 50% of the females had produced cubs.

because losses occurred among several age classes of radiocollared females and all were relatively young (3–5 years old). Using our method, the same estimate is obtained regardless of the existence or pattern of mortality or other losses among reproductive-age bears.

Our method differs from other methods in that it considers the percent of females that produced cubs based on those that were available to do so. Garshelis (1993) previously illustrated the problem with the conventional estimate of the average age of first reproduction and suggested calculating the percent of nulliparous females that produced cubs at each age, which is the first step in the process that we developed further here.

In work with marine mammals, DeMaster (1978, 1981) also devised methods of estimating average age of maturity and of first birth that include the number of

females available to produce at each age. However, his assumptions are not appropriate for bears. In his first paper, DeMaster (1978) assumed that once an animal gave birth, it did so every year thereafter. In his second paper, DeMaster (1981) incorporated the possibility of animals skipping annual births, but he assumed that all females of the same age had an equal probability of giving birth, whether or not they previously produced. With regard to bears, this assumption would mean that a female that had cubs at 3 years old would be no more likely to produce again at 5 than a nulliparous 5-year old. DeMaster (1981) also assumed that the age of first reproduction did not fluctuate yearly. If not for the probable violation of these assumptions in most bear populations, DeMaster's (1981) method would yield the same result as ours, even with mortalities and other losses.

Table 4. Production of first surviving litters by radiocollared female black bears in northcentral Minnesota and western Massachusetts, based on direct observations and spacing of annuli in teeth collected during 1981–96.

Age (yr)	Number of nulliparous females available to produce	Number producing	% of nulliparous females producing (A)	% of females in population available to produce (B)	% of females in population producing (C)	Age weighted by % of population producing (D)
Minnesota						
3	93	3	3.2	100.0	3.2	0.10
4	67	22	32.8	96.8	31.8	1.27
5	40	28	70.0	65.0	45.5	2.27
6	7	4	57.1	19.5	11.1	0.67
7	3	2	66.7	8.4	5.6	0.39
8	1	0	0	2.8	0	0
9	1	0	0	2.8	0	0
10	1	1	100.0	2.8	2.8	0.28
Sum		60			100.0	4.98
Mean age		4.75 ^a				4.98 ^b
Median age		4.68 ^c			4.83 ^d	
Massachusetts						
3	49	2	4.1	100.0	4.1	0.12
4	37	13	35.1	95.9	33.7	1.35
5	17	9	52.9	62.2	32.9	1.64
6	5	3	60.0	29.3	17.6	1.06
7	1	0	0	11.7	0	0
8	1	1 ^e	100.0	11.7	11.7	0.94
Sum		28			100.0	5.11
Mean age		4.61 ^a				5.11 ^b
Median age		4.42 ^c			4.87 ^d	

^a Conventional estimate of mean age of first production of surviving cubs.

^b Our estimate of mean age of first production of surviving cubs. Ages of females in Minnesota and Massachusetts were not different ($P > 0.7$).

^c Estimate of the median based only on those that produced using Sokal and Rohlf's (1969) procedure.

^d Our estimate of the median, derived by interpolating the age at which 50% of the females had produced cubs.

^e This bear had not produced a surviving litter by 7 years of age, based on the pattern of annuli in its teeth, but was assumed to produce a litter at age 8; deleting this bear from the sample would have biased the estimate low.

Taylor et al. (1987) formulated a method for estimating age of first reproduction in polar bears (*Ursus maritimus*) from visual surveys during the spring after females emerged from maternity dens. Their method also compares those that had cubs to those available to have cubs, and like DeMaster (1981), they assume that all available females of the same age (whether they had just broken up with a set of offspring, skipped a year since breaking up, or never had cubs before) were equally likely to produce cubs the next year. To determine the percent of females of each age available to produce cubs, they subtract those that died at the previous age; in contrast, we use the percent that would have been available if none had died. Our estimate thus represents the expected age of first reproduction had all bears lived to produce, whereas theirs represents the average age of primiparity among those that lived. Consequently, their estimate is

like the conventional estimate, and as Taylor et al. (1987) acknowledge, would change with changes in mortality rate. Although their estimate was appropriate for the type of population model they used, it would not be appropriate for many other population models or for cross-population comparisons of reproductive potential.

In Minnesota, we use year-specific estimates of the percent of nulliparous females producing at each age (Table 3, column A) as inputs for population modeling, rather than the mean age of primiparity. The values obtained in the other steps of the process of calculating a mean age are also useful, and for some purposes more useful than the mean age. For statistically comparing age of primiparity between 2 or more populations, 2 groups of bears in 1 population (e.g., Rogers 1987), or 1 population at 2 different time periods, we would employ values for the percent of females in the population

that are still nulliparous at each age (Table 3 or 4, column B), which is analogous to a comparison of survivorship curves (e.g., PROC LIFETEST). To calculate a median age of primiparity, we would use the percent of females in the population producing a first litter at each age (Table 3 or 4, column C). Lee (1992) recommended a graphical approach using survivorship curves (i.e., the percent of females available to produce, column B), but we believe that our procedure for calculating the median is simpler and more exact.

The advantage of the median is that, unlike the mean, it is not affected by the shape of the tail of the distribution. For example, the bear in our Minnesota study that had her first litter at 10 years old (Tables 3 and 4) could have produced several years earlier or later without affecting the median. If bears like this are considered outliers, the median age of primiparity may better represent the population. However, if these bears in the tail of the distribution are thought to characterize a small but significant portion of the population, a portion that may distinguish this population from another, then differences between these populations would be more evident in a comparison of means.

The relative advantages of means versus medians also depend on the length of the study. In relatively short term studies, when several nulliparous females may be older than the median age of first reproduction, assumptions regarding their ages of primiparity would be necessary to calculate a mean, but not a median. Similarly, in a study comparing ages of primiparity between 2 time periods, the mean might appear to decline only because the most recent period included bears who would have produced cubs at an old age but were not observed to do so because the observation period ended; a comparison of median ages of primiparity would avert this potential problem.

No numerical procedure can totally avoid the potential bias arising from a monitoring period that is too short to document relatively old ages of first reproduction. For this reason, estimates of the average age of primiparity will invariably be biased low during the early years of a study, when the sample may include nulliparous females that are older than the oldest observed age of primiparity. Schwartz and Franzmann's (1991) and Miller's (1994) method of assuming that each of these bears would produce cubs the following year provides a reasonable, albeit imperfect remedy. We made this assumption for the oldest nulliparous bear in Massachusetts (Table 4). However, there is no way to truly correct for a biased sample that stems from insufficient data.

Anomalous data also may bias the sample. In some places there may be a few females that never produce cubs (e.g., LeCount 1987), either because of infertility or insufficient weight. If females like this are included in the sample, they would, with each year of monitoring, stretch out the tail of the distribution, thereby increasing the mean (but not the median). Such cases could be handled by partitioning out the anomalous individuals, reporting how many there were, and then proceeding with the calculation of relevant statistics. One problem with this approach is that it is difficult to determine with certainty that a bear will never produce cubs. In our Minnesota study there was little evidence that the 10-year-old female (Tables 3 and 4) would ever produce, as her weights in the den were consistently below the minimum threshold for reproduction (Noyce and Garshelis 1994). When she finally did have cubs they were small, and when checked in the den as yearlings were so light (<6 kg) that they had a negligible chance of survival the following spring. However, for litter survival we considered only the first year of life. These considerations and others regarding what bears to include and how to include them (see Methods) are as important as the calculations themselves. If the Minnesota bear that had her first cubs at age 10 had not produced during the course of our study and had consequently been excluded from the sample (i.e., considered anomalous), the mean age of primiparity would have been 0.3 years lower, and thus closer to the mean age in Massachusetts (although, even without this bear, the distributions would still have been significantly different, $P < 0.0001$).

An explanation of the difference between ages of primiparity in Minnesota and Massachusetts (Table 3) is beyond the scope of this paper. Our purpose for presenting the 2 data sets was to demonstrate that the conventional estimate of the mean can be significantly biased both in heavily hunted populations like Minnesota, where losses were due mainly to death, as well as lightly hunted populations like Massachusetts, where radiocollars failed or were removed from bears before they produced cubs.

As shown by these examples, the conventional method yields a low-biased estimate because late-maturing bears are more likely than early-maturing bears to die or otherwise drop out of the sample before reproducing. The extent of bias varies with the proportion of the sample lost prior to production of a first litter. In our 2 studies, the discrepancy between the biased estimate and our estimate of the mean and median ages of primiparity varied from 0.2–0.5 years. This amount of bias is not trivial considering: (1) the fairly narrow range of ages that bears normally reach sexual maturity (i.e., about 90% of black

bears in North America produce their first cubs during a 4-year age-span [Garshelis 1994]), (2) the effects of small samples and individual or year-specific variability on study results, and (3) the sensitivity of population growth rate and sustainable mortality to small changes in the age of first reproduction (Bunnell and Tait 1981). If ages of first reproduction are used to compare populations or to assess trends within a population, it is clearly advantageous to eliminate known biases in order to more effectively detect real differences.

The bias in conventional estimates of the average age of primiparity is analogous to the bias in estimates of mortality derived by dividing the number of deaths by the total number of animals monitored (Heisey and Fuller 1985). In both cases, the estimate becomes skewed by the loss or "censoring" of animals during the study. Most bear studies now employ mortality estimators that deal with censored data (e.g., Heisey and Fuller 1985, Pollock et al. 1989). We used an analogous procedure to calculate average ages of first reproduction and to make statistical comparisons among groups of bears across populations.

It is important to reiterate that our approach yields the expected age of first reproduction that would be realized had there been no censored data. If all bears were lost due to radio failure, emigration beyond the range of monitoring, or other events related to deficiencies in the study, the estimate obtained using our method would represent the real mean age of primiparity in the living population. However, if some losses were due to death, our estimate would represent the expected age of first reproduction had all bears lived to produce a litter. That is, the estimate generated using our method is free of the effects of mortality. We believe that this is the most appropriate estimator for cross-population comparisons aimed at assessing relative habitat quality because differences in average age of primiparity would not be confounded by differences in rates of mortality of young, reproductive-age females. Similarly, this procedure yields results more suitable for population models, which typically employ separate (independent) inputs (or outputs) for mortality and reproduction.

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