

Reproductive maturation and senescence in the female brown bear

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Abstract: Changes in age-specific reproductive rates can have important implications for managing populations, but the number of female brown (grizzly) bears (*Ursus arctos*) observed in any one study is usually inadequate to quantify such patterns, especially for older females and in hunted areas. We examined patterns of reproductive maturation and senescence in female brown bears by combining data from 20 study areas from Sweden, Alaska, Canada, and the continental United States. We assessed reproductive performance based on 4,726 radiocollared years for free-ranging female brown bears (age ≥ 3); 482 of these were for bears ≥ 20 years of age. We modeled age-specific probability of litter production using extreme value distributions to describe probabilities for young- and old-age classes, and a power distribution function to describe probabilities for prime-aged animals. We then fit 4 models to pooled observations from our 20 study areas. We used Akaike's Information Criterion (AIC) to select the best model. Inflection points suggest that major shifts in litter production occur at 4–5 and 28–29 years of age. The estimated model asymptote (0.332, 95% CI = 0.319–0.344) was consistent with the expected reproductive cycle of a cub litter every 3 years (0.333). We discuss as-

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sumptions and biases in data collection relative to the shape of the model curve. Our results conform to senescence theory and suggest that female age structure in contemporary brown bear populations is considerably younger than would be expected in the absence of modern man. This implies that selective pressures today differ from those that influenced brown bear evolution.

Key words: AIC, Akaike's information criteria, brown bear, grizzly bear, maturation, modeling, reproduction, senescence, *Ursus arctos*

Effects of aging on survival and reproductive success are key elements of life history theory and demographic modeling. Senescence is an age-related decrease of an organism's survivorship or fecundity (Williams 1957) associated with declining physiological function (Adams 1985). Patterns of reproduction and survival for many long-lived mammals tend to follow a roughly bell-shaped curve (Gaillard et al. 1994). Reproductive senescence has been documented in many long-lived mammals, including humans (Williams 1957, Hamilton 1966, Rogers 1993, Hawkes et al. 1997), non-human primates (Paul et al. 1993, Johnson and Kapsalis 1995), and ungulates and carnivores (Eberhardt 1985, Fisher et al. 1996, Packer et al. 1998, Bérubé et al. 1999, Ericsson et al. 2001).

Senescence has been attributed to cellular breakdown or other long-term diminishment of an animal's physiological state (Adams 1985). Evolutionary theory explains senescence as a consequence of age-specific selective pressures and reproductive costs (Williams 1957, Hamilton 1966). For some long-lived mammals (i.e., humans and some non-human primates, Paul et al. 1993), reproductive senescence occurs well before the limits of physical longevity are reached. Williams (1957) postulated that selection could favor continued survival of post-reproductive individuals if the survival and successful reproduction of offspring required extended parental care. The adaptive menopause hypothesis assumes that post-reproductive females actively enhance the fitness of their prior offspring and their young (Williams 1957, Hamilton 1966, Hawkes et al. 1997). For mammals that do not provide maternal care to prior offspring, one would expect post-reproductive survival to be short in wild populations (Williams 1957). Current theory suggests a tendency for individuals not to survive beyond the normal age of last reproduction (Gaulin 1980, Mayer 1982) because there is no selective advantage in doing so.

Theory suggests that age-specific reproduction in brown (grizzly) bears should be well described by the bell-shaped curve of Gaillard et al. (1994). Moreover, because brown bears do not provide extended maternal care to previous offspring or their young, patterns of

reproductive senescence should mirror patterns of survival, giving insights into physical longevity and expected female age structure under the conditions in which brown bears evolved. Such patterns have not previously been quantified, however. Reviews by Craighead and Mitchell (1982:527) and Pasitschniak-Arts (1993:5) concluded that "reproductive longevity approximates physical longevity." Later, Craighead et al. (1995:414) recognized that "young and old adult females (4–8 and 21–25 years of age, respectively) had lower fertility than prime-aged females (9–20)," but they lacked sufficient information for older age classes to quantitatively characterize senescence patterns. Caughley (1977) and Eberhardt (1985) discussed the application of Lotka's equations (Lotka 1907) to summarize rates of increase using age-specific survivorship and fecundity. Eberhardt (1985) suggested constructing a reproductive curve with 3 stages. The first stage was early reproduction, the second included prime years of adulthood, and the third reflected reduced reproduction due to senescence. Eberhardt (1985) suggested that, with adequate data, a continuous curve across all ages could be fit, recognizing that only values corresponding to discrete ages were relevant. He recommended fitting a 3-parameter growth curve (Brody 1945) to the early reproductive data, and a 3-parameter Gompertz curve to the senescence component. Multiplying the curves together generated a continuous model. Eberhardt (1985) fit curves to several data sets, setting age of senescence subjectively in cases where fits to the Gompertz curve were unsuccessful.

There are discrepancies in the literature regarding effects of reproductive senescence on the finite rate of population change (λ), with some studies suggesting pronounced effects (Noon and Biles 1990) and others (Packer et al. 1998) showing little impact. In either case, however, quantifying age-specific reproduction is prerequisite to making such a determination.

In this paper we model age-specific reproductive changes in the brown bear by combining data from multiple studies, then fitting those data to models describing the processes of maturation and senescence.

Table 1. Geographic area, years of study, and sample size ($n = 4,726$ radiocollar years) for the 20 data sets used to model reproductive maturation and senescence in the brown bear. References provide descriptions for each study area.

Geographic area	Study area	Years sampled	Females observed (n)	Reference
Sweden	Southern area	1985–99	199	Björvall and Sandegren (1987)
	Northern area	1984–99	177	Björvall and Sandegren (1987)
Alaska	Kodiak Island	1982–97	943	Barnes and Smith (1998)
	Black Lake	1988–96	251	Miller et al. (1997)
	Game Management Unit 13	1980–97	358	Miller et al. (1997)
	Katmai National Park	1989–96	223	Sellers and Miller (1999)
	Denali National Park	1991–98	162	Keay (2001)
	Canning River	1973–75	51	Reynolds et al. (1976)
	Western Brooks Range	1977–95	489	Reynolds and Garner (1987)
	Arctic National Wildlife Refuge	1982–90	326	Reynolds and Garner (1987)
	North Central Alaska Range	1981–2000	398	Reynolds (1999)
Canada	Bow River	1994–99	112	Gibeau (2000)
	Kluane	1989–98	124	McCann (unpublished data)
	West Slopes	1994–2000	54	Woods et al. (1999)
	Flathead	1979–2000	163	Hovey and McLellan (1996)
Continental USA	Selkirk Mountains	1983–2000	67	Wielgus et al. (1994)
	Cabinet–Yaak Mountains	1983–2000	46	Kasworm et al. (1998)
	Northern Continental Divide	1986–96	53	Mace and Waller (1998)
	Yellowstone Ecosystem	1975–99	359	Eberhardt et al. (1994)
	Yellowstone National Park	1959–70	171	Craighead et al. (1995:181)

We followed the approach recommended by Eberhardt (1985). However, rather than fitting separate models to each stage, we simultaneously fit a continuous function describing both the maturation and senescence processes, thereby eliminating the need to arbitrarily estimate age at senescence. We fit and compared 4 variations of a general model describing reproduction, maturation, and senescence, and used AIC to select the best model (Anderson et al. 2001).

Study area and methods

We obtained data from 20 brown bear studies; all but 2 were from geographically distinct areas. We used recent data from the Greater Yellowstone Ecosystem and historic data from Yellowstone National Park; these are effectively the same area, but the data span different periods (Table 1). Each bear was aged by sectioning a premolar tooth and counting annuli (Stoneberg and Jonkel 1966) or was monitored from birth. Radio-telemetry and visual observations were used to determine the reproductive status of each female each year. Descriptions of study areas, sampling protocols, and other details can be found in previously published literature (Table 1). Authors are listed in order of sample size provided except for first author (Schwartz) and second author (Keating), who developed the models.

Each investigator provided information on the reproductive status of each collared female bear each year. Data were treated as binomial: females were classified as with cubs-of-the-year or without. Because many collared bears were observed in multiple years, observations were not independent. Only bears whose reproductive status was visually ascertained were included in the sample. Females known to have lost litters were classified as producing cubs for this analysis. We did not include bears <3 years of age because brown bears do not reach sexual maturity (age at first breeding) until at least age 3.5 in North America (Schwartz et al. 2003), and there are few records of 3-year olds producing first litters elsewhere (Zedrosser et al. 1999, Frkovič et al. 2001).

Modeling and data analysis

General model. To model age-specific probabilities of litter production, we defined $N_{R,t}$ as the number of reproductive females of age t in the population; i.e., the numbers that were reproductively mature, but not yet senescent. Let $N_{R,t}$ be a binomial random variable, such that

$$E(N_{R,t}) = N_t p_t,$$

where N_t is the total number of females of age t and p_t is the probability that a female of age t is reproductively

mature and non-senescent. Next, let L_t be the number of litters produced by females of age t , and assume $E(L_t) \propto E(N_{R,t})$, with proportionality constant m_t . It follows that,

$$E(L_t) = m_t E(N_{R,t}) = m_t N_t p_t \tag{1}$$

where m_t is the expected productivity (in this case, number of litters) per reproductively mature, non-senescent female of age t , per year. In this case, bear biology constrains annual productivity, such that $0 \leq m_t \leq 1$; thus, L_t also is a binomial random variable [$L_t \sim \text{Binomial}(N_t, mp_t)$]. Now, let

$$p_t = p_{M,t}(1 - p_{S,t})$$

where $p_{M,t}$ is the probability that a female will be reproductively mature by age t and $p_{S,t}$ is the probability that a female will be reproductively senescent by age t . It follows that $1 - p_{S,t}$ is the probability that a female is not reproductively senescent by age t . Substituting into Eq. (1) gives the most general form of our model:

$$E(L_t) = m_t N_t p_{M,t}(1 - p_{S,t}) \tag{2}$$

Theoretically, $p_{M,t}$ and $p_{S,t}$ can each be modeled using any cumulative distribution function (cdf) with domain $t \geq 0$. It is not necessary to use the same cdf to describe both. Also, either could be modeled as the product of multiple cdfs (each with domain $t \geq 0$) to describe situations where more complex relationships between age and reproductive performance are suspected. We considered the case where the relationship between age and productivity might differ between prime- and old-aged females, as suggested by Eberhardt (1985). Thus, we modeled the age-specific probability of senescence as

$$p_{S,t} = 1 - (1 - p_{P,t})(1 - p_{O,t}) \tag{3}$$

where $p_{P,t}$ is the probability that a female will be reproductively senescent by age t due to factors operating on prime-aged animals, and $p_{O,t}$ is the corresponding probability due to factors operating on old-aged animals. Lacking age-specific information on annual per capita productivity, we also simplified our general model by assuming that m_t is constant with age, so that $m_t = m$. We expected that $m \approx 0.333$ because adult female brown bears typically produce a litter about every third year. Substituting Eq. (3) into Eq. (2) gives the general model we evaluated,

$$E(L_t) = m N_t p_{M,t}(1 - p_{P,t})(1 - p_{O,t}). \tag{4}$$

The slope of the model, $d[E(L_t)]/dt$, gives the age-specific rate of change in per capita litter production

and can be used to characterize important aspects of the maturation and senescence processes. We estimated age of maximum per capita litter production by setting $d[E(L_t)]/dt = 0$ and solving for t . We estimated modal ages of primiparity and senescence as the maximum and minimum, respectively, of $d[E(L_t)]/dt$ by examining the second derivative at $d^2[E(L_t)]/dt^2 = 0$.

Specific forms of the model parameters. We derived a specific model for $p_{M,t}$ from the cdf for the generalized extreme value distribution (Johnson et al. 1995:75),

$$F_T(t) = e^{-\{1-\gamma[(t-\xi)/\theta]\}^{1/\gamma}}, \quad t \geq \xi + \theta/\gamma, \quad \gamma < 0 \tag{5}$$

where γ , ξ , and θ are parameters of the distribution. Setting $t \geq 0$ (because age must be positive) gives $\gamma = -\theta/\xi$. Substituting into Eq. (5) gives our model for $p_{M,t}$,

$$p_{M,t} = e^{-(t/\xi)^{-\xi/\theta}}, \quad t \geq 0, \quad \theta > 0, \quad \xi > 0. \tag{6}$$

We selected this model largely because the probability density function (pdf) is right-skewed, a form that is qualitatively consistent with the few reported distributions of age at primiparity (see York 1983, Reiter and Le Boeuf 1991).

Using the cdf for the power distribution function (Johnson et al. 1995:672), we modeled senescence for prime-aged animals as

$$p_{P,t} = \left(\frac{t}{\xi}\right)^\theta, \quad 0 \leq t \leq \xi. \tag{7}$$

The value $1 - (t/\xi)^\theta$ gives the probability of not being reproductively senescent at age t , and equals zero when $t = \xi$. This model was selected to mimic a process in which litter production declines steadily until some upper age threshold is reached. Such a pattern might be expected if fecundity declined with, say, the number of remaining oocytes or increased embryonic mortality, as suggested by Adams (1985).

We modeled senescence among old-aged animals using a variation of the cdf in Eq. (5),

$$p_{O,t} = 1 - e^{-(t/\xi)^{\xi/\theta}}. \tag{8}$$

This model is similar to the one for $p_{M,t}$, except that the pdf is left- rather than right-skewed. We selected this model to describe reduced reproductive success resulting from overall physical senescence. Selection should favor individuals that delay physical and, hence, reproductive senescence as long as possible; it follows that the probability of becoming reproductively senescent due to overall physical deterioration should increase at a more rapid rate late in life (Adams 1985). A left-skewed pdf is consistent with this reasoning.

Model comparisons. Substituting various combinations of Eqs. (6)–(8) for $p_{M,t}$, $p_{P,t}$ and $p_{O,t}$ in Eq. (4), we fit and compared 4 variations of our general model:

$$\begin{aligned}
 \text{Model A: } E(L_t) &= mN_t e^{-(t/\xi_M)^{-\xi_M/\theta_M}} \\
 \text{Model B: } E(L_t) &= mN_t e^{-(t/\xi_M)^{-\xi_M/\theta_M}} [1 - (t/\xi_P)^{\theta_P}] \\
 \text{Model C: } E(L_t) &= mN_t e^{-(t/\xi_M)^{-\xi_M/\theta_M}} e^{-(t/\xi_O)^{\xi_O/\theta_O}} \\
 \text{Model D: } E(L_t) &= mN_t e^{-(t/\xi_M)^{-\xi_M/\theta_M}} \\
 &\quad \times [1 - (t/\xi_P)^{\theta_P}] e^{-(t/\xi_O)^{\xi_O/\theta_O}} \quad (9)
 \end{aligned}$$

where (ξ_M, θ_M) is the parameter set for the cdf describing the age-specific probability of litter production in young-aged animals, and (ξ_P, θ_P) and (ξ_O, θ_O) are the parameter sets for the cdfs describing the age-specific probabilities of senescence among prime- and old-aged animals, respectively. Reproductive maturation (Eq. 6) was included in all models, but the form of reproductive senescence varied. In Model A, animals exhibit no reproductive senescence (i.e., $p_{P,t} = p_{O,t} = 0$). In Model B, $p_{P,t}$ increases with age according to Eq. (7) and $p_{O,t} = 0$. This model was intended to mimic a situation in which senescence is due solely to some mechanism (e.g., ovarian depletion) that steadily diminishes reproductive capacity, while imposing a finite upper bound on that capacity. In Model C, $p_{O,t}$ increases with age according to Eq. (8) and $p_{P,t} = 0$. This model was intended to mimic a situation in which reproductive senescence increases with age-related physical senescence. As we show below, Model C was not entirely successful in this regard. Model D combines both patterns of reproductive senescence, allowing senescence to increase according to Model B in prime-aged animals and according to Model C in old-aged animals.

We fit Models A–D using the simplex method in the SYSTAT (2000) nonlinear regression module. To achieve convergence, it was necessary to specify starting values close to the final estimates. This was particularly true for ξ_O and θ_O , as sample sizes for old-aged animals were understandably small. We used the following starting values, obtained by visually fitting the model to the data: $\hat{m} = 0.33$, $\hat{\xi}_M = 4.5$, $\hat{\theta}_M = 0.7$, $\hat{\xi}_P = 40.0$, $\hat{\theta}_P = 2.0$, $\hat{\xi}_O = 28.0$, and $\hat{\theta}_O = 2.0$. Results were robust to small changes in starting values, while large changes usually led to a failure to converge or, less often, to a clearly unrealistic model. This suggested that convergence to locally rather than globally optimum estimates was not a serious problem when using these starting values.

Being a binomial random variable with parameters (N_t, mp_t) , the variance of L_t is (Johnson et al. 1993)

$$\text{var}(L_t) = N_t(mp_t)^{L_t}(1 - mp_t)^{N_t - L_t}.$$

Because N_t and p_t vary with age, $\text{var}(L_t)$ is not constant, thereby violating an important assumption of least squares regression. We therefore used iterative reweighting (Cox and Snell 1989) to fit our model. Each case (i.e., age class) was assigned a weight, w_t , proportional to $1/\text{var}(L_t)$ and calculated as

$$w_t = \frac{N_t}{\hat{L}_t(N_t - \hat{L}_t)}$$

where \hat{L}_t is the estimate of L_t following each iteration in the nonlinear regression procedure. This method yields maximum likelihood estimates of the model parameters (Cox and Snell 1989).

We fit Models A–D to data from all 20 studies, treating each observation with equal weight and giving no consideration to possible differences among the 20 study populations (including whether they were increasing or declining) or the fact that sample size varied among areas. To graph modeled relationships, results were expressed as estimated per capita annual litter production, rather than predicted numbers of litters produced; i.e., the models were divided by N_t . We compared models using AIC (Burnham and Anderson 1998)

$$\text{AIC} = -2 \ln(\mathcal{L}) + 2K$$

where \mathcal{L} is the model likelihood and K is the number of parameters estimated. We calculated \mathcal{L} as the product across all age classes of the binomial probabilities of observing exactly L_t litters among the N_t females in our sample

$$\mathcal{L} = \prod_{t=3}^{34} \binom{N_t}{L_t} (\hat{m}\hat{p}_t)^{L_t} (1 - \hat{m}\hat{p}_t)^{N_t - L_t},$$

where the binomial coefficient

$$\binom{N_t}{L_t} = \frac{N_t!}{L_t!(N_t - L_t)!}$$

and

$$\hat{p}_t = \hat{p}_{M,t}(1 - \hat{p}_{P,t})(1 - \hat{p}_{O,t}).$$

Again, we treated m as a part of the binomial parameter because, in this study, it represents the proportion of reproductive females that produce a litter in a given year and thus is constrained to the domain $0 \leq m \leq 1$. Use of a different measure of productivity (e.g., litter size) would require a different formulation of \mathcal{L} .

Only the best model, as determined by AIC, was examined further because model averaging performed

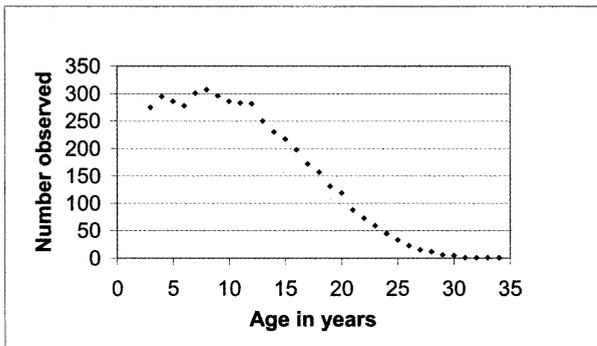


Fig. 1. Age distribution of 4,726 observations of the reproductive status of female brown bears ≥ 3 years of age for 20 study sites in Sweden, Alaska, Canada, and the continental United States for studies occurring from 1959 to 2000.

poorly in this instance. We calculated standard errors and 95% confidence intervals for parameter estimates for the best model using a first-order jackknife procedure (Efron and Tibshirani 1993:141), whereby we omitted data for each study area from the data set then refit the model. We also examined jackknife results for evidence that data from any particular study area might have exerted undue influence on parameter estimates. No evidence of such influence was found.

Results

Our data contained 4,726 observations, with 482 (10.2%) and 98 (2.1%) from age classes ≥ 20 and ≥ 25 , respectively (Fig. 1). The oldest bear observed was 34. In our sample, none of the 275 3-year olds or the 15 bears ≥ 29 years of age was observed with cubs-of-the-year.

Our models fit the data well according to traditional regression criteria (all 4 r_{Adj}^2 values were between 0.96 and 0.97). Based on AIC, however, Model A (no reproductive senescence) was not supported by the data ($\Delta_{\text{AIC}} = 17.917$). Models B–D all supported the conclusion that reproductive senescence occurs in the brown bear (Fig. 2, $0 \leq \Delta_{\text{AIC}} \leq 1.441$). Based on Akaike weights (w_{AIC}), we could not pick a single best model, suggesting that model averaging might best estimate the age-specific probability of litter production. We calculated average estimates based on AIC weights, but the resulting output provided an unrealistic shape to the reproductive curve. Consequently, we focused on Model D because it received the lowest AIC score and it made the most biological sense. Examination of the derivatives for this model suggested that the most rapid increase in per capita litter production occurs at 4.3 years of age (i.e.,

modal age of primiparity is between ages 4 and 5 years). Estimated per capita litter production peaked at age 8.7 (i.e., $d[L_{8.7}/N_{8.7}]/dt = 0$), suggesting that animals are most productive between ages 8 and 9. Maximum decline in per capita litter production occurred at 28.3 years, suggesting that maximum rate of reproductive senescence occurs between ages 28 and 29. From our fitted model (Table 2), we estimated that per capita litter production declined about 7.5% among 16-year-old females, 15.2% among 20-year olds, 68.2% among 28-year olds, and 100% by age 31. The model asymptote of $\hat{m} = 0.332$ (Table 3) was nearly identical to the value of 0.333 that we would expect if bears had 1 litter every 3 years, and the maximum predicted value for the model ($L_{8.7}/N_{8.7} = 0.322$) was only slightly lower.

Discussion

Each database contains potential biases. First, some bears likely lost litters prior to observation. The consequence of this would depend on the rate of loss among age classes. If loss is independent of age, then the general shape of the curve is correct but the asymptote, m , is biased low. However, if litter loss is greater in younger age classes (Sellers and Aumiller 1994), then age at first litter production and the left inflection point may be biased high. If older females lose litters at a greater rate than prime-aged females, then senescence may occur later than indicated; i.e., the right inflection point may be biased low. Second, sightability of bears varied greatly among areas. Our study sites varied from arctic tundra with high sightability to heavily forested environments with low sightability. Age at first reproduction and sampling effort also varied among areas. Although all of these factors influenced the fit and ultimate shape of the curve, by combining data from many brown bear study sites, we generated an adequate sample size to obtain reasonable model fits and to demonstrate reproductive senescence in the brown bear. Moreover, the excellent fit of our model suggests that, although local variation among populations may introduce noise, the overarching patterns of maturity and senescence are relatively fixed and therefore unaffected by such variation. Selective forces common to the species likely predetermined the pattern we observed.

Even though our results are based on a very large sample size, the oldest age classes had few observations. For example, we only had a single observation in each age class from 31–34, and those were of the same individual. Interestingly, that female was sighted during routine radiotracking with 2 different males during the

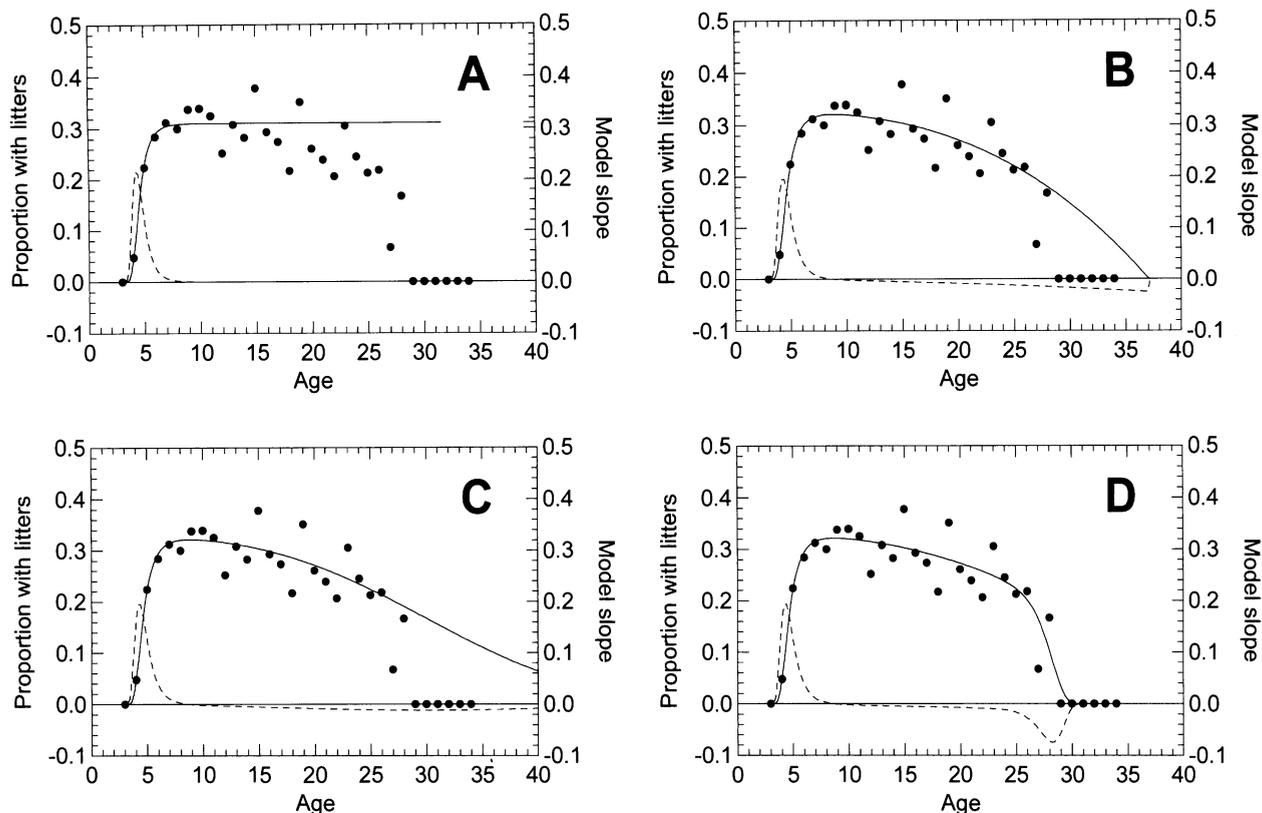


Fig. 2. Observed age-specific per capita litter production (dots) versus predicted values for Models A–D (solid lines; see text, Eqs. 9). Model slopes (derivatives) are shown by dashed lines. For Model D (the best model based on Akaike's Information Criterion), the predicted litter production rate increased most rapidly at 4.3 years of age, declined most rapidly at 28.3 years of age, and peaked at a value of 0.32 at 8.7 years of age.

breeding season for several days at a time when she was 29 and 30 years of age, suggesting she exhibited signs of estrus. Whether breeding was attempted or successful is unknown. However, by combining information from 20 studies we were able to increase our sample for bears >20 years nearly 10-fold over any single study. This larger sample improved our ability to detect and model reproductive senescence in aged animals.

Our reproductive data for brown bears took the form of a classic mammalian productivity curve, with reproductive rates increasing rapidly during sexual maturation, reaching a maximum and stabilizing or declining only slowly in prime-aged individuals, and decreasing rapidly in very old animals (Eberhardt 1985, Gaillard et al. 1994, Lunn et al. 1994, Jorgenson et al. 1997, Ericsson et al. 2001). Consistent with this pattern, our model indicated major shifts in litter production early in life and again with old age. The first major change occurred between ages 4 and 5, where Model D suggests the maximum rate of change in litter production occurred at 4.3 years of age; after this, per capita litter

production increased at a slower rate, until peaking at about 0.32 litters/female for animals 8–9 years of age. We believe that the value 4.3 is a good approximation of modal age at primiparity, although it may be slightly biased. Our model predicts that approximately 5% of females produce their first litter at age 4, and that 22.3% of 5-year olds will be observed with cubs-of-the-year. However, once a female reaches age 5, it is not always possible to determine if the observed litter is an animal's first. Consequently, litter production for ages >4 represents a mix of primiparous individuals producing their first litter and pluriparous individuals producing a subsequent litter. Hence, our estimate only approximates modal age at primiparity. Error associated with the estimate would be related to the rate of first litter loss and subsequent rebreeding in primiparous females.

Our top model also predicted that maximum per capita litter production occurred at age 8.7 and that reproductive performance remained relatively high between about 8 and 25 years of age. Thereafter, productivity declined rapidly, with the rate of decline peaking around

Table 2. Parameter estimates, Akaike's Information Criterion (AIC), Δ_{AIC} , and w_{AIC} values for 4 brown bear litter production models evaluated for data from Sweden and North America and collected from 1959 to 2000. Models are listed by AIC rank.

Model	Parameter estimate							AIC	Δ_{AIC}	w_{AIC}
	m	ξ_M	θ_M	ξ_P	θ_P	ξ_O	θ_O			
D	0.332	4.384	0.626	40.269	2.460	28.430	1.013	163.429	0.000	0.441
B	0.330	4.379	0.618	37.065	2.803	—	—	163.919	0.490	0.345
C	0.329	4.378	0.616	—	—	34.048	11.041	164.870	1.441	0.214
A	0.311	4.328	0.528	—	—	—	—	181.346	17.917	0.000

age 28. The derivative of the model (dashed line, Fig. 2) showed more variability after peak maturity (the point where the derivative becomes negative), suggesting that senescence is more drawn out than maturation. The interval between the estimated modal ages of primiparity and senescence (28.3–4.3) suggested an expected reproductive lifespan of about 24 years. Although no bears in our sample had a litter after age 28, reproduction in older age classes has been documented (Aoi 1985, Kawahara and Kadosaki 1996).

Does senescence have a major impact on finite rate of population change in brown bears? Noon and Biles (1990) modeled the demography of spotted owls (*Strix occidentalis caurina*) to evaluate attributes most affecting changes in population size. The finite rate of population change (λ) was most sensitive to variation in adult survival and relatively insensitive to variation in fecundity, age at first reproduction, and subadult survival. Effects of an age-related decline in fecundity were explored by incorporating a maximum age beyond which no reproduction occurred. Rates of population change were strongly affected by reproductive senescence. The effects of senescence on λ became progressively more pronounced as age of senescence decreased. Effects were most pronounced with high rates of adult survival and low rates of pre-adult survival. Noon and Biles (1990) demonstrated dramatic effects of senescence because in modeling zero reproduction beyond a maximum age they effectively truncated their adult population well before adult mortality reduced numbers of individuals in these older age classes to levels where their contribution to recruitment was not significant. By doing so, they effectively reduced adult survival.

Packer et al. (1998) modeled population growth in olive baboons (*Papio hamadryas anubis*) and African lions (*Panthera leo*) using a population projection matrix. They estimated population growth (λ) for each species, using both observed vital rates that included reproductive senescence in older females and vital rates of a hypothetical cohort whose fertility at older ages was

the same as for younger females. Among baboons, the observed λ was 1.1329 compared with 1.1355 for a non-menopausal population. Among lions, the observed λ was 1.1970 compared with 1.1985 for the hypothetical population. Reproductive senescence in older animals had little impact on estimates of λ . In both species, senescence occurred late in life, the number of individuals surviving to these older age classes was small, and their overall contribution to recruitment was minimal.

Eberhardt et al. (1994) modeled the population trajectory for the Yellowstone grizzly bear using Eberhardt's (1985) polynomial approximation to the Lotka equation. Physical and reproductive senescence were incorporated into the equation by approximating the reproductive curve with a rectangular function that was bounded on the left by the estimated age at first parturition and on the right by the estimated maximum age of reproduction (Eberhardt 1985). The maximum age was chosen to compensate for likely lower reproductive and survival rates in older age-classes. By taking the partial derivatives of the polynomial equation, Eberhardt et al. (1994) were able to demonstrate that the most important determinant of rate of increase was adult survival, followed by reproductive rate and subadult survival. They did not evaluate effects of physical or reproductive senescence.

When modeling rate of change in grizzly bear populations, Eberhardt et al. (1994), Eberhardt (1995), and Hovey and McLellan (1996) set senescence at 20 years of age; Wielgus and Bunnell (1994) used 21.5 years after reviewing data presented for 22 grizzly bear populations by LeFranc et al. (1987). McLellan (1989) set senescence at age 23, Wielgus et al. (1994) used 20.5. All used the Lotka equations, as suggested by Eberhardt (1985), and set the maximum reproductive age at the chosen value, which effectively truncates the population at that age. In each case, reproduction was assumed to remain high until the maximum reproductive age was reached. Only McLellan (1989) evaluated potential impacts of reproductive or physical senescence on estimates of λ . He concluded that the model was

relatively insensitive to changes in maximum reproductive age, similar to Packer et al. (1998).

Our results support the conclusion that rapid senescence among old-aged brown bears ($t > 25$) is probably not very important when modeling finite rate of increase because few individuals survive that long. However, our results do suggest that studies that assume a constant rate of production among prime-aged animals may bias estimates of λ high because they fail to account for the approximately 1%/year decline in litter production among those animals. Models of finite rate of increase should take this decline into account unless there is sufficient information suggesting rates of reproduction remain high. Without such consideration of these senescence effects, sustainable yield or allowable human-caused mortality estimates may be too liberal. This could have long-term impacts on population trajectory for both hunted populations or for remnant populations in need of recovery. Conversely, estimates of population size (e.g., Eberhardt and Knight 1996) that assume constant productivity of 0.333 litters/female/year likely are biased low.

The estimated asymptote of our model ($\hat{m} = 0.332$, Table 2) was nearly identical to the value of $m = 0.333$, expected if bears have 1 litter every 3 years. Moreover, our confidence interval for m (95% CI = 0.319–0.344) spanned 2.9–3.1 years, suggesting an interbirth interval that very closely approximates 3 years. Empirically observed interbirth intervals for most populations recorded in the literature span 2–4 years (Schwartz et al. 2003). We expected a slightly greater confidence interval for m because bears from one study area (South Sweden, Bjärvall and Sandegren 1987) tend to breed and wean offspring every other year. However, this had little influence on the overall fit and was not deemed an outlier based on the jackknife procedure (Table 3). Our assumption that m is a constant is not entirely correct. For example, primiparous 3-year olds could theoretically all breed and produce a litter at age 4. However, this was not the case, suggesting that onset of primiparity and litter production in younger bears is a gradual process that builds to a maximum around age 8.

Our sample showed that female brown bears in the wild can live until at least age 34. This is younger than recorded longevity for brown bears in captivity (age 50 for a male and 42 for a female, Karr 2002). Our results indicated that reproductive senescence begins well before maximum physical longevity is attained. Craighead and Mitchell (1982:527) concluded that reproductive longevity approximated physical longevity, but did not quantify either one. They recognized,

Table 3. Parameter estimates and 95% jackknife confidence bounds for Model D, the best model as determined by Akaike's Information Criterion (AIC). Estimates are based on data from Sweden and North America, from 1959 to 2000.

Parameter	Estimate	95% Confidence limits	
		Lower	Upper
m	0.332	0.319	0.344
ξ_M	4.384	4.359	4.410
θ_M	0.626	0.598	0.653
ξ_P	40.269	37.728	42.880
θ_P	2.460	2.146	2.768
ξ_O	28.430	28.322	28.536
θ_O	1.013	0.964	1.065

however, that old females (21–25 years of age) had lower fertility than prime-aged females (9–20) (Craighead et al. 1995:414). This later approximation of peak breeding ages is close to what we found here. Our results suggested that reproductive longevity might very well approximate physical longevity in the sense that the pattern of senescence roughly approximates the pattern of survival. Indeed, if theories about the evolution of senescence are correct, then the 2 are inextricably linked and should parallel one another. If our data are representative of the mean age structure of our 20 study populations, then Fig. 1 approximates a survival curve for the 4,726 bear years sampled. Comparing the general shape of the curve in Fig. 1 with the one in Fig. 2D, suggests that female survival declined rapidly after about 12 years of age, whereas a similar decline in per capita litter production did not occur until about 25 years of age. Because the majority of the populations in our sample came from either hunted populations or protected populations in which human-caused mortality is the major cause of adult mortality, one would expect a younger age structure than what might have occurred evolutionarily in the absence of a large amount of human-caused mortality. If this theory is correct, our model of reproductive senescence may approximate natural survival in adult female brown bears in the absence of human-caused mortality.

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