Paper 36

Reproductive Cycles and Rates in the Grizzly Bear, *Ursus arctos horribilis,* of the Yellowstone Ecosystem

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INTRODUCTION

Since the early 1800s grizzly bears, *Ursus arctos horribilis,* rapidly declined in the contiguous United States to a number that probably does not now exceed 600 or 700 (Craighead and Craighead 1973). They are found only in high mountain country and wilderness areas of our large national parks and forests. In Alaska and western Canada, grizzly bears are still relatively abundant.

Female grizzlies are characterized by a long life span, a relatively late sexual maturity, protracted reproductive cycles and, as adults, high survivorship rates (Craighead *et al.* 1974). Their low reproductive capacity compared to that of other mammals is an evolutionary characteristic that relates to size and power, competence and aggressiveness of mothers, self-sufficiency of cubs, and social facilitation among females with offspring. Because of the long-term continuity necessary to obtain quantitative data on a slowly reproducing mammal, precise reproductive rates have not been obtained for any bear population. Yet information on reproductive rates is essential for intelligent management since neither mortality rates nor population trends can be evaluated without it.

We describe in this paper how reproductive rates were obtained and how this biological parameter relates to the population dynamics of the grizzly bear in the Yellowstone ecosystem.

METHODS

From 1959 to 1971, bears were captured in culvert traps or shot with propulsive syringe darts containing immobilizing drugs. Following capture and immobilization, each grizzly was ear-tagged and individually color-marked. Used in combination with numbered colored ear-tags, several hundred color combinations were possible. Many color-markers lasted 6 or 7 years without replacement and some for the entire study period (Craighead *et al.* 1960).

Computing Reproductive Cycle

To determine age at first pregnancy, animals of known or established age were observed annually during the mating seasons (Craighead *et al.* 1969). To obtain quantitative data on length of the reproductive cycle, the reproductive histories were recorded for 30 marked females, over extended periods of time. Among these females, all but five were aged by the cementum layer technique (Craighead *et al.* 1970). Litter sizes were determined from annual counts of individually identifiable females with cubs.

The reproductive cycle for a female begins when fertilization occurs during June to mid-July and terminates with weaning (Craighead *et al.* 1969). The cycle for a female or for a population is obtained by dividing the reproductive period in years by the number of cycles. A female with two cycles during a 7-year period, for example, has a reproductive cycle of 3.5; a population with a total of 33 cycles and 99 reproductive years exhibits a 3.00 average reproductive cycle. The reproductive rate was calculated by dividing litter size by length of the reproductive cycle. This is expressed as a number of cubs produced per adult female per year.

Data from the 30 females were grouped into four samples based on number of reproductive cycles. The samples show the variation in reproductive rate that occurs with an increase in the number of cycles used in the computations. Samples 1 and 2 included data from 19 females with the most complete reproductive histories. Sample 3 included the 19 bears from Samples 1 and 2 plus five additional females. The fourth sample included reproductive histories of all 30 females. Nine females were sub-adult when record-keeping began.

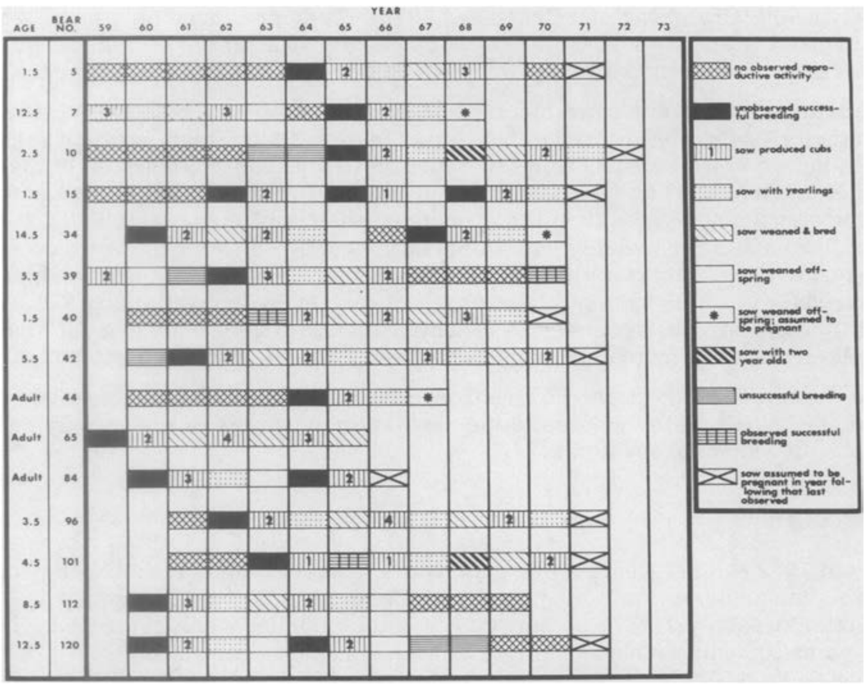

Fig. 1 Method of recording reproductive histories of females. The continuity of observations could be quickly checked for each female each year, as well as the female's reproductive performance.

Number of litters, cubs per litter, length of reproductive cycles, and reproductive period in years, were recorded for each female. The reproductive period for each female is the sum of her reproductive cycles. A cycle is the period in years from pregnancy to pregnancy or to an assumed pregnancy. Assumed pregnancy dates were projected for the females in samples 2, 3 and 4 in order to maximize information on the reproductive chronology of each female. It was assumed that when observation of a given female terminated, pregnancy ensued at the earliest possible date. This assumption tended to minimize values for average length of the reproductive cycle and thus to elevate the reproductive rate. The methodology used to record the annual sequence of reproductive events, with assumed dates of last pregnancy, is shown in Fig. 1.

Determining Age at First Pregnancy

A female was recorded as pregnant following observed copulation resulting in offspring or by extrapolation from observations of females with cubs. A female was considered sexually mature at 5.5 years, the earliest that females were known to produce litters (Craighead *et al.* 1969). We termed the period in years between the earliest recorded pregnancy (age 4.5) and the actual age at which a first pregnancy occurred, the pre-pregnancy period. Among 30 females with reproductive histories, this period ranged from 0 to 4 years. The effect of an extended pre-pregnancy period on length of reproductive cycle for individual females and for the population of females will be considered in calculating values for reproductive cycles.

The age at first pregnancy was recorded for 16 of 30 marked females. Eleven of these (69%) first became pregnant at 4.5, one at 5.5, three at 6.5, and one at 8.5 years of age. Although younger females copulated, none became pregnant before they were 4.5 years old (Craighead *et al.* 1969). The average age at first pregnancy was 5.2 years for 16 females. It was possible, but unverifiable, that some females having protracted pre-pregnancy periods conceived earlier and suffered miscarriages or fatalities of entire litters in the den. The effect on the reproductive rate is, nonetheless, the same as failure to conceive.

RESULTS

Reproductive Cycles

The chronology of events occurring in a cycle varies with the cycle length. The length of a cycle is dependent on when the female weans and how soon thereafter she comes in estrus.

In a 2-year cycle, the female becomes pregnant in June or July, whelps the following February, suckles cubs through summer and winter, weans them as yearlings in the spring, then comes in estrus, breeds, and becomes pregnant following weaning.

In a 3-year cycle, the female becomes pregnant, whelps cubs, attends them as yearlings, dens with them, weans them as 2-year olds soon after leaving the den, and then comes in estrus and breeds to begin another cycle.

In a 4-year cycle, the female follows the 3-year cycle, but after weaning 2-year olds, she either remains anestrous or she comes into estrus but is not fertilized. She is bred the following year and becomes pregnant. In longer cycles, the female may remain anestrous or for various reasons fail to bring forth cubs.

TABLE 1. REPRODUCTIVE RATES OF 19 MARKED FEMALE GRIZZLY BEARS (33 REPRODUCTIVE CYCLES) 1959-1972.

Bear No.	Age Marked	No. of Repro. Cycles in Years 2	3	4	5	Total Cycles	Repro. Period in Years	Date of Last Known Pregnancy	No. Cubs	Repro. Rates
5	1.5		1			1	3	1967	2	0.667
7	12.5		1	1		2	7	1965	6	0.857
10	2.5			1		1	4	1969	2	0.500
15	1.5		2			2	6	1968	3	0.500
34	14.5	1			1	2	7	1967	4	0.571
40	1.5	2				2	4	1967	4	1.000
42	5.5	1	2			3	8	1969	6	0.750
65	Adult	2				2	4	1963	6	1.500
84	Adult			1		1	4	1964	3	0.750
96	3.5		2			2	6	1968	6	1.000
101	4.5	1		1		2	6	1969	2	0.333
120	12.5			1		1	4	1964	2	0.500
125	5.5		3			3	9	1970	8	0.889
128	10.5	1	2			3	8	1969	10	1.250
144	0.5			1		1	4	1970	2	0.500
150	4.5			1		1	4	1966	3	0.750
172	11.5	1	1			2	5	1967	4	0.800
173	2.5		1			1	3	1969	2	0.667
175B	Adult		1			1	3	1962	2	0.667
Totals		9	16	7	1	33	99		77	

Reproductive cycles of 19 marked females were calculated from known pregnancies as shown in Table 1. The number of cycles per female varied from one to three and totalled 33 for all 19 animals during a cumulative reproductive period of 99 years. Sample 1 contains no assumed pregnancies, so usable data on cycles, reproductive period and litter size are minimal. The reproductive cycle varied from 2 to 5 years. Of the 33 cycles, 9 were 2 years; 16, 3 years; 7, 4 years; and 1, a 5-year cycle. Three-year cycles were more prevalent than 2-year cycles (64 to 36 percent). For some females the reproductive period consisted of a single reproductive cycle, but for others it included two or more cycles.

An average reproductive cycle of 3.00 years is obtained when the total of reproductive periods in years for all 19 females (99) is divided by the total number of cycles (33). This parameter can then be refined by including pre-pregnancy data. For example, among 19 females recorded in Table 1, five were older than 4.5 years at first pregnancy. The average reproductive cycle of

TABLE 2. REPRODUCTIVE CYCLE OF 30 MARKED FEMALE GRIZZLY BEARS (68 REPRODUCTIVE CYCLES) 1959-1972.

Bear No.	Age* Marked	No. of Repro. Cycles in Years 2	3	4	5	6	7	Total Cycles	Repro. Period In Years	No. Cubs	Repro. Rates
5	1.5		1	1				2	7	5	0.714
7	12.5		2	1				3	10	8	0.800
10	2.5		1	1				2	7	4	0.571
15	1.5		3					3	9	5	0.556
34	14.5	1	1		1			3	10	6	0.600
39	5.5		1	1	1			3	12	7	0.583
40	1.5	2	1					3	7	7	1.000
42	5.5	2	2					4	10	8	0.800
65	Adult	3						3	6	9	1.500
84	Adult	1		1				2	6	5	0.833
96	3.5		3					3	9	8	0.889
101	4.5	2		1				3	8	4	0.500
112	8.5		1			1		2	9	5	0.556
120	12.5			1			1	2	11	4	0.364
125	5.5		4					4	12	10	0.833
128	10.5	2	2					4	10	13	1.300
144	0.5	1						2	6	4	0.667
150	4.5			1	1			2	9	5	0.556
163	1.5	1						1	2	2	1.000
172	11.5	1	2					3	8	7	0.875
173	2.5	1	1					2	5	3	0.600
175	10.5	1	2					3	8	4	0.500
175B	Adult		2					2	6	4	0.667
200	3.5			1				1	4	2	0.500
44	Adult						1	1	7	2	0.286
140	8.5				1			1	5	3	0.600
141	1.5		1					1	3	2	0.667
160	Adult					1		1	6	2	0.333
180	11.5		1					1	3	3	1.000
187	1.5		1					1	3	1	0.333
Totals		18	32	10	4	2	2	68	218	152	

*Bears designated as 'Adult' were assumed to be at least 4.5 years of age.

TABLE 3. COMPARISON OF FOUR CALCULATIONS OF REPRODUCTIVE CYCLES AND RATES OF MARKED FEMALE GRIZZLIES.

	Sample Group 1	2	3	4
Number of Marked Females	19	19	24	30
Number of Reproductive Cycles	33	52	62	68
Reproductive Period in Years (Adjusted)	99(110)	156(167)	191(202)	218(231)
Total Number of Cubs	77	119	139	152
Average Litter Size	2.33	2.29	2.24	2.24
Average Unadjusted Reproductive Cycle	3.00	3.00	3.08	3.21
*Adjusted Average Reproductive Cycle	3.33	3.21	3.26	3.40
Reproductive Rate for Population of Marked Females	0.700	0.713	0.687	0.659

*Adjusted by including pre-pregnancy data.

3.00 was adjusted for the 11 years that these females were not pregnant. With this adjustment (99 years + 11 = 110/33 = 3.33), the average reproductive cycle is 3.33 years.

By assuming when each of 30 females would become pregnant following her last litter (see Methods), it was possible to use a larger number of cycles and reproductive years to compute reproductive rate.

With longer reproductive histories to examine, changes occurred for individual females in average length of the reproductive cycle and in reproductive rates. In sample 2, 52 cycles representing 167 reproductive years yielded an average reproductive cycle of 3.21.

In sample 3, 24 females having 62 reproductive cycles during a combined reproductive period of 202 years gave an average reproductive cycle of 3.26 years.

A fourth sample of 30 females (Tables 2 and 3) yielded 68 reproductive cycles, a reproductive period of 231 years, and an average reproductive cycle of 3.40 years. Data used to calculate average reproductive cycles for marked females included in the four data samples are summarized in Table 3. The values of 3.33, 3.21, 3.26, and 3.40 years for reproductive cycles indicate the range occurring in this parameter with changes in sampling. They also indicate that a representative reproductive rate for a population of long-lived animals can be obtained only from a relatively large sample of animals over an extended period of time since the accuracy of this biological parameter is dependent on an accurate measurement of cycle length.

Litter Sizes

The thirty marked females produced 68 litters. Nine were 1-cub litters; 38, 2-cub; 18, 3-cub; and 3, 4-cub litters. Fifty-six and twenty-six percent were 2-

TABLE 4. COMPARISON OF REPRODUCTIVE RATES OF 19 MARKED FEMALE GRIZZLIES (EXCLUDING PRE-PREGNANCY DATA).

Bear No.	Repro. Rates from 33 Repro. Cycles	Repro. Rates from 52 Repro. Cycles	Change in Repro. Rates with Change in Sample Size 33 R.C.	52 R.C.
5	0.666	0.714		+0.048
7	0.857	0.800	−0.057	
10	0.500	0.571		+0.071
15	0.500	0.555		+0.555
34	0.571	0.600		+0.029
40	1.000	1.000		0.000
42	0.750	0.800		+0.050
65	1.500	1.500		0.000
84	0.750	0.833		+0.083
96	1.000	0.888	−0.112	
101	0.333	0.500		+0.167
120	0.500	0.364	−0.136	
125	0.888	0.833	−0.055	
128	1.250	1.300		+0.050
144	0.500	0.666		+0.166
150	0.750	0.555	−0.195	
172	0.800	0.875		+0.075
173	0.666	0.600	−0.066	
175B	0.666	0.666		0.000
Totals	14.447	14.620	−0.621	+0.794
	+0.173		+0.173	
	R.R. =0.760	R.R. =0.769		

and 3-cub litters, respectively. The average litter size for the females recorded in each sample are shown in Table 3. These parameters and those for length of cycle were used to compute reproductive rates for the population.

Reproductive Rates

In sample 1, reproductive rates for individual females ranged from a low of 0.333 to a high of 1.500. The low represented two cubs produced in two cycles totalling 6 years, whereas the high resulted from six cubs produced in two cycles of 4 years. Of the 19 females, 4 exhibited reproductive rates of 1.000 or higher (Table 1). The average rate for all 19 females was 0.700 (Table 3).

In sample 2, we calculated reproductive rates for the same 19 females but used a longer time period. We increased the length of the reproductive period

TABLE 5. CALCULATION OF AVERAGE REPRODUCTIVE RATE FOR 30 ADULT FEMALES.

Cycle Length (yrs) 2	3	4	5	6	7	Total Cycles	Repro. Period (yrs) Un-adjusted	Adjusted	No. Cubs	Repro. Un-adjusted	Rate Adjusted
18	32	10	4	2	2	68	218	(+13)231	152	0.697	0.658

Calculations

$$\frac{\text{Total Cubs}}{\text{Total No. Litters}} = \frac{152}{68} = 2.24 = \text{Average Litter Size}$$

$$\frac{\text{Total Reproductive Period in Years}}{\text{Total Number Cycles}} = \frac{218}{68} = 3.21$$

= Unadjusted Reproductive Cycle

$$\frac{\text{Total Cubs}}{\text{Total Reproductive Period in Years}} = \frac{152}{218} = 0.697$$

= Unadjusted Reproductive Rate

218 + 13 = 231 (Total Reproductive Period in Years Adjusted by Pre-Pregnancy Data)

$$\frac{\text{Adjusted Total Reproductive Period in Years}}{\text{Total Number Cycles}} = \frac{231}{68} = 3.40$$

= Average Reproductive Cycle

$$\frac{\text{Total Cubs}}{\text{Adjusted Total Reproductive Period in Years}} = \frac{152}{231} = 0.658$$

= Average Reproductive Rate

examined from 110 to 167 years. Total cub production then showed an increase from 77 to 119 and number of reproductive cycles 33 to 52. Calculating reproductive rates with these parameters altered the rates for individual females (Table 4). Three rates remained unchanged, 10 increased by an average of 0.079, but 6 decreased by 0.104, for a 0.009 overall average increase in all rates. This gave a 0.713 average reproductive rate for all 19 females in sample 2 compared to 0.700 for the same females in sample 1 (Table 3).

In the third sample, the number of marked females was increased to 24 and a reproductive rate calculated from a total of 62 cycles and 202 reproductive years (191 plus 11 years pre-pregnancy). This gave a reproductive rate of 0.687.

In sample 4 involving 30 females, a reproductive cycle of 3.40 years, and a reproductive period of 231 years, gave a reproductive rate of 0.658 (Table 5).

A comparison of reproductive rates based on only one recorded reproductive cycle per female (Table 2) illustrates how the cycle length and litter size affect the reproductive rate of individual females. As an example, one female had a very low reproductive rate (0.286) because of a long 7-year cycle, while another had a moderately high reproductive rate (0.600) despite the production of three cubs during a 5-year cycle. The 0.667 reproductive rate of still another female exceeded the average for all females (0.658) because a 3-year cycle compensated for her low production of two cubs. The average reproductive rate was 0.482 for six females, each with only one reproductive cycle.

Because even minor changes in reproductive rate affect the population growth of a slowly reproducing species, four different rates were calculated to show the variation that could occur. We believe the reproductive rates from sample 4 shown in Table 3 are more accurate than those from samples 1, 2 and 3, because they represent the reproductive behavior of a large number of females over a longer period of time than the other samples. The higher rates of 0.700 and 0.713 obtained with samples 1 and 2 are due to higher values for litter size and may represent optimum rates attained over relatively short reproductive periods.

Maximum and Minimum Reproductive Rates of Marked Females

Maximum and minimum reproductive rates for individual females or a group of females are useful because they indicate the potential of a population to grow or to decline. A population exhibiting compensatory reproduction following a population decline should contain females with high reproductive rates. Similarly, a declining population under environmental stresses could be expected to have females with low reproductive rates. Both maximum and minimum reproductive rates for grizzly bears in Yellowstone are shown so that data obtained in the future can be compared with these parameters.

Maximum reproductive rates of individual bears, including variations resulting from changes in sampling, are presented in Table 6. For example, female No. 128 exhibited a reproductive rate of 1.250 during a period of 8 reproductive years and 1.300 in a 10-year period. Female No. 96 had a reproductive rate of 1.000 during 6 reproductive years, but this declined to 0.889 over a period of 9 years. Although the data indicate that one female exhibited a reproductive rate of 1.500 during a 6-year period, it is highly unlikely that she could sustain this throughout her entire reproductive life. Data suggest that a maximum for several females averaged 1.17 or, in round figures, about one cub per adult female per year. A reproductive rate of this magnitude for a population of females would indicate a potential for that population to grow if mortality was not excessive.

Although the minimum reproductive rate recorded for an individual female was 0.286, this was for only one reproductive cycle and was not considered representative. Bears with minimum rates as calculated for samples 1, 2, and 3 are shown in Table 7. The reproductive rate for female No. 120 averaged 0.364 over an 11-year period. The average of four females in samples 2 and 3 was 0.498; therefore, an average minimum reproductive rate among marked females was approximately half the maximum or, in round numbers, 0.5 cub per adult female per year. A rate of this magnitude among female grizzlies in Yellowstone would clearly indicate a declining population even if man caused mortalities were kept to a minimum (Craighead *et al.* 1974).

The maximum and minimum reproductive rates presented illustrate the range in this parameter and clearly show that a valid long-term reproductive rate for a population of grizzly bears must be obtained from a large sample of females observed over a long period of time.

TABLE 6. MAXIMUM REPRODUCTIVE RATES ILLUSTRATED BY CERTAIN GRIZZLY BEARS FOR WHICH MORE THAN ONE REPRODUCTIVE CYCLE WAS OBSERVED, 1959–1972.

Bear No.	Sample 1 (19)	Sample 2 (19)	Sample 3 (24)
40	1.000	1.000	1.000
65	1.500	1.500	1.500
96	1.000	0.889	0.889
128	1.250	1.300	1.300
Average	1.188	1.172	1.172

TABLE 7. MINIMUM REPRODUCTIVE RATES ILLUSTRATED BY CERTAIN GRIZZLY BEARS FOR WHICH MORE THAN ONE REPRODUCTIVE CYCLE WAS OBSERVED, 1959–1972.

Bear No.	Sample 1 (19)	Sample 2 (19)	Sample 3 (24)
101	0.333	0.500	0.500
120	0.500	0.364	0.364
10	0.500	0.571	0.571
15	0.500	0.556	0.556
Average	0.458	0.498	0.498

Reproductive Rate for Ecosystem Population

The reproductive cycle of 3.40 and rate of 0.658 are average parameters for 30 marked females over a 12 year period. To obtain a reproductive rate that would more accurately represent the entire population of grizzly bears inhabiting Yellowstone National Park and adjacent areas, we increased the sample size. This was accomplished by combining data from an additional 25 marked females omitted from reproductive cycle calculations because of observational discontinuities. These data were valid for calculating litter size and when combined with data from the 30 females, gave a long-term reproductive rate of 0.626 for the population. This long-term rate, derived from annual counts of 55 marked and recognizable females with litters extending over a 15-year period, we consider to be the most accurate long-term average rate for the population between 1959 and 1970.

Reproductive Longevity

One female was 14.5 years old when marked, and produced her last litter of

TABLE 8. REPRODUCTIVE PERFORMANCE OF 30 FEMALE GRIZZLIES, 1959–1972.

Bear No.	Age Marked*	Repro. Years Prior to Pregnancy	Age at First Pregnancy	Age at First Recorded Pregnancy	Sequence of Cycles in Years 1st	2nd	3rd	4th	Repro. Period in Years	Age When Last Observed	Age When Last Litter was Produced
5	1.5	2	6.5	6.5	3	4			7	12.5	10.5
7	12.5	—	—	11.5	3	4	3		10	21.5	19.5
10	2.5	4	8.5	8.5	4	3			7	14.5	13.5
15	1.5	0	4.5	4.5	3	3	3		9	12.5	11.5
34	14.5	—	—	14.5	2	5	3		10	24.5	22.5
39	5.5	0	4.5	4.5	4	3	5		12	16.5	12.5
40	1.5	0	4.5	4.5	2	2	3		7	10.5	9.5
42	5.5	2	6.5	6.5	2	3	3	2	10	15.5	15.5
44	Adult	—	—	—	7				7	Min. 10.5	9.5
65	Adult	—	—	—	2	2	2		6	Min. 10.5	9.5
84	Adult	—	—	—	4	2			6	Min. 9.5	9.5
96	3.5	0	4.5	4.5	3	3	3		9	12.5	11.5
101	4.5	2	6.5	6.5	2	4	2		8	13.5	13.5
112	8.5	—	—	8.5	3	6			9	17.5	12.5
120	12.5	—	—	12.5	4	7			11	22.5	17.5
125	5.5	1	5.5	5.5	3	3	3	3(2)	12(11)	15.5	15.5
128	10.5	—	—	10.5	3	2	3	2	10	19.5	19.5
140	8.5	—	—	10.5	5				5	12.5	11.5
141	1.5	1	5.5	5.5	3				3	7.5	6.5
144	0.5	0	4.5	4.5	4	2			6	9.5	9.5
150	4.5	0	4.5	4.5	4	5			9	12.5	9.5
160	Adult	—	—	—	6				6	Min. 9.5	5.5
163	1.5	0	4.5	4.5	2				2	5.5	5.5
172	11.5	—	—	11.5	3	2	3		8	19.5	17.5
173	2.5	0	4.5	4.5	3	2			5	8.5	8.5
175	10.5	—	—	10.5	3	2	3		8	17.5	16.5
175B	Adult	—	—	—	3	3			6	Min. 10.5	8.5
180	11.5	—	—	11.5	3				3	14.5	12.5
187	1.5	1	5.5	5.5	3				3	7.5	6.5
200	3.5	0	4.5	4.5	4				4	8.5	5.5
Totals		13			100	72	39	7	218 + 13 = 231		

*Bears designated as 'Adult' were assumed to be at least 4.5 years of age.

TABLE 9. SEQUENCE OF CYCLE LENGTHS FOR 30 FEMALE GRIZZLIES, 1959-1972.

Bear No.	Sequence of Cycles in Years				Sequence of Litter Sizes				Cubs Produced/Year			
	1st	2nd	3rd	4th	1st	2nd	3rd	4th	1st	2nd	3rd	4th
5	3	4			2	3			0.67	0.75		
7	3	4	3		3	3	2		1.00	0.75	0.67	
10	4	3			2	2			0.50	0.67		
15	3	3	3		2	1	2		0.67	0.33	0.67	
34	2	5	3		2	2	2		1.00	0.40	0.67	
39	4	3	5		2	3	2		0.50	1.00	0.40	
40	2	2	3		2	2	3		1.00	1.00	1.00	
42	2	3	3	2	2	2	2	2	1.00	0.67	0.67	1.00
44	7				2				0.29			
65	2	2	2		2	4	3		1.00	2.00	1.50	
84	4	2			3	2			0.75	1.00		
96	3	3	3		2	4	2		0.67	1.33	0.67	
101	2	4	2		1	1	2		0.50	0.25	1.00	
112	3	6			3	2			1.00	0.33		
120	4	7			2	2			0.50	0.29		
125	3	3	3	3	2	3	3	2	0.67	1.00	1.00	0.67
128	3	2	3	2	3	3	4	3	1.00	1.50	1.33	1.50
140	5				3				0.60			
141	3				2				0.67			
144	4	2			2	2			0.50	1.00		
150	4	5			3	2			0.75	0.40		
160	6				2				0.33			
163	2				2				1.00			
172	3	2	3		3	1	3		1.00	0.50	1.00	
173	3	2			2	1			0.67	0.50		
175	3	2	3		1	2	1		0.33	1.00	0.33	
175B	3	3			2	2			0.67	0.67		
180	3				3				1.00			
187	3				1				0.33			
200	4				2				0.50			
≤	100	72	39	7	65	49	31	7				
$\overline{X}$	3.33	3.27	3.00	2.33	2.17	2.23	2.38	2.33	0.65	0.68	0.80	1.00

TABLE 10. LENGTH OF CYCLE VERSUS NUMBER OF CUBS PRODUCED, 1959–1972.

	2-Yr	3-Yr	4-Yr	5-Yr	6-Yr	7-Yr
1.	2	2	2	3	2	2
2.	2	3	2	2	2	2
3.	2	2	3	2	≤=4	≤=4
4.	2	2	2	2	$\overline{x}$=2.0	$\overline{x}$=2.0
5.	1	3	2	≤=9		
6.	2	2	3	$\overline{x}$=2.25		
7.	2	3	2			
8.	4	2	3			
9.	2	3	3			
10.	3	2	1			
11.	2	1	≤=23			
12.	1	2	$\overline{x}$= 2.30			
13.	1	3				
14.	2	1				
15.	3	2				
16.	2	1				
17.	2	3				
18.	3	2				
19.	≤=38	4				
20.	$\overline{x}$= 2.11	3				
21.		2				
22.		2				
23.		2				
24.		2				
25.		3				
26.		2				
27.		2				
28.		3				
29.		4				
30.		3				
31.		1				
32.		2				
		≤=74				
		$\overline{x}$= 2.31				

two cubs at the age of 22.5, weaning them when she was 24.5. Two females produced litters when they were 19.5 years old and two others when 17.5 (Table 8). The greatest age attained by a female was 25 years; therefore, the data suggest that reproductive longevity approximates physical longevity and that most adult females could produce offspring as long as they lived. The minimum breeding age is 4.5 years, but a female cub born into the population requires an average of 6.3 years to whelp her first litter. With an average reproductive cycle of 3.40 years and 2.24 average litter size, a 25-year old female would experience 6 reproductive cycles and produce 13 cubs.

Sequence of Reproductive Cycles

We examined data to determine if any sequence of reproductive cycle lengths was more prevalent than others among the 30 females. The sequence of reproductive cycles varied greatly among individual females (Tables 8 and 9). For example, one female's first reproductive cycle was 3 years and her second, 4 years. Another female had a sequence of 3, 4, and then 3.

Among females with at least two reproductive cycles, cycle length consisted of 12 combinations: 6 occurred once, 4 were repeated, and 2 (3-3 and 3-2) occurred four times each.

Among females with 3 reproductive cycles, 9 combinations occurred. Seven occurred once, while 2 sequences (3-3-3 and 3-2-3) occurred three times each. Since (3-3 and 3-2) occurred four times each in two-cycle sequences, one would expect them to predominate, as they did, in three-cycle sequences. The significance of these repetitive patterns is unclear, but they definitely relate to physiological differences which are responses to extrinsic factors such as food, climate and population density. Variations in both cycle length and litter size appear to be natural population-regulating mechanisms. However, Table 9 shows no relation between cycle length and litter size, so compensatory processes may not be highly developed.

Length of Cycle Versus Cubs Produced

A Spearman Rank Correlation Coefficient (S.R.C.C.) was computed to determine if length of reproductive cycle was related to number of cubs produced per litter (Table 10). No significant correlation was obtained; the 'rho' value equalled +0.124, a statistically insignificant positive correlation.

EVALUATION OF PROCEDURAL BIAS ON RESULTS

To determine whether procedural biases were present in evaluations of reproductive cycle, reproductive rate and litter size, the data for these parameters were tested statistically.

Productivity Related to Age of Females

Ages of the 30 females varied from 0.5 to 14.5 years when marked; eleven were between 0.5 and 3.5 years, 10 were 4.5 to 5.5 years, and 9 were between 8.5 and 14.5. If productivity was dependent on age of the female, then the age composition of a sample could affect the values obtained for reproductive cycles and reproductive rates. This was tested by arranging data on number of

TABLE 11. PRODUCTIVITY OF 28 FEMALE GRIZZLIES RELATED TO AGE, 1959–1972.

Age Class	No. of Litters	No. of Cubs	Ave. No. of Cubs	Age Class	No. of Litters	No. of Cubs	Ave. No. of Cubs
5½	13	28	2.2	14½	2	5	2.5
6½	4	6	1.5	15½	5	10	2.0
7½	5	11	2.2	16½	2	5	2.5
Total 5½- 7½	22	45	2.0	Total 14½-16½	9	20	2.2
8½	4	8	2.0	17½	3	7	2.3
9½	11	26	2.4	18½	0	0	0.0
10½	1	3	3.0	19½	2	5	2.5
Total 8½-10½	16	37	2.3	Total 17½-19½	5	12	2.4
11½	4	8	2.0	20½	0	0	0.0
12½	6	15	2.5	21½	0	0	0.0
13½	3	6	2.0	22½	1	2	2.0
Total 11½-13½	13	29	2.2	Total 20½-22½	1	2	2.0

litters and number of cubs produced by 28 females into one-year age groups (5.5 to 25.5 years of age). A S.R.C.C. was calculated to compare individual age of post-parturient females with number of cubs per litter. The 'rho' value was −0.021, a statistically insignificant negative correlation.

Other correlation coefficients compared adult age-groups with number of cubs per litter. These tests determined whether females were more productive during certain periods of life. Grouping female grizzlies into six 3-year age categories (Table 11) and ranking them against numbers of cubs gave a 'rho' value of +0.132. The six groups were then consolidated into 3 arbitrary age categories of reproductive females: young (5.5—9.5 years); prime (10.5—17.5); and old (18.5—22.5). A S.R.C.C. calculation produced a 'rho' value of +0.118 when age categories were ranked with number of cubs in litters. Neither of these positive 'rho' correlations were statistically significant. We concluded that age of females in our sample did not appreciably affect litter size.

Variations in length of reproductive cycles for individuals and between individuals, and variation in the sequential combinations of reproductive cycles for individuals, indicated that a relationship might exist between a female's age and the length of her reproductive cycles. A S.R.C.C. calculated to examine this relationship resulted in a 'rho' equal to +0.256, which is not statistically significant. Correlation between the female's age at her last litter and the length of her last reproductive cycle was also found to be statistically insignificant. The coefficient of correlation was +0.025.

From our statistical analyses, we concluded that age of the females sampled

TABLE 12. NUMBER OF IMMOBILIZATIONS RELATED TO REPRODUCTIVE PERFORMANCE FOR 12 ADULT FEMALE GRIZZLIES, 1959—1970.

Bear No.	Age Marked	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	Total	Age 1st Observed Litter	Repro. Rate
7	12.5	1	—	1	—	2	—	—	—	1	—	—	—	5	12.5	0.800
23	14.5	—	2	—	—	1	1	1	—	1	—	1	—	7	15.5	0.600
39	5.5	—	1	1	—	1	1	—	—	1	2	5	—	12	5.5	0.583
42	5.5	—	1	—	—	1	1	—	—	1	3	—	—	7	7.5	0.800
65	Adult	—	1	1	—	—	—	—	—	—	—	—	—	2	Min. 5.5	1.500
84	Adult	—	—	1	—	—	—	—	—	—	—	—	—	1	Min. 5.5	0.833
112	8.5	—	—	1	—	—	—	—	1	2	3	—	—	7	9.5	0.556
120	12.5	—	—	1	—	—	—	—	1	—	—	—	—	2	13.5	0.364
125	5.5	—	—	—	1	—	—	—	—	—	—	—	—	1	6.5	0.833
128	10.5	—	—	—	1	1	—	—	—	1	—	1	—	4	11.5	1.300
172	11.5	—	—	—	—	—	1	—	—	1	—	—	—	2	12.5	0.875
175	10.5	—	—	—	—	—	1	—	—	1	—	—	—	2	11.5	0.500
Totals		1	5	6	2	6	5	1	2	9	8	7	—	52		

TABLE 13. NUMBER OF IMMOBILIZATIONS RELATED TO REPRODUCTIVE PERFORMANCE FOR 15 SUB-ADULT FEMALE GRIZZLIES, 1959—1970.

Bear No.	Age Marked	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	Total	Age 1st Litter	Repro. Rate
5	1.5	1	1	1	—	—	—	1	—	1	1	—	—	6	7.5	0.714
6	0.5	1	2	2	2	—	2	1	—	—	—	—	—	10	7.5	Killed-Blastocysts Recovered
10	2.5	1	—	1	—	—	1	—	—	1	—	—	—	4	9.5	0.571
15	1.5	1	—	1	—	—	—	—	—	—	—	—	—	2	5.5	0.556
29	0.5	1	—	2	—	—	—	1	—	—	—	—	—	4	6.5	0.250
40	1.5	—	2	1	1	1	2	2	2	2	3	1	—	17	5.5	1.000
81	2.5	—	—	1	—	—	—	1	—	—	—	—	1	3	6.5	0.250
96	3.5	—	—	1	1	3	—	—	—	1	—	—	—	6	5.5	0.889
101	4.5	—	—	1	—	—	1	—	—	3	2	—	—	7	7.5	0.500
200	3.5	—	—	—	—	—	—	1	—	1	1	—	—	3	5.5	0.500
187	1.5	—	—	—	—	—	1	1	1	1	2	—	—	6	6.5	0.250
163	1.5	—	—	—	—	1	—	—	—	3	—	—	—	4	5.5	1.000
144	0.5	—	—	—	—	1	—	1	4	—	—	1	1	8	5.5	0.667
150	4.5	—	—	—	—	2	1	—	—	1	—	—	—	4	9.5	0.556
173	2.5	—	—	—	—	—	1	—	—	1	—	—	—	2	5.5	0.600
Totals		5	5	11	4	8	9	9	7	15	9	2	2	86		

caused no significant bias in our calculations of litter size, length of reproductive cycle, or reproductive rate.

Immobilizations Related to Reproductive Rate

Female grizzlies were drugged with succinylcholine chloride or phencyclidine hydrochloride to obtain reproductive and other types of information. Females captured as adults were immobilized 1-12 times each, and females captured as sub-adults were immobilized 2-17 times.

To test the possibility that frequent use of drugs may have altered long-term productivity, we correlated the number of immobilizations with the reproductive rate for each of 12 adult and 14 sub-adult females. A correlation coefficient between number of immobilizations and reproductive rates of 12 adult females (Table 12) was not statistically significant ('rho' value of —0.332). A similar test for 14 sub-adult females (Table 13) yielded no significant correlation between number of immobilizations per female and reproductive rate ('rho' value of +0.345). A third S.R.C.C. indicated no significant correlation between number of immobilizations per female before age 5.5 and the age at which these females first littered ('rho' value of +0.496). We concluded that drugs did not significantly alter reproduction and did not bias the data.

Food Supply Related to Reproductive Rates

Both intrinsic and extrinsic factors affect reproductive rates but are difficult to isolate and analyze. Lack of comparative data prevents us from thoroughly evaluating whether the food available at the long-established open pit garbage dumps increased the reproductive rate of female grizzlies or changed the carrying capacity of the pristine habitat. We have much evidence, however, that the abrupt closing of garbage dumps in Yellowstone during 1969 and 1970, did stress the population and that this coincided with lower reproductive rates (Craighead *et al.* 1974). Feeding habits of many females were observed when reproductive histories were recorded. We cannot, at this time, show a statistically significant correlation between food supply and the reproductive rates of specific females. However, a drop in the annual reproductive rate of the population during 1970-72, can be related to a marked decrease in food supply associated with the abrupt closing of open pit garbage dumps (Craighead *et al.* 1974). Studies of other animals have shown that a decrease in nutritional level can affect reproductive success (Cheatum and Severinghaus 1950; Beuchner 1955; Knowlton 1972). Jonkel and Cowan (1971) presented inconclusive data suggesting an increased black bear reproductive rate coinciding with an increase in food.

The major food types used by grizzlies in the Yellowstone ecosystem were green vegetation, roots and tubers, berries, pine nuts, small rodents, large herbivores, and garbage. Relatively slight annual fluctuations occurred in the availability of green vegetation, roots, tubers and garbage, while great variations occurred annually in the other major foods (Craighead *et al.* in press). With garbage available to bears, the nutritional level of the Yellowstone population was more stable and this may have elevated reproductive rates. Our data suggest that for a period of years, a lowered reproductive rate associated with the decreased food base is more probable than a rising rate attributable to compensatory density-dependent factors.

DISCUSSION

We have shown that reproductive parameters of Yellowstone grizzlies are highly variable. Ages at first pregnancy ranged from 4.5 to 8.5 years, reproductive cycles from 2 to 7 years, litters from 1 to 4 cubs, and reproductive rates from 0.286 to 1.500 for the individual females studied. Presumedly, flexibility of these biological parameters should enable the species to adjust to environmental factors that affect the population favorably or unfavorably. However, for a long-lived species exhibiting delayed maturity these compensatory reproductive processes (increases in litter size, decreases in length of reproductive cycle, and/or higher survivorship rates for sub-adult bears) would act slowly. On the other hand, population regulating mechanisms (infanticides from aggressive males and hormonal activity regulating the intervals between estrus in females) are factors that can offset compensatory processes. Infanticide was low (eight records). The great variability in the sequences of reproductive cycles could be important in regulating reproduction, but it will be difficult to draw conclusions from this information until similar data are obtained from other populations and norms established.

The grizzly bear is at the top of its food chain, and under primitive conditions has had few natural enemies, partially explaining the relatively low reproductive rate. In modern times, man has developed the capability of inflicting rapid and heavy mortality. There is no scientific evidence that the grizzly bear has the capacity to compensate for the high mortality rates inflicted by man. On the contrary, Craighead *et al.* (1974) have shown that the Yellowstone grizzly cannot sustain a high death rate for even a short period of time without critically lowering the population level. Any abnormal mortality such as undue control by man or excessive hunting, or both, should be viewed with concern because it can cause a rapid irreversible decline in population size. The historic decline of the grizzly bear in the western United States has probably resulted from the species' low reproductive rate and its inability to cope with man-induced mortality and drastic habitat changes. The grizzly has been able to survive only in large national parks and national forest wilderness areas where spacious habitats have, until recently, insulated the species from excessive mortality. If threatened with high mortality rates, the grizzly will face extinction just as surely as it did in California some 50 years ago.

Where mortality rates are known to be high (Yellowstone ecosystem) or are of uncertain status (Bob Marshall-Scapegoat Wilderness), we believe it would be prudent for game managers to apply the long-term average reproductive rates presented in this paper. To assume higher rates for other populations, in the absence of any other long-term scientific evidence, is to take unjustifiable risks with a threatened species.

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