SYNCHRONOUS REPRODUCTION BY MAINE BLACK BEARS

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Abstract: We studied reproduction by black bears (*Ursus americanus*) in 3 dissimilar Maine study areas from 1982 to 1991. Nuts of American beech (*Fagus grandifolia*) were the primary fall food source in Spectacle Pond, a major fall food in Stacyville, and rarely available in Bradford. We visited 396 dens, including 303 dens of 96 adult females, and examined 154 newborn litters. Alternate-year beechnut crop failures appeared to maintain reproductive synchrony at Spectacle Pond, where 73 of 77 (95%) litters were produced on odd-numbered years following abundant beechnut crops. Most bears at Spectacle Pond began to reproduce at 6 years of age, and had 2-year intervals between litters, even after litter loss. Eighty percent of breeding females (i.e., adults without cubs) produced litters at Spectacle Pond when beechnuts were abundant, but breeding females lost weight and only 13% produced litters when beechnuts were scarce. Reproductive synchrony was less pronounced at Stacyville and Bradford, where most bears began to produce litters at 4 years of age, and generally produced subsequent litters 1 year after litter loss. At Stacyville and Bradford, bears maintained stable weights regardless of beechnut abundance, and most breeding females produced litters every year. Where bears depend upon few fall foods, food failures may synchronize female reproductive schedules and impact population age structures. Adequate understanding of bear reproductive biology includes estimates of litter losses and resulting inter-litter intervals for projections of cub production.

Int. Conf. Bear Res. and Manage. 9(1):471-479

Black bear reproduction is influenced in a density-independent manner by the abundance, diversity, and quality of food sources (Rogers 1976, 1987; Bunnell and Tait 1981; Elowe 1987; Eiler et al. 1989; Elowe and Dodge 1989). Age of first breeding, litter size, and interval between litters are linked to the physical condition of females (Jonkel and Cowan 1971, Rogers 1976, Elowe 1987). Despite their opportunistic foraging behavior, black bear nutritional planes may vary considerably from year to year due to fluctuating abundance of mast crops (Rogers 1976, 1987; Elowe 1987). Periods of food scarcity may severely reduce reproduction (Rogers 1987), and within populations, the reproductive success of individuals may vary with their ability to obtain high-energy food (Rogers 1976, Elowe 1987). In Maine, nuts of American beech (*Fagus grandifolia*) are the primary mast crop used by black bears during the fall months (Spencer 1955, Hugie 1982, Caron and McLaughlin 1984). Regular, 2-year cycles of alternating high and low beechnut abundance have occurred in much of northern Maine since 1980 (Schooley 1990).

We studied reproduction of black bears on 3 dissimilar study areas (Spectacle Pond, Stacyville, and Bradford) from 1982 to 1991. Beech was available at Spectacle Pond and Stacyville, and bears had access to active agriculture at Stacyville. Beech was essentially absent from Bradford, where bears used other mast and agricultural crops in the fall. This paper compares the reproductive parameters of black bears living on these areas, and examines relationships between litter production and abundance of beechnuts.

Field data collection was completed with the assistance of Maine Department of Inland Fisheries and Wildlife (MDIFW) biologists R.B. Allen, M.A. Caron, J. Connolly, R.A. Cross, K.D. Elowe, D.M. Kane, K.I. Morris, and L.M. Tudor. Additional assistance was provided by many student interns, of which L.M. Comly, S.R. Fennel, C.A. Lombardo, M.L. Merchant, A. Starr, C.W. Whitman, and T.E. Vecchiolli were particularly helpful. Pilots J. McPhee and R.P. Treadwell helped locate dens. Discussions with K.D. Elowe improved the manuscript immeasurably. This work is part of Maine black bear research, funded under Federal Aid in Fish and Wildlife Restoration Projects W-67-R and W-82-R.

STUDY AREAS

Hugie (1982) and Schooley (1990) provided detailed descriptions of the 3 MDIFW study areas, each of which encompassed about 172 km^2. Brief summaries of their narratives follow.

The Spectacle Pond study area was located 27 km SW of Ashland in northern Maine (Fig. 1). This area was >95% forested, with elevations ranging from 226 to 692 m. Higher, well-drained sites were covered with northern hardwood associations (sugar maple-american beech-yellow birch) (*Acer saccharum-F. grandifolia-Betula alleghaniensis*). Spruce-fir (*Picea* spp.-*Abies balsamea*) associations and northern white cedar (*Thuja occidentalis*) are found along drainages and in valleys. The area was commercial forestland managed primarily for production of pulp wood. It contained no permanent residences, paved roads, or agricultural areas. Bears in this area fed largely upon herbaceous vegetation in spring, soft mast during summer, and hard mast (primarily beechnuts) in the fall months (Hugie

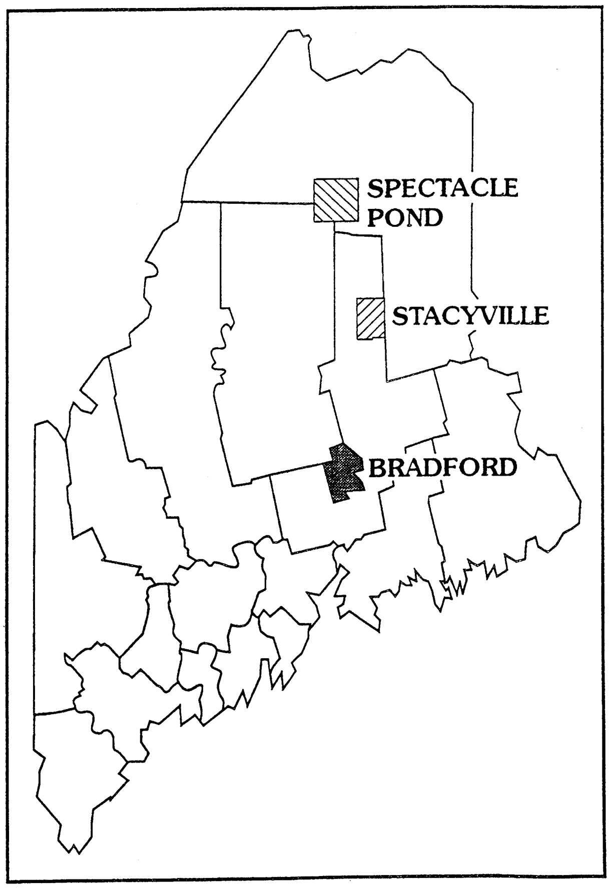

Fig. 1. Location of Maine black bear study areas.

1982, Caron and McLaughlin 1984, MDIFW file data).

Stacyville study area was located in northcentral Maine, about 88 km SE of Spectacle Pond, and was about 80% forested (Hugie 1982). The area was bisected by the east branch of the Penobscot River. Terrain and vegetation west of the river were similar to Spectacle Pond. Terrain east of the river was flatter, and commercial forestland was interspersed with agriculture (dairy, potato, and small grain) and small towns. Bears used a variety of vegetation as food in this area, including herbaceous forage in spring, soft mast crops in summer, and a range of soft mast and grain crops associated with agricultural areas, in addition to hard mast in the form of beechnuts, in fall (Hugie 1982, MDIFW file data).

Bradford study area was located in central Maine, nearly 90 km SW of Stacyville. Bradford was 92% forested and relatively flat. Vegetation differed from the other 2 study areas, with an abundance of spruce-fir forests intermixed with bogs and wooded swamps. Northern hardwoods were less common; red maple (*A. rubrum*), aspen (*Populus tremuloides* and *P. grandidentata*), and ash (*Fraxinus* spp.) were prevalent hardwoods. Red oak (*Quercus rubra*) occurred along the Penobscot River on the area's eastern border. Several towns were present, as were agricultural areas (primarily dairy farms) and abandoned apple (*Malus* spp.) orchards. Bears in this area consumed herbaceous vegetation during spring, soft mast in summer, and had access to grain and apple crops during fall. Beechnuts were very rare in this area, but there was some hard mast available in the form of red oak acorns along the Penobscot river (MDIFW file data).

METHODS

MDIFW biologists visited the Spectacle Pond study area each fall and subjectively surveyed food abundance, particularly beechnut crops. Beechnuts were classified as scarce or abundant based upon ocular estimates (Rogers 1976, Schooley 1990).

Bears were captured with foot snares, and occasionally with culvert-style traps and trained bear dogs, during spring, summer, and fall. Captured bears were immobilized with a 2:1 mixture of ketamine hydrochloride and xylazine hydrochloride (Addison and Kolenosky 1979), or a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Stirling et al. 1985). Bears were measured and weighed, and premolars extracted for age estimation (Willey 1974). Female bears were radiocollared, and all bears were marked with numbered ear tags prior to release. Reproductive status of female bears was determined by observations of offspring. Age of first reproduction was known for bears captured as cubs or yearlings. Nipple measurements were used to determine previous production by solitary bears initially captured at 2-6 years of age. Second thoracic nipples of pre-production females measured <7 mm in length; after nursing a litter, nipples generally remained ≥ 7 mm long (MDIFW file data). Each den-year of reproductive history for each female was classified according to the following levels of reproductive experience: pre-production, first litter, subsequent litter, or unknown (first or subsequent) litter.

Movements and survival of radio-collared female bears and their offspring were monitored by tracking from fixed-wing aircraft (Hugie 1982, Mech 1983). Bears were usually located weekly during the active seasons as conditions permitted. They were immobilized in their dens each winter for collar replacement and collection of physical and reproductive data. Dens of solitary females, and females accompanied by yearling offspring, were generally visited in January or February. Dens of females expected to give birth during January-February were visited in mid to late March. In-den counts of newborn offspring provided data on cub production. Offspring of collared bears were tagged, and yearling females were radiocollared at den sites.

Cubs were assumed to have died if they were absent from the female's den as yearlings, or if the female died prior to July in the year of their birth. Mortality of female bears ≥1 year of age was documented through collar returns and in-field visits to sites of stationary collars.

Following analysis of age of first reproduction, we classified females ≥4 years of age as adults. To estimate number of potential breeding females (available cub producers), we considered any female bear ≥4 years of age that was not accompanied by yearling offspring in a den to have been available for mating the previous summer. Records of bears that abandoned newborn cubs immediately following our visits, or bears that received orphaned cubs, were removed from estimates of cub survival.

Mean in-den weights of potential cub-producing adults ≥7 years old (females that were solitary or accompanied by cubs) were used as a condition index for examining relationships between beechnut abundance and condition of breeding females. Weights of younger breeding adults were excluded from the index because bears continued body growth through 6 years of age (MDIFW file data).

We examined differences in weight of adult females among study areas, reproductive experience, and beechnut abundance using ANOVA. We also used ANOVA to test for differences in litter size among study areas, reproductive experience, and beechnut abundance. Linear categorical models (Freeman 1987) were used to test for differences in litter loss rates among litter size, study areas, reproductive experience, and beechnut abundance. Confidence intervals were used to compare proportions of available females producing litters following years of high and low beechnut abundance. Statistical tests were considered significant if $P < 0.05$.

RESULTS

Food Abundance

Beechnut abundance fluctuated regularly throughout the study period, with alternate years of high and low crops. Although bumper crops of nuts were recorded only in 1982 and 1988, beechnuts were common to abundant every even-numbered year (1982, 1984, 1986, 1988, 1990). Beechnut crops were scarce in odd-numbered years (1983, 1985, 1987, 1989, 1991) (Schooley 1990).

Reproductive Parameters

We visited 396 dens of 142 female bears, including 216 dens at Spectacle Pond, 67 at Stacyville, and 113 at Bradford (Table 1). We monitored 7-31 females annually at Spectacle Pond, 5-9 bears per year at Stacyville, and 5-23 bears each year at Bradford. Individual bears were monitored for up to 10 years at Spectacle Pond and Stacyville, and up to 7 years at Bradford.

We examined 154 litters (77 at Spectacle Pond, 29 at Stacyville, and 48 at Bradford) (Table 1). Our den visits probably caused bears to abandon 8 litters of cubs, and we introduced orphaned cubs to the dens of 19 females with newborn litters of their own. These 27 litters were removed from analyses of litter survival.

We compared weights of adults between first and subsequent litters, and among study areas and mast abundance categories. Weights of females increased between first and subsequent litters ($F = 30.41$; 1, 209 df; $P = 0.0001$) and showed a study area-beechnut abundance interaction, identifying a decline in weights of Spectacle Pond bears when beechnuts were scarce.

During winters following abundant beechnut crops, in-den weights of ≥7-year-old potential producing females were similar in all 3 areas, averaging 68.5 kg, $n = 47$ (Table 2). However, during years of scarce beechnuts, weights of older potential producers at Spectacle Pond declined 16 kg ($\bar{x} = 53.8$, $n = 10$, SD $= 12.8$) ($F = 17.95$; 1, 40 df; $P = 0.0001$), but remained relatively constant at Stacyville and Bradford. Small sample sizes prevented rigorous testing for

Table 1. Reproductive status of denned female black bears in 3 Maine study areas, 1982-91.

Study area	Subadult[a]	Pre-prod.[b]	W/Cubs	W/Yrlings	Solo adult	Total
Spectacle Pond	52	26	77	43[c]	18	216
Stacyville	10	3	29	23	2	67
Bradford	31	3	48	26	5	113

[a] Solitary bears ≤3 years of age.
[b] Bears 4-5 years of age that had not produced litters.
[c] Includes 1 den of adult accompanied by 2-year-old female offspring.

Table 2. In-den weights of older (≥7 years) breeding female bears in Maine, 1982-91.

	Odd years—following high mast			Even years—following low mast		
Study area	$\bar{x}$ weight (kg)	SD	*n*	$\bar{x}$ weight (kg)	SD	*n*
Spectacle Pond	69.8	9.7	32	53.8[a]	12.8	10
Stacyville	65.9	9.0	5	70.2	9.8	16
Bradford	65.4	7.8	10	65.5	9.1	12

[a] Significant ($F = 17.55$; 1,40 df; $P = 0.0001$).

differences between weights (i.e., condition) of solitary females and those with cubs within mast categories. However, mean weights of solitary females (≥7 years) were similar to weights of females with cubs.

At Spectacle Pond, 73 (95%) of 77 litters were produced in odd-numbered years, following abundant beechnut crops. At Stacyville, 10 (34%) of 29 litters were produced in odd-numbered years (following high beechnut production), and 32 (67%) of 48 litters recorded at Bradford were produced in odd-numbered years.

At Spectacle Pond, 80% of available (i.e., breeding) females ($n = 91$) produced litters in odd-numbered years following high mast (95% CI = 76-91%) (Table 3), but only 13% of available females produced litters in even-numbered years following low mast ($n = 30$, 95% CI = 3.5-31%). The proportion of available females that produced litters remained high in both odd and even years at Stacyville and Bradford (Table 3).

Age of First Reproduction.—Earliest reproduction occurred at 4 years of age in all 3 areas (Table 4). Most (14 of 23) known-age females at Spectacle Pond produced their first litters at 6 years of age. At

Table 3. Proportion of available female bears[a] producing cubs in Maine during 1982-91, by even and odd years of study.

	Odd years—following high mast				Even years—following low mast[b]			
	Number	Producing cubs			Number	Producing cubs		
Study area	potential	No.	%	95% CI	potential	No.	%	95% CI
Spectacle Pond	91	73	80	76-91	30	4	13	3.5-31
Stacyville	11	10	94	54-100	23	19	88	61-94
Bradford	34	32	85	80-98	22	16	96	47-87

[a] Females ≥4 years that were not accompanied by yearlings in the den the following winter.
[b] Beechnut abundance, based upon field surveys at Spectacle Pond.

Table 4. Age of first reproduction by Maine black bears, 1982-91.

		Age of bear producing first litter		
Study area	*n*	4 yrs	5 yrs	6 yrs
Spectacle Pond	23	4	5	14
Stacyville	6	3	1	2
Bradford	12	7	3	2

Stacyville, 3 of 6 bears produced first litters as 4-year-olds, and 7 of 12 females produced first litters at 4 years of age at Bradford.

At Spectacle Pond, 4 of 18 available 4-year-olds produced first litters on odd-numbered years, following high beechnut crops; all available 5-year-olds ($n = 4$) and 6-year-olds ($n = 13$) did as well. However, during even-numbered years only 2 of 14 potential first-breeders actually produced litters. At Stacyville all 3 potential first-time producers on odd-numbered years had litters, and 2 of 5 potential first-producers had litters on even-numbered years. At Bradford, most available first-producers produced litters in both odd-numbered (8 of 9 bears) and even-numbered years (4 of 6 bears).

Litter Size.—Litters ranged from 1 to 4 cubs and averaged 2.48 cubs ($n = 154$, SD = 0.73) (Table 5). Overall sex ratio of litters was 120 M:100 F. Litter size did not differ among areas or by beechnut abundance, but first litters were smaller than subsequent litters ($P = 0.045$). First litters averaged 2.05 cubs ($n = 41$, SD = 0.67), subsequent litters averaged 2.64 cubs ($n = 113$, SD = 0.70).

Litter Losses.—Litter losses occurred in all areas. At Spectacle Pond, 6 of 21 first litters were lost, as was 1 of 44 later litters, including 1 litter lost when the entire family group was killed by another bear. At Stacyville,

Table 5. Litter size of black bears in Maine, 1982-91.

			No. cubs in litter					
Study area	Litter class	*n*	One	Two	Three	Four	$\bar{x}$	SD
Spectacle Pond	First	23	3	13	6	1	2.22	0.74
	Subsequent	54	2	19	28	5	2.61	0.68
Stacyville	First	6	1	4	1	0	1.83	0.41
	Subsequent	24	0	6	17	1	2.70	0.56
Bradford	First	12	3	8	1	0	1.83	0.58
	Subsequent	34	2	14	15	3	2.64	0.79

1 of 3 first litters was lost; all 18 subsequent litters survived. Bradford females lost 3 of 10 first litters and 4 of 23 subsequent litters, including 2 litters lost when older adult females died of suspected bear predation at or soon after den emergence.

Litter loss did not differ with litter size, study area, or beechnut abundance, but was higher for first litters than for subsequent litters (χ^2 = 6.31, 1 df, P = 0.012). Ten of 34 (29.4%) first litters were lost, compared to 5 of 85 (5.9%) subsequent litters.

Time Between Litters.—At Spectacle Pond, 1 of 7 females losing entire litters produced another litter the following year (Fig. 2). The remaining 6 females each produced another litter 2 years after the year of litter loss. Two females at Stacyville that lost litters (including 1 that abandoned a litter following our den visit) reproduced the following year. In Bradford, 9 of 10 females losing litters (including all of 4 females known to abandon litters at/prior to den emergence) reproduced the following year.

Twenty-two of 23 females with surviving litters produced subsequent litters 2 years later at Spectacle Pond (Fig. 2). The remaining female was accompanied by her solitary female offspring through 2 winters, and produced another litter on the third year.

At Stacyville, 16 of 17 females raising at least 1 cub through yearling age produced another litter 2 years later; 1 female remained solitary and produced a litter the third year. In Bradford, 11 of 12 females raising litters to yearling age produced another litter 2 years later; 1 female cycled again 3 years later.

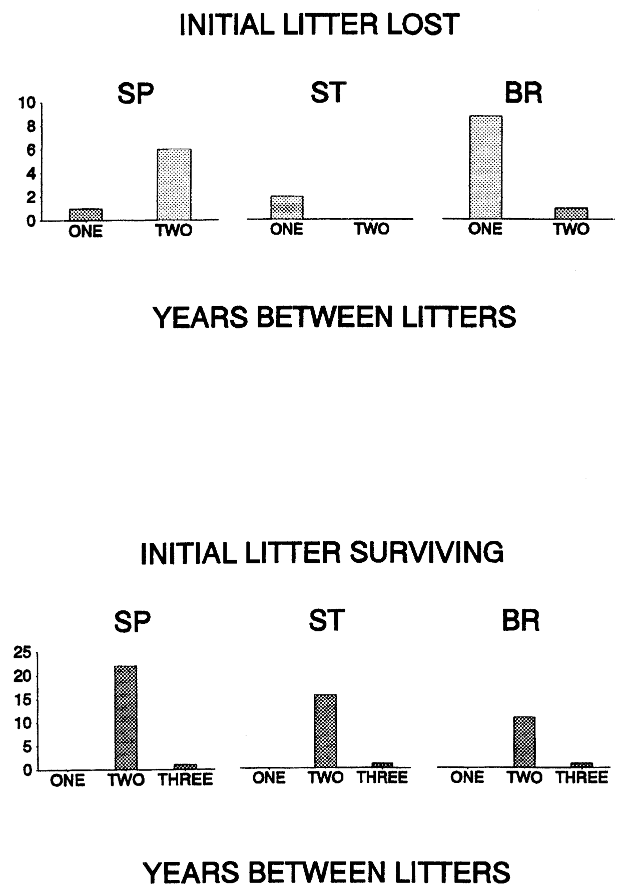

Fig. 2. Length of intervals (years) between litters produced by black bears at Spectacle Pond (SP), Stacyville (ST), and Bradford (BR) Maine, 1982-91, relative to initial litter loss or survival.

DISCUSSION

Food Abundance

Although beechnut mast surveys were conducted only in Spectacle Pond, bear habitat-use data collected concurrent with this study (Schooley 1990, MDIFW file data) indicated bears at both Spectacle Pond and Stacyville responded similarly to beechnut production. Schooley (1990) reported bears at Spectacle Pond and Stacyville used hardwood stands containing beech more than expected during falls of abundant beechnut crops. In years of beechnut scarcity, bears at Spectacle Pond used softwood stands near riparian areas, but bears at Stacyville moved to agricultural areas, apparently utilizing grain crops and feral apples (Schooley 1990, MDIFW file data). Beech was uncommon at Bradford, and bears used other foods during fall, including feral apples, grain crops, and acorns (MDIFW file data).

The alternate-year cycle of beechnut abundance was also associated with a long-term pattern of fluctuating den-entry dates of bears at Spectacle Pond and Stacyville throughout the study period (Schooley 1990, MDIFW file data). During years of high mast production, most bears in both areas delayed den-entry until mid-November; in years of mast failure, they generally entered dens in mid-October. Bears usually entered dens in late October at Bradford.

Reproductive Parameters

Despite their omnivorous feeding habits, black bears require abundant foods high in fat and carbohydrates (Elowe 1987, Rogers 1987) for reproduction. Weight is associated with differences in reproductive performance among populations (Stringham 1990). Female bears with access to high-energy food during fall months have demonstrated weight gains and increased reproductive success (Rogers 1976, Elowe 1987). Consequently, weight of adult breeding females should be a useful indicator of their condition.

Weights of females were strongly related to the abundance of beechnuts at Spectacle Pond, where bears were lighter and few breeding females produced litters in years following beechnut scarcity. This relationship was not observed in Stacyville or Bradford, where weights of available breeders remained relatively stable and most produced cubs.

Our data suggest that reproductive performance of bears in Spectacle Pond was controlled by beechnut mast failures through recurring reduction of the nutritional planes of adult females. Fluctuating beechnut crops at Spectacle Pond were associated with the following aspects of female bears' reproductive schedules: a) age of first breeding, b) time between litters following litter loss, and c) proportion of available breeders actually producing litters. Regular, alternate-year beechnut crop failures in this area resulted in synchronization of the reproductive cycles of most adult female bears living on the area.

Most bears in Spectacle Pond delayed litter production until 6 years of age, and females losing litters generally produced subsequent litters 2 years later. The strong synchrony of litter production appeared to be maintained by alternating years of food abundance and scarcity, as the condition of females fluctuated around a threshold required for reproduction. Few potential cub-producing females actually produced litters following low mast crops. Therefore, most adult females were available for breeding and potential litter production in the following year. Given an abundant fall beechnut crop in the alternate year, their nutritional planes became elevated, and a high proportion produced litters, thus reinforcing the synchronous pattern with another strong cub pulse.

Bears at Stacyville and Bradford did not exhibit strong reproductive synchrony. Stacyville and Bradford bears matured earlier, maintained relatively stable weights, and generally re-cycled to produce subsequent litters in years immediately following litter loss. Also, most available adult females produced litters each year. Bears at Stacyville had access to a wider array of fall foods than bears in Spectacle Pond (Hugie 1982). They used beechnut crops when available, but apparently maintained a relatively high nutritional plane by using agricultural areas when beechnuts were scarce. Bradford bears were generally removed from the influence of beechnut abundance. In 1986 and 1988, a few bears at Bradford traveled up to 78 km to exploit concentrations of beechnuts, but most bears remained on the study area and used other foods during the fall months, including apples, red oak acorns, and grain crops.

Age of First Reproduction.—First reproduction occurred at 4 years of age in all 3 areas, similar to age of first litter production for other northeastern bear populations (Willey 1974, Sauer 1975, Hugie 1982, Elowe 1987, Kolenosky 1990). Most females at Spectacle Pond delayed litter production until 6 years of age, as did bears in an Ontario population (Kolenosky 1990). The later maturation schedule of Spectacle Pond bears, compared to females at Stacyville and Bradford, may reflect their lower nutritional plane. Periodic shortages of beechnuts probably slowed their growth and prevented most 4- and 5-year-old females from attaining sufficient body size and condition for successful gestation.

Time Between Litters.—The longer (2-year) inter-litter interval exhibited by bears losing litters at Spectacle Pond may also reflect reduced nutritional levels associated with alternate-year beechnut scarcity, as suggested by the wide fluctuation of in-den weights of adult females at Spectacle Pond between high and low mast years. In northeastern Pennsylvania, where bears exhibit extremely fast growth and begin producing litters at 3 years of age (Alt 1980), 4 of 5 females losing litters re-cycled to produce subsequent litters the following year (Alt 1981).

We measured intervals between litters separately for females losing entire litters, and for those with surviving litters, since litter survival influences length of inter-litter interval. Most reports of inter-litter intervals (LeCount 1983, Rogers 1987, Kolenosky 1990, Stringham 1990, Swartz and Franzmann 1991) omitted females losing entire litters from their calculations. While such inter-litter intervals can provide a baseline for comparing nutritional planes and crude reproductive rates of bear populations (Stringham 1990), they have limited utility in population modeling unless they are accompanied by measures of litter loss and the inter-litter interval for bears losing litters. In populations with high first litter mortality, the proportion of females experiencing litter loss in a given year has a major influence on the number of females available for breeding that year.

Litter Size.—Litter size did not differ among study areas, probably because most litters were produced when females at Spectacle Pond were in similar condition to those in Stacyville and Bradford. In years of low beechnut abundance, most available females at Spectacle Pond may have been in too poor condition to produce offspring, as suggested by the 16 kg decline in mean weights of potential cub producers ≥7 years of age.

Litters of Maine bears were similar in size to litters from Massachusetts (Elowe 1987), and Ontario (Kolenosky 1990). Our data from Spectacle Pond and Stacyville indicate larger litters than reported by Hugie (1982) for the same areas in the late 1970s. However, Hugie's estimates of litter sizes (SP: $\bar{x}$ = 2.07, ST: $\bar{x}$ = 2.15) were based on spring-summer observations, and cub mortality during spring probably accounted for the observed difference.

Litter Losses.—The timing of litter loss was not known for most litters; we considered a litter lost if no yearlings were present in the female's den the following year. Our few observations of litter losses suggest that most occurred soon after emergence from dens, when cubs are dependent on the female's nutritional resources and are less able to avoid predators. In Massachusetts, 76% of cub mortality occurred between 1.5 and 5 months of age (Elowe 1987). Kolenosky (1990) reported cubs in Ontario had higher mortality in the first 5-8 months of life than later in their first year.

Litter loss patterns in this study were comparable to losses reported in Massachusetts (Elowe 1987), where 57% of first litters and 7% of subsequent litters were lost. The higher loss rate for early litters may be related to the smaller size and poorer condition of first-time producers, or to their lack of experience in raising and caring for cubs (Elowe and Dodge 1989).

Because we used den records to estimate numbers of females available for breeding the previous year, we may have included a few females losing litters too late to participate in the breeding season. Consequently, we may have overestimated the number of females available for litter production, which would lead to underestimates of the proportion of available females that actually produced litters, and to overestimates of between-litter intervals for females losing litters.

Synchronous breeding and litter production has been reported in black bears in New York (Free and McCaffery 1972), Washington (Lindzey and Meslow 1977), and Arizona (LeCount 1984). Free and McCaffery attributed unstable age distributions in harvests to a 4-year maturation schedule and alternate-year cub production of individual female bears. By assuming most females produced first litters at 4 years of age and subsequent litters at 2-year intervals, they simulated synchronous breeding and a population of unstable age distribution. They suggested such a synchronous pattern would be broken by a disaster (such as wide-spread food scarcity) causing the loss of a particular age class. LeCount (1984) reported synchronous reproduction by Arizona bears over a 6-year period, with means of 78% and 25% of adult females with litters in alternate years. He attributed this to the same reproductive schedule reported by Free and McCaffery, and noted a consistent food supply in Arizona. At Stacyville and Bradford the reproductive schedules of bears would detract from synchrony. Bears in these areas experienced relatively high litter loss rates for first litters, and most females losing litters re-cycled to produce subsequent litters the following year, thereby strengthening the "weak" year-classes born on alternate years.

Projections of bear populations must accommodate the variation in recruitment rates caused by their multi-year reproductive cycles. The dynamic nature of natural systems and long maturation schedule of bears promote unstable age distributions in bear populations. Annual cub production is modified by interactions between dynamic age structures and proportion of breeding females within each year class (Taylor et al. 1987). Consequently, realistic projections of cub production require age-specific data on maturity schedules, numbers of available females, proportion of available females producing litters, litter loss rates, and measures of inter-litter intervals for females for both surviving and lost litters.

Numbers of litters produced in a given year are dependent on the number of females available for breeding during the previous summer, and the proportion of those potential females that breed and subsequently attain a nutritional plane high enough to produce a litter. All adult females unencumbered with litters (i.e., solitary adults, adults with recently weaned offspring, and first-year breeders) are available for breeding. Assuming the polygynous breeding habits of bears ensure nearly all potential producers will conceive during a breeding season, nutrition during the late summer and fall months apparently determines the proportion of available females that produce litters.

Where bears do not have a diverse fall food base, beechnut crops may strongly influence annual reproductive success. Severe reduction in beechnut availability through removal of mature beech trees, or through disease such as beech bark disease (Houston 1975), would probably cause a substantial, long-term reduction in the reproductive vigor of bear populations in northeastern habitats that are isolated from influences of agriculture.

The implications of reproductive synchrony and unstable age distributions on bear population dynamics have not been fully explored. In areas where bear populations are lightly exploited and contain many older individuals, synchrony of production may have little impact on densities. However, exploited populations with truncated age structures may have reduced resilience to overharvest, because their recruitment rates may be lowered by high litter loss associated with first litters. Consequently, short-term (1-2 year) food shortages, combined with over-harvest of adult females, may lead to severe, long-term reduction in bear densities.

MANAGEMENT IMPLICATIONS

In regions similar to northern Maine, where bears have a limited number of fall foods, the abundance of a major fall food source appears able to control bear reproductive schedules. Mast scarcity may control reproductive schedules of bears in such areas and promote reproductive synchrony by reducing the nutritional planes of bears during fall and winter months.

Adequate assessments of bear populations require documentation of reproductive parameters that allow age-specific monitoring of their multi-year reproductive cycles. The proportion of adult females available for breeding each year is influenced by litter loss rates and inter-litter intervals. Therefore, both parameters need to be measured to describe reproduction of bears.

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