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Relationship of variable mast production to American black bear reproductive parameters in New Mexico

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Abstract: We examined the relationship of variable mast production to American black bear (*Ursus americanus*) reproductive parameters in 2 areas of New Mexico during 1993–2000. Mast production differed across years for each of 10 species surveyed ($P < 0.001$). Black bear reproductive characteristics were documented during 266 den investigations of 80 females ≥ 4 years old. On both study areas, acorn production by the 2 dominant oak (*Quercus* spp.) species appeared to have the greatest influence on natality and recruitment ($P < 0.001$). Neither natality nor recruitment varied following oak production indexed as “poor” to “good”. However, natality among eligible parous females decreased by more than 60% following years categorized as oak “failure”, and recruitment decreased by more than 70% 2 years after oak failure ($P = 0.05$). This suggested that only a minimum threshold of high quality food was needed for successful reproduction. Cub survival was positively associated with juniper (*Juniperus* spp.) production during the previous fall and combined production of juniper during the previous fall and oak production during the birth year ($P \leq 0.009$). During 1999–2000, New Mexico Department of Game and Fish officers subjectively assessed mast production in our study areas. These assessments were highly correlated with our survey results ($r_s \geq 0.73$, $P < 0.001$, $n = 12$), indicating subjective criteria were adequate to distinguish variation in mast production. Documenting annual mast production in New Mexico, especially occurrence and frequency of mast failures, may be an effective index to subsequent black bear reproductive output during the following 2 years.

Key words: American black bear, cub survival, food abundance, Juniper, *Juniperus* spp., mast production, New Mexico, oak, *Quercus* spp., reproduction, trend monitoring, *Ursus americanus*

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As in much of North America, the primary foundation for American black bear management in New Mexico is information obtained from hunter-killed bears. Wildlife managers often make inferences about status and trend of bear populations based on number and sex–age composition of harvested bears. However, harvest data are not necessarily representative of actual bear populations because of differences in vulnerability and

hunter selectivity among sex and age groups (Miller 1990, Garshelis 1991). One common circumstance, subject to misinterpretation, is an observed increase in the percentage of young bears in the harvest sample. Is this increase due to previous overharvest of mature individuals or an increase in recent reproductive output?

During the late 1980s and the early 1990s, interpretation of New Mexico black bear harvest data was stymied by these very circumstances. Increasing, stable, and decreasing trends were all plausible explanations for observed changes in the harvest data. Clearly, additional information was necessary to interpret these data and determine the true status and trend of New Mexico bear populations. During 1992, an 8-year research project was initiated to understand ecology and population

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dynamics of black bears in New Mexico and to develop a population model to help estimate and predict trend in population size and structure.

A primary focus of the study was to document reproductive characteristics, especially as influenced by mast production. A positive correlation between food abundance and black bear reproduction has been widely reported, based on annual variability in foods (Jonkel and Cowan 1971, Rogers 1976, Eiler et al. 1989, Elowe and Dodge 1989, McLaughlin et al. 1994, Miller 1994), geographic variability in foods (Schwartz and Franzmann 1991, McLaughlin et al. 1994, Miller 1994), and differential feeding behaviors among bears (Rogers 1976, Elowe and Dodge 1989). Black bear productivity has also been linked to female nutritional condition (Kolenosky 1990, Noyce and Garshelis 1994, Samson and Huot 1995).

In the Southwest, abundance and productivity of food plants can be quite limited by the arid climate and short growing season. In particular, soft mast producers common in other regions of North America, such as *Rubus*, *Vaccinium*, *Sorbus*, *Sambucus*, *Prunus*, *Ribes*, *Shepherdia*, and *Amelanchier* are restricted or absent in southwestern forests. Only 3 mast producers, oak (*Quercus* spp.), juniper (*Juniperus* spp.), and pinyon (*Pinus edulis*), are widespread within this region.

We studied mast production and black bear reproduction on 2 study areas in New Mexico. Our objectives were: (1) to document annual variation in mast production for 10 plant species consumed by bears; (2) to document black bear reproductive parameters, including age of primiparity, natality, cub survival, recruitment, and litter interval; (3) to investigate relationships between mast production and reproductive parameters; and (4) to evaluate the feasibility of evaluating annual changes in bear reproductive output based on state-wide mast production surveys.

Study areas

Research was conducted on 2 study areas. The Northern Study Area (NSA) was located in the Sangre de Cristo Mountains of northern New Mexico, between the towns of Eagle Nest and Cimarron. The NSA was approximately 310 km² and encompassed mostly private and state lands. Recreation and livestock grazing were primary land uses.

Elevations ranged from 2,070 m to 3,793 m. At lower elevations, dominant habitat types included pinon-juniper (*Pinus edulis*–*Juniperus* spp.) woodland and oak–mountain mahogany (*Quercus* spp.–*Cercocarpus*

spp.) scrub. Mid-elevations were dominated by ponderosa pine (*Pinus ponderosa*), mixed conifer (*Pseudotsuga menziesii*–*Abies concolor*), and aspen (*Populus tremuloides*) forests. Meadows of fescue (*Festuca* spp.), mountain muhly (*Muhlenbergia montana*), grama (*Bouteloua* spp.), and bluegrass (*Poa* spp.) existed throughout wooded habitats at lower and mid elevations. Spruce–fir (*Picea engelmannii*–*Abies lasiocarpa*) and bristlecone pine–limber pine (*Pinus aristata*–*Pinus flexilis*) forests dominated higher elevations. An alpine tundra community, consisting of sedge (*Carex* spp.), alpine avens (*Geum rossii*), mountain current (*Ribes montigenum*), shrubby cinquefoil (*Potentilla fruticosa*), and groundsel (*Senecio* spp.) surrounded scree and talus slopes at the highest elevations.

Climate varied with elevation. Period of record average temperatures were –7° to 0°C in January and 16° to 21°C in July. The frost-free growing season was 70–120 days at higher elevations and 145–190 days at lower elevations. Annual precipitation ranged from 37.8 to 41.4 cm, with most occurring as snowfall or rainfall during July and August (Western Regional Climate Center 2001).

The Southern Study Area (SSA) was located in the Mogollon Mountains of west-central New Mexico, near the towns of Reserve and Glenwood. The SSA was 420 km² and was within Gila National Forest. Livestock grazing and timber harvest were primary land uses. Recreational use primarily occurred during summer months and during spring or fall hunting seasons.

Elevations on the SSA were lower than the NSA and ranged from 1,750 m to 3,035 m. Dominant habitat types coincided with those described for the NSA, with some variation in species composition. The high elevation bristlecone pine–limber pine and alpine communities were not present on the SSA.

Period of record average temperatures were –1° to 5°C in January and 19° to 24°C in July. The frost-free growing season was 110–155 days at higher elevations and 180–230 days at lower elevations. Annual precipitation ranged from 37.6 to 40.4 cm, with most occurring as snowfall or rain during July and August (Western Regional Climate Center 2001).

Methods

Study area mast surveys

We conducted annual mast production surveys on each study area from 1993–2000. Surveys were limited to those genera contributing most to bear diets (Costello

et al. 2001). Species surveyed on the NSA were Gambel oak (*Q. gambelii*), wavyleaf oak (*Q. undulata*), pinyon, Rocky Mountain juniper (*J. scopulorum*), one-seed juniper (*J. monosperma*), and chokecherry (*Prunus virginiana*). Species surveyed on the SSA were Gambel oak, gray oak (*Q. grisea*), pinyon, alligator juniper (*J. deppeana*), Utah juniper (*J. osteosperma*), and orange gooseberry (*Ribes pinetorum*). Timing of surveys coincided with the period just prior to peak ripening (mid-August to mid-September) to ensure that most fruits were fully formed but consumption by wildlife was minimal.

We surveyed 100 plants of each species of oak, juniper, pinyon, and gooseberry. Due to limited distribution, only 40 chokecherry plants were classified. Plants were surveyed on 10 permanent transects established on each study area. Survey transects followed roads, jeep trails, or foot trails and encompassed variation in elevation and aspect. Prior to establishing transects, we could not predict presence of each species at each plot. Total transect length ranged from approximately 0.8 to 8.0 km, and 2–10 survey plots were designated at intervals of 0.2–1.6 km, as necessary to achieve target sample sizes. At each plot, we walked 10 paces perpendicular from the road or trail and classified production for the closest 1–10 (usually 5) plants of each species. We attempted to classify 5 plants/species at each plot; however, we were sometimes constrained by availability. We did not search more than approximately 100 m in any direction for plants. For some species with limited distribution, 10 plants were classified at each plot. The same survey transects and plots were revisited each year, with the same number of plants classified at each plot.

Ratings were assigned as described by Graves (1980): no visible fruit; fruit visible after very close inspection; fruit readily visible, but not covering entire plant; or fruit readily visible and covering entire plant. This method was selected because it was shown to be robust against observer bias (Graves 1980). We assigned values of 0, 2, 4, and 8 to this sequence of ratings, which roughly represented a minimum ratio of fruit/plant among the 4 classifications. We used the Kruskal-Wallis (KW) rank procedure to test for annual differences (by genus) and the Student-Newman-Keuls (SNK) test to identify homogeneous subsets (or to pool years by genus). We used mean values for homogeneous subsets to assign mast “production categories across genera: ≤ 1.4 = “failure”; 1.5 – 2.4 = “poor”; 2.5 – 3.9 = “moderate”; 4.0 – 4.9 = “good”; ≥ 5.0 = “excellent”. We used the same procedure to produce mast indices that included 2–4 genera within 1 year and across 2 years.

District mast surveys

During 1999–2000, we distributed mast survey forms to 2 New Mexico Department of Game and Fish (NMDGF) officers whose districts encompassed the study areas. These surveys were used to assess mast production at genus level for oaks, junipers, and pinyon. Officers were asked to observe mast production any time during September and answer the following questions for each genus:

- What percentage of plants had fruit? (circle one category)
 $<25\%$ = 1; 25 – 50% = 2; 51 – 75% = 3;
 $>75\%$ = 4
- In general, of plants bearing fruit, how would you characterize the number of fruit per plant? (circle one or two categories)
scarce = 2; moderate = 3; abundant = 4;
super abundant = 5
- How would you characterize overall fruit production? (circle one category)
mast failure = 1; poor = 2; moderate = 3;
good = 4; bumper crop = 5

Numerical values to questions (a) and (b) were multiplied to produce a mast production “score.” Numerical values for question (c) were used as a mast production “assessment.” We used Spearman’s rank correlation (r_s) procedure to compare our detailed mast survey results to scores and assessments provided by officers.

Capture, marking, and den investigations

During 1992–99, we used foot snares and culvert traps to capture bears during late April to early November (Costello et al. 2001). We chemically immobilized bears and recorded chest girth, weight, and a subjective fat index (with values ranging from 1–5, based on our ability to palpate the spine, pelvic, and shoulder bones). For female bears, we noted vulval swelling, teat length, teat width, teat color, occurrence of lactation, evidence of suckling (swollen teats or hair matting), and presence of offspring. A vestigial premolar tooth was extracted from bears ≥ 1 year old for age determination using cementum annuli counts (Willey 1974). We marked all females with eartags, tattoos, and radio-telemetry transmitters.

We visited dens of radiocollared adult females each year 1993–2000 to determine their reproductive status. Dens of 2- and 3-year-old bears were visited annually or biennially to change or refit collars as necessary. Typically, we did not remove adult bears from dens unless it was necessary to reach their head or to reach offspring. Yearlings and cubs were removed from dens for handling. For adult females, we recorded chest girth

and fat index when possible but did not attempt to measure weight.

Black bear reproduction

We estimated mean age of primiparity using the Garshelis et al. (1998) non-biased method. We included bears whose reproductive status was verified during annual den investigations or capture beginning at age 4. We also included bears captured at age 5 and judged to be nulliparous from teat measurements (Beck 1991, Brooks 1997) and weight, but we did not backdate these individuals to age 4.

We determined cub survival by revisiting dens of females whose cubs were handled or observed the previous year. Cubs were assumed to have died if they were absent from dens as yearlings and if this assumption was supported by lack of observations of cubs in later captures. Cubs were also assumed to have died if their mother died prior to 1 July in their birth year, but cubs whose mother died after 1 July and cubs whose fate was unknown were excluded from analyses.

For estimating mean litter interval, we included intervals verified during annual den investigations. We also included intervals known from sightings of offspring during capture and incomplete intervals known to be at least 3 years. We included these latter observations because long intervals were more difficult to document than short intervals and because they bracketed a failed reproductive opportunity.

We included repeated measures in the data set by treating annual reproductive events for the same female and offspring from the same female as independent observations. We believe this strategy was justified given that year-to-year variation in reproduction by individuals was as great as variation among individuals. When appropriate, we separated females into 2 subsets: previously nulliparous females and parous females. We further categorized parous females as eligible or non-eligible for cub production based on absence or presence of yearlings at the current observation. We categorized females as eligible for yearling recruitment based on absence of yearlings the previous year.

Analyses of relationships: mast production and black bear reproduction

We tested for differences in annual natality and physical characteristics relative to mast indices from the previous fall. Cub survival was investigated relative to mast production during the birth year and previous years. Recruitment was investigated relative to mast indices for the two previous years.

For analyses of binomial reproductive parameters (cub production, yearling recruitment, and cub survival), we used logistic regression. We produced a model for each mast index using production as the predictor variable (with values of 1–5 corresponding with failure to excellent production) and entered reproductive class and study area as indicator variables (with interactions). We used likelihood ratio tests to reduce models to significant ($P \leq 0.10$) predictor and indicator variables. Among significant models with different mast indices, we used Akaike information criteria (AIC) to identify models with the best fit (Anderson et al. 2000).

For analyses of continuous reproductive parameters (natality, recruitment, and litter size), we used analysis of variance (ANOVA). We entered mast indices as random factors and entered reproductive class and study area as fixed factors. For significant models, we tested for differences among levels of mast production using Bonferroni tests. All statistical analyses were performed using SPSS statistical software (SPSS, Chicago, Illinois, USA). Statistical tests were considered significant if $P \leq 0.10$.

Results

Mast production

Mast production varied across years for all genera on both study areas (KW $P < 0.001$). Mast production was more variable on the SSA than the NSA (Table 1). Production of juniper was most variable, with crops ranging from failure to excellent. Oak and orange gooseberry crops were slightly less variable. Pinyon production failed during all but one year. On the NSA, oak and chokecherry were most variable, with crops ranging from failure to moderate. Production of pinyon was generally poor and production of juniper failed every year.

Mast production was rarely synchronized across all genera for either study area. We observed one year (1998, SSA) when all genera produced moderate to excellent crops, and 2 years (1997, NSA and 2000, SSA) when all genera produced poorly or failed. Although production by the 3 dominant producers (oak, juniper, and pinyon) ranged from failure to excellent, mast failures were most common, accounting for 31% of oak crops, 73% of juniper crops, and 67% of pinyon crops. Combined production by all 3 genera failed during 7 of 15 (47%) study area-years for which complete data were available.

District officer responses were highly correlated with corresponding study area mast survey data (Fig. 1) for both scores ($r_s = 0.73$, $P = 0.007$, $n = 12$) and assessments ($r_s = 0.76$, $P = 0.004$, $n = 12$).

Table 1. Annual mast production indices determined from surveys of 10 plant species on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993–2000.

Area	Species, genus, or group	n	Mean mast production rating and index by year							
			1993	1994	1995	1996	1997	1998	1999	2000
NSA	oak	200	0.9 ^a F ^b	3.4 M	2.0 P	2.6 P	2.3 P	3.2 M	1.9 P	4.0 M
	juniper	200	1.4 F	0.5 F	0.1 F	0.3 F	1.2 F	1.1 F	0.9 F	0.5 F
	pinyon	100	2.4 P	0.5 F	1.2 P	2.2 P	0.3 F	1.4 P	1.8 P	0.4 F
	chokecherry	40		2.9 M	2.4 M	1.6 M	0.6 F	3.9 M	3.1 M	
	oak + juniper	400	1.2 F	2.0 P	1.1 F	1.5 F	1.8 P	2.2 P	1.4 F	2.3 P
	oak + juniper + pinyon	500	1.4 F	1.7 P	1.1 F	1.6 F	1.5 F	2.0 P	1.5 P	1.9 P
	oak + juniper + pinyon + chokecherry	540		1.8 P	1.2 F	1.6 F	1.4 F	2.1 P	1.6 F	
	oak + juniper (year-1)	400		2.4 P	1.3 F	1.4 F	1.3 F	2.2 P	1.5 F	2.5 P
	oak + juniper + juniper (year-1)	600		1.8 P	0.9 F	1.0 F	1.3 F	1.8 P	1.3 F	1.8 P
SSA	oak	200	2.1 P	1.2 F	3.1 M	0.9 M	2.5 P	4.5 G	0.4 F	0.7 F
	juniper	200		2.5 M	2.7 M	1.3 M	3.2 M	5.2 E	1.1 F	0.6 F
	pinyon	100	1.3 F	0.2 F	1.1 F	0.8 F	0.4 F	3.6 M	0.1 F	0.1 F
	orange gooseberry	100	4.4 G	1.7 P	0.2 F	3.3 F	2.2 P	3.6 M	3.4 M	
	oak + juniper	400		1.9 P	2.9 M	1.1 M	2.9 M	4.9 G	0.8 F	0.7 F
	oak + juniper + pinyon	500		1.5 F	2.5 M	1.0 M	2.4 P	4.6 G	0.6 F	0.5 F
	oak + juniper + pinyon + gooseberry	600		1.5 P	2.2 P	1.2 P	2.3 P	4.5 G	1.1 F	
	oak + juniper (year-1)	400			2.8 M	1.8 M	1.9 P	3.9 G	2.8 M	0.9 F
	oak + juniper + juniper (year-1)	600			2.8 M	1.6 M	2.4 P	4.3 G	2.3 P	0.8 F

^aIndividual plants were visually rated using the following criteria: no visible fruit = 0; fruit visible after very close inspection = 2; fruit readily visible, but not covering entire plant = 4; or fruit readily visible and covering entire plant = 8.

^bLetters refer to the following relative scale of production: F = failure, P = poor, M = moderate, G = good, and E = Excellent. By genus, annual estimates with different letters were different based on Kruskal-Wallis rank sum and Student-Newman-Keuls tests ($P \leq 0.10$).

Black bear reproduction

Reproductive data were obtained during 266 den investigations of 80 female bears aged 4–27 years. This sample included 115 observations of cub litters, 62 observations of yearling litters, and 89 observations of no offspring (Table 2).

Age of Primiparity. Minimum age of primiparity was judged to be 4 years, because no 1-, 2-, or 3-year-old bears were observed with cubs in the den ($n = 76$) and no 1- or 2-year-old bears were observed in estrus when captured between May and September ($n = 21$). Analyses of mean age included 48 bears monitored prior to primiparity. We documented age of primiparity for 30 of these bears, but others were censored before primiparity because of collar removals, mortalities, shed transmitters, or lost signals. Mean age of primiparity was 5.8 years on the NSA ($n = 60$ bear-years), 5.6 years on the SSA ($n = 37$), and 5.7 years combined ($n = 97$). Although age of primiparity ranged from 4–9 years old, analyses indicated most bears (73%) produced their first litter either at age 5 or 6.

Natality. Natality of female bears ≥ 4 years old was 0.78 cubs/female/year, and proportion of females observed with cubs was 43% ($n = 266$). Natality appeared slightly higher on the NSA than the SSA; however, the

difference was not significant at our α level (0.86 vs. 0.67, $t = 1.6$, 264 df, $P = 0.11$). Proportion of females with cubs did not differ by study area ($P = 0.32$). Natality was higher for parous females than for previously nulliparous females (0.90 vs. 0.53, $t = 3.0$, 264 df, $P = 0.003$) as was proportion of females with cubs (48% vs. 33%, $\chi^2 = 5.1$, 1 df, $P = 0.03$).

Litter size. Litter size ranged from 1–3 cubs with a mean of 1.8 among 115 litters handled or observed in dens. Two-cub litters were most common (71%), followed by 1-cub litters (24%). Neither mean litter size nor frequency of 1-, 2-, and 3-cub litters differed by study area ($P \geq 0.27$). First litters were smaller than subsequent litters (1.6 vs. 1.9, $Z = -2.7$, $P = 0.008$, $n = 115$). Specifically, 1-cub litters were more common among first litters than among subsequent litters ($\chi^2 = 7.18$, 2 df, $P = 0.03$).

Cub survival. Survival data were obtained for 148 cubs from 82 litters (Table 3). First-year survival for all cubs was 0.55. Excluding cubs presumed dead following their mother's death, cub survival was 57% ($n = 143$). Survival was lower for cubs in first litters than for cubs in subsequent litters (38% vs. 62%, $\chi^2 = 6.2$, 1 df, $P = 0.01$, $n = 143$). Cub survival did not differ by study area for all litters ($P = 0.59$), first litters ($P = 0.25$), or subsequent litters ($P = 1.0$).

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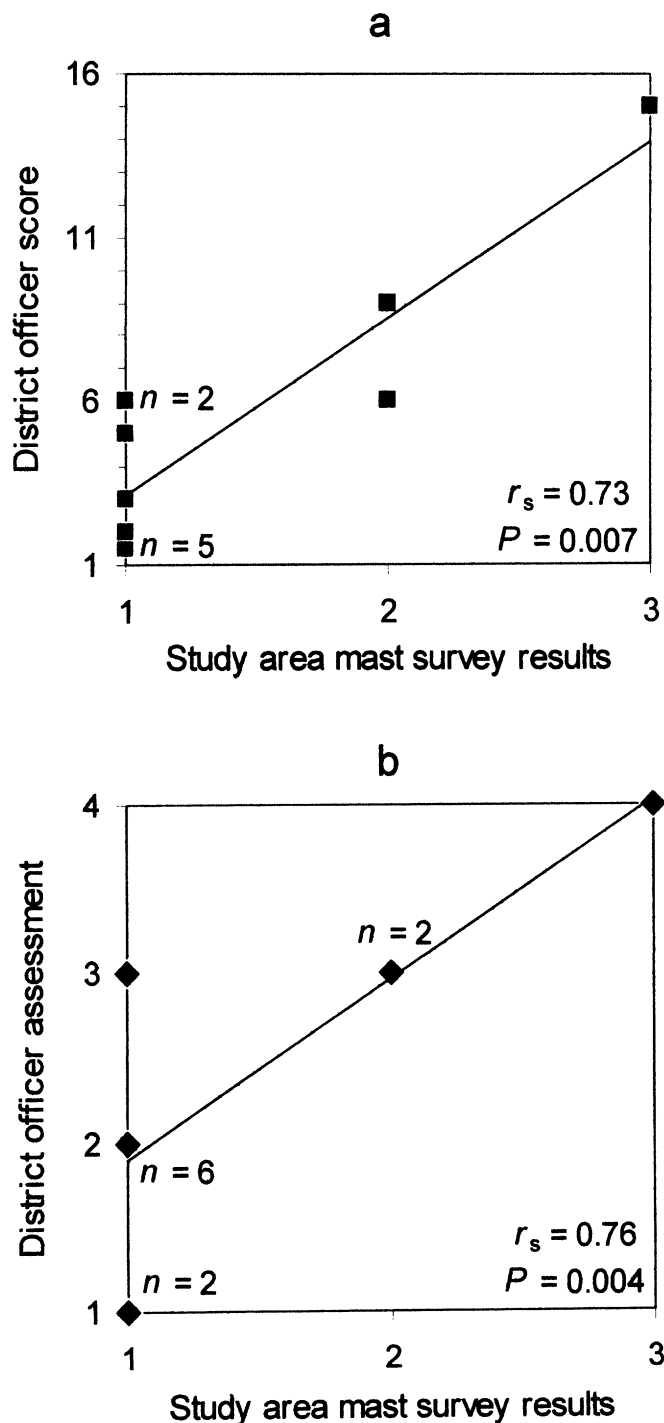


Fig. 1. Relationships between results of intensive mast production surveys conducted on the Northern and Southern Study Areas and subjective scores (a) and assessments (b) recorded within corresponding New Mexico Department of Game and Fish districts, New Mexico, 1999–2000.

Recruitment. Recruitment of females ≥ 5 years old was 0.40 yearlings/female/year, and proportion of females observed with yearlings was 27% ($n = 232$). Neither recruitment nor percent of females with yearlings differed by study area ($P \geq 0.62$). Recruitment was higher for parous females than for previously nulliparous females (0.51 vs. 0.17, $t = 3.5$, 231 df, $P = 0.001$), as was proportion of females with yearlings (28% vs. 13%, $\chi^2 = 6.5$, 1 df, $P = 0.01$).

Litter interval. We documented 65 complete litter intervals and 6 incomplete intervals ≥ 3 years (Table 4). Litter interval ranged from 1 to ≥ 5 years. Most intervals were 2 years (61%), but 1-year intervals were also common (28%). Mean litter interval was at least 1.9 years and was shorter on the NSA than the SSA (1.7 vs. 2.1, $t = -2.4$, $P = 0.02$, $n = 71$). Excluding 1-year intervals, mean interval was at least 2.2 years and was shorter on the NSA than the SSA (2.1 vs. 2.4, $t = -2.0$, $P = 0.05$, $n = 51$). Intervals ≥ 3 years were more common on the SSA ($\chi^2 = 6.1$, 2 df, $P = 0.5$, $n = 71$).

Relationships between mast production and black bear reproduction

Nativity. Among 4 significant logistic regression models relating proportion of eligible females producing cubs to mast production (Table 5), the lowest AIC value was obtained for “reproductive class, oak (year-1), reproductive class \times oak (year-1)” ($\chi^2 = 57.2$, 3 df, $P < 0.001$). This model showed a significant increase in females producing cubs relative to increasing oak production (Wald = 15.8, 1 df, $P < 0.001$) and a significant difference in the rate of increase between previously nulliparous females and eligible parous females (Wald = 3.5, 1 df, $P = 0.06$; Fig. 2). Study area was not a significant

Table 2. Reproductive status of female black bears (≥ 4 years old) documented during annual den investigations on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993–2000.

			Number of observations by year								
Area	Reproductive class	Status	1993	1994	1995	1996	1997	1998	1999	2000	Total
NSA	previously nulliparous	cubs	1	0	2	1	2	8	2	1	17
		no offspring	1	2	3	8	10	4	5	3	36
		total	2	2	5	9	12	12	7	4	53
	parous	cubs	4	0	8	4	12	8	9	9	54
		yearlings	0	3	0	8	3	8	8	6	36
		no offspring	0	4	1	1	0	0	2	3	11
		total	4	7	9	13	15	16	19	18	101
SSA	previously nulliparous	cubs		0	0	1	1	5	4	1	12
		no offspring		0	4	2	7	3	3	3	22
		total		0	4	3	8	8	7	4	34
	parous	cubs		4	0	11	3	5	4	5	32
		yearlings		0	1	0	8	3	8	6	26
		no offspring		2	8	1	1	3	1	4	20
		total		6	9	12	12	11	12	15	78
NSA total			6	9	14	22	27	28	26	22	154
SSA total				6	13	15	20	19	20	19	112
Grand total			6	15	27	37	47	47	46	41	266

indicator variable ($P \geq 0.44$) and was excluded from this model.

Although the proportion of previously nulliparous females producing cubs was positively associated with oak production, strength of the test was compromised by an age bias in the sample. Of the 18 previously nulliparous females observed following oak failure, 72% were 4 years old, but following poor, moderate, and good oak production, 4-year-old females comprised 29% ($n = 45$), 40% ($n = 15$), and 0% ($n = 7$) of the sample, respectively. Among 4 year olds, 0 of 26 produced their

first cubs following years with poor or failed oak production, whereas 1 of 6 produced cubs following a moderate crop ($\chi^2 = 4.4$, 2 df, $P = 0.11$). Among bears >4 years old, 2 of 5 (40%) gave birth for the first time following oak failure, 17 of 32 (54%) following poor production, 4 of 9 (44%) following moderate production, and 4 of 7 (57%) following good production ($P = 0.91$).

The model “reproductive class, oak (year-1)” was the only ANOVA model detecting significant differences in natality relative to mast production (Fig. 3). Natality differed by reproductive class ($F = 53.9$, 1 df, $P < 0.001$)

Table 3. Fate of cubs documented during consecutive annual den investigations on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1993–2000.

			Number of observations by birth year							
Area	Reproductive class of mother	Status	1993	1994	1995	1996	1997	1998	1999	Total
NSA	previously nulliparous	survived	0	0	1	0	0	3	2	6
		died	2	0	2	0	3	8	0	15
		total	2	0	3	0	3	11	2	21
	parous	survived	5	0	7	5	13	9	7	46
		died	3	0	8	4	7	4	7	33
		total	8	0	15	9	20	13	14	79
SSA	previously nulliparous	survived		0	0	0	0	3	3	6
		died		0	0	2	0	3	0	5
		total		0	0	2	0	6	3	11
	parous	survived		1	0	6	6	8	2	23
		died		8	0	5	0	2	0	14
		total		9	0	11	6	10	2	37
NSA total			10	0	18	9	23	24	16	100
SSA total				8	0	13	6	16	5	48
Grand total			10	8	18	22	29	40	21	148

Table 4. Intervals between litters documented for female black bears on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1992–2000.

Area	Fate of litter	Interval (years)			Total
		1	2	≥3	
NSA	≥1 cub survived	0	23	1	24
	no cubs survived	15	3	1	19
	fate unknown	0	1	0	1
	total	15	27	2	44
SSA	≥1 cub survived	0	10	5	15
	no cubs survived	5	3	0	8
	fate unknown	0	3	1	4
	total	5	16	6	27
Grand total		20	43	8	71

and oak index ($F = 10.7$, 3 df, $P < 0.001$). Study area was not a significant factor ($P = 0.93$) and was excluded from the model. Among eligible parous females, natality was lower during years following oak failure than other years (0.6 vs. 1.6, Bonferroni $P = 0.05$). Among previously nulliparous females, no significant differences in natality were detected relative to oak production (Bonferroni $P > 0.15$).

Fat index and chest girth, our best indicators of nutritional condition, were also positively associated with oak production during the previous fall. Among all eligible females, fat index was positively correlated with oak index ($r_s = 0.42$, $P < 0.001$, $n = 133$). Fat indices of 1 or 2 were only recorded following failed or poor oak production. Mean fat index was lower in years following oak failures than other years for previously

nulliparous females (3.5 vs. 2.5, $t = 3.1$, 44 df, $P = 0.004$, $n = 46$) and eligible parous females (3.8 vs. 2.4, $t = 5.8$, 85 df, $P < 0.001$, $n = 87$). Girth was positively correlated with oak production for previously nulliparous females ($r_s = 0.44$, $P = 0.06$, $n = 18$) and eligible parous females ($r_s = 0.56$, $P = 0.001$, $n = 31$). Among previously nulliparous females, mean girth was 75.9 cm in years following oak failures but was 84.6 cm in other years ($t = 1.8$, 16 df, $P = 0.10$, $n = 18$). Based on a regression of \ln (chest girth) and \ln (weight) ($R^2 = 0.90$, $P < 0.001$, $n = 116$), these measurements corresponded to predicted weights (PW) of 54 kg and 71 kg, respectively. Among eligible parous females, mean girth was 83.6 cm (PW = 69 kg) in years following oak failures, but 95.8 cm (PW = 97 kg) in other years ($t = 3.7$, 29 df, $P = 0.001$, $n = 31$).

Production of cubs was related to fat index and chest girth. No eligible females with a fat index of 1 and only 29% of females with an index of 2 produced cubs. Mean fat index differed between females that produced cubs and those that did not for previously nulliparous females (3.7 vs. 2.7, $t = 4.1$, 45 df, $P < 0.001$, $n = 47$) and eligible parous females (3.8 vs. 2.3, $t = 7.0$, 88 df, $P < 0.001$, $n = 90$). Mean girth was 76.4 cm (PW = 55 kg) for previously nulliparous females that did not produce cubs, but 89.3 cm (PW = 82 kg) for those that did produce cubs ($t = 2.8$, 16 df, $P = 0.01$, $n = 18$). Mean girth was 82.1 cm (PW = 66 kg) for eligible parous females without cubs and 94.2 cm (PW = 93 kg) for those with cubs ($t = 3.2$, 29 df, $P = 0.003$, $n = 31$). No previously nulliparous females with a chest girth <80 cm (PW = 62 kg) produced cubs and only 1 parous

Table 5. Akaike information criteria (AIC) for logistic regression models relating reproductive parameters to mast production.

Response	Model	AIC	ΔAIC	W _i
Percent of eligible females producing cubs	class ^a , oak (year-1), class × oak (year-1)	44.99	0.00	0.873
	class, area ^b , oak + juniper + pinyon + softmast	48.85	3.86	0.127
	class, area, oak + juniper + pinyon (year-1)	59.01	14.02	0.001
	class, area, oak + juniper (year-1), class × oak + juniper (year-1)	67.52	22.53	0.000
Cub survival	litter ^c , juniper (year-1)	26.71	0.00	0.613
	litter, oak (birth year) + juniper (year-1)	27.76	1.04	0.364
	litter, oak (birth year)	34.04	7.32	0.016
	litter, oak (year-1), litter × oak (year-1)	35.47	8.75	0.008
Percent of eligible females producing yearlings	class, oak + juniper + pinyon (year-2)	33.10	0.00	0.685
	class, oak (year-2)	34.65	1.56	0.315
	class, area, oak + juniper (year-2), class × oak + juniper (year-2)	52.61	19.52	0.000

^aReproductive class (previously nulliparous or eligible parous).

^bStudy area (Northern Study Area or Southern Study Area).

^cLitter order (first or subsequent).

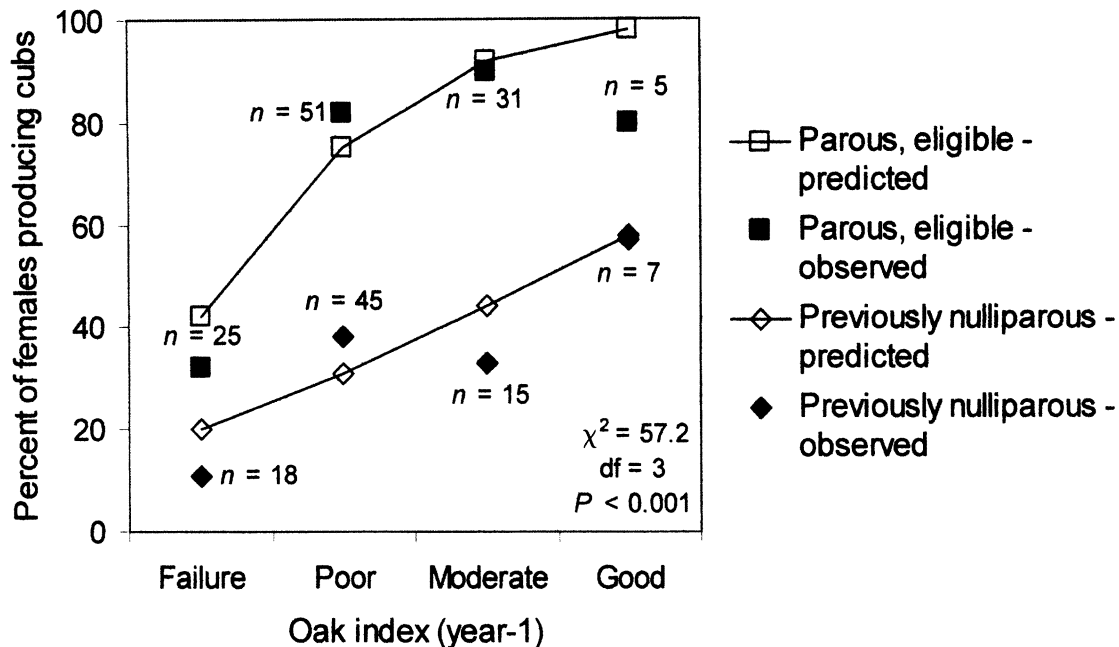


Fig. 2. Observed and predicted values for logistic regression model relating percent of females producing cubs to oak production on the Northern and Southern Study Areas, New Mexico, 1993–2000. Oak index was entered into the model as a predictor variable with values of 1–4 corresponding to failure to good production. Reproductive class was entered into the model as an indicator variable.

female under this threshold produced a litter. Above this threshold, 66% of previously nulliparous females produced cubs, but proportion did not increase with increasing girth.

Litter size. All mast production indices were insignificant ($P \geq 0.15$) in ANOVA models relating litter size to mast production. Neither mean litter size nor frequencies of 1-, 2-, and 3-cub litters differed relative to fat index ($P \geq 0.56$). Sample sizes were inadequate for assessing relationships between chest girth and litter size.

Cub survival. Among 4 significant logistic regression models estimating the relationship of cub survival to mast production (Table 5), lowest AIC values were obtained for “litter order, juniper (birth year-1)” ($\chi^2 = 9.4$, 2 df, $P = 0.009$) and “litter order, oak (birth year) + juniper (birth year-1)” ($\chi^2 = 11.6$, 2 df, $P = 0.003$). The first model detected a slight increase in survival relative to increasing juniper production (Wald = 2.7, 1 df, $P = 0.10$) and a significant difference in survival between first litters and subsequent litters (Wald = 7.5, 1 df, $P = 0.06$). The second model detected a significant increase in survival relative to increasing oak and juniper production (Wald = 4.7, 1 df, $P = 0.03$) and a significant difference in survival by

litter order (Wald = 9.0, 1 df, $P = 0.003$; Fig. 4). Study area was not a significant indicator variable in either model ($P \geq 0.40$) and was excluded. Cub survival did not differ relative to fat index of mother ($P = 0.88$).

Recruitment. Among 3 significant logistic regression models relating proportion of eligible females producing yearlings to mast production (Table 5), lowest AIC values were obtained for “reproductive class, oak (year-2)” ($\chi^2 = 46.5$, 3 df, $P < 0.001$) and “reproductive class, oak + juniper + pinyon (year-2)” ($\chi^2 = 43.6$, 2 df, $P < 0.001$). The first model detected a significant increase in females producing yearlings relative to increasing oak production (Wald = 20.0, 1 df, $P < 0.001$) and a significant difference between previously nulliparous females and eligible parous females (Wald = 19.8, 1 df, $P < 0.001$). The second model detected a significant increase in females producing yearlings relative to increasing oak, juniper, and pinyon production (Wald = 15.1, 1 df, $P < 0.001$) and a significant difference between previously nulliparous females and eligible parous females (Wald = 22.2, 1 df, $P < 0.001$; Fig. 5). Study area was not a significant indicator variable in either model ($P \geq 0.44$).

Two significant ANOVA models detected differences in recruitment relative to mast production. The first

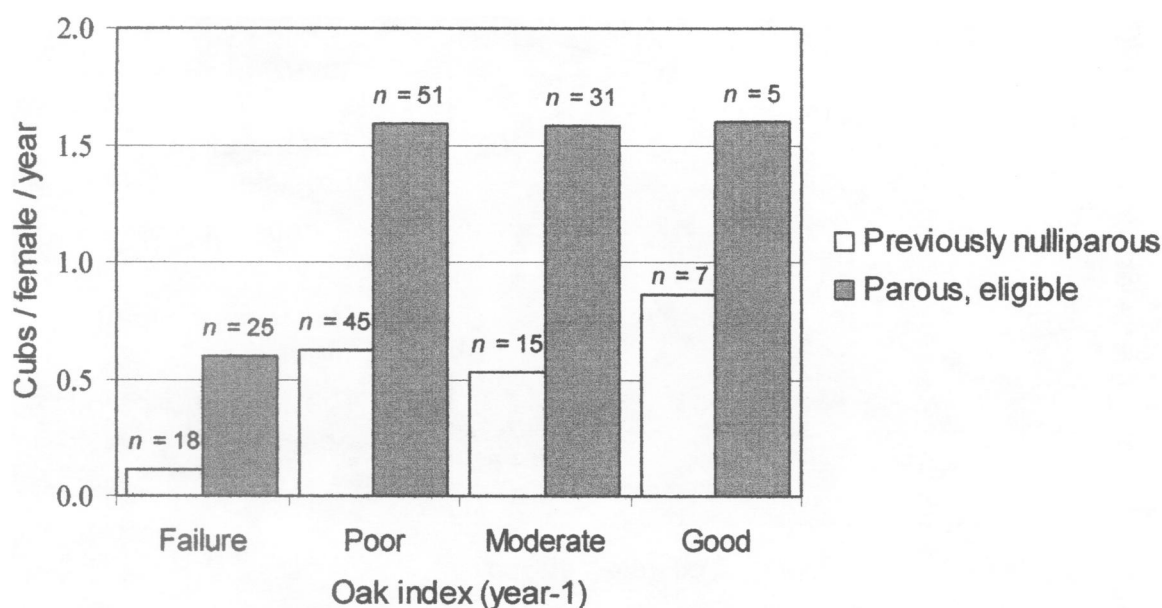


Fig. 3. Natality (cubs/female/year) of female black bears (≥ 4 years old) relative to oak index during the previous year on the Northern and Southern Study Areas, New Mexico, 1993–2000.

model, “reproductive class, oak (year-2)”, indicated a significant difference in recruitment between previously nulliparous females and eligible parous females ($F = 28.2$, 1 df, $P < 0.001$) and relative to oak index ($F = 6.7$, 3 df, $P < 0.001$). Study area was not a significant factor ($P = 0.71$) and was excluded from this model. For eligible parous females, recruitment was significantly lower 2 years after oak failures than all other years (0.25 vs. 0.87, Bonferroni $P = 0.05$). For previously nulliparous females, recruitment was higher 2 years after good oak production than all other years (1.00 vs. 0.13, Bonferroni $P = 0.10$; Fig. 6).

The second model “reproductive class, juniper (year-2)”, indicated a difference in recruitment between previously nulliparous females and eligible parous females ($F = 31.3$, 1 df, $P < 0.001$) and differences in recruitment relative to juniper index ($F = 3.9$, 2 df, $P < 0.02$). However, no significant difference in recruitment relative to juniper production was apparent for eligible parous females (Bonferroni $P > 0.15$). For previously nulliparous females, recruitment was higher 2 years after excellent juniper production than following failed or moderate production (1.0 vs. 0.1, Bonferroni $P = 0.10$).

Litter interval. Variation in litter interval was related to mast production. We observed 18 failed reproductive opportunities, of which 61% coincided with oak failures during the previous fall, 22% coincided

with poor production, and 17% coincided with moderate production. We observed 52 successful reproductive opportunities, of which only 14% coincided with oak failures, while 54%, 25%, and 8% coincided with poor, moderate, and good oak production, respectively ($\chi^2 = 16.5$, 3 df, $P = 0.001$, $n = 70$).

Discussion

Periodic lack of mast production appeared to influence bear productivity; the effect of oak failures appeared to be most pronounced. For eligible parous females, natality decreased by more than 60% following years of oak failure and recruitment decreased by more than 70% 2 years after oak failure. Lack of hard and soft mast has been tied to declines in reproduction in several regions (Jonkel and Cowen 1971, Rogers 1976, Eiler et al. 1989, Elowe and Dodge 1989, McLaughlin et al. 1994, Miller 1994). Neither natality nor recruitment varied following good, moderate, or even poor oak production. This suggests only a minimum threshold of high quality food is needed for successful reproduction. Although weight thresholds necessary for reproduction have been cited (Rogers 1976, Kolenosky 1990, Samson and Huot 1995), we found no previous references to the existence of a minimum food abundance threshold.

Differences in fat index and girth measurements demonstrated that a lack of fall mast resulted in lower

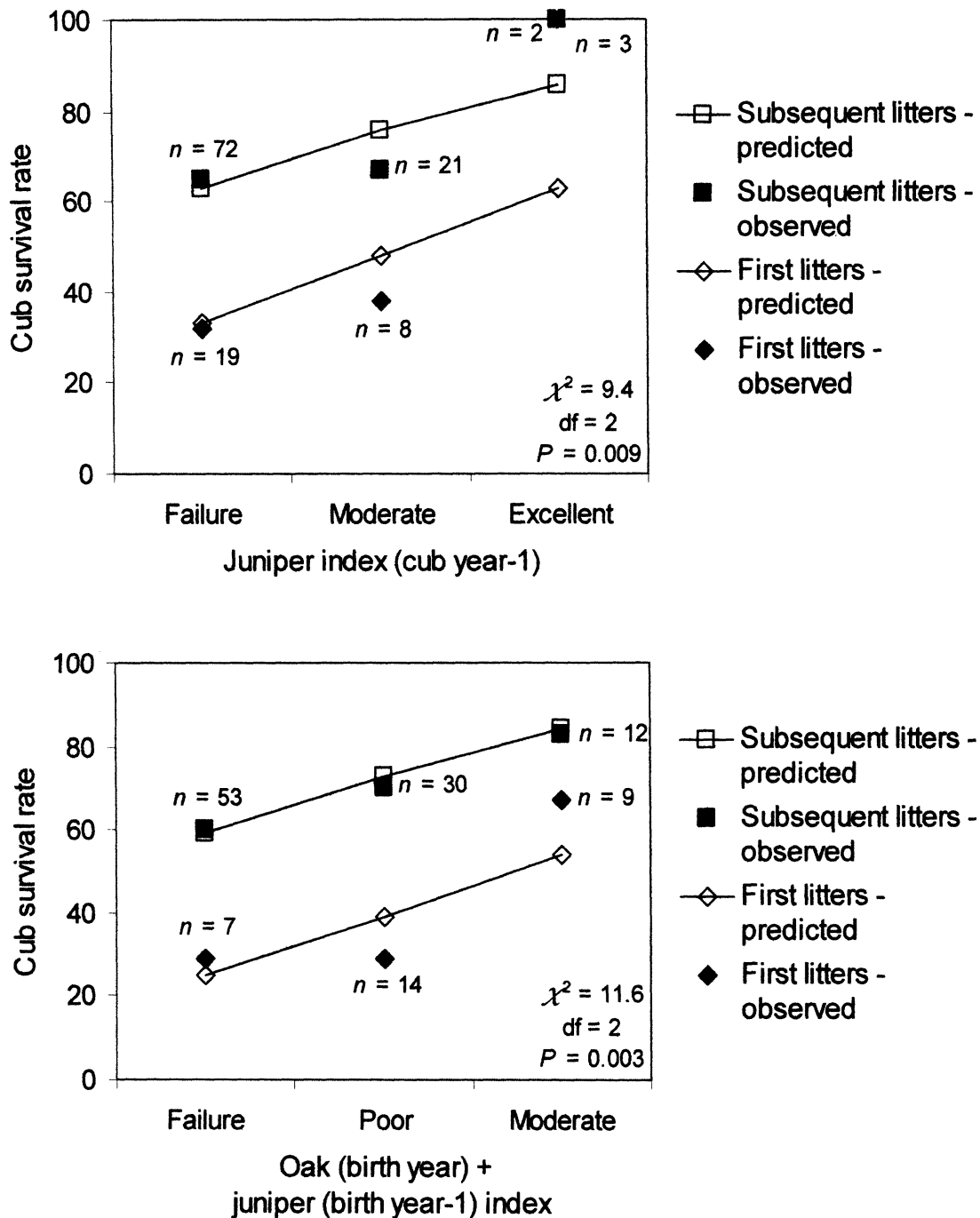


Fig. 4. Observed and predicted values for logistic regression models relating black bear cub survival to mast production on the Northern and Southern Study Areas, New Mexico, 1993–1999. Mast index was a predictor variable with values of 1–5 corresponding with failure to excellent production. Litter order was an indicator variable.

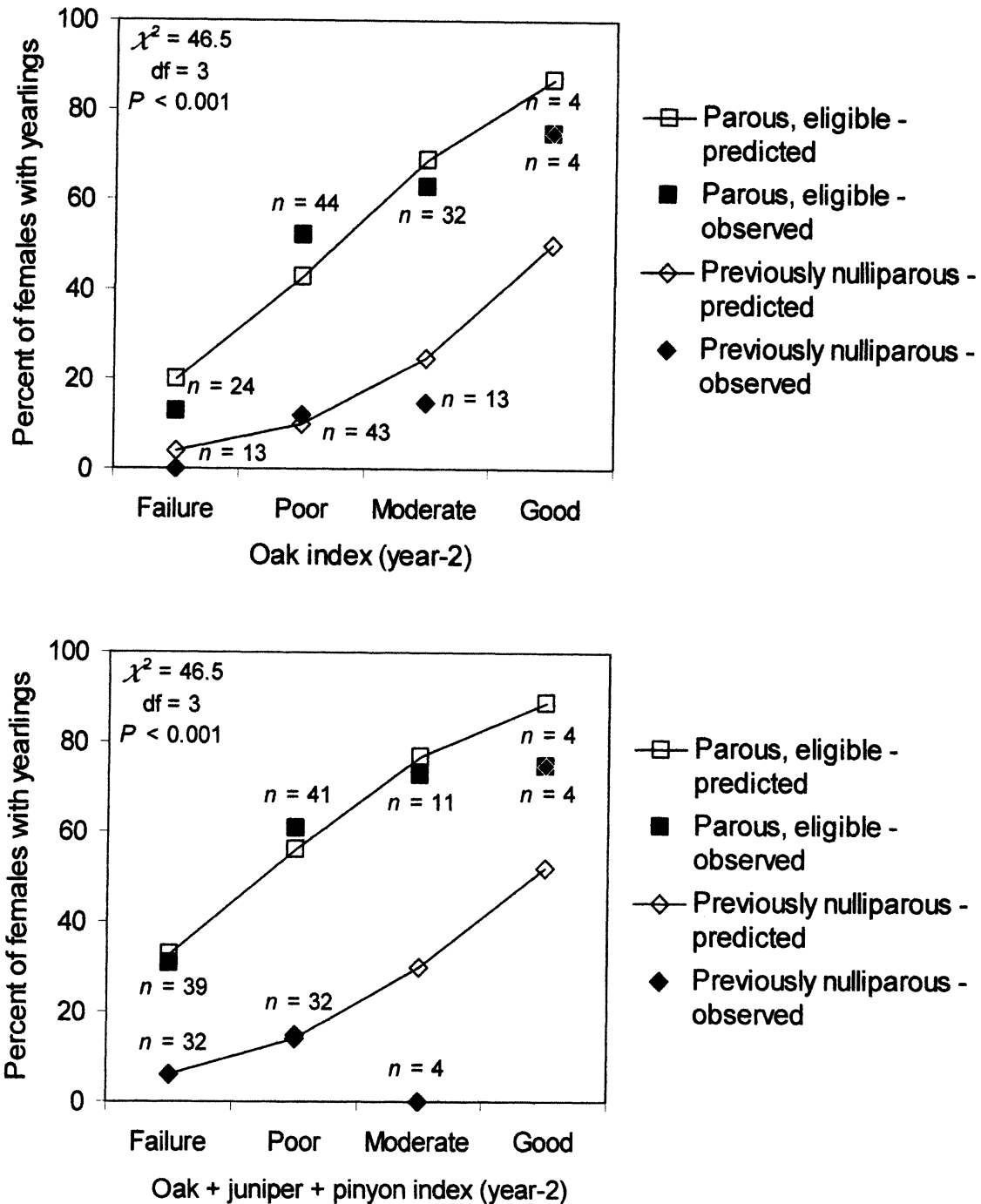


Fig. 5. Observed and predicted values for logistic regression models relating percent of females producing yearlings to mast production 2 years previous on the Northern and Southern Study Areas, New Mexico, 1993–2000. Mast index was a predictor variable with values of 1–5 corresponding with failure to excellent production. Reproductive class was an indicator variable.

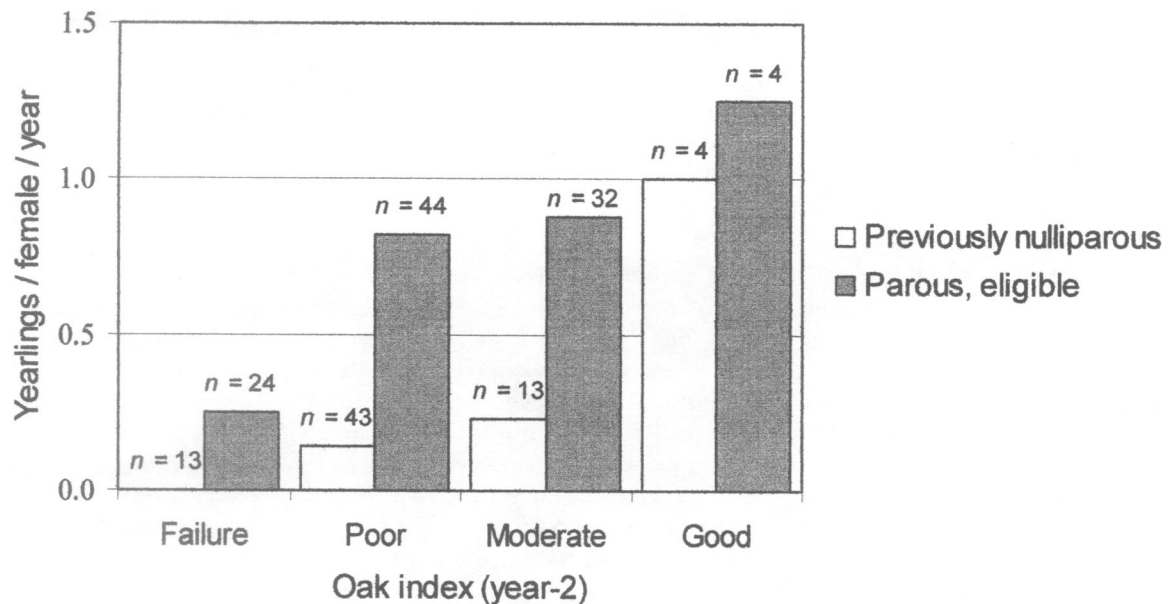


Fig. 6. Recruitment (yearlings/female/year) of black bears (≥ 5 years old) as related to oak index 2 years previous on the Northern and Southern Study Areas, New Mexico, 1993–2000.

nutritional condition of bears. Predicted mean weight of eligible parous females that did not produce was 66 kg, very close to the threshold weight of 62 kg identified as necessary for reproduction by previously nulliparous females. This indicates a single year of oak failure was adequate for reducing weights of some parous females to levels experienced prior to reproductive maturity. Low weights have been associated with a lack of reproduction by parous females in other regions (Rogers 1976, Elowe and Dodge 1989, Kolenosky 1990, Noyce and Garshelis 1994, Samson and Huot 1995).

No positive association was found between juniper or pinyon production and natality or recruitment, except for the relationship between recruitment and combined production of oak, juniper, and pinyon. Although higher levels of juniper and pinyon production occurred in conjunction with acorn failures, it appeared this production did not compensate for lack of acorn production. In fact, moderate juniper production coincided with oak failure on the SSA in 1994 and poor pinyon production coincided with oak failure on the NSA in 1993. Nonetheless, subsequent natality and recruitment were zero. Only 1 year of moderate pinyon production occurred during the study (SSA, 1998), but it coincided with a good oak crop and an excellent juniper crop. These simultaneous events did not allow us to determine the impact of moderate pinyon production alone on reproduction. Pinyon cones mature and open approxi-

mately 6 to 8 weeks after ripening of acorns, possibly limiting foraging opportunities of bears preparing for hibernation. We observed pregnant females denning earlier than other classes of bears and many were denned by mid-October, especially on the NSA (Costello et al. 2001). More study is needed to determine the influence of pinyon production on bear reproduction, especially in the absence of other foods.

We found no evidence that chokecherries or gooseberries influenced bear productivity. Compared to other species surveyed, these soft mast species were more limited in distribution and were probably available to only a fraction of the bear population. Analyses of foraging habits indicated these species accounted for <10% of scat volume during fall (Costello et al. 2001).

Cub survival appeared to increase slightly relative to juniper production during the previous fall and relative to combined production of juniper during the previous fall and oak production during the birth year. Other studies have documented a positive relationship between cub survival and mast production during the previous year, which was generally attributed to better nutritional condition of mothers (Rogers 1976, Eiler et al. 1989, Elowe and Dodge 1989). Noyce and Garshelis (1994) found that cubs born of lightweight mothers were less likely to survive, because they were unable to attain adequate weights. Our results suggest cub survival was related not only to abundance of fall mast (which

determines condition of females during denning, parturition, and early lactation), but also to availability of mast during spring and summer. In New Mexico, juniper berries began to ripen in September to October but remained on trees through late fall. Berries began to drop during winter and early spring. We observed bears consuming substantial quantities of juniper berries during all seasons, especially on the SSA when production was high (Costello et al. 2001). Therefore, more than any other mast genera, juniper could continue to affect nutritional condition of females and their cubs long after emergence from dens.

Although mean rates of cub survival did not differ between study areas, annual rates appeared to fluctuate more on the SSA. On the NSA, lack of juniper production, combined with failed to moderate oak production, resulted in relatively consistent annual cub survival rates (50–62%). The more variable annual cub survival observed on the SSA (13–100%) appeared to be associated with varying levels of juniper and oak production. We suspect there may be differences in the productivity of the juniper species existing on the SSA versus those on the NSA; however, future mast production surveys will be necessary to determine if these inter-specific differences exist.

Cub survival in New Mexico averaged only 57% and appeared typical of bear populations in the Southwest (LeCount 1982, 1987, 1990; Beck 1991). Rates were also similar to those observed in Tennessee (Eiler et al. 1989), Massachusetts (Elowe and Dodge 1989), and Ontario (Kolenosky 1990), but were generally lower than those observed in Alaska (Schwartz and Franzmann 1991), Maine (McLaughlin et al. 1994), and Minnesota (Noyce and Garshelis 1994). The lower survival of cubs in New Mexico compared to these regions cannot be explained merely by condition of maternal females during winter because no difference appeared to exist in mean weight of lactating females in dens. This also suggests availability of foods upon den emergence may be as important to cub survival as maternal condition in the den. Arid climate may limit abundance of green vegetation for bears in the Southwest, possibly accounting for some of the observed difference in cub survival.

In our study, we found no correlation between annual mast production and litter size. Our results support suggestions that regional differences in litter size, such as those compiled by Alt (1989) and Beck (1991), were not related to nutritional condition (Beck 1991, Noyce and Garshelis 1994). In contrast to cub survival and litter interval, which vary annually as a consequence of food availability and maternal condition, litter size and age

of primiparity appear to be relatively insensitive to these changes even under the most extreme conditions. MacDonald and Fuller (2001) also concluded that litter size is relatively invariable locally because no relationship could be found between food abundance, bear nutritional traits, and litter size. In the Southwest, smaller litter size and older mean age of primiparity may be evolutionary strategies for maximizing fitness by increasing cub survival and residual reproductive value in an environment with variable and unpredictable food availability. The fact that only 57% of nulliparous females above the girth threshold produced cubs indicates factors other than current condition may be involved.

Noyce and Garshelis (1994) determined relationships among reproductive parameters of black bears and several potential indicators of nutritional condition in Minnesota. They proposed that, as nutritional plane declines from a theoretical maximum, black bears respond by modifying reproductive performance in the following sequence: (1) litter size, (2) age of primiparity, (3) juvenile survival, (4) cub survival, and (5) litter frequency. They acknowledged that their model extended beyond the range of values in their data because few individuals approached either extreme of nutritional condition. To broaden their perspective, they also drew upon published reproductive data obtained from a highly productive population in Pennsylvania (Alt 1989) and more marginal populations in Alaska (Miller 1994) and Ontario (Kolenosky 1990). With low diversity of mast producing plants in New Mexico, coupled with frequent occurrences of mast failures, reproductive data from New Mexico may contribute valuable information for refinement of the Noyce and Garshelis (1994) model.

The most notable contrast between our results and those of Noyce and Garshelis (1994) pertains to litter interval. They found no relationship between maternal condition and litter interval, and litter interval varied from the expected 2 years in only 4 of 64 observations. In New Mexico, differences in the proportion of eligible females producing cubs and resulting variation in litter interval appeared to be the reproductive parameters most closely associated with mast production. This contrast does not appear to be related to a lower nutritional plane in New Mexico but to a more variable nutritional plane. Following adequate crops of oak, individuals were observed with physical traits (fat index and girth) indicative of nutritional condition equal to or higher than that of individuals in Minnesota. However, bears were observed to drop below weight thresholds necessary for cub production following frequent oak failures. We

believe this variation in nutritional condition in New Mexico is related to a lack of alternative foods when acorn failures occur. Nutritional condition may also be related to a lack of quality foods during spring and summer. Further analyses may show whether the time between den emergence and fall mast availability represents a negative foraging period. Noyce and Garshelis (1998) found that several classes of bears in Minnesota gained weight during this period, but that lactating females generally lost weight.

Our analyses provide insight into the variability in reproductive traits that can be observed within a population, or even in an individual over time, relative to more extreme fluctuations in food abundance than those apparent in Minnesota. Our results support the Noyce and Garshelis (1994) model with respect to the response of bears to declining nutrition from a theoretical maximum. But for understanding the effects of food shortages on local populations, we suggest the following addition. For populations in environments where annual supplies of food are highly variable and unpredictable, the reproductive parameters most sensitive to periodic declining nutrition are, in order: (1) litter frequency, (2) cub survival, (3) age of primiparity, and (4) litter size.

Management implications

Documenting annual mast production, particularly occurrence and frequency of mast failures, may be an effective tool for forecasting changes in black bear reproductive output in New Mexico. Annual mast and bear harvest data may provide wildlife managers with an opportunity to identify periods of reduced or increased natality and recruitment. Examination of proportions of 1-, 2-, and 3-year age classes of bears in 3 successive years of NMDGF harvest records from 1985–2000 revealed striking differences by birth year. Some cohorts appeared to be virtually absent from harvest records, while others appeared large. In regions surrounding our 2 study areas, these patterns in cohort size corresponded with observed variation in natality and birth years of captured bears estimated from cementum ages (Costello et al. 2001). Simultaneous observations of missing cohorts and mast failures would provide compelling evidence of periodic declines in black bear productivity. Potential effects of these declines could then be explored with simulations using population modelling.

Long-term collection of mast production data may also provide insight into relative productivity of bear populations in different regions of New Mexico. Dur-

ing the study period, the NSA experienced only 1 oak failure, while the SSA experienced 4. As a consequence, observed natality was slightly lower on the SSA. Only long-term documentation of annual mast will allow us to determine if these frequencies were real or were due to random variation during the short sampling period.

Besides providing data relevant to bear reproduction, mast surveys may also help elucidate other patterns in harvest data. In regions surrounding our study areas, increases in hunter effort, hunter success, and proportion of females in the kill were associated with documented oak failures (Costello et al. 2001). In Minnesota, results of well established mast surveys, along with hunter effort, explained most of the year-to-year variation in hunting success and sex–age composition of the harvest (Noyce and Garshelis 1997).

Results of simplified surveys conducted by NMDGF officers were highly correlated with our more intensive survey results, indicating subjective criteria were adequate to distinguish variation in mast production. Results were most consistent with the “score” of relative numbers of fruit/plant and relative numbers of plants bearing fruit. We believe these simplified surveys are an acceptable alternative to the more intensive surveys and may be a more feasible option for long-term, statewide use. We suggest continuation of these mast surveys in New Mexico and recommend implementation of similar surveys in other regions, especially where hard mast is a primary fall food of black bears. In the future, an effort to establish specific survey routes, revisited each year, may reduce unnecessary variability and ensure quality data.

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