PREDICTION OF LITTER SIZE IN AMERICAN BLACK BEARS

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Abstract: American black bear *(Ursus americanus)* litter production is likely dependent on maternal condition, which is in part dependent on the availability of fall foods. To date, no indices for black bear demographic parameters have been reported that particularly aid in population modeling. Thus, black bear population model parameterization is usually based on extensive field work with radiocollared animals. However, long-term, intensive field research can not be carried out indefinitely. We attempted to classify production of different litter sizes by black bears in Massachusetts using environmental and harvest-derived variables combined with individual black bear variables (weight, age, reproductive status). We used linear discriminant function analysis to classify litter events into categories (1 cub, 2 cubs, 3 cubs, or 4 cubs) and thus to identify variables that may index reproductive output. We also used 2 types of Bayesian analysis to estimate the probability distribution of litter sizes for Massachusetts black bears. During 1981-97, we observed 20 known first litters and 66 subsequent litters. We could not derive a predictable relationship among food abundance, bear traits, and litter size. This was due in part to black bears' propensity to use human-related food sources (primarily corn) in years of poor natural food abundance. Simple Bayesian estimates tended to overestimate the proportion of 2-cub first litters and 3-cub subsequent litters in Massachusetts. A different approach based on the multinomial distribution produced estimates of litter size distributions very close to that observed for subsequent litters. The observed distribution of first litters in Massachusetts was skewed much lower than other reported distributions, thus complicating our use of prior information in the Bayesian estimates. We suggest that litter size is relatively invariate locally and can be reliably estimated for modeling purposes using Bayesian techniques. Thus, researchers and managers can use the extensive data collected on black bear reproduction to help estimate sensitive parameters for their own specific populations in the absence of annual field data collection.

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Key words: Bayesian estimation, American black bear, corn, hard mast, linear discriminant function, litter order, litter size, Massachusetts, *Ursus americanus*

Recent efforts to estimate black bear populations have generally taken one of two approaches. One approach involves intensive capture and radiocollaring efforts, with subsequent den visits, to estimate demographic parameters (e.g., litter size, cub sex ratio, age of first reproduction) for inclusion in a population model (Yodzis and Kolenosky 1986, Fuller 1993, McLaughlin 1998). The other approach also involves intensive capture and marking, usually with radiocollars, and the use of mathematical models to estimate bear densities (Garshelis 1992, Fuller 1993, Miller et al. 1997). Garshelis and Visser (1997) used a variation of this technique with tetracycline-laced baits that allowed bears to mark themselves by consuming the baits. They used harvested bears as the recapture sample and identified marked individuals by examining tooth and bone samples for tetracycline marks. This technique requires that sufficient samples of harvested bears be obtained.

Most states with black bear hunting seasons use some harvest-derived measures to index population trends; however, there are several problems with using these data to estimate population status or trend (Beck 1991, Garshelis 1993, Noyce and Garshelis 1997). For species such as white-tailed deer (*Odocoileus virginianus*), indices have been developed that estimate key demographic parameters such as age-specific reproductive rates (Severinghaus and Moen 1983) from harvested animals. For black bears, no such index has been developed for any key demographic parameter (Noyce and Garshelis 1994).

In Massachusetts, the University of Massachusetts, Amherst and the Massachusetts Division of Fisheries and Wildlife have collaborated in an ongoing black bear field research project since 1980. Several other states and provinces also have conducted long-term black bear radiocollaring studies (Alt 1989, McLaughlin et al. 1994, Noyce and Garshelis 1994, Pelton and van Manen 1996). These studies have generated the type of information needed for the population model approach, but are extremely labor intensive and expensive.

Because black bears do not reach sexual maturity in most areas until 2.5 years of age and have cubs at intervals of 2 years, cub production and cub survival are usually identified as important population model inputs (Fuller 1993). Body weight, age, and overall nutritional condition of female black bears have been hypothesized to be related to reproductive parameters (Rogers 1987, Alt 1989, Elowe and Dodge 1989, Stringham 1990). Further, natural food abundance has been speculated to influence bear reproductive success and could possibly serve as a surrogate for bear condition.

Stringham (1990) demonstrated a positive relationship between adult bear weight and litter size. Noyce and Garshelis (1994) could not predict litter size from physical and blood parameters of black bears but litter order was related to litter size, as first litters were smaller than subsequent litters. They suggested that litter size is relatively insensitive to maternal condition except at extremes.

Our objectives in this paper were (1) to predict litter

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size in Massachusetts black bears based on environmental and physical variables and, (2) to use a Bayesian approach to estimate Massachusetts black bear litter size from data collected in eastern North America. Our null hypothesis was that we could not assemble a suite of environmental variables that could accurately predict litter size in black bears, even given some data (age, weight, litter order) for individual bears. Bayesian techniques use existing information to predict the probability of future events (Winkler 1972). Because Bayesian methods result in a probability distribution for a given set of outcomes, we thought that this statistical style was better suited to estimate a discrete variable like litter size than traditional frequentist approaches (i.e., mean and standard deviation).

STUDY AREA

We collected data in western Massachusetts (42°27'N, 72°41' W) on the 150-km² Conway–Williamsburg study area (CWSA). The CWSA was 70% forested and >90% privately owned; elevations ranged from 30 m to 450 m (Fuller 1993). Hardwood-dominated forests consisted of northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta*), sugar maple (*A. saccharum*), and hickories (*Carya* spp.). Major softwoods were eastern white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*).

The major agricultural crop present in the CWSA and used by bears was feed corn for dairy cattle. Usually 10–20, 0.4 to 4.0-ha cornfields were present in the CWSA each year. Other human-related food sources included apiaries, apple orchards, and home bird feeders, but none of these were enumerated.

METHODS

We captured bears during 1980–96 with foot snares and trained bear hounds (Elowe 1984, Fuller 1993) and immobilized them with a mixture of ketamine hydrochloride (10–17 mg/kg body weight) and xylazine hydrochloride (1–2 mg/kg body weight) or tiletamine hydrochloride (3.9–7.3 mg/kg body weight). We used ketamine (6–10 mg/kg body weight) alone on small bears (<50 kg). We placed radiocollars on adult and yearling females. During January–March each year we tracked radiocollared females to winter dens and counted new cubs. We marked some cubs with numbered aluminum or plastic ear tags for future identification. We visited the dens of females expected to have litters between 20 February and 20 March. We determined litter order (first litter, subsequent litter) through visits to dens of known-age females collared as yearlings with their mothers, or captured as 1- or 2-year olds (determined by counting cementum annuli). If the order of a female's first observed litter could not be determined it was not included in our analyses, but her subsequent litters were used.

We estimated abundance of natural fall foods in several ways during the study. Between 1980 and 1996 we estimated fall mast (e.g., oak, beech [*Fagus grandifolia*], black cherry [*Prunus serotina*]) visually and classified it as poor, good, or excellent (Elowe 1987). Between 1991 and 1996 we sampled 7–12 line transects and made visual estimates of hard mast abundance (Fuller 1993, McDonald et al. 1994). Between 1993 and 1996 we used seed traps (Christisen and Kearby 1984) to estimate hard mast production and correlate hard mast abundance in the CWSA to that in the Quabbin Reservation in central Massachusetts (about 30 km east of the CWSA). We used the indices to red oak acorn crop size in the Quabbin Reservation during 1986 to 1990 as surrogates for fall mast production in the CWSA for those years. This index was derived by dividing the annual total of acorns collected in seed traps by the 1995 total annual collection (W. Healy, U.S. Forest Service Northeast Experiment Station, Amherst, Massachusetts, personal communication, 1998). Because we did not have quantitative mast data for the early years of the study, we used 3 classifications, poor, good, and excellent, when analyzing the entire data set. We also performed analyses on reduced data sets for which we had quantitative mast data (kg/ha or index values).

Between 1993 and 1996 we conducted aerial surveys of cornfield damage during early September. We surveyed the entire CWSA and some adjacent areas, and we identified all cornfields and visually estimated the percent of each field damaged by bears.

We used data collected from harvested bears at mandatory, state-operated check stations to calculate mean dressed weights of harvested bears, ages of harvested bears, and percent females among harvested bears. We obtained the percent females and mean dressed weights of bears in the early season (Sep or Oct) harvest from 1982 to 1996. Ages were derived primarily from cementum annuli readings performed by Matson's Laboratory, Milltown, Montana. Some harvested bears were tagged as part of this study and their ages were known because they were first captured in dens with their mothers (see above). We pooled harvested bears into 4 age classes for analysis: cubs-of-the-year (1.0 year old), yearlings (1.7 years old), young bears (2.7–4.7 years old), and adults (>5.0 years old). Cubs and yearlings were considered sexually immature. Young bears (3 to 5 year olds) included the age classes in which we observed first litters, although some 3.7- and 4.7-year-old bears may have been multiparous. All adult bears would have been multiparous.

We estimated den entry weights of female bears weighed at dens in late winter by (1) assuming a den entry date of

December 1 and using the daily weight loss rate of 260g/ day reported by Hellgren et al. (1990), and (2) using the weight loss equation (early weight = 9.41 + 2.16 [litter weight] + 0.96 [late winter weight]) reported in Samson and Huot (1995) to estimate late December weight. We assessed all variables for normality using the UNIVARIATE procedure in SAS (SAS Institute 1985). Proportions were transformed for analysis with the arcsine square root transformation.

We used a stepwise procedure (PROC STEPDISC) to select variables for the discriminant function analysis (PROC DISCRIM) after examining the data for correlated variables. We entered variables with $P \leq 0.20$ into the model. We derived prior probabilities of group membership from data on litter size distributions from unknown order litters presented in the literature (Table 1). We classified litters as 1 cub, 2 cubs, 3 cubs, or 4 cubs. We did not observe any 5 cub litters during this study.

We considered 80% overall correct classification as a successful model. Because we used the same data to assess classification success as to develop the classification functions, we used a cross-validation procedure (Lachenbruch 1967, SAS Institute 1989) to estimate classification success. This technique uses (n -1) observations to develop the classification functions and applies those functions to the observation left out. By doing this for all n observations, an unbiased estimate of classification success is obtained (Efron and Gong 1983).

We performed Bayesian estimation of the probabilities of observing different sized litters in Massachusetts. Simple Bayesian analysis uses conditional probabilities (likelihoods) to estimate the probability of an outcome given some specified prior probability distribution (Winkler 1972; e.g., we estimated the probability of a female having a litter of 2 cubs given that it is her first litter: P[2 cubs | first litter]). The conditioning variable must be one that can be determined without error. We used litter order (first litter, had prior litter) as the conditioning variable in our analysis. First litters tend to be smaller and have lower survival rates than subsequent litters (Elowe 1987, Beck 1991, Fuller 1993, McLaughlin et al. 1994, Noyce and Garshelis 1994). Thus, litter order should be an effective and meaningful conditioning variable.

Bayesian analysis combines the assumed prior probability distribution with a likelihood measure to estimate the posterior probability distribution. These estimates can be updated as new data are added (Cohen 1988). We derived the prior probability distribution of litter size from sources in the literature and from communication with other bear researchers using only data from in-den litter observations. These data contain both first and subsequent litters. We restricted our search to eastern North America because many western studies estimated litter size from spring and summer family group observations. Also, there is evidence that in western black bear populations, litter size distribution may be skewed lower than eastern populations (Alt 1989).

We calculated likelihood functions (conditional probabilities) for litter sizes from known first litters and subsequent litters from studies that determined litter order, excluding Massachusetts data (Table 2). We used Bayes theorem to combine the "known" prior distribution of black bear litter sizes with the observed likelihood functions for first and subsequent litters to estimate a poste-

Table 1. Black bear litter sizes for litters of unknown order reported from in-den counts in eastern North America.

Location	n[a]	$\bar{x}$	Litter size 1	2	3	4	5	Source
GSMNP[b]	83	1.99	23	40	18	2	0	McLean (1991)
Western North Carolina	34	2.24	7	14	11	2	0	McLean (1991)
East-central Ontario	18	2.50	1	8	8	1	0	Kolenosky (1990)
SNP[c]	21	2.00	6	9	6	0	0	Carney (1985)
Northeast Minnesota	70	2.54	5	26	35	4	0	Rogers (1987)
West Virginia	41	2.73	4	9	22	6	0	Alt (1989)
Northeast Pennsylvania	211	2.98	10	45	102	48	6	Alt (1989)
Arkansas, Dry Creek study area	13	2.38	2	5	5	1	0	Clark (1991)
Arkansas, White River study area	14	1.36	9	5	0	0	0	Clark (1991)
SNP	26	2.31	1	17	7	1	0	Kasbohm (1994)
Maryland	13	3.08	0	2	8	3	0	Mathews and Garner (1993)
Mexico	12	2.75	0	5	5	2	0	Doan-Crider and Hellgren (1996)
Quebec	15	2.53	0	9	4	2	0	Samson and Huot (1995)
Ontario	10	2.70	0	4	5	1	0	Smith and DeAlmeida (1991)
Vermont	14	2.07	3	8	2	1	0	F. Hammond[d]
Total	595	2.56	71	206	238	4	6	

[a]Number of litters observed.
[b]Great Smoky Mountains National Park, Tennessee.
[c]Shenandoah National Park, Virginia.
[d]Vermont Department of Fish and Wildlife, Springfield, Vermont, personal communication, 1997.

rior distribution of litter size frequencies for eastern North America (Berger 1985). These posterior distributions were used as prior distributions in a second analysis in which observed first and subsequent litter size frequencies from Massachusetts were used as likelihood functions.

Because our "known" prior distribution of litter sizes was derived from samples presented in the literature (Table 1), we also estimated the probability of observing different sized litters (1–5 cubs) using the method of Cohen (1988). This method assumes that the prior distribution can be approximated by the multinomial distribution and produces mean and variance estimates for each category. We used equations 6–8 from Cohen (1988) that provide for an informative prior:

$$mean(\phi_i) = \frac{\propto_i + \chi_i}{2n}$$

where ϕ_i is the posterior probability of a litter of size *i*, $\propto_i$ is the expected number of litters of size *i* as derived from previous data or expert opinion, x_i is the observed number of litters of size *i*, and *n* is the total number of litters observed. We derived the expected number of litters of each size from the literature-derived distribution of litter sizes.

RESULTS

We observed 93 litters in dens from 1981 to 1997 in western Massachusetts and determined litter order for 86 of them; 20 were first litters and 66 were subsequent litters (Table 2). The distribution of first litters was skewed lower than that of subsequent litters (Kolmogorov-Smirnov test $P < 0.001$). Twelve bears (60%) produced first litters as 3-year-olds, 5 (25%) as 4-year-olds, and 3 (15%) as 5-year-olds. All bears had produced first litters (though not always first surviving litters) by age 5; no bears produced litters at age 2.

Red oak production indices for 1993–96 were correlated for the Quabbin Reservation and CWSA (Spearman rank correlation $r_s = 1.0$, $P \leq 0.0001$). Four of 17 years were rated as excellent mast years; 1993 had the highest estimated production of the 11 years with quantitative data (Table 3). Seven of the 17 years were rated as poor mast years. Crop damage was estimated only during 1993 to 1996 and was highest in 1995 and lowest in 1996 (Table 3).

Mast scores were not correlated with estimated early winter female weights or with weights of harvested adult and young males (all P's > 0.10). Mast scores were negatively correlated with adult ($r_s = -0.66$, $P = 0.0007$) and young ($r_s = -0.26$, $P = 0.03$) female harvest weights. Age of females and estimated den entry weights were not correlated with litter size production for either first litters or subsequent litters (all P's > 0.10), although both were correlated if first and subsequent litters were pooled (all P's < 0.05). Sow age, both measures of early winter weight (considered separately), and all mast scores failed to enter the discriminant function model. Litter order, young female weight, adult male weight, and young male weight were selected to enter the full discriminant function (Table 4).

Classification success of models fit with all years of data (1982–96) and various reduced data sets (to incorporate years with quantitative mast scores and cornfield damage estimates) were all low (52–60%; Table 4). Litter sizes of 1 and 3 had the highest classification success rates; most litters of 2 were incorrectly classified as litters of 3.

Table 2. Black bear litter sizes from litters of known order.

			Litter size					
Location	n[a]		1	2	3	4	5	source[b]
First litters								
Minnesota	36	2.06	5	24	7	0	0	Noyce
Maine, Spectacle Pond	41	2.07	6	27	7	1	0	McLaughlin
Maine, Stacyville	11	1.91	2	8	1	0	0	McLaughlin
Maine, Bradford	17	1.82	4	12	1	0	0	McLaughlin
Massachusetts	20	1.55	10	9	1	0	0	This study
Total	125	1.94	27	80	17	1	0	
Subsequent litters								
Minnesota	87	2.74	6	17	60	2	2	Noyce
Maine, Spectacle Pond	91	2.53	9	31	45	6	0	McLaughlin
Maine, Stacyville	30	2.53	1	13	15	1	0	McLaughlin
Maine, Bradford	69	2.45	6	31	27	5	0	McLaughlin
Massachusetts	66	2.58	3	24	36	3	0	This study
Total	343	2.58	25	116	182	17	2	

[a]Number of litters observed.
[b]Noyce data from K. Noyce, Minnesota Department of Natural Resources, Grand Rapids, Minnesota, USA. McLaughlin data from C. McLaughlin, Maine Department of Inland Fisheries and Wildlife, Bangor, Maine, USA.

Table 3. Harvest-derived variables (weights in kg), hard mast measures, and cornfield damage index values for western Massachusetts, 1980–96.

		Average weight						
		Females		Males				
Year	Harvest F (%)	Adult	Young	Adult	Young	Hard mast rating	Red oak index[c]	Cornfield damage index[d]
1980	50.0	na	na	na	na	excellent	na	na
1981	0.0	na	na	na	na	poor	na	na
1982	30.8	62.7	na	na	54.6	good	na	na
1983	20.0	na	na	na	58.9	good	na	na
1984	52.9	na	na	na	na	excellent	na	na
1985	64.3	65.3	65.5	na	57.3	poor	na	na
1986	55.6	na	54.1	na	42.7	good	2.73	na
1987	58.8	62.1	58.7	na	68.0	poor	0.40	na
1988	48.7	66.8	52.1	135.0	68.6	poor	0.46	na
1989	51.7	61.6	58.8	109.6	75.6	good	3.78	na
1990	34.5	71.4	53.0	111.4	50.6	good	3.93	na
1991	48.0	67.7	52.1	111.4	67.3	excellent	9.83	na
1992	50.0	61.9	54.8	89.1	80.7	poor	0.19	na
1993	45.8	58.5	52.8	109.6	68.6	excellent	41.59	4.25
1994	43.6	61.1	47.4	110.6	69.9	good	3.37	9.25
1995	60.5	70.7	54.2	124.0	68.8	poor	1.00	12.12
1996	55.4	69.1	55.1	100.1	71.4	poor	1.19	1.72

[a]Ad = adult (5.7 + years old at time of harvest).
[b]Y = young (2.7–4.7 years old at time of harvest).
[c]1986–92 = total Quabbin acorn count/1995 Quabbin total (W. Healy, U.S. Forest Service, Amherst, Mass., personal communication, 1998); 1993–96 = total annual Conway-Williamsburg Study Area acorn count/1995 Conway-Williamsburg Study Area acorn count.
[d]Sum of estimated % damage in all fields observed/number of fields observed.

Litter order contributed the most to the classification functions and entered each stepwise model first. Other variables selected in the stepwise procedure (young female weight, young male weight, adult male weight) only marginally improved classification success.

Because discriminant function calculation requires that all variables associated with each observation have non-missing values, no stepwise models could use all observed litters when fitting classification functions. We attempted to chose a model that would use the maximum number of observations available (Table 4, model 3). We deliberately excluded litter order from this model to examine its effect on classification. Excluding litter order, this model correctly classified 53.3% of 2 cub litters but 0% of 1 cub litters. Various other force-fit combinations of variables did not result in higher classification rates and likely violated model assumptions more severely by having too many categorical variables. Thus, attempts to develop a model that would accurately predict litter size in Massachusetts black bears failed.

Simple Bayesian estimates of litter size overestimated the observed proportion of 2-cub litters in first litters and 3-cub litters in subsequent litters (Table 5, Post. 1). We calculated estimates by segregating Massachusetts data into 2 groups (1981–90 and 1991–97) using the 1981–90 data as initial likelihoods and using the 1991–97 data to update the estimates. These updated estimates also overestimated the observed probabilities and by a slightly greater percentage (Table 5, Post. 2 and 3). The Cohen method overestimated the proportion of 2-cub first litters, but not as much as the simple Bayesian technique (Table 6). Estimates of the litter size distribution of subsequent litters were very close to the observed distribution (Table 6).

DISCUSSION

Effect of Natural Food on Reproduction

Black bear reproductive patterns have been reported to be related to the interaction between natural food abundance and female condition (Jonkel and Cowan 1971, Rogers 1976, Elowe and Dodge 1989). Female condition is difficult to quantify, although body weight may be a useful index (Alt 1989, Stringham 1990). We demonstrated in this study, as others have suggested (Noyce and Garshelis 1994), that litter order is the most important variable in estimating litter size. Other variables (e.g.,

Table 4. Model variables, years, and number of litters included, and cross-validation[a] classification success rates for several discriminant function classification models of black bear litter sizes, western Massachusetts, 1981–97.

Model	Variables[c]	Years	*n*	% Classification success[b] 1	2	3	4	Total
1	Order YFEMWT YMALWT AMALWT	1988–97	66	66.7	17.4	93.1	0.0	52.3
2	Order YFEMWT	1993–97	41	100.0	5.3	94.7	na	60.0
3	Age ENTERWT MAST1	1981–97	74	0.0	53.3	69.0	0	52.6

[a] Cross-validation derives classification functions for *n* -1 observations and applies them to the observation left out.
[b] Success rates = # observations litter size *i* classified as litter size *i*.
[c] Order = litter order; YFEMWT = dressed weights of harvested females 2.7–4.7 years old; YMALWT = dressed weights of harvested males 2.7–4.7 years old; AMALWT = dressed weights of harvest males >5.7 years old; Age = female age; ENTERWT = estimated female den entry weight; MAST1 = qualitative hard mast score for previous fall.

age and weight of individual bears, hard mast abundance) did not improve classification success of Massachusetts black bear litters. We think this is due mostly to Massachusetts bears' ability to access agricultural crops, primarily corn, in years of hard mast scarcity.

Alt (1989) reported that litter size was correlated with female age and weight. However, Alt (1989) pooled first and subsequent litters, as do most others cited in the literature. In our study, both age and weight were correlated with litter size when first and subsequent litters were pooled, but neither variable was correlated to litter size when first and subsequent litters were considered separately.

Elowe and Dodge (1989) reported that the proportion of females producing litters in Massachusetts was higher in years following good mast crops than years following poor mast crops. However, they failed to account for litter order in those calculations. At least 5 of the 10 females they reported as failing to produce litters following a poor mast year were only 3 years old (we could not determine ages of the others used in their results); 40% of Massachusetts bears fail to have their first litters at age 3. Poor mast crops may increase the percent of females that delay first litter production until a later age. However, since Elowe and Dodge's study, 5 of 6 3-year olds in the same area have produced first litters following poor mast years.

Rogers (1987) noted that age of first reproduction for wild bears in northeast Minnesota appeared linked to hard and soft mast availability or use of human foods. Bears that supplemented their diets with garbage in late summer and fall had first litters at earlier ages (4.4 years vs. 6.3 years for bears without garbage supplementation). Rogers also noted that most (15 of 17) bears eating only natural foods produced first litters following good mast crops. McLean (1991) noted that panhandler bears in Great Smoky Mountains National Park had earlier ages of first reproduction and greater litter sizes than "wild" bears.

McLaughlin et al. (1994) noted that in Maine litter production was unaffected by mast abundance for bears that had access to human-related foods. Schwartz and Franzmann (1991) reported that black bears on the Kenai Peninsula in Alaska moved to areas with abundant American devilsclub (*Oplopanax horridus*) fruit during fall; however, they could not detect any effect of fruit abundance on litter production the following year. Kasbohm et al. (1996) documented the ability of bears in Virginia to adapt to a loss of oak mast production caused by gypsy moth (*Lymantria dispar*) infestation by feeding on soft mast. They observed no adverse effects of acorn crop failure on female reproductive output in terms of age of first reproduction or litter size frequencies.

Advantages of Alternate Foods

In our study, female den entry weights were not related to hard mast production. In fact, dressed weights of harvested females were negatively correlated with hard mast abundance. We interpret this to indicate that bears feeding in cornfields were better able to gain weight than bears feeding on natural foods. Although cornfields were a small percentage of the study area, bears used them heavily in poor mast years. The advantages of foraging at a high density food source include decreased search time and increased intake per bite. In this respect, cornfields are analogous to high-density berry patches. Thus, we speculate that Massachusetts black bears feeding primarily in cornfields may attain near-maximum growth rates because of the interaction of foraging efficiency and body size (Welch et al. 1997). Conversely, bears feeding on abundant hard mast may be restricted in their ability to gain weight because of increased search times (relative to ag-

Table 5. Simple Bayesian estimates of the posterior probability distributions of litter size in Massachusetts black bears, for first and subsequent litters.

n cubs	Prior[a]	First likelihood[b]	Post. 1[c]	Mass. 1981–90[d]	Post. 2	Mass. 1991–97[e]	Post. 3
First litters							
1	0.1193	0.1619	0.0612	0.4286	0.0583	0.5385	0.0797
2	0.3462	0.6762	0.7419	0.5714	0.9417	0.3846	0.9203
3	0.4000	0.1524	0.1932	0.0000	0.0000	0.0769	0.0000
4	0.1244	0.0095	0.0038	0.0000	0.0000	0.0000	0.0000
5	0.0101	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Subsequent litters							
1	0.1193	0.0788	0.0272	0.0500	0.0030	0.0435	0.0003
2	0.3462	0.3411	0.3414	0.4000	0.3063	0.3696	0.2323
3	0.4000	0.5306	0.6135	0.5000	0.6885	0.5435	0.7673
4	0.1244	0.0496	0.0178	0.0500	0.0020	0.0435	0.0002
5	0.0101	0.0058	0.0001	0.0000	0.0000	0.0000	0.0000
Subsequent litters without Pennsylvania data in prior							
1	0.1589	0.0788	0.0361	0.0500	0.0041	0.0435	0.0038
2	0.4193	0.3411	0.4124	0.4000	0.3765	0.3696	0.2927
3	0.3542	0.5306	0.5419	0.5000	0.6183	0.5435	0.7069
4	0.0677	0.0496	0.0097	0.0500	0.0011	0.0435	0.0001
5	0.0000	0.0058	0.0000	0.0000	0.0000	0.0000	0.0000

[a] Prior probability distribution from data in Table 1.
[b] First likelihood (probability of litter size *i* given first litter or subsequent litter) derived from known order litters in Table 2 (excluding Massachusetts data).
[c] Posterior probability of litter size *i* given litter order. Posterior probabilities are used as prior probabilities for estimates with Massachusetts data as likelihoods.
[d] Data observed in Massachusetts between 1981 and 1990.
[e] Data observed in Massachusetts between 1991 and 1997.

ricultural crops) and intake of non-digestible items along with nut meats.

Our results fit the pattern of adaptability by black bears to variable food resources. In the modern era, natural food abundance appears to influence litter production and litter size only in extremely remote areas (Rogers 1987, Beck 1991, McLean 1991, McLaughlin et al. 1994). Black bears will either use local human-related foods, travel to relatively distant areas with more abundant natural or human-related food, or shift to alternative natural foods in their area if possible. Only if these options are not available (e.g., requiring long-distance movements) does natural food supply appear to limit reproductive output in female black bears. Indeed, in Massachusetts, abundant natural foods may decrease reproductive potential among those females that would otherwise have fed in cornfields, especially young females that could have their first litter.

Black bear behavioral plasticity in using alternative food sources is supported by several analyses of harvest patterns in black bears. In years of low natural food abundance, bear harvests increased in New Hampshire, Massachusetts, Tennessee, and Minnesota (Kane 1989, McDonald et al. 1994, Pelton and van Manen 1996, Noyce and Garshelis 1997) as bears moved to agricultural and other human-related food sources. Rogers (1987) documented extensive movements (>20 km) by adult females in late summer and fall to areas with hard and soft mast. In Massachusetts specifically, we have observed adult females traveling >20 km from their normal home ranges to uncut cornfields during poor mast years. The apparent paradox is that most bears do not travel to cornfields every year, preferring to feed on hard mast when abundant and only visiting cornfields in their home range. This may be due to the proximity of most cornfields to roads and human development in western Massachusetts.

Means vs. Proportions

Overall mean litter size can be misleading and is an unrealistic representation of reproductive performance of black bears. The distribution of litter sizes is more meaningful. This is especially relevant given the small samples of litters usually observed (Table 1). For example, the addition of 1 5-cub litter to the 10 studies with <30 reported litters in Table 1 increased the estimates of mean litter size by between 4% and 18%. Litters have discrete values over a short range (1, 2, 3, 4, or 5 cubs). Thus, as Cohen (1988) argued for clutch size in birds, there can be no real expectation that litter sizes will be distributed normally because they can only have a small number of integer values. In this circumstance, the distribution of litter sizes provides better information regarding reproductive output and is easier to interpret.

Bayesian Estimation

We overestimated the proportions of some litter sizes produced in Massachusetts with simple Bayesian analy-

Table 6. Estimates of mean posterior probabilities of litter size in Massachusetts black bears for first and subsequent litters using the method of Cohen (1988).

	First litters			Subsequent litters		
n cubs	observed		variance	Observed		Variance
1	0.5000	0.2750	0.00490	0.0455	0.0379	0.0003
2	0.4500	0.6000	0.0059	0.3788	0.3636	0.0017
3	0.0500	0.1250	0.0027	0.5303	0.5682	0.0015
4	0.0000	0.0000	0.0000	0.0455	0.0303	0.0002
5	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

sis. This was partly because the assumed prior distribution of litters (containing both first and subsequent litters) and the separate likelihood functions for first and subsequent litters differed from our observed distributions. Sixty percent of Massachusetts first litters were produced by 3-year-old bears, and most of these were single cub litters. Conversely, the majority of first litters used to derive our likelihood functions were 2-cub litters.

For subsequent litters, 3-cub litters dominated both our data and the literature reports; however, the percent of 3-cub litters in the literature was higher. Inclusion of data from Pennsylvania, which accounted for 35% of all observations and had a high proportion of 3-cub litters, may have accounted for some of this overestimation. When the Pennsylvania data were omitted from the prior probability distribution, the 3-cub bias was reduced; however, the probability of 3-cub litters still was overestimated by 30%.

Because of differences in productivity across black bear range, our prior probability distribution encompassed too much variability to accurately estimate litter size production in Massachusetts. In trying to estimate first litter proportions, we were hampered by a lack of reported data on first litters. We observed a high proportion of single cub first litters in Massachusetts compared to other areas. Thus, we think that our assumed prior distribution did not represent the "true" distribution of litter sizes in Massachusetts.

Cohen's approach produced estimates of litter size proportions very close to those observed in Massachusetts from multiparous females. For first litters, the Cohen approach overestimated the proportion of 2-cub litters, but by less than the simple Bayesian approach. Our study is unique among the few reported distributions of first litters in its proportion of single cub litters.

Our efforts to use simple Bayesian analysis to reliably estimate litter size were hampered by lack of a proper prior probability distribution. This was due to our choice of representing the "true" prior with a compilation of litter sizes derived from the literature from across eastern North America. This placed undue weight on the prior in the calculations and resulted in poor estimates of litter size distributions. Reducing the geographic scope of the prior distribution to the northeast likely would have resulted in better estimates of the litter size distribution in Massachusetts. Also, annual updates of the posterior distribution, instead of pooling several years of data, would likely have reduced the role of the initial prior distribution in the results.

The method of Cohen can provide useful estimates of litter size in black bears. This method allows the incorporation of prior information (or expert opinion) in estimating the posterior distribution of litter sizes. Thus, it can be updated when new information becomes available, either from local sources or in the literature. Because most estimates of litter size are based on small numbers of observed litters in a restricted study area, we think that incorporating data from other research in similar areas will improve the depiction of the true distribution of litter sizes.

MANAGEMENT IMPLICATIONS

We suggest that black bear litter size is relatively invariate locally. There is obvious regional variation (Table 1), likely associated with primary food sources. However, in most areas litter size likely coalesces around a stable distribution. Thus, in the East, the primary use of field data collection relative to estimation of reproductive output (i.e., litter size) is to determine the relative proportions of 2 and 3 cub litters for adult females (and 4 cub litters in some populations) in the particular location. Also, more data are needed on first litter sizes to adequately estimate productivity of young female bears.

Collection of local field data can help managers using the population model approach to determine the appropriate prior probability distribution to use when estimating litter size proportions using a simple Bayesian approach. For example, do other populations exhibit a distribution skewed toward single cub first litters as did the Massachusetts population? After a sufficient sample has been obtained to capture annual variation in litter size proportions by litter order, we think that estimating future litter sizes using the simple Bayesian approach or Cohen's approach will provide useful results for modeling without never-ending field data collection.

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