

Demography of Black Bears in Hunted and Unhunted Areas of the Boreal Forest of Ontario

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ABSTRACT We estimated relative density, survival, and reproduction of American black bears (*Ursus americanus*) from capture–recapture and telemetry data collected from 1989 to 1999 in the unhunted Chapleau Crown Game Preserve (CCGP) and nearby hunted areas in the boreal forest of Ontario, Canada. We tested for combinations of effects of age class, sex, year, years of food shortage, encumbrance status, and residency (on or off the Game Preserve) on vital rates. Results from live captures, remote captures, and bait-station hit rates indicated that density was highest inside CCGP. Total survival of adult females, subadults, and cubs were similar among residents and nonresidents of CCGP, but yearling survival was lower among CCGP residents. Adult females were approximately twice as likely to die and nearly 10 times as likely to be cannibalized (risk ratio [RR] = 9.62, 95% CI = 2.088–44.29) while encumbered with cubs of the year. Nonresidents of CCGP had greater risk of being harvested (RR = 4.00, 95% CI = 1.19–13.46) but similar risk of being cannibalized (RR = 0.875, 95% CI = 0.300–2.55) relative to CCGP residents, suggesting that harvest mortality was additive to other forms of mortality. Residents of CCGP had older ages at primiparity and lower litter-production rates than bears resident in hunted areas. Few litters were produced in years following food shortages, but litter size was unaffected. We recommend that managers allow for additive harvest mortality and reduced survival of bears encumbered with cubs of the year, and we caution that assuming density-compensatory increases in cub production could optimistically bias estimates of population growth. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):869–880; 2008)

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Effective wildlife management requires an understanding of demographics to estimate population growth and predict effects of management action. Population growth, sustainable harvest, and extinction risk in bears are most sensitive to survival of adult females (Taylor et al. 1987, Horino and Miura 2000, Boyce et al. 2001), but our understanding of natural and cause-specific mortality is limited because most documented mortality among bears is human-caused (Bunnell and Tait 1985, Koehler and Pierce 2005, Haroldson et al. 2006). Forms and mechanisms of density dependence are not well understood in bears (Taylor 1994), including American black bears (*Ursus americanus*; Miller 1990, Garshelis 1994, Sargeant and Ruff 2001), but are expected only when populations are near carrying capacity (Miller et al. 2003) and may include effects on movements (Sargeant and Ruff 2001), survival (LeCount 1987, Czetwertynski et al. 2007), or reproduction (Rogers 1987, Czetwertynski et al. 2007). The current consensus is that compensatory increases in survival and reproductive rates should not be assumed when bears are harvested (Boyce et al. 2001, Sargeant and Ruff 2001, Miller et al. 2003; but see Czetwertynski et al. 2007). Here, we present measures of relative density and demographic data from a 10-year study of black bears in a large, unhunted area, and nearby hunted areas, in the boreal forest of Ontario, Canada. A large, radiocollared sample ($n = 101$ ad F) enabled us to document many cases of cause-specific, natural mortality and to make comparisons among years and between residents and nonresidents of the unhunted preserve. We hypothesized

that the population in the unhunted area would have higher density and lower survival or reproductive rates. We also suspected that risk of mortality by different causes would respond differently to individual survival covariates.

STUDY AREA

The study area in the Chapleau Crown Game Preserve (CCGP) and nearby hunted areas in Ontario, Canada (47°10'N, 83°20'W; Fig. 1) was within the Missinaibi–Cabonga Forest Section of the Southern Boreal Forest Region (Rowe 1972). Sandy outwash plains and glaciolacustrine deposits were dominated by jack pine (*Pinus banksiana*). Poorly drained areas were occupied by black spruce (*Picea mariana*), occasionally mixed with tamarack (*Larix laricina*) and eastern white cedar (*Thuja occidentalis*). Higher, better-drained sites were occupied by mixed stands of poplars (*Populus tremuloides* and *P. balsamifera*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), black spruce, and white spruce (*Picea glauca*; Rowe 1972). Timber harvest was ongoing across the area, including within the CCGP. Logging and periodic wildfires resulted in a mosaic of different-aged forest stands (Ontario Ministry of Natural Resources 1984). Mean temperatures in January and July were -15.8°C and 16.7°C , with mean annual precipitation of 79 cm (Chapman and Thomas 1968). We sampled in 3 study areas: 1) CCGP; 2) Borland's Bear Management Area (Borland's), adjacent to the Game Preserve but separated from it by the Chapleau–Nemegosenda River; and 3) Ivanhoe, approximately 50 km east of the CCGP (Fig. 1). Spring and fall harvests of bears occurred in both the Borland's and Ivanhoe study areas, but hunting and trapping

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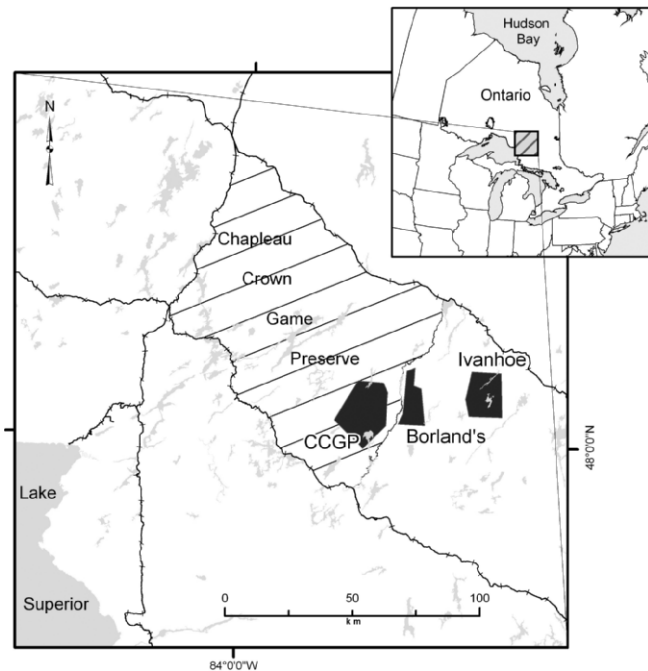


Figure 1. Location of study areas (Chapleau Crown Game Preserve [CCGP], Borland's, Ivanhoe) in relation to CCGP in northern Ontario, Canada, 1989–1999. Inset shows location relative to the entire province. Areas trapped for black bears by live and remote trapping appear in black.

in the 7,220-km² CCGP had been prohibited since 1925 (Ontario Ministry of Natural Resources 1984).

METHODS

Capture, Handling, and Radiomonitoring

We trapped bears in barrel traps during 1989–1995, 1997, and 1998 in CCGP; during 1990–1995, 1997, and 1998 in Borland's; and during 1992–1995, 1997, and 1998 in Ivanhoe. Field work was delayed in 1996 because of a late-spring melt, so we trapped in each part of the study area only to target bears whose radiocollars were likely to fail before winter den visits. We trapped separate lines of ≥ 10 traps covering different sections of contiguous areas within each of the CCGP, Borland's, and Ivanhoe study areas on 1 or 2 5-day sessions per year. There were 4 trap lines in CCGP and 3 in each of the Borland's and Ivanhoe study areas. We spaced traps approximately 2.5 km apart. Area trapped increased after 1993 in Ivanhoe but was constant in CCGP and Borland's. Trapping began in early May in CCGP, and after 15 June when the spring hunting season ended in Borland's and Ivanhoe, and ended in mid July before bears left their core ranges on summer foraging excursions (Schenk et al. 1998).

We anesthetized captured bears, uniquely marked them with numbered aluminum ear tags (Ketchum Kurl-Lok tags; Ketchum Manufacturing, Ottawa, ON, Canada), and released them after recording morphometric and reproductive data. We removed a first premolar for age estimation via cementum analysis (Stoneberg and Jonkel 1966). We fitted all adult females and some males with very high frequency

(VHF) radio transmitters with motion-sensitive mortality switches (Lotek Wireless, Newmarket, ON, Canada).

We monitored radiocollared bears by ground and aerial telemetry throughout the active season. When radiocollars emitted mortality signals, we visited the site to confirm mortality and determine cause of death. We interpreted evidence of a struggle, carcasses with everted hides, large, canine punctures in the skull, and presence of bear tracks, scats, or daybeds as evidence of cannibalism. If skeletal remains were scattered, wolf scats were present, or cub tags were found in wolf scats, we concluded the event was wolf predation. We handled radiocollared females in winter dens in late February or March (1990–1999). We also tagged cubs or yearlings first observed in winter dens, and we fitted some yearlings with expandable radiocollars (Strathearn et al. 1984). Animal handling protocols were approved annually by the Animal Care Committee of the Ontario Ministry of Natural Resources and followed guidelines of the American Society of Mammalogists (Committee for Field Methods in Mammalogy 1987).

Relative Density

We estimated abundance of female bears aged ≥ 2 years in each area from capture–recapture data obtained by live-trapping and by remote DNA sampling using barbed-wire hair traps (Woods et al. 1999). Average radius of the home range of adult females in the study area was about 2.5 km (Schenk et al. 1998), so we estimated the effective trap area (A_E) as the area of a buffer with a radius of 2.5 km around all traps in each area.

For live capture, we estimated abundance from capture–recapture data using the Garshelis (1992) version of the Petersen–Chapman estimator, which weights animals based on the proportion of locations on the study area during the recapture period. Following Garshelis (1992), we considered all bears radiocollared before an annual trapping session to be the marked sample and all within-year trapping the recapture period. We calculated animal equivalents as the sums of the proportions of radiolocations on the trapping area during capture periods (Garshelis 1992). Limited or incomplete telemetry records for some bears during the trapping period prevented us from applying the Garshelis (1992) method in all years. We calculated minimum densities as sums of animal equivalents for all collared females divided by A_E by livetrapping and estimated densities as the estimated abundance divided by A_E .

We conducted barbed-wire hair-trap sampling once annually in late spring 1997–2000, inclusive, in CCGP and Borland's and 1998–2000, inclusive, in Ivanhoe. We spaced hair traps approximately 1 km apart. We initially profiled DNA from hair samples at 5 microsatellite loci to identify unique individuals (if necessary, we profiled samples at an additional 10 loci) and subjected them to a gender test at the Natural Resources DNA Profiling and Forensics Centre, Trent University, Peterborough, Ontario. We used Program RELEASE (Burnham et al. 1987) to test for violations of Cormack–Jolly–Seber model assumptions. We modeled apparent survival, probability of entry, recapture

probability, and superpopulation size of female bears aged ≥ 2 years in the 3 areas simultaneously using the POPAN data type (Schwarz and Arnason 1996) in Program MARK (White and Burnham 1999). We fixed capture probability in 1997 in Ivanhoe at zero. The data set was insufficient to support the full complexity of available models, so we ignored time variation. We tested for differences in parameters among the 3 study areas and between CCGP and the hunted study areas by comparing models using Akaike's Information Criterion (AIC; Akaike 1981) adjusted for small sample size (AIC_c; Anderson and Burnham 1999). We estimated area-specific densities as model-averaged abundance estimates divided by A_E for hair traps.

We indexed bear density in each study area by recording visits to bait stations spaced 1 km apart (Carlock 1986). We located survey lines along secondary or tertiary roads with a minimum of 50 stations per line. We then calculated proportion of stations visited by a bear each year. We used canine punctures in sardine tins, claw marks or hair left on the bait tree, tracks, and scats as evidence of visitation. We conducted bait-station surveys from 1989 to 1998 in CCGP, 1990 to 1998 in Borland's, and 1992 to 1998 in Ivanhoe.

Demographic Rates

We estimated, and tested for effects of covariates on the following vital rates: survival and cause-specific mortality of adult (aged ≥ 4 yr) females; survival of subadults (aged 2–3 yr), yearlings, cubs, and litters of cubs; age at primiparity; litter-production rate of available females; and litter size. We evaluated covariate effects on survival of subadults, yearlings, and cubs, and litter-production rate and size by comparing AIC_c weights among candidate models, and effect sizes on demographic rate estimates.

We estimated survival of adult females and age at primiparity using Cox's proportional-hazards regression adapted to allow discontinuous time intervals (Andersen and Gill 1982). We used survival times (in days) and ages at primiparity (in yr) as dependent variables and evaluated covariate effects by performing Z-tests and comparing risk ratios (RR). We tested the assumption of proportional hazards among levels of covariates using the test on rescaled Schoenfeld residuals described in Grambsch and Therneau (1994).

We selected covariates and defined candidate model sets to test research hypotheses while accounting for biological realism and data limitations. Covariates were sex, age class, residency (on or off CCGP), year, and years of food shortage, and in the case of adult females, survival and encumbrance status. We excluded most interactions because of data limitations but included interaction between residency and years of food shortage in some candidate model sets to test whether demography of residents and nonresidents of the Game Preserve responded differently to food shortages. In the case of litter-production rate of available females, we also included an interaction between residency and age class.

We assigned residency of bears in each year based on

proportion of radiolocations on CCGP. We considered bears with $\geq 80\%$ of radiolocations in CCGP to be CCGP residents and those with $\leq 20\%$ in CCGP to be non-residents. We did not assign residency to bears we located less than once per month during the active season and those with between 20–80% of locations in CCGP.

Several researchers experienced at assessing bear foods in the boreal forest and on the study area noted that mast crops were poor or failed in 1992, 1995, and 1998. Bear food shortages in 1992 and 1995 were nearly Ontario-wide phenomena brought on by late-spring frosts and summer droughts and were associated with elevated problem-bear activity and hunter success rates in those years (Obbard et al. 2003). Poor fruit-set in 1992 relative to 1991 and 1993 in CCGP was quantified by Usui et al. (2005).

We determined encumbrance status during winter den visits and modeled it as a binomial individual covariate where we considered females with cubs of the year to be encumbered. We considered solitary females and females with yearlings to be unencumbered.

Excluding handling mortalities, no deaths of radiomonitored bears occurred during the November–April denning period, so we modeled adult female survival over the May–October active season but present annual survival-rate estimates. We assumed that survival of adult females was age-constant and that radiocollars did not affect survival rates. We expect modeling age classes separately and including only females in adult survival analyses prevented violation of the assumptions of independent fates and equal survival within groups pooled. We analyzed cause-specific mortality of radiocollared adult females in a competing-risks context with 3 mortality types: harvest, cannibalism, and other. We estimated total survival using a null Andersen–Gill model and the nonparametric cumulative incidence function estimator (NPCIFE; Heisey and Patterson 2006) and cause-specific mortality using the NPCIFE.

We estimated effects of encumbrance status, residency, year, and years of food shortage on total survival times by fitting 2 Andersen–Gill proportional-hazard models stratified by cause of mortality. One model included additive effects of encumbrance, residency, and years of food shortage, and in the other model, individual year effects replaced years of food shortage. We tested for effects of encumbrance status and residency on risks of cause-specific mortality as follows. Following Lunn and McNeil (1995) and Heisey and Patterson (2006), we duplicated the data set once for each type of mortality while censoring records for all types of mortality except the one that occurred (if any). We created binomial indicator variables for each mortality type and fit an Anderson–Gill proportional-hazards model, stratified by cause of mortality, with terms for interactions between each covariate and indicator variables for harvest and cannibalism.

We included a cluster term on individuals when fitting Anderson–Gill models to allow nonindependent repeat observations for the same individual and to avoid underestimating variance of coefficients (Lee et al. 1992). We

Table 1. Effective area trapped by barbed-wire hair traps, number of unique female black bears identified by genotyping, model-averaged estimates of superpopulation size of females aged ≥ 2 years and its 95% confidence interval estimated using the POPAN data type in Program MARK, and minimum and estimated densities of females aged ≥ 2 years in each of 3 areas (Chapleau Crown Game Preserve [CCGP], Borland's, Ivanhoe) in the boreal forest of Ontario, Canada, 1997–2000.

Study area	Area trapped	No. of F captured	Superpopulation size		Density (F/km ²)		
			Estimate	95% CI	Min.	Estimate	95% CI
CCGP	123 km ²	32	43.3	35.9–64.7	0.260	0.352	0.29–0.53
Borland's	174 km ²	36	39.7	37.2–46.4	0.207	0.228	0.21–0.27
Ivanhoe	194 km ²	21	27.2	22.7–43.8	0.108	0.140	0.12–0.23

conducted replicate adult female survival analyses: one in which we right-truncated data for adult females with which we permanently lost contact, assuming noninformative censoring, and one where we assumed lost bears to have died 1 day after their last location alive.

We modeled annual survival of subadults, yearlings, individual cubs, and litters of cubs using the known-fate data type in Program MARK. We used break-away collars on yearlings and 2-year-old bears (Strathearn et al. 1984). We assumed survival rates were similar for 2- and 3-year-old bears and in all years from 1990–1998 when modeling subadult survival and fit 4 models with additive combinations of sex and residency covariates. We monitored no yearlings in 1990. We fit 10 models of yearling survival to test for effects of residency, food shortages, sex, and interaction between residency and food shortages.

We assigned noninstrumented cubs the same residency as their mother. We excluded data from cubs of mothers for which we did not assign residency, cubs fostered to new mothers after handling mortalities of birth mothers, cubs that died as a result of handling, and cubs with unknown fates in dens at age 1 year. We considered cubs that were missing from their mother's winter den as yearlings and cubs of females known to have died before cubs reached age 1 year to be dead at age 0 years. We fit 14 models to test for effects of residency, sex, food shortages, annual variation, and interaction between residency and food shortages on individual cub survival and 7 models to test for the same effects, except sex, on litter survival.

We compared frequencies, means, and medians of ages at primiparity on and off CCGP. We also estimated mean age of primiparity following Garshelis et al. (1998) to avoid negative bias. We fit a Cox proportional-hazards model with primiparity as the response variable to test for a residency effect. Monitored bears entered the risk set at age 5 years, and we censored them if they died while still nulliparous.

We obtained data on litter size during winter den visits and on litter-production rate of available females from ≥ 2 consecutive den visits. We used binomial and multinomial logistic regression to fit models to litter-production rate and litter-size data, respectively. We fit the same set of 16 candidate models to test for effects of age class (aged 5–7 yr or ≥ 8 yr), residency, year, food shortages (in yr $t - 1$), and 2-way interactions between residency and age class and between residency and food shortages. We estimated the

variance inflation factor as the chi-square statistic divided by its degrees of freedom for the most general model in the candidate set, and where overdispersion occurred, we compared models using the AIC statistic adjusted for both quasi-likelihood and small sample size (QAIC_c; Burnham and Anderson 2002). Sample sizes for nonresidents of CCGP were low before 1993, so only data from 1993–1999 were included.

RESULTS

Relative Density

In CCGP, we livetrapped 59 female bears aged ≥ 2 years 153 times. In Borland's, we caught 34 bears 56 times, and in Ivanhoe, we caught 23 bears 24 times. Minimum densities ranged from 0.07–0.11 female bears/km² and averaged 0.087 in CCGP; ranged from 0.01–0.043 female bears/km² and averaged 0.024 in Borland's; and ranged from <0.01 –0.02 female bears/km² and averaged 0.01 in Ivanhoe. Annual density estimates ranged from 0.09–0.16 female bears/km² and averaged 0.12 in CCGP, ranged from 0.042–0.093 female bears/km² and averaged 0.069 in Borland's, and ranged from 0.04–0.06 female bears/km² and averaged 0.05 in Ivanhoe.

Number of hair traps and the corresponding effective trap area varied among study areas (Table 1). Barbed-wire hair trapping and genotyping to identify unique individuals and gender yielded 32 females caught a total of 49 times over 4 occasions in CCGP, 36 females caught 57 times over 4 occasions in Borland's, and 21 females caught 33 times over 3 occasions in Ivanhoe. We did not detect unequal survival probabilities among animals within encounter occasions; all RELEASE test 3 *P*-values were >0.10 or had insufficient data. Data were insufficient to test the assumption of equal recapture probabilities within encounter occasions. Only 2 of 27 candidate models had AIC_c weights >0.01 . Some models yielded an estimate of superpopulation size in Ivanhoe equal to the number of unique animals captured with a zero boundary standard error, indicating that the parameter was not estimable, so we model-averaged across all models under which all parameters were estimable. Female bear density determined by remote sampling was highest in CCGP, followed by Borland's, and then Ivanhoe (Table 1).

Mean of annual bait station visitation rates was higher in CCGP ($\bar{x} = 89.7 \pm 3.0\%$ SE) than in Borland's ($\bar{x} = 55.8 \pm 5.7\%$ SE) or Ivanhoe ($\bar{x} = 42.5 \pm 9.1\%$ SE).

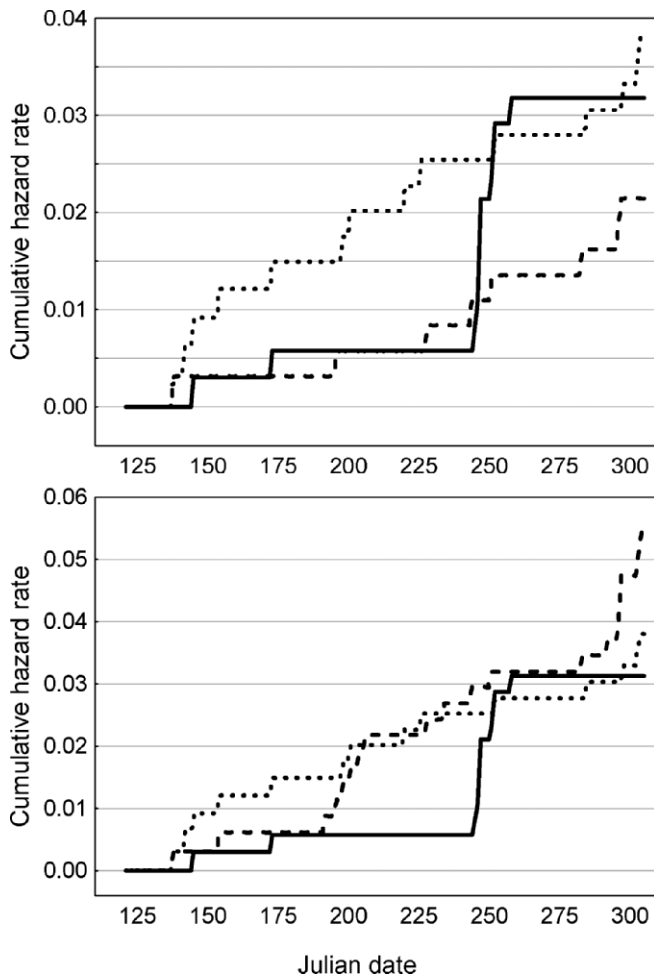


Figure 2. Nonparametric cumulative incidence function estimates of cause-specific mortality of adult female black bears in the boreal forest of Ontario, Canada, during May–October of 1990–1998, assuming noninformative censoring of lost animals (top panel) and assuming lost animals had died (bottom panel). Causes of mortality were harvest (solid lines), cannibalism (dotted lines), and other (dashed lines).

Demographic Rates

More than 90% of bears had >80% of their radiolocations within an active season either on or off CCGP. Number of radiolocations per bear per active season ranged from 1–130 and averaged 31.5 (SD = 27.8). Bears with few locations within an active season were those entering the risk set in mid season, those with which we lost radio contact, and those that died.

After excluding data from bear–seasons for which encumbrance status was unknown or we did not assign residency, data were available for survival analyses from 101 adult females monitored for a total of 64,537 days over 395 bear–seasons. We observed 34 mortality events: 12 harvest mortalities, 14 cases of cannibalism, and 8 bears dying of other causes, including wolf predation ($n = 4$), unknown forms of natural mortality ($n = 2$), one bear killed by a moose (*Alces alces*; Obbard et al. 2000), and one bear killed in defense of property. We permanently lost contact with 13 radiocollared animals over the course of the study.

The NPCIFE hazard functions for different mortality

Table 2. Annual cause-specific mortality and total survival rates of adult female black bears in the boreal forest of Ontario, Canada, 1990–1998, estimated by right-truncating data and by assuming death when we lost radiocontact. We estimated cause-specific mortality rates using the nonparametric cumulative incidence function estimator. We estimated total survival rates using a null Andersen–Gill model.

Cause of mortality	Right-truncated		Assumed death	
	Estimate	95% CI	Estimate	95% CI
Harvest mortality	0.032	0.015–0.049	0.031	0.014–0.048
Cannibalism mortality	0.039	0.019–0.058	0.038	0.016–0.060
Other mortality	0.021	0.007–0.035	0.055	0.033–0.077
Total survival	0.908	0.880–0.938	0.876	0.843–0.910

types crossed because most harvests occurred during the fall hunting season but other forms of mortality were relatively evenly distributed over time (Fig. 2). Assuming that bears with which we lost contact had died caused cumulative hazards for other mortality to exceed those for harvest or cannibalism (Fig. 2) and reduced total annual survival estimates by 3.2% (Table 2).

The assumption of proportional hazards was met for all covariates in both data sets and all models we used to test for effects of covariates on total and cause-specific mortality (Table 3). In the data set where we right-truncated data for lost animals, we detected a significant effect of encumbrance status on survival times ($Z = 1.967$, $P = 0.049$ from the model with food-shortage yr; $Z = 2.02$, $P = 0.044$ from the model with individual-yr effects). Encumbered bears were at greater risk of mortality based on models with food-shortage years (RR = 1.98, 95% CI = 1.002–3.91) and individual-year effects (RR = 2.059, 95% CI = 1.021–4.15). In the data set where we assumed lost animals died, risk ratios for encumbrance were similar ($P = 0.067$ for models with food-shortage yr; $P = 0.055$ for models with individual-yr effects) and confidence intervals for risk ratios included 1.0. We did not detect effects of residency, food-shortage years, or individual years. In the data set with lost bears assumed dead and individual-year effects in the model, all P -values were >0.10, except for the effect of residency ($Z = -1.75$, $P = 0.081$), suggesting that CCGP residents may have been at lower risk of mortality (RR = 0.55, 95% CI = 0.285–1.08).

Adult females were nearly 10 times as likely to be cannibalized (RR = 9.62, 95% CI = 2.088–44.29) but no more or less likely to be harvested (RR = 0.693, 95% CI = 0.216–2.222) while encumbered with cubs. Residents of CCGP were at lower risk of being harvested than nonresidents (RR = 0.25, 95% CI = 0.074–0.838) but were at similar risk of being cannibalized (RR = 1.143, 95% CI = 0.392–3.334). Risk of other mortality was similar regardless of encumbrance status (lost animals right-truncated: RR = 1.020, 95% CI = 0.236–4.415; lost animals assumed dead: RR = 1.186, 95% CI = 0.465–3.024) or residency (lost animals right-truncated: RR = 1.557, 95% CI = 0.308–7.869; lost animals assumed dead: RR = 0.705, 95% CI = 0.283–1.757).

We monitored most radiocollared females until they died

Table 3. Chi-square and *P*-values from tests of the assumption of proportional hazards among levels of covariates in Andersen–Gill models of total and cause-specific mortality risks for adult female black bears in the boreal forest of Ontario, Canada, 1990–1998.

Mortality	Covariates					
	Encumbrance		Residency		Time	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Total mortality (time covariate)						
Lost bears right-truncated						
Food-shortage yr	0.970	0.33	1.675	0.20	0.101	0.75
All yr	0.653	0.42	0.021	0.89	0.107	0.74
Lost bears assumed dead						
Food-shortage yr	0.223	0.63	0.046	0.83	0.001	0.97
All yr	0.271	0.60	0.045	0.83	0.002	0.97
Cause-specific mortality						
Lost bears right-truncated						
Harvest	0.079	0.78	0.429	0.51		
Cannibalism	0.243	0.62	3.32	0.07		
Other	0.551	0.46	0.686	0.41		
Lost bears assumed dead						
Harvest	0.066	0.80	0.457	0.50		
Cannibalism	0.230	0.63	3.13	0.08		
Other	0.116	0.73	0.078	0.78		

or the study ended. Of 13 bears with which we lost contact, 8 involved premature transmitter failure from one shipment, and 2 were dropped collars that we recovered far from roads with no evidence of a struggle or disturbance at the site, so we believe the collars were simply fitted too loosely. Censoring of these 10 animals was, therefore, unrelated to survival probability. In 3 cases, we were uncertain about fate of the bear and collar, so censoring may have been informative. Resulting bias to estimated survival rates and effects of covariates from the data set where we right-truncated data from these bears would be slight, but total survival was underestimated and other mortality overestimated by the data set in which we assumed these 13 bears had died.

Of 29 radiocollared 2-year-old bears with known fates, 10 died as 2-year-olds. Of the surviving 19 2-year-old bears, only 8 contributed data as 3-year-olds, and one died as a 3-year-old. We captured 2 bears for the first time as 2-year-old—both survived through age 3. Causes of subadult death included cannibalism, harvest, and nuisance kills. The model with sex-specific survival and the null model had the most support with AIC_c weights (w_i) of 0.378 and 0.375, respectively. Models including the effect of residency had much less support ($w_i = 0.12$). We averaged across all 4 models to estimate subadult survival (Table 4).

Of 72 yearlings with known fates, we excluded 3 because we could not assign residency, 14 died as yearlings, and 55 survived to age 2 years. The model of yearling survival with an effect of residency ($w_i = 0.275$) and the null model ($w_i = 0.237$) had the most support. All 10 candidate models had $\Delta AIC_c < 6.0$ and were included in model averaging. Estimated survival rates were higher among nonresidents of CCGP (Table 4).

Excluding 2 cubs that died during handling and 5 fostered cubs, we observed 331 cubs in winter dens during 1990–1998. We excluded data for 25 cubs with no residency assigned and 55 with unknown fates on their first birthday. We observed 112 cubs to be alive as yearlings in winter dens, whereas 139 died or were assumed dead because their mother died or they were absent from their mothers' dens as yearlings. Models of cub survival including residency and food-shortage covariates and their interaction ranked first and third and had a combined AIC_c weight of 0.457. However, the null model ranked second and could not be excluded as the most appropriate model ($\Delta AIC_c = 1.00$, $w_i = 0.195$). Models with residency and food-shortage covariates alone or in additive combinations had less support ($\Delta AIC_c > 2.5$). We averaged across all 14 candidate models to estimate cub survival. Food shortages were associated with lower cub survival in CCGP but higher cub survival off CCGP (Table 5). We estimated survival from the residency model to compare with other studies. There was no difference in cub survival between residents of CCGP ($S =$

Table 4. Model-averaged survival rates of yearling and subadult (aged 2–4 yr) black bears in or outside the Chapleau Crown Game Preserve (CCGP) in the boreal forest of Ontario, Canada, 1990–1998. Models included effects of residency, sex, and food shortages (FS).

Residency	Sex	FS	Survival	95% CI	% model variation
Yearlings					
CCGP	F	0	0.758	0.566–0.883	22.8
Off CCGP	F	0	0.855	0.603–0.958	43.0
CCGP	M	0	0.768	0.593–0.882	19.2
Off CCGP	M	0	0.860	0.611–0.960	45.4
CCGP	F	1	0.771	0.580–0.891	18.9
Off CCGP	F	1	0.855	0.589–0.961	40.6
CCGP	M	1	0.780	0.615–0.887	12.9
Off CCGP	M	1	0.861	0.603–0.962	43.3
Subadults					
CCGP	F	n/a ^a	0.758	0.528–0.898	26.8
Off CCGP	F	n/a	0.766	0.504–0.913	27.9
CCGP	M	n/a	0.646	0.391–0.873	31.5
Off CCGP	M	n/a	0.567	0.382–0.855	27.5

^a n/a = not applicable.

Table 5. Model-averaged survival rates (S) of black bear cubs in the Chapleau Crown Game Preserve (CCGP) and in hunted areas in the boreal forest of Ontario, Canada, 1990–1998.

Yr	CCGP				Off CCGP			
	F		M		F		M	
	S	95% CI	S	95% CI	S	95% CI	S	95% CI
1990	0.488	0.371–0.607	0.480	0.368–0.594	0.413	0.289–0.551	0.405	0.280–0.544
1991	0.489	0.371–0.608	0.480	0.368–0.595	0.414	0.288–0.552	0.406	0.280–0.545
1992	0.405	0.280–0.543	0.397	0.268–0.541	0.489	0.319–0.661	0.480	0.314–0.651
1993	0.489	0.373–0.606	0.480	0.369–0.593	0.414	0.290–0.550	0.406	0.281–0.544
1994	0.489	0.374–0.605	0.481	0.371–0.592	0.414	0.290–0.550	0.406	0.282–0.543
1995	0.405	0.280–0.545	0.397	0.268–0.542	0.489	0.320–0.661	0.481	0.316–0.651
1996	0.489	0.374–0.606	0.481	0.370–0.594	0.415	0.290–0.551	0.406	0.281–0.545
1997	0.489	0.374–0.605	0.481	0.371–0.593	0.414	0.290–0.550	0.406	0.282–0.544
1998	0.405	0.280–0.543	0.397	0.269–0.541	0.489	0.319–0.661	0.480	0.314–0.651

0.456, 95% CI = 0.379–0.534) and nonresidents ($S = 0.430$, 95% CI = 0.333–0.532).

Of 145 litters of cubs observed during 1990–1998, we excluded 38 because we could not assign residency or they had unknown fates at age 1 year. Whole-litter mortality occurred in 43 cases, whereas 64 litters included ≥ 1 cub that survived to age 1 year. The null model of litter survival had more than twice the support of any other model with 51.0% of the total AIC_c weight. The estimate of litter survival from the null model was 0.598 (95% CI = 0.503–0.687). Models including effects of residency, food shortage, or both had ΔAIC_c values < 6.0 , and models with individual-year effects had little support ($\Delta AIC_c > 13.0$). We averaged across all candidate models to estimate litter survival rates. Litter survival was similar in both areas in all years (Table 6).

Mean and median ages at primiparity were higher among residents of CCGP than among nonresidents (Table 7). Cox's regression revealed an effect of residency ($Z = -3.06$, $P = 0.002$, $RR = 0.289$, 95% CI = 0.131–0.641). All nonresidents of CCGP produced a litter by age 8 years, whereas 40% of 8-year-old CCGP residents were nulliparous (Fig. 3).

During 1993–1999, we observed 185 cases (131 for CCGP residents and 54 for nonresidents) where females were available to mate in year $t - 1$, and we determined litter production in dens in year t . The estimate of the variance

Table 6. Model-averaged survival rates (S) of litters of black bear cubs in the Chapleau Crown Game Preserve (CCGP) and in hunted areas in the boreal forest of Ontario, Canada, 1990–1998.

Yr	CCGP		Off CCGP	
	S	95% CI	S	95% CI
1990	0.601	0.486–0.706	0.586	0.459–0.703
1991	0.601	0.485–0.706	0.586	0.458–0.704
1992	0.607	0.480–0.721	0.597	0.455–0.724
1993	0.601	0.486–0.706	0.586	0.459–0.703
1994	0.601	0.487–0.705	0.587	0.460–0.703
1995	0.607	0.480–0.721	0.597	0.455–0.724
1996	0.601	0.487–0.705	0.587	0.460–0.703
1997	0.601	0.487–0.705	0.587	0.460–0.703
1998	0.607	0.480–0.721	0.597	0.455–0.724

inflation factor from the most general model in the candidate set (yr + age + residency) indicated mild overdispersion ($\chi^2/df = 1.018$), so we compared models using $QAIC_c$. The model with additive effects of age class, food shortages, and residency ranked first with 59% of total $QAIC_c$ weight. The second-ranked model ($w_i = 0.155$) included the same effects plus interaction between age class and residency. Sums of $QAIC_c$ weights for supported covariates were 0.998 for food shortages, 0.974 for age class, and 0.912 for residency. Litter production was lower following years of food shortage, among younger bears, and among residents of CCGP; the effect of residency was primarily because of differences among younger bears (Fig. 4).

We observed 9 1-cub litters, 51 litters each of 2 and 3 cubs, and 1 4-cub litter shortly after birth in winter dens. Litter-size data were slightly overdispersed ($\chi^2/df = 1.101$). The model with additive effects of age class and food shortages ranked first with 71% of the total $QAIC_c$ weight, and the model with only an age-class effect ranked second ($w_i = 0.171$). Summed $QAIC_c$ weights for age class, food shortages, and residency were 1.00, 0.81, and 0.12, respectively. Only age class had an appreciable effect size. Mean litter size of females aged 5–7 years was 2.00 ($n = 2$) following years of food shortage and 1.82 ($n = 11$, 95% CI =

Table 7. Ages at primiparity among female black bears resident on and off the Chapleau Crown Game Preserve (CCGP) in the boreal forest of Ontario, Canada, 1990–1999. The bottom row presents mean age of primiparity calculated following Garshelis et al. (1998).

Age (yr)	CCGP	Off CCGP
5	4	1
6	2	3
7	4	5
8	8	2
9	4	
10	2	
11	1	
12	1	
Median	8	7
\bar{x}	7.81	6.73
Alternate \bar{x}^a	8.09	7.19

^a Method of Garshelis et al. 1998.

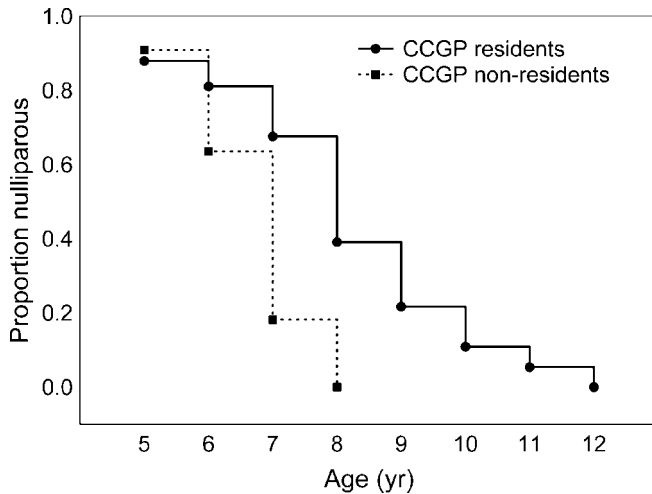


Figure 3. Proportions of nulliparous female black bears at age among residents and nonresidents of the Chapleau Crown Game Preserve (CCGP) in the boreal forest of Ontario, Canada, 1990–1998.

1.41–2.22) in other years. Mean litter size of bears aged ≥ 8 years was 2.40 ($n = 20$, 95% CI = 2.08–2.72) following years of food shortage and 2.48 ($n = 79$, 95% CI = 2.34–2.62) in other years.

DISCUSSION

Relative Density

Three independent data sources and estimation methods showed the same pattern of decreasing abundance from CCGP, to Borland's, to Ivanhoe. We believe it is more parsimonious to infer that a gradient in bear density existed among our study areas than to assume some form of bias created this pattern in all 3 data sets. Robust density estimation of bears using capture–recapture is complicated by such factors as low, heterogeneous probabilities of capture (Noyce et al. 2001, Boulanger et al. 2002), small sample sizes relative to the number of parameters in models (Schwarz and Seber 1999), and uncertainty in the effective trap area (Efford 2004). In our study, among-year differences in abundance estimated following the method of Garshelis (1992) were likely a result of sampling error, though they may have been affected by unknown additions of unmarked animals. Higher abundance estimates derived from hair-trap versus live-capture data may have been due to different spacing of traps, methods of capture, or methods of abundance estimation. However, genotyping errors, such as allelic dropout and false alleles, can cause overestimation of abundance (Waits and Leberg 2000); these may have been present in our data.

Survival

A disproportionate number of the radiocollars that failed prematurely were worn by nonresidents of CCGP. We suspect the weak evidence for an effect of residency on survival from the data set in which we assumed bears with which we lost contact had died was an artifact of the pessimistic bias introduced by this assumption on survival of nonresidents. Therefore, total mortality estimates and

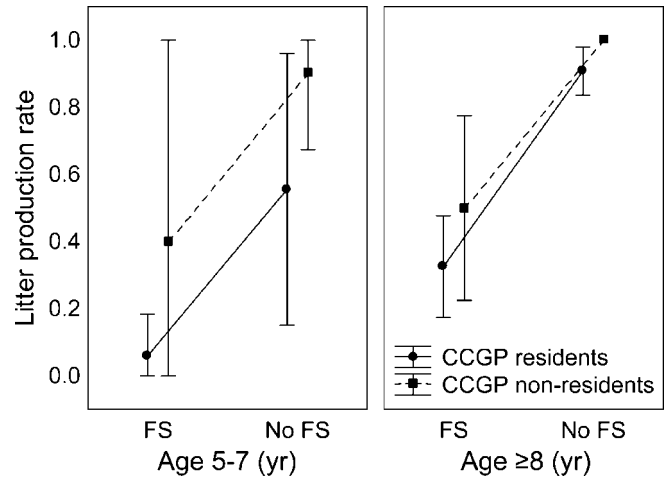


Figure 4. Litter-production rates of available female black bears of 2 age classes in the boreal forest of Ontario, Canada, 1993–1999, for residents and nonresidents of the Chapleau Crown Game Preserve (CCGP), in food-shortage years (FS) and years of good or average food production (No FS). Error bars show 95% confidence intervals.

estimates of other mortality from the data set in which we assumed these 13 bears died were overestimated.

Lower survival of adult females encumbered with cubs of the year was due to their greater risk of being cannibalized. It was predicted that adult female bears would be more vulnerable to cannibalism when encumbered with cubs of the year. Our data showing similar risk of cannibalism in CCGP relative to lower-density hunted areas suggest that cannibalism rates were neither density-dependent nor affected by removals of resident males.

Despite being at higher risk of harvest mortality, nonresidents of the Game Preserve were not at lower risk of death by other causes, suggesting that harvest mortality was additive to other forms. Similarly, studies of black bears inside and outside sanctuaries in North Carolina indicated that a compensatory increase in natural survival in harvested populations was absent or insufficient to compensate for harvest mortality. There, total survival rates of black bears were higher among those spending more time in a sanctuary, and survival rates of adult females in the greater study area, including hunted areas and a refuge, were lower than those in the refuge alone (Powell et al. 1996, Beringer et al. 1998).

Lower survival of subadult males than of subadult females (Beringer et al. 1998; Lee and Vaughan 2003, 2005; this study) or adult males (Bunnell and Tait 1985, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beringer et al. 1998) has been attributed to greater mobility and other risks associated with dispersal (Schwartz and Franzmann 1992, Beringer et al. 1998, Lee and Vaughan 2005). In our study, AIC_c model selection criteria and model averaged-parameter estimates showed differences between sexes in subadult survival but not yearling survival. Survival of subadult males

was lower than that of subadult females and of yearlings of both sexes. In Virginia, Lee and Vaughan (2005) showed that females aged 1–3 years had similar survival rates, but survival rates of subadult (aged 2 and 3 yr) males were lower, and those of yearling males were lower still. It is possible that survival of male yearlings was lower than that of female yearlings in our study and that the effect was simply not detected in our sample; however, in our boreal study area, bears may have grown more slowly and so delayed dispersal until 2 years of age more frequently than in Virginia, resulting in lower survival of male subadults but not male yearlings.

We detected an effect of residency on survival of yearlings but not on survival of subadults. Models including effect of residency on yearling survival were only slightly better supported than models without the effect, but unconditional parameter estimates showed a large effect size where yearlings in CCGP had lower survival. If this difference was attributable to higher bear density in CCGP, we would expect similar effects on survival of other age classes, particularly cubs and subadults, which we did not observe. We expected that harvest mortality would cause lower subadult survival off CCGP, but the sample size for subadults with known fates may have been insufficient for a meaningful test. Among bears marked but not radio-collared, few yearlings but many subadults were harvested on our study areas (M. E. Obbard, Ontario Ministry of Natural Resources, unpublished data). We lost contact with subadults of both sexes when breakaway collars were dropped, and dispersal of males further reduced our sample size because bears left the greater study area while wearing collars (we subsequently removed these during winter den visits), or remained on the study area but moved between CCGP and hunted areas precluding us from assigning residency.

Cubs had lower survival than did other age classes. Cub survival estimates are affected by the time of census such that estimates based on winter den surveys (such as ours) are lower than those based on spring and summer captures (e.g., Kolenosky 1990) due to deaths occurring between birth and capture in spring or summer. Nevertheless, winter-to-winter cub survival estimates <0.5 are uncommon in the literature (Elowe and Dodge 1989, Kolenosky 1990, McDonald and Fuller 2005, Czetwertynski et al. 2007). This suggests that cub survival in our study area was lower than in most areas. Similar ($<50\%$) cub survival rates were observed in White River National Wildlife Refuge (NWR), Arkansas (USA), and Ocala National Forest (NF), Florida (USA; Clark and Eastridge 2006, Garrison et al. 2007). In White River NWR, winter and spring flooding and infanticide were suggested causes of low cub survival, but neither cause was strongly supported by data (Clark and Eastridge 2006). Infanticide was the most common cause of cub mortality in Ocala NF (Garrison et al. 2007). We assumed cubs died when their mother died, or when cubs were absent from dens as yearlings, and we did not document causes of mortality for many of the cubs included in our analysis.

However, high risk of encumbered females to cannibalism suggests infanticide was likely an important cause of cub mortality on our study areas.

Previously it was proposed that natural survival rates of bears, particularly cubs, may depend on density of adult bears, especially males (Bunnell and Tait 1981, LeCount 1987, McLellan 1993, Clark and Smith 1994, Taylor 1994). Schwartz et al. (2006) showed that survival of grizzly bear cubs was lower in the interior of Yellowstone National Park where bears were considered to be near carrying capacity. Czetwertynski et al. (2007) demonstrated lower survival of black bear cubs in a higher-density, un hunted area than in a lower-density, hunted area during a short-term study in Alberta, Canada, and concluded differences were consistent with a density-dependent response. Nevertheless, the effect of hunting, bear density, or proximity of the population to carrying capacity on survival of bear cubs remains controversial (Miller 1994, Sargeant and Ruff 2001, Miller et al. 2003, McLellan 2005). In our study, though an effect of residency was included in models of cub survival receiving the most AIC_c support, cub survival among nonresidents of CCGP was not consistently higher or lower than among residents, so our long-term data do not support an effect of bear density or harvest on cub survival.

The interaction between residency and years of food shortage was included in models ranking higher than the null model, but additive effects of residency and food shortages were not. Reduced cub survival in years of food shortage in CCGP could have resulted from nutritional stress in cubs or from increased cannibalism, but neither of these factors explains higher cub survival in the same years off the CCGP. Of 18 cubs monitored off CCGP in 1995, 11 (61%) survived, contributing to the high estimate of cub survival in years of food shortage. In 1998, 7 of 16 cubs (44%) monitored off CCGP survived—a rate similar to the overall mean for cubs off CCGP. We can suggest no plausible mechanism to explain increased cub survival outside the preserve in years of food shortage, so we suggest that the apparent increase in cub survival off CCGP in years of food shortage was a sampling artifact.

Reproduction

Median and mean ages of primiparity on our study areas appear to be the highest reported for black bears (Beecham 1983, Rogers 1987, Kolenosky 1990, Schwartz and Franzmann 1991, Garshelis et al. 1998), likely reflecting the lower productivity of the boreal ecosystem. For example, Miller (1994) showed that female black bears in less-productive habitats in Alaska had older ages at primiparity.

We suggest that higher bear density in CCGP contributed to lower reproductive rates among younger bears there. Similarly, Czetwertynski et al. (2007) inferred a density-dependent response based on greater ages of first reproduction and first successful reproduction in un hunted than in hunted areas. Rogers (1987) suggested that in a food-limited system, density effects on black bear reproduction would be more pronounced in younger animals because older animals would outcompete them in, or exclude them

from, food-rich patches. However, Young and Ruff (1982) did not observe decreased bear weights as population density increased. Czetwertynski et al. (2007) suggested that low body mass was the proximate cause of delayed reproduction in their higher-density study area. In contrast, several nulliparous females in CCGP were handled in winter dens ≥ 1 year before producing a litter and were old enough and of sufficient body mass (estimated to have been ≥ 90 kg in fall based on body mass in winter) to have successfully produced cubs, yet they did not. Support for a food-limitation hypothesis was further complicated by the fact that CCGP bears frequently left the preserve on summer foraging excursions, often feeding on soft mast in the same general areas as bears from the hunted portions of the study area (Obbard and Kolenosky 1994). We cannot attribute delayed reproduction in the higher-density population to a food-limitation hypothesis or to effects of nutritional condition. Perhaps there was reproductive suppression of young females in the higher-density population through dominance hierarchies analogous to that proposed by Stoen et al. (2006) for brown bears (*Ursus arctos*) in Scandinavia. Though Schenk et al. (1998) showed there was little correlation between relatedness of neighboring females and home-range overlap in our study area, and our study showed a similar risk of cannibalism in CCGP relative to the lower-density areas, the threat of infanticide might still result in delayed reproduction as proposed by Stoen et al. (2006). Such a dominance hierarchy could be induced behaviorally (e.g., Samson and Huot 2001) or chemically by scent marking (see DeBruyn 1999).

In black bear populations, the annual proportion of females that reproduce successfully varies considerably with food supply or nutritional condition of mothers (Rogers 1987, Eiler et al. 1989, Kolenosky 1990, McLaughlin et al. 1994). Reproductive failure following years of food shortage is common in black bears (Jonkel and Cowan 1971, Miller 1994, Costello et al. 2003, Dobey et al. 2005). In our study, reproductive success was strongly affected by food availability, with few litters produced following years of food shortage. Residents and nonresidents of both age classes were similarly affected. Although litter-production rates differed between high- and low-density areas, annual differences in response to changes in food supply were independent of any effects of density (Fig. 4), as previously demonstrated for black bear recruitment rates (Bunnell and Tait 1981, Beecham 1983, Rogers 1987, Elowe and Dodge 1989).

Miller (1994) observed that recruitment interval, cub survival, and age at first maturity were affected by differences in productivity among study areas, but litter size was not. Similarly, Noyce and Garshelis (1994) found no relationship between litter size and habitat quality. In our study, litter size was unaffected by either food shortages or density. Black bears are induced ovulators and mating occurs before periods of major food abundance so females likely have no ability to predict food resources and adjust litter size accordingly. Alternatively, it is possible that we failed to

detect reduced litter size following years of food shortage because few litters were produced in those years, so statistical power was low.

Reproductive failures in black bear populations following years of food shortage can result in reproductive synchrony (McLaughlin et al. 1994, Clark et al. 2005). If female black bears are generally at greater risk of being cannibalized when encumbered with cubs, as shown here, an adverse effect of food shortages on adult female survival with a 2-year lag could be expected. However, detecting such an effect would require a high ratio of natural to anthropogenic deaths in the population. We did not detect annual variation in adult female survival or effects of food shortages on survival in the same year, and we did not consider a lagged response. Nevertheless, the number of cannibalism events was highest and adult female survival lowest in 1994, 2 years after a food-shortage year, though a similar effect of the 1995 food-shortage year on survival in 1997 was not apparent.

MANAGEMENT IMPLICATIONS

Effects of encumbrance status on female survival should be considered when modeling black bear populations, especially when natural survival is an important predictor of population growth rate. Harvest mortality of adult females was additive in our study, so managers assuming that harvest mortality is compensatory to natural mortality should do so cautiously. We did not observe higher cub survival in lower-density, hunted areas in our long-term study. Increased cub survival following density reduction is not ubiquitous in black bear populations, so we urge caution when interpreting results from short-term studies. Cub production, especially by younger adults, was greater on the lower-density, hunted areas than in CCGP, suggesting a density-dependent response. However, we did not demonstrate a functional relationship between density and litter-production rate or age at primiparity, and litter-production rates in lower-density areas were affected by changes in food supply. Furthermore, our study design lacked the randomization and replication necessary to make general inferences regarding density dependence in black bears. Therefore, managers should not assume a subsequent increase in reproduction when opening a hunting season or when further reducing bear density in an area where anthropogenic mortality already occurs.

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