Effects of hunting on demographic parameters of American black bears

Sophie M. Czetwertynski[1,3], Mark S. Boyce[2], and Fiona K. Schmiegelow[1]

[1]*Department of Renewable Resources, University of Alberta, Edmonton, AB, T6G 2H1, Canada*
[2]*Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada*

Abstract: We conducted an experiment to test competing hypotheses regarding the effects of hunting on American black bear (*Ursus americanus*) demographic parameters. Specifically, we tested for the existence and the relative influence of sexually selected infanticide (SSI) and density dependence in regulating demographic parameters. We monitored 290 bears in 2 hunted areas and an adjoining unhunted area in the boreal forest of Alberta, Canada, during a 4-year study (2002–2005). We manipulated the areas using a modified before–after control–impact (BACI) design whereby bait sites for hunting were closed in 1 of the 2 hunted areas in years 3 and 4 and adult males in the unhunted area were removed in year 3. Results did not support a significant influence of SSI, if it occurs, on population parameters compared with the effects of density dependence. We found lower cub survival (66% versus 83%) and older age of first reproduction in the unhunted, higher-density area than in the lower-density, hunted area. We found no difference in body condition of males and females between areas, suggesting that if SSI restricted females to suboptimal areas, the effect was not strong enough to affect reproduction. We did not detect an influx of new males or a change in cub survival after removal of adult males from the unhunted area (66% before versus 73% after). Our results suggest that SSI does not affect the population growth rate of hunted black bear populations, and that target hunting quotas do not require including potential effects of SSI in population projections. However, SSI should be considered in unhunted or lightly hunted populations approaching carrying capacity (*K*). We advocate the inclusion of density dependence in population projection models for bear populations. However, for specific cases where harvesting maintains a population size well below *K*, density-dependent effects are predicted to be negligible due to the non-linear relationship between demographic parameters and density.

Key words: Alberta, American black bear, body condition, cub mortality, density dependence, hunting, sexually selected infanticide, *Ursus americanus*, vital rates

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Black bear populations are considered stable or increasing throughout most of North America (Servheen 1990, Williamson 2002, Garshelis and Hristienko 2006), and in most Canadian jurisdictions there are no limits on the number of hunting permits issued to residents, only on the number of bears per hunter. Harvest pressure in an area often is related to the degree of access (e.g., roads, seismic lines, pipelines; Gratson and Whitman 2000*a,b*; Trombulak and Frissell 2000). Removal of animals through harvest typically reduces population size below carrying capacity (*K*), the maximum number of animals a particular area can sustain at a time (Caughley 1979). Density-dependent responses of populations reduced below *K* include increased reproduction or diminished natural mortality (Caughley 1966, Fowler 1987). The existence of density dependence is attractive to wildlife managers because it can potentially compensate for harvest mortality (Miller 1990*a*).

Density-dependent effects on survival and reproduction are difficult to observe across study areas because of confounding effects of habitat differences (Garshelis 1994) and their strong influence on these parameters (Rogers 1987, Eiler et al. 1989, Elowe and Dodge 1989). Even in a high-density bear population on Long Island, Washington, reduced cub survival could not be attributed to the high density of bears because of forest maturation and a gradual decrease in food availability (Lindzey and Meslow 1977*a,b*). A few bear studies offer insight into the effects of density dependence

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[3]smc3@ualberta.ca

on population parameters (McLellan 1994, Miller et al. 2003). In Yellowstone, where a grizzly bear population approaching carrying capacity was reduced and allowed to rebound (Boyce et al. 2001; Schwartz et al. 2006*a,b*), authors recommend that density-dependent effects be considered in modeling and decision making. However, other studies did not find evidence of density-dependent responses to hunting in bear populations (Miller 1990*a*, Derocher and Taylor 1994, Garshelis 1994, McLellan 1994, Taylor 1994) and recommended against considering the effects of this mechanism in management practices (Peek et al. 2003) and sustainable yield projections for hunted populations below *K* (Miller 1990*a*, Taylor 1994).

In addition to questions on the existence and form of density dependence in bear populations are questions on the potential indirect effects of hunting in response to changes in the age–sex and social structure in hunted populations. Hunting usually affects certain cohorts disproportionately. Male bears usually are more susceptible than females to hunting mortality because of legal harvest restrictions on females with cubs in some jurisdictions and larger home ranges of males; also, males have a greater likelihood of encountering hunters (Bunnell and Tait 1980, Miller 1990*b*). The hunting method also can affect harvest, particularly in the case of hunting with hounds or baits, where hunters can target large trophy males (Litvaitis and Kane 1994). Bear hunting pressure thus tends to target the adult male cohort. For populations experiencing high hunting pressure, this results in not only in reduced population density but also changes to the age and sex structure of populations (Clark 1991).

Populations where hunting pressure is relatively low and targeted toward trophy males may undergo changes in population structure without substantial changes to density. Trophy hunts often are justified in small populations because they are seen as not having any effect beyond that of removing a few old individuals (Whitman et al. 2004). However, potential indirect effects of sex-biased harvests could have impacts beyond those of removing individuals from the population. Recent debates offer competing hypotheses regarding the role of adult male bears in population regulation, which could alter the effects of harvest (Swenson et al. 1997, Miller 2003).

McCullough (1981) and Stringham (1980, 1983) suggested that the reduction of adult males from a population may increase survival of young bears by decreasing intraspecific predation or infanticide. This scenario is supported by field evidence of adult male bears killing subadults and cubs (Jonkel and Cowan 1971, LeCount 1982) and the observation that younger bears are less aggressive (Reynolds and Beecham 1980). Kemp (1972, 1976) claimed that adult male bears regulate density through exclusion of subadult male bears. That conclusion was based on a perceived population increase after the removal of adult male bears from an unhunted population and an increase in the proportion of subadult males; this conclusion has often been used by managers as evidence of density dependence and sustainable bear hunting. However, Garshelis (1994) reinvestigated the trapping data and concluded that there was insufficient evidence for that claim. Subsequent analysis of those data by Sargeant and Ruff (2001) showed that the number of bears using the study area increased after the removals, but they detected no effect on birth and death rates. Furthermore, bears in the study area experienced human-caused mortality and were likely not at *K*. Thus, Sargeant and Ruff (2001) concluded that the removal of male bears resulted in increased use of the area by subadults and females, but that no inferences regarding density dependence or population regulation could be made.

An alternative hypothesis suggests a negative relationship between hunting and cub survival whereby adult male bears might protect their own offspring by excluding subadult males from their home range (Rogers 1976). The removal of resident males through hunting could alter the established social structure and result in increased infanticide by males encountering females with which they were unlikely to have bred (Swenson 2003), termed sexually selected infanticide (SSI, Hrdy and Hausfater 1984). SSI is possible in bears because females are induced ovulators (Boone et al. 2004) and because by killing cubs sired by other males, a male bear can mate with their mother and sire his own cubs. Larger males are more likely to sire cubs (Kovach and Powell 2003, Bellemain et al. 2006*a*) and thus may not exhibit sexually selected infanticide within their home range. Studies in Scandinavia showed decreases in cub and yearling survival after the removal of adult male bears and attributed the cause to SSI by immigrant males (Swenson et al. 1997, 2001*a,b*). However, more recent results suggested that remaining resident adult males were responsible for the deaths, possibly because of shifts in home ranges of males (Swenson 2003). In Scandinavia, SSI was considered to be one of the most important factors affecting cub survival (Swenson et al. 1997, 2001*b*). Immigrant male bears also were believed to displace female bears from optimal habitats, resulting in lower nutritional condition and litters sizes in Alberta, Canada (Wielgus and Bunnell 1994*a,b*; 1995; 2000), but sample sizes used to draw these conclusions were small.

Convincing evidence of SSI in North American bear populations is lacking. McLellan (2005) proposed a potential alternate form of SSI to the immigrant male hypothesis described in the Scandinavian study, which he termed the mate-recognition hypothesis. This suggests that both resident and non-resident bears kill cubs they were unlikely to have sired to increase breeding opportunities. High survival of cubs in a hunted population (annual cub survival = 0.85, n = 81) as well as simulations favored the mate-recognition hypothesis but could not differentiate between SSI and predation-driven infanticide (McLellan 2005). Furthermore, density and sex ratio probably influence the expression of this mate-recognition form of SSI, if it exists (McLellan 2005). Specifically, a population with few adult males should experience low infanticide because males would have access to many potential mates. Conversely, a low density of female bears could lead to increased infanticide because males would have difficulty finding estrus females. In Alaska, however, Miller et al. (2003) found greater cub survival in low-density hunted populations than in higher density unhunted populations. He concluded that cub survival was driven by density dependence and the proximity of unhunted populations to K. Therefore, in contrast to results from the Scandinavian study where removing males resulted in decreased cub survival (Swenson et al. 1997, 2001*b*; Swenson 2003), both Miller et al. (2003) and McLellan (2005) concluded that hunting male bears did not increase cub mortality.

Part of the difficulty in describing the effects of hunting stems from the potentially confounding effects of changes in population density and structure associated with an annual legal harvest and potential indirect effects due to the disruption in social structure (i.e., an increase or decrease in infanticide). The theory of density dependence predicts that populations below K will have increased reproduction and survival (Fowler 1981*a*, Owen-Smith 2006). Important management questions stemming from this debate are (1) whether the effects of density dependence are actually occurring in hunted black bear populations and (2) whether there are positive, negative, or negligible indirect effects to reproduction and survival that should be considered when setting harvest targets.

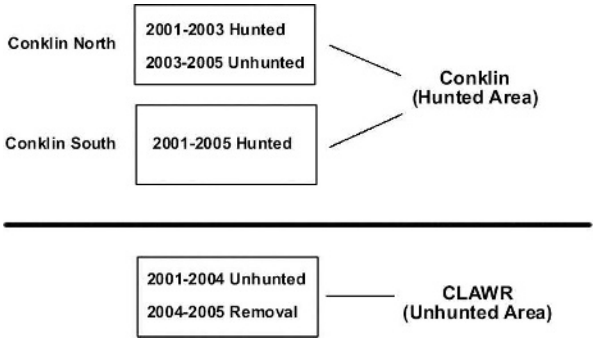

Fig. 1. Study design (2001–2005) depicting experimental closure of hunting in the Conklin North (CN) area and experimental removal of adult male black bears in the Cold Lake Air Weapons Range (CLAWR), Alberta, Canada.

We tested several predictions of responses to hunting using a modified BACI (before–after control–impact) design in 2 hunted and 1 nearby unhunted black bear populations (Fig. 1). We thus addressed the effects of hunting in a series of 3 population comparisons: (1) between a hunted (sites 1 and 3, Fig. 1) and unhunted (site 4, Fig. 1) population, (2) of a hunted population before (sites 1 and 3, Fig. 1) and after (site 2, fig. 1) an experimental closure of hunting, and (3) of an unhunted population before (site 4, Fig. 1) and after (site 4, Fig. 1) the experimental removal of adult males. We implemented the experimental design in northeastern Alberta, Canada, from 2001 to 2005 and simultaneously monitored annual reproduction, cub survival, and body mass in all study areas.

Study areas

Unhunted area (Cold Lake Air Weapons Range)

The Cold Lake Air Weapons Range (CLAWR) covers 11,600 km^2 and straddles northeastern Alberta and northwestern Saskatchewan. All civilian traffic was restricted within its borders. Our study was concentrated in the 5,100 km^2 Alberta portion of the range and all further mention of CLAWR or unhunted area refers to this section. Our study differs from the Cold Lake study area of Kemp

(1972, 1976), which was outside CLAWR and had no access restrictions.

Oil and gas extraction was prominent on CLAWR, but there was no timber harvesting. However, several large-scale burns were present within the study area. Many kilometers of seismic lines, created in the initial phases of oil exploration, were present on the landscape. A 42-km all-season main road (MR) provided the main north–south connection to most oil and gas extraction activities in the area. Five camps for oil-company staff were located along the MR and all were surrounded by electrified fencing to reduce human–bear conflicts. Our access permits allowed trapping within 1 km of the main road and access was further restricted by muskeg scattered throughout the area and in the vicinity of the MR.

Feeding bears along the MR was strictly forbidden to all people operating in CLAWR. Hunting has been prohibited since 1954. However, under the 2002 Cold Lake First Nations (CLFN) Agreement, CLFN members were permitted to hunt in specific areas away from roads. Moose (*Alces alces*) hunting was the primary interest of natives and no bears were harvested within CLAWR during the study. The only harvest mortality of CLAWR bears occurred when bears traveled beyond the range to Crown and private lands.

Hunted area (Conklin)

Conklin (~8,000 km^2) was north of CLAWR on Crown land, divided into 2 study sites north (CN) and south (CS) of Christina and Winefred Lakes. Although the lakes did not impede movement between the 2 areas, most radiomarked bears were captured far enough within each study area that transboundary travel was minimal. We assumed that bears remained within the capture area for the duration of the study.

Oil and gas extraction was ongoing throughout the study area and was the main anthropogenic disturbance on the landscape. Forestry activity occurred, but affected a relatively small portion of the area during the study; fire was the main large-scale natural disturbance within the study area. Bears could be legally hunted over bait in spring and fall, and several outfitters operated guided hunts during spring. Residents seldom hunted black bears in this remote area and although they could legally hunt bears in both Conklin areas, we considered their effect negligible. Hunters regularly report tagged bears to local conservation officers and no tagged bears from this area were reported shot by a resident during the study. Females with cubs of the year (cubs, hereafter) were protected.

Expandable radiocollars were used to minimize chaffing at the neck and outfitters were asked to inform their clients that collars should be ignored when selecting bears. Many hunters admitted not noticing the black collars when hunting, and we do not believe that hunter selectivity was significantly affected by the study.

CLAWR and Conklin vegetation

Vegetation in CLAWR and Conklin was similar. The northern border of CLAWR was adjacent to Crown land which was extended the boreal mixed-wood forest in CLAWR. Both areas consisted of rolling mixed-wood boreal forest interspersed with burned areas and wetlands. The forest was composed of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce (*Picea glauca*) at higher elevations. Black spruce (*Picea mariana*) and tamarack (*Larix laricina*) dominated wet areas at lower elevations and stands of jackpine (*Pinus banksiana*) were dispersed throughout the dry areas. The main habitat difference between the areas resulted from the lack of forestry activities in CLAWR. However, early seral stages were available in burned areas within the CLAWR study area.

Methods

Fieldwork

We captured bears using modified bucket traps (Lemieux and Desrosiers 2001, Lemieux and Czetwertynski 2006) and L-83 ground snares (Lemieux and Jolicoeur 1984, Jolicoeur and Lemieux 1992). Once restrained, bears were immobilized with tiletamine–zolazepam, individually marked with colored ear tags, measured and weighed; a premolar was extracted for age determination (Animal care 322104 University of Alberta). Ages were determined by cementum annuli counts performed by Matson's Laboratory (Milltown, Montana, USA). A subset of captured bears was equipped with VHF and GPS 2200L (programmed to acquire fixes hourly) radiocollars within each study area (Lotek Wireless Inc., Newmarket, Ontario, Canada).

We alternated trapping sessions between study areas to sample population structures as accurately as possible. Bears were trapped on CLAWR from 24 April to 10 May 2001 and 25 September to 15 October 2001. Trapping occurred in the 2 Conklin study areas from 21 June to 19 August 2001. Shorter capture sessions were scheduled annually in the spring and fall of the following years to replace lost collars.

Collared bears were located periodically throughout summer using fixed-wing aircraft, and extensive transects were flown during winter to locate dens. We visited dens of collared bears yearly between mid-January and mid-March to record mass, body measurements, reproduction, and cub survival. All yearlings in dens ($n = 98$) were sexed, weighed, and measured, whereas cubs ($n = 160$) were sexed and weighed only.

Study design and hypotheses

The 2 Conklin study sites were hunted during spring 2001 and 2002. Outfitters agreed to close bait sites within the trapped area of CN during 2003 and 2004 (Fig. 1), thus reducing hunting pressure and food supplementation in the area compared with previous years. The CS area was hunted for the duration of the study. Trophy hunting in CLAWR was simulated by euthanizing collared male bears in January 2004. Our simultaneous monitoring of both areas reduced the potential bias of annual environmental fluctuations which influences reproductive parameters (Beecham 1980, Bunnell and Tait 1981, Rogers 1987). Thus, we attempted to control for the confounding effects of habitat quality often encountered when comparing remote populations (Bunnell and Tait 1981).

In our first comparison (i.e., hunted versus unhunted), we hypothesized that if density dependence was the most important factor affecting population parameters and if the indirect effects of hunting were negligible, we should observe higher body condition index (BCI), reproduction, and cub survival in the hunted population than in the unhunted population. Conversely, if the effects of social disruption affected population parameters negatively and were substantial, they should counteract the effects of density dependence and we should detect lower BCI, reproduction, and cub survival in the hunted population than in the unhunted population.

Secondly, we compared a hunted population before and after the closure of hunting sites. We assumed that density would increase in the 2 years following the hunting closure but that the population structure would not have time to reestablish as in an unhunted population at *K*. We predicted no changes to cub survival and BCI because the population likely did not have sufficient time to reach a population density at which density-dependent effects would be detected.

Thirdly, we compared an unhunted population near *K* before and after the removal of adult males. In this case, the density of bears was little affected, and we considered potential changes a response to the social perturbation. To test whether adult males regulated population density, we intensively trapped the area to detect new bears following the removal. We hypothesized that if adult male bears regulated density through exclusion of subadults, we would observe an influx of new subadult males into the area after the experimental removal. Second, dens of females were visited to test for a change in survival of cubs. If density dependence were the most important factor affecting population parameters, we expected to see no change after the experimental removal. However, if the removal of males led to an increase in SSI, we would expect a decline in cub survival.

Bear density

Bear density index. The number of unique individuals captured was used to compare the relative density of bears in our hunted and unhunted areas in 2001. This index is considered robust when underlying population attributes are unknown (McKelvey and Pearson 2001). However, the duration of trapping effort and the total area trapped varied between the study areas. Therefore, we calculated a bear-density index based on the number of individual bears trapped/10 km of road per night to control for these differences.

Trapping duration was determined by available radiocollars and field-related constraints. Specifically, both capture sessions in the unhunted CLAWR area were limited by time whereas the capture session in the hunted Conklin area lasted until all available radiocollars were deployed on a pre-determined number of bears of each sex.

We created trap sites at approximately 1-km intervals in the unhunted area where access was restricted to a 43-km all-season road, saturating the length of the road. In the hunted area, our intention was to restrict each study site to 40 km of road, and trap sites were initially constructed at approximately 1-km intervals in each area to mimic the trapping effort in the unhunted CLAWR area. However, we realized that we could not collar the desired number of bears without expanding the study areas. Therefore, we increased the spacing between traps to approximately 2 km and expanded each of the areas until all radiocollars were deployed. Thus, the total area trapped was modified in the hunted area to capture our pre-determined sample size of bears. Given that 29 of the 92 bears (32%) trapped in the hunted area were recaptured a second time that summer at a different trap location, we believe that this additional spacing between traps approximated the trap saturation described for CLAWR. Therefore, given the spatial proximity of our trap sites and the difference in the length of road saturated with traps in each area, we consider the number of individuals trapped/km per night a better estimate of unit effort than the more conventionally reported number of bears/trap-night.

Because the 2 hunted study areas were trapped simultaneously, we summed the number of bears trapped/10 km in each area and divided by the total trapped in both areas to calculate the overall density index for the hunted area. All bears captured in 2001 excluding cubs were used in the analysis.

Home-range analysis. We calculated home ranges of individual bears with 90% fixed kernel density estimates (Worton 1987,1989; Seaman and Powell 1996) using the Home Range Extension (Version 1.1c, Ontario Ministry of Natural Resources, Ontario, Canada) in ArcView 3.2 (Environmental Systems Research Institite, Inc. [ESRI], Redlands, California, USA). Only animals from non-manipulated areas with a minimum of 80 days and 650 locations were included in the analysis. Some bears traveled in a straight-line distance far beyond their home range and remained there for several weeks (mostly CLAWR bears in fall). Those long-distance excursions were not included in the analysis because we were interested in comparing distinct home ranges within the study areas. All available locations were used because home-range estimates are less biased with increasing temporal autocorrelation (De Solla et al. 1999). The smoothing factor (h) should be the same for all individuals to compare home ranges (Kernohan et al. 2001). Therefore, we calculated the reference bandwidth (h_{ref}) for each individual bear (Worton 1989) and used the mean value to calculate the 90% fixed kernel density of bear home ranges for comparisons. Because reproductive status affects home range size (Dahle and Swenson 2003*a*,*b*) we used only home ranges of females with cubs. We used a Mann-Whitney *U*-test to compare home-range size between hunted and unhunted areas.

Population structure

We compared population sex and age structure using data from the 2001 captures only because traps were operational for a longer time than in later years, possibly biasing data from those years. Capture data from the 2 hunted study areas were merged and compared with animals captured in the hunted CLAWR. Only the first capture was included in the data set, and captures of cubs were excluded because they were not independent of their mothers. Ages could not be obtained for 1 female and 1 male from Conklin. We also compared the population structure obtained in 2001 to bears captured throughout the remainder of the study.

Bear mortality

Bear hunting season in Alberta occurred from mid-April to mid-June and the beginning of September to the end of November. Outfitters in the Conklin area reported all bears killed by their clients. Resident hunters returned radiocollars and provided information on bears they had killed. Annual mortality was calculated using the number of tagged bears reported killed compared with the total number of tagged bears available each year. Because the minimum age of hunted bears was 2 years, only bears aged 2 and older were considered available in each year.

Population parameters

Body condition. Due to large variation in mass throughout the summer (Noyce and Garshelis 1998), we used winter mass and body measurements to compare populations and recorded the date of weighing. Because mass is only a surrogate of nutritional condition, we used the residual index (Jakob et al. 1996) to estimate BCI of bears. For this method, we regressed body mass on total body length (TBL), and used the residuals from the regression line as an index of condition. This index has proven reliable for bears because it is independent of body size and highly correlated to true BCI (Cattet et al. 2002). Mass and TBL values were transformed to natural logarithms to meet the assumptions of linear regression. We contrasted BCI among cohorts in non-manipulated areas (we withheld 2004–2005 data from Conklin north and 2005 data from CLAWR and CS) using ANOVA and controlled for the year in which bears were weighed. We also compared the BCI of cohorts before and after experimental manipulations. Given the small sample sizes for the manipulated areas, we also compared the BCI of individual bears for which there was information before and after manipulations.

Survival of dependent young. Survival of cubs from birth to age 1 was determined by visiting winter dens of radiocollared female bears in successive years. Cubs were considered dead if they were not present with their mother as yearlings. Two litters consisted of 4 cubs; we coded them as 3-cub litters for analyses. Because litters of nulliparous females are often less successful than later litters (Elowe and Dodge 1989), we excluded first litters from comparisons of litter size between areas. Reproductive synchrony was calculated by comparing the number of females with young with the total number of females available to reproduce. Females were considered available only if they had previously reproduced or produced cubs the following spring.

Age of first reproduction and first successful litter. We used log-rank tests to compare age of first reproduction and age of first successful litter of hunted areas with unhunted areas (Garshelis et al. 1998). We used only data from non-manipulated areas. We determined age of first reproduction by field observation. Bears were considered not to have reproduced based on the size and color of nipples and their age of first reproduction was determined during winter den visits. When it was clear that a newly trapped bear had previously reproduced and its age was below or equal to the median age of first reproduction for that study area, it was included in the sample as having reproduced that spring (due to the possibility of having lost its cubs in early spring). Similarly, bears not having reproduced but aged equal to or older than the median age for that study area were considered to have reproduced the following winter, and data were right censored. This reduced the potential bias of undersampling bears that would have reproduced later but were eliminated from the sample due to hunting, a dropped collar, or the end of the study. To estimate the age of a first successful litter, we used a combination of cementum annuli data (Coy and Garshelis 1992) and field observations. Because litters lost even later in the summer may not be detectable by cementum analysis (Coy and Garshelis 1992), we considered litters successful if at least 1 yearling was present with the mother in the den. Bears having reproduced at a younger age than the median age of first reproduction for the study area were not included because survival of at least 1 cub could not be assessed. However, bears that did not reproduce or bears that reproduced but with which contact was lost the following year at an age equal to or above the median for the study area were considered to have their first successful litter the following winter and were right censored.

Results

Fieldwork

In the summer of 2001, we made 194 captures of 133 individual bears. Between spring 2002 and fall 2004, 110 captures resulted in 58 unmarked bears being tagged. This included a fall trapping session in 2004 during which we trapped 11 bears (5 recaptured females, 5 new adult females, 1 male yearling of a resident female) between 31 August and 12 September 2004. All yearlings present in dens (n = 98) were sexed, weighed, and measured whereas cubs of the year (COY) were sexed and weighed (n = 160). During the winters of 2002–2005, we visited 101 dens in CLAWR and 142 dens in Conklin. Five of 7 radiocollared adult males in CLAWR were euthanized in January of 2004, and the 2 remaining collared males, not located that winter, were killed by hunters south of the range in spring 2004.

Bear density index and home range

In CLAWR, 39 bears were trapped along 43 km of road in 38 days, resulting in a bear-density index of 0.24 bears/10 km/day. In CN and CS, 4.5 and 4.7 bears/10 km of road were trapped (n = 45, 47) in 60 days resulting in an overall density index of 0.08 bears/10 km/day. Bear-density index was greater in CLAWR than CN and CS by a factor of 3.

Home ranges of unhunted CLAWR bears were smaller than those of hunted Conklin bears. CLAWR females with cubs had smaller home ranges (27.5 km^2, range = 15–63 km^2, n = 8 home ranges, n = 17,887 locations) than hunted females in Conklin (58 km^2, range = 21–233 km^2, n = 12 home ranges, n = 28,523 locations, mean h_{ref} = 0.28, P = 0.017). Unhunted CLAWR males also had smaller home ranges (123.5 km^2, range = 90–245 km^2, n = 6 home ranges, n = 13,632 locations) than hunted Conklin

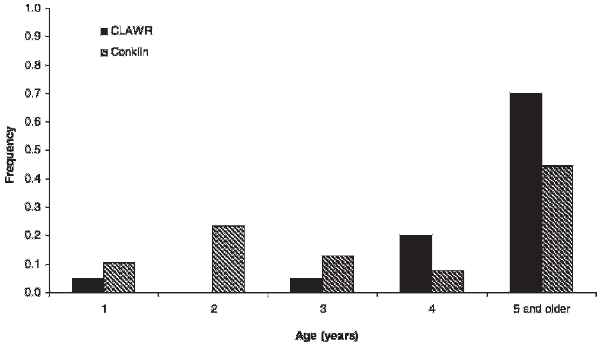

Fig. 2. Age distribution of female black bears captured in the hunted Conklin (n = 38) and unhunted CLAWR (n = 20) areas in 2001, Alberta, Canada.

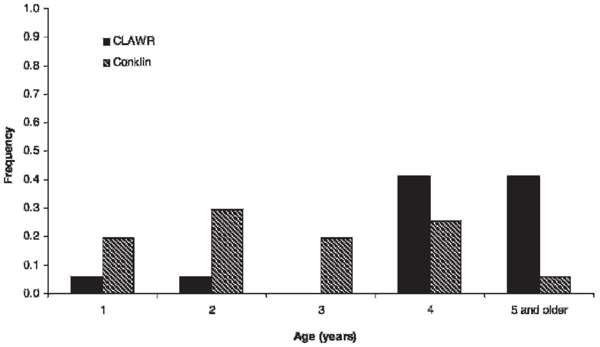

Fig. 3. Age distribution of male black bears captured in the hunted Conklin (n = 51) and unhunted CLAWR (n = 17) areas in 2001, Alberta, Canada.

males (378 km^2, range = 269–686 km^2, n = 7 home ranges, n = 15,933 locations, mean h_{ref} = 0.28, P = 0.003).

Population structure

Bears in CLAWR were older than bears in Conklin. The median age of female bears was 2 years older in CLAWR than in Conklin (6.0 yr in CLAWR, n = 20, and 4.0 yr in Conklin, n = 38; Mann-Whitney U = 270, P = 0.070; Fig. 2). The oldest bear trapped in 2001 was a 22-year-old female from CLAWR. Females ≥5 years old represented 90% of all females trapped in CLAWR and 53% of all trapped females in Conklin. Male bears in CLAWR were older than their counterparts in Conklin (CLAWR: median = 4.0, n = 17; Conklin: median = 3.0, n = 51; Mann-Whitney U = 188, $P <$ 0.001; Fig. 3). Trapped males ≥4 years old in CLAWR were 82% of all trapped males, but 31% of bears trapped in Conklin. Only 6% of bears trapped in Conklin were ≥5 years old compared with 41% of bears in CLAWR. Captures in Conklin between 2002 and 2004 for which we had age data revealed a similar trend; 63% of male bears were 2–3 years old and only 16% were ≥4 years old (n = 19). No 3-year-old males were captured summer of 2001 in CLAWR.

Sex ratios did not differ between areas (χ^2 = 1.45, 1 df, P = 0.230), although more males than females were captured in Conklin (53M:39F); the opposite was true in CLAWR (17M:20F). Captures during fall 2004 in CLAWR included 11 bears (1M:10F), of which 6 were recaptures. The only male trapped was the yearling offspring of one of the resident females. Ages of the 5 new females trapped in 2004 were 3 to 7 years (median = 4.0).

Bear mortality

Between 2001 and June 2005, we recorded 4 deaths of females in CLAWR, 1 of which was a yearling bear that died of unknown cause. An adult female in a snare was killed by another bear, a second died of unknown cause within CLAWR, and another was found dead near a farmhouse south of CLAWR.

We trapped 15 male bears ≥3 years old (14 in 2001 and 1 in 2002) in the unhunted CLAWR area; 5 of them were never relocated within the range and we did not consider them residents for the purpose of this study. Two resident males dropped their collars, 2 resident bears were not located in the winter of 2004 but were located in the range in 2005, and 1 resident bear died within CLAWR. This last bear was one of the largest bears we collared (138 kg, 11 yr). It died of unknown causes in a remote section of the Range and evidence at the scene suggested there had been a fight with another bear (the GPS antenna had been chewed off and claw marks were evident on nearby trees). We trapped one 2-year-old male bear in CLAWR in 2001; little information is available but hunters shot the bear south of the range in the spring of 2004.

Most bear mortality in the hunted area was due to spring hunting over bait (89%, n = 206). In the Conklin south area, mean annual hunting mortality was 21% (n = 35 bears killed) between 2002 and 2004. In the Conklin north area, hunting mortality was 14% in 2002, 11% in 2003, and 8% in 2004 (n = 17 bears killed). Hunters selected for older males; 35% of tagged male bears killed by hunters in 2002–

Table 1. Changes in body condition index (BCI) of female black bears with cubs in the Conklin North (CN) and Conklin South (CS) areas before (2002–2003) and after (2004–2005) experimental closure (EM) of bait sites in the CN area, Alberta, Canada.

		BCI before EM		BCI after EM		
Bear ID	Area	BCI	Year	BCI	Year	Change in BCI
32	CS	0.234	2002	0.085	2004	−0.149
36	CS	−0.130	2002	0.030	2004	0.160
43	CS	0.112	2002	−0.068	2004	−0.180
56	CS	−0.018	2002	0.044	2004	0.061
81	CS	−0.222	2002	−0.308	2005	−0.086
38	CN	0.184	2003	−0.177	2005	−0.360
68	CN	0.096	2002	0.071	2004	−0.026
88	CN	0.005	2003	−0.053	2005	−0.058
89	CN	0.172	2002	0.050	2004	−0.122
103	CN	0.068	2002	0.296	2004	0.228
177	CN	−0.041	2003	0.107	2005	0.148

2004 were $\geq$5 years old ($n = 31$ bears hunted), whereas this cohort represented only 6% of the population based on 2001 captures ($\chi^2 = 10.87$, 1 df, $P < 0.001$). Fifty three percent of females killed by hunters during 2002–2004 were $\geq$5 years old ($n = 15$ bears killed), which was similar to the population structure observed (45% of females captured in 2001; $\chi^2 = 0.32$, 1 df, $P = 0.581$).

Physical condition

After controlling for the year an animal was weighed, there was no difference in BCI between males in the hunted areas and the unhunted CLAWR ($F = 0.03$; 1, 37 df; $P = 0.858$). Similarly, we found no difference in BCI between solitary females ($F = 0.91$; 1, 28 df; $P = 0.347$), females with cubs ($F = 0.17$; 1, 43 df; $P = 0.687$), females with yearlings in the den ($F = 0.08$; 1, 24 df; $P = 0.777$), or yearlings ($F = 0.53$; 1, 60 df; $P = 0.470$). In the hunted area, we compared BCI of bears from the unmanipulated hunted area in 2004 and 2005 with bears in the manipulated area where hunting was curtailed. For males, we found no difference in BCI between CS (mean BCI = −0.075, SD = 0.188, $n = 6$) and CN (mean BCI = −0.026, SD = 0.093; $t = 0.53$, 9 df, $P = 0.609$), and no difference in BCI of females with yearlings between CS (mean BCI = −0.009, SD = 0.054, $n = 7$) and CN (mean BCI = −0.017, SD = 0.125; $t = 0.16$, 14 df, $P = 0.878$). The difference in BCI of females with cubs in the CN area (mean BCI = 0.049, SD = 0.159, $n = 6$) and in CS approached significance (mean BCI = −0.094, SD = 0.120; $t = 2.10$, 15 df, $P = 0.053$), but our sample size in the CS area was almost double that of the CN sample. Given the skewed samples, we also compared the BCI of individual females with cubs for which we had BCI information before and after manipulations in Conklin (Table 1). We found no difference in the mean change in BCI before and after manipulations between CS (mean change in BCI = −0.032, SD = 0.208, $n = 6$) and CN (mean change in BCI = −0.039, SD = 0.145; $t = 0.06$, 9 df, $P = 0.950$). Sample sizes of female bears with cubs and yearlings in CLAWR were too small for inference.

Annual cub survival

Mean yearly survival of cubs by study area ranged from 57 to 100% (Table 2). Cub survival was greater in the hunted area (83%, $n = 30$) than in the unhunted CLAWR (66%, $n = 29$; S. Czetwertynski,

Table 2. Cub survival (%) in the unhunted Cold Lake Air Weapons Range (CLAWR), 2002–2004 and after removal of males 2004–2005, in the hunted Conklin South (CS) area, and in the hunted Conklin North (CN) area before (2002–2003) and after (2003–2005) bait closures, Alberta, Canada. Rates calculated based on the presence or absence of yearlings in dens with radiocollared females.

	2002–2003			2003–2004			2004–2005		
	Survival % (*n*)	Litters	Litters lost	Survival % (*n*)	Litters	Litters lost	Survival % (*n*)	Litters	Litters lost
Conklin N	86(14)	5	0	83(18)	7	0	63(8)	3	1
Conklin S	70(10)	6	1	83(6)	3	0	85(13)	6	1
CLAWR	57(23)	10	3	100(6)	2	0	73(15)	5	0

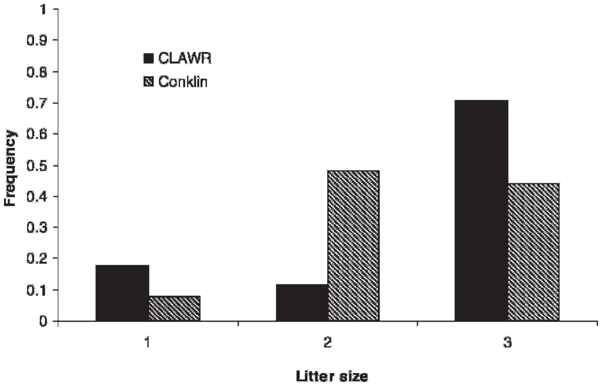

Fig. 4. Distribution of litter sizes for the unhunted CLAWR area (2002–2004, n = 17) and the hunted Conklin area (CS 2002–2004 and CN 2002–2003, n = 25) for black bears, Alberta, Canada.

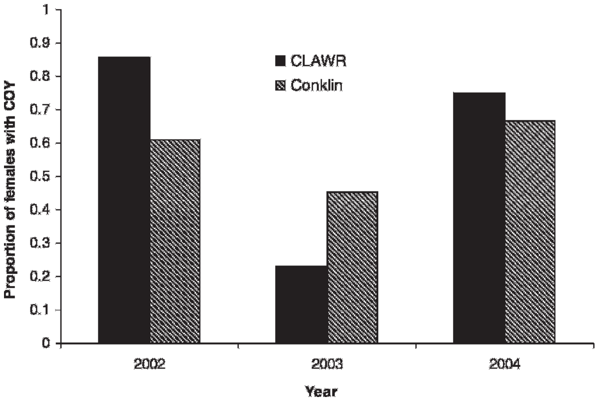

Fig. 5. Annual proportion (2002–2004) of female black bears with cubs of the year compared to the number of females available to reproduce in the unhunted CLAWR (n = 39) and hunted Conklin areas (n = 55), Alberta, Canada.

unpublished data). Furthermore, cubs were equally likely to survive before and after experimental manipulations in both Conklin (81% non-manipulated versus 77% manipulated) and CLAWR (66% pre-removal versus 73% post-removal) areas. Of the 47 litters of cubs observed over 4 winters, 6 (13%) were completely lost (3 in CLAWR before experimental removal, 2 in the hunted area before the experimental closure, and 1 after the closure), and only 1 of those females produced cubs the following winter. Furthermore, 2 of the lost litters were 1-cub litters. Only 1 of the lost litters was a first litter (CS, 2004–2005) and 3 of the 5 females not producing cubs were heavier than they had been the previous winter (mean mass 72.80 kg, SD = 8.23). Mean body mass of females with cubs having lost at least one cub (82.44 kg, SD = 14.41) did not differ from mass of females having kept their entire litter to age 1 (78.63 kg, SD = 11.26; t = 0.75, 22 df, P = 0.460) in non-manipulated areas.

Reproductive rate

Three-cub litters were more common in the unhunted CLAWR (71%, n = 17) than in the hunted Conklin area (44%, n = 25, χ^2 = 0.98, P = 0.045; Fig. 4). We found a correlation between the mass of females and their litter size (F = 6.53; 1, 47 df; P = 0.014). However, we found no effect of area (F = 0.12; 1, 47 df; P = 0.728) on litter size and no interaction of female mass and area (F = 0.09; 1, 47 df; P = 0.762). The lowest body mass of a female with cubs encountered was in the CS area (55 kg, 2-cub litter in 2004). Reproduction in the unhunted CLAWR was synchronized (n = 39, χ^2 = 0.10, P = 0.002; Fig. 5), and most adult females produced cubs in alternate years; no reproductive synchrony was detected in the hunted Conklin area (n = 55, χ^2 = 0.82, P = 0.398).

Conklin females had their first litters at younger ages (median = 5.0 years) than CLAWR females (median = 7.0 years; log rank test P = 0.01, n = 30). Females in Conklin also had their first litters with surviving cubs at an earlier age (median = 5.0 years) than females in CLAWR (median = 6.0 years, log-rank test P = 0.02, n = 37). In Conklin, several females had their first litters at age 3, and 43% of first litters (n = 14) occurred by age 4. Several females in CLAWR did not have their first litters until the age of 9. Of the 9 bears that had their first litters between 2002 and 2004 in CLAWR, we had mass information on 3 individuals for years prior to primiparity.

Sample sizes of intervals between litters were too small to assess differences between areas. However, within the non-manipulated study areas, there were 10 instances in which females that previously reproduced had neither cubs nor yearlings with them when visited in winter. Six of these instances occurred in CLAWR; 4 of the females had successfully weaned yearlings in the spring and the other 2 lost litters from the previous winter. Based on their winter mass (mean = 75.3 kg, SD = 8.7), all females were physically able to produce litters. However, 2 of the females were old (19 and 24 years). Four females in the CS area also did not reproduce. Two (80 kg each) lost litters from the previous winter and 1 (6 yr, 105 kg) weaned 1 yearling in the spring. The fourth female weighed only 52 kg and had a 2-year-old cub with her in the den. Following the experimental removal of males in CLAWR, all females of breeding age except 1 had either cubs or yearlings with them in the den during 2005. The one solitary female was 25 years old and weighed 87 kg. In the CN area, there were a total of 4 solitary females during 2004–05. Of these, 2 females weighed 75 kg (one of which had 3 2-year olds in the den, the other 2), one (18 yr, 65 kg) lost a litter of 3 cubs, and one (8 yrs, 60 kg) weaned 3 yearlings in the spring

Discussion

Infanticide as a factor influencing demographic parameters

Although infanticide has been widely reported in bears (McLellan 1994, Miller et al. 2003), the motivation for killing cubs is not well understood. The SSI model predicts that, to increase their breeding opportunities, males kill cubs they are unlikely to have sired (Hrdy 1979). Our comparisons of the unhunted CLAWR before male removal with the hunted Conklin areas (excluding CN 2003–05) do not support the immigrant male SSI hypothesis proposed by Swenson (2003), in which hunting disrupts the social structure and increases infanticide by adult males. A strong effect of this form of SSI would have been higher cub mortality in the hunted Conklin area than the unhunted CLAWR; we observed the opposite. Similarly, this hypothesis predicted an increase in cub mortality in the unhunted CLAWR after the removal of adult males, but we documented no change in cub survival. Researchers in Scandinavia detected increased cub mortality only 1.5 years after the removal of males (Swenson et al. 1997, 2001*b*). Because our study ended 1 year post-removal, we could not measure a possible delayed response.

One of the conditions of immigrant male SSI is the immigration of new bears following the removal of adult resident males. This claim of subadult ingress has been suggested by several authors (Kemp 1976, Wielgus and Bunnell 1994*a*, Sargeant and Ruff 2001) and is consistent with the observation that male subadults are the dispersing cohort (Schwartz and Franzmann 1992, Lee and Vaughan 2003). In the Cold Lake study, an increase in subadults was observed the year after removals took place (Sargeant and Ruff 2001). However, persuasive evidence of increase in subadult immigration is lacking (Taylor 1994, Kontio et al. 1998, Miller et al. 2003, McLellan 2005) and we did not observe it in CLAWR after male removal. Males in our study were removed during the winter of 2004, but our trapping session in the fall of 2005 did not detect the presence of new subadult males. Although the capture session was short (12 days), we believe we would have captured new individuals had such an influx occurred because we saturated the study area with traps.

Neither the predictions of the mate-recognition form of SSI (McLellan 2005) nor the immigrant-male form (Swenson 2003) are supported by our litter-loss data. By definition, SSI is the act of eliminating the dependent offspring of a prospective mate to increase breeding opportunities (Hrdy and Hausfater 1984). In our study, most cub mortality did not result in entire litter loss (87%), which would be required for females to come into estrus. Because the dense forest in the study area did not permit visual observations of bears during telemetry flights, accurate information on the timing of litter loss is not available. However, litter loss driven by SSI should occur in the spring and result in cub production the following spring; black bears can breed within 48 hours of losing their cubs (LeCount 1983). Conversely, litter loss in which the female is without cubs the following winter is more suggestive of other events such as a predatory infanticide or starvation. Of the 6 females that lost complete litters during the study, only 1 reproduced the following spring, although based on their body mass, 4 of the 5 remaining bears would have physically been able to do so. These results differ from the Scandinavian study where mothers that lost entire litters reproduced a year earlier than females with surviving cubs (Bellemain et al. 2006*b*). We observed no complete litter loss after the removal of resident males in CLAWR, but our power to detect litter losses was low because of small sample sizes. Most cub mortality occurs during the breeding season (LeCount 1987, Elowe and Dodge 1989, Kolenosky 1990, Swenson et al. 2001*b*, Miller et al. 2003), but this could be explained by the increased mobility of male bears in spring (Rogers 1987) and thus higher likelihood that they would encounter females with cubs. Cubs also are more vulnerable earlier in the season (Miller et al. 2003). Although infanticidal males may have been responsible for the deaths of cubs in our study, the lack of female cub production following litter losses in both areas is inconsistent with a strong effect of SSI.

Wielgus and Bunnell (2000) claimed that females in a hunted area tended to avoid potentially infanticidal males and foraged in poorer habitats, resulting in smaller litter sizes. Miller et al. (2003) found the opposite response: litter sizes were larger in the hunted Black Lake area than in unhunted Katmai National Park, and 3-cub litters increased after increased harvest pressure. In our study, results were similar to those of the Alberta study (Wielgus and Bunnell 2000); 3-cub litters were more common in the unhunted CLAWR area than in the hunted area. However, this was probably because the unhunted population, with an older average age for females, included more females in their most productive years of cub production (Yodzis and Kolenosky 1986). Schwartz et al. (2006*a*) also found that older females were more likely to produce 3-cub litters than younger females.

Unlike the brown bear (*Ursus arctos*) study that inferred nutritional condition from observed litter sizes (Wielgus and Bunnell 2000), we compared actual BCI of black bears between study areas. We did not detect a difference in the BCI of female bears between the hunted Conklin and unhunted CLAWR areas after accounting for reproductive status and, similarly, found no change in BCI of CLAWR females after the removal of males. These results are unlikely to be affected by habitat type because we also found no difference in male BCI between areas. Therefore, if adult females were restricted to poorer habitats, the effect was not strong enough to significantly affect BCI.

Results from McLellan's (2005) study did not support the immigrant male hypothesis but could not differentiate between mate recognition SSI and infanticide due to predation. McLellan (2005) predicted that the level of expression of infanticide or predation would depend on the breeding opportunities available to males (sex ratio and density of bears). For example, killing cubs may be more profitable in lower density areas where males are less likely to encounter estrus females. Our results appear to contradict these predictions; cub mortality was lower in the lower-density area where males and females had larger home ranges. However, cub production in the unhunted area appeared to be more synchronized than in the hunted area, effectively reducing the number of solitary estrus females available in alternate years. Synchronous breeding of black bears has been reported elsewhere and is more common in populations with low litter-loss rates and areas where bears depend on few fall foods (McLaughlin et al. 1994, Clark et al. 2005). The difference in reproductive synchrony between our areas cannot be explained by habitat characteristics, but could be a consequence of the younger age of first reproduction in the hunted Conklin area. Long-term data on grizzly bears (*U. a. horribilis*) in Yellowstone showed that cubs of younger females had lower survival than those of older females (Schwartz et al. 2006*b*). Under such conditions, the high density of females in the unhunted CLAWR would not produce increased breeding opportunities for males and might create conditions favorable to mate-recognition SSI or predation. Furthermore, because both males and females can have multiple mates and multiple paternity within litters is possible (Schenk and Kovacks 1995, Sinclair et al. 2003, Bellemain et al. 2006*b*), males may gain a reproductive advantage by killing cubs even if they bred with the female the previous year. But if the higher rate of cub mortality in the unhunted CLAWR was caused by mate recognition SSI, we would have expected litter losses (and subsequent cub production the following spring) to be more common during years of cub production when few females were available for breeding. Thus, our results are more consistent with infanticide due to predation by either male or female bears than SSI.

Our results suggest that immigrant male SSI, if it occurs in black bears, is rare and does not explain the differences in cub mortality observed between our study areas. Furthermore, our data do not support predictions made by the habitat segregation hypothesis proposed by Wielgus and Bunnell (2000). In our study, habitat segregation could have occurred, but if so it was insufficient to affect the BCI. The lack of reproduction in females that lost complete litters is more consistent with the hypothesis that infanticide is predation driven and opportunistic than it is with the mate recognition hypothesis.

Density dependence in black bears

Results from our study are consistent with a density-dependent response wherein reproduction and survival are inversely proportional to density. Bears are difficult to census and accurate estimates of density are costly and labor intensive (Garshelis and Visser 1997, Stirling et al. 1997, Mowat and

Strobeck 2000, Boulanger et al. 2004). Although our data are not adequate for calculating actual bear densities within each study area, the lower bear-density index and larger home-range sizes in the hunted Conklin area provide evidence of a population below *K*. The older population of male bears we sampled and the lack of subadults in CLAWR at the initiation of the study indicated a relatively low impact of harvest and the likelihood that the population was near carrying capacity.

Differences in cub survival observed in our study are also consistent with a density-dependent response. Cub mortality was higher in the unhunted CLAWR population than in the hunted Conklin population and did not change after the removal of a few adult males from CLAWR. Miller et al. (2003) attributed greater brown bear cub survival in several hunted populations compared with higher-density areas in Alaska to differences in density. Density-dependent reproductive output also was detected in Yellowstone, although authors could not differentiate between changes in litter size and cub survival (Schwartz et al. 2006*a*). Because cub deaths were not investigated, we do not know whether cubs died of natural causes or if they were killed by other bears. However, the difference in cub survival cannot be explained by the BCI of females, and the large proportion of 3-cub litters in the unhunted CLAWR indicates that females were not food-stressed. Therefore, our data suggest that the greater number of cubs killed in the unhunted CLAWR was due to infanticide by male or female bears. This is consistent with other studies that found the threat of infanticide to be highest in high-density populations (Wolff 1997).

Age of first reproduction and the age of first successful litter were greater in the unhunted CLAWR than in the hunted Conklin, consistent with a density-dependent response. Several studies provide evidence that density-dependent effects are exhibited sequentially as population density increases (Eberhardt 1977, 2002). Specifically, survival of young is affected first, followed by an increase in the age of first reproduction, a decrease in female reproductive rate, and lastly, decreased survival of adults. We suspect that insufficient body mass was the proximate cause of some females not reproducing until age 7–9 in the unhunted CLAWR. Female–female competition can influence dispersal of brown bears (Stoen et al. 2006) and thus could also influence competition for food resources. Stoen et al. (2005) found that overlap in female home ranges was correlated to their relatedness and hypothesized that this type of spatial arrangement could influence reproductive success. Moyer et al. (2006) found a similar pattern in female black bears where females with overlapping core home ranges were more related than females with non-overlapping core home ranges. In such cases, females related to more dominant females could have a reproductive advantage over other females of the same age. However, this type of spatial organization and space sharing is not necessarily universal across populations; Schenk et al. (1998) found no correlation between relatedness and home range overlap. Future analyses of habitat use of individual bears may shed some light on these possible explanations. Regardless of the mechanism for delayed primiparity in CLAWR, the results are consistent with a density-dependent response in a population approaching *K*.

The high density of adult females in CLAWR and the lack of subadult males in the area suggest that the density of adult females could be just as important as overall population density or density of males. Females have smaller home ranges than males (Young and Ruff 1982, this study), and their movements and daily foraging opportunities are more likely to be affected by surrounding females than males roaming through their home ranges periodically. Furthermore, larger bears are more aggressive (Reynolds and Beecham 1980) and females are known to kill cubs of other females (LeCount 1987, Garshelis 1994, Hessing and Aumiller 1994), so adult female density also could influence cub survival (Lindzey and Meslow 1977*b*, LeCount 1987). Females could potentially gain a competitive advantage by reducing competitors likely to remain near their home range. This high density of females also could be a factor in the lack of an influx of subadult males after adult male removal in the unhunted CLAWR.

Definitive evidence for density-dependent effects has been elusive (Miller 1990*a*, Derocher and Taylor 1994, Garshelis 1994, McLellan 1994, Taylor 1994). A possible explanation is that density-dependent effects on vital rates in large mammals generally operate only when population are near carrying capacity (Fowler 1981*a*,*b*, 1987; Miller et al. 2003; Owen-Smith 2006). This may explain why comparisons of hunted populations do not show measurable change in vital rates corresponding to different densities below *K*, whereas studies comparing hunted and unhunted areas (e.g., Miller et al. 2003; this study) are able to detect such differences. Miller et al. (2003) found no change in cub survival when hunting pressure changed, and we observed no difference in cub survival after the closure of hunting at bait sites in one of our hunted study areas. These observations are also consistent with populations below *K* where changes in hunting pressure should not result in a detectable density-dependent response.

Confounding effect of bait sites on cub survival

Use of bait for hunting in Conklin was a potential confounding factor in our study because no such food source was available to bears in CLAWR. Outfitters baited bears every spring for 4–5 weeks, creating a temporary dependence on this high-energy food source when few natural foods are available. This supplementation may offer a nutritional advantage to bears and increase female nutritional condition and cub survival. However, we do not believe that baiting influenced the difference in cub survival observed between areas. First, that advantage would be incurred only by females that visited bait sites, which was only a portion of our collared bears and would not greatly affect mean cub survival. Secondly, the female BCI was similar between the baited Conklin area and non-baited CLAWR, and 3-cub litters were more frequent in CLAWR (71%) than in Conklin (44%). This suggests that females with cubs in the unhunted CLAWR were in good condition, and nutritional factors were unlikely to have caused the lower cub survival observed. Lastly, we found no difference in cub survival before and after the removal of bait sites from the hunted CN area, and no trend in female BCI after the removal of bait sites from the hunted CN area.

Bait sites also could have affected cub survival by increasing the likelihood of females with cubs encountering males or more dominant females. Several studies have found minimal overlap in female home ranges in northern forests (Jonkel and Cowan 1971; Rogers 1976, 1987; Young and Ruff 1982). Dahle and Swenson (2003*a*) described adult female bears altering their behavior in years when they have cubs to avoid contact with other resident bears. The presence of an attractive food source could lead to a breakdown of this adaptive behavior and create situations where females with cubs are more likely to meet adult bears. Pacas and Paquet (1994) found that hunter bait sites attracted bears and that home-range overlap was greater for bears using bait sites. Similarly, Fersterer et al. (2001) found that feeding stations did not reduce home-range sizes of bears but did attract and concentrate bears at these locations. Because both male and female bears are known to kill cubs (Garshelis 1994), bait sites could lead to increased cub mortality rates. However, our results show greater cub survival in the baited area (Table 2). Therefore, although we cannot accurately account for the potential effect of bait sites, we do not consider baiting to be an important factor for the differences in cub mortality we observed.

Management implications

Our results indicate that harvesting of black bear populations in Alberta is sustainable. We advocate the inclusion of density dependence in population models for bears, and agree with Miller et al. (2003) that its influence is most important for populations approaching *K* because they are more likely to experience physiological thresholds (Fowler 1987, Owen-Smith 2006). For cases where hunted populations are predicted to be well below *K*, density-dependent effects may be negligible because of the non-linear relationship between demographic parameters and density.

We do not think that SSI should be a concern in designing harvest policies for American black bears. Most black bear populations in boreal forests are considered healthy (Garshelis and Hristienko 2006), range over large areas, and do not depend on a single dominant food source. These characteristics increase the likelihood that populations would respond to hunting similarly to the hunted populations in our study, and that SSI is either not expressed or has a negligible effect on population parameters. However, given the unexplained influence of reproductive synchrony on the mate-recognition form of SSI, we recommend that managers monitor the ratio of females with cubs observed by hunters to the number of non-lactating females of reproductive age killed in the harvest. The presence of reproductive synchrony may warrant a closer examination of cub survival rates in some areas. We acknowledge that black bears and brown bears might respond differently with regard to density dependence and SSI.

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