University of Alberta

EFFECTS OF HUNTING ON THE DEMOGRAPHICS, MOVEMENT, AND HABITAT SELECTION OF AMERICAN BLACK BEARS
(*Ursus americanus*)

by

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ABSTRACT

I conducted a large-scale experiment to determine the effects of hunting on the demographics and behaviour of American black bears (*Ursus americanus*). I monitored 290 bears, a subset of which were equipped with VHF and GPS radio-collars, in 2 hunted areas and an adjoining unhunted area in the boreal forest of Alberta, Canada, during a 4-year study (2002–2005). I implemented a modified before–after control–impact (BACI) design whereby bait sites for hunting were closed in 1 of the 2 hunted study areas in years 3 and 4 and adult males in an unhunted area were removed in year 3. I found population density to be the most important factor affecting population parameters and suggest that the potential effects of sexually selected infanticide (SSI), if it exists, are negligible in populations reduced below carrying capacity (K). I show that spatial and temporal movements of females with cubs were most influenced by the density of female neighbors. This differs from current interpretations of female movement where food availability and male avoidance are suggested as the main determinants. Lastly, I found that females with cubs adjusted their habitat selection in response to the probability of encountering a male and reduced their selection for high-quality habitats as the density of adult males increased. These results demonstrate that population density is the most important factor regulating behaviour and demographic parameters. Therefore, black bears can be harvested sustainably without concern for potential indirect effects such as increased infanticide and reduced productivity of females.

DEDICATION

I dedicate this thesis to all those who made it possible

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Chapter 1: General Introductionon

1. Project motivation: why study the effects of hunting?

With the exception of native communities, hunting in North America has evolved from its traditional use for food and shelter to modern sport hunting subject to wildlife management regulations. Wildlife management truly began in the US and Canada in the early 1900s under Theodore Roosevelt and Sir Wilfred Laurier as a response to the devastating consequences of settlement on forests and wildlife species (Gilbert and Dodds 1987). Sport hunters in North America and the hunting organizations to which they belonged were the major force behind the conservation movement and the push for "sustainable use" of wildlife (Reiger 1975).

Today, wildlife management regulations are pressured by several distinct lobbies with divergent goals including hunters, natives, farmers, conservation organizations, and anti-hunting groups. Hunter numbers have been steadily declining over the years and the mean age of hunters has increased (Enck et al. 2000, Dizard and Muth 2001) and in Alberta hunter numbers have been declining since the 1980s (Watson and Boxall 2005). Rural living appears to be the most important factor influencing participation in hunting activities (Heberlein et al. 2002). Therefore, with the projected continuing trend of human migration toward larger urban centers, hunters must acknowledge that they no longer represent as powerful a political force as they did in the late 19th and early 20th centuries. Wildlife in North America is legally designated as public property (Gilbert and Dodds 1987), therefore, the reality is that the management of any species must take into account public concerns (Bath 1995) and utilitarian attitudes toward wildlife are declining in Western cultures (Schwartz et al. 2003). Consequently, the field of wildlife management cannot do otherwise but evolve with changing demographics.

One aspect of this evolution has been the expansion of government agency wildlife management goals from providing a harvestable surplus of species for hunting enthusiast to managing entire ecosystems which include non-game species (Holsman 2000). Within this context, harvest management also has broadened its scope by addressing possible indirect effects of removing individuals from populations (Frank and Woodroffe 2001, Festa-Bianchet 2003). Examples of demographic consequences of the selective removals of animals (reviewed in Milner et al. 2007) include biased age and sex-ratios resulting in reduced fecundity (Solberg et al. 2002), changes in timing and synchrony of birth (Saether et al. 2003), reduced body growth (Garel et al. 2006), and decreased juvenile survival (Whitman et al. 2004). Interest in the behavioral impacts of exploitation is relatively recent, in part because behavioral ecologists are most interested in the evolutionary explanations of animal behavior (Frank and Woodroffe 2000). The importance of incorporating studies of animal behaviour into wildlife management (Singh and Kaumanns 2005) and considering possible behavioral changes caused by hunting have gained attention because of their link to demographic parameters (Tuyttens and Macdonald 2000). Lastly, biologists have also begun to consider the possible evolutionary consequences of selective hunting pressure for particular traits (Harris et al. 2002, Willson 2002, Coltman et al. 2003, Festa-Bianchet and Apollonio 2003, Proaktor et al. 2007). Such evolution in the scope of wildlife management is a benefit to the field and also may help reconcile divergent stakeholder demands. Specifically, hunter participation in projects that go beyond traditional "surplus production" studies demonstrate ecological stewardship (Holsman 2000) and also are an advantage to managers if they hope to keep hunting as a source of funding (Powers et al. 2000) and a valuable tool within a broad conservation agenda.

The papers in this thesis address the effects of hunting on American black bears (*Ursus americanus*) and are the result of a successful cooperation among academia, hunting organizations, conservation groups, industry, and government agencies. In Canada, black bears are considered healthy over most of their range (Garshelis and Hristienko 2006). Population estimates range between 735,000 and 941,000 and a minimum of 26,000 bears are harvested annually (Williamson 2002). In Alberta, Black bears range over 74% of the province's land area and the population is estimated at 40,000 (Gunson 1993). They are classified as big game and are an important component of the province's outfitting industry, particularly in the spring, generating in excess of $6.5 million of "new money" into the province's economy (Kubursi 2003).

The closure of the spring black bear hunt in Ontario in 1999 as a result of public pressure epitomizes the need for detailed information on the effects of hunting of this charismatic megafauna and the dissemination of this information to the general public.

Specifically, spring hunting was closed because of the perception that a large number of cubs were orphaned (Ontario Ministry of Natural Resources 1999), although no scientific evidence to substantiate this claim was available. The Alberta Professional Outfitters Association (APOS) funded a study to ascertain Albertan's perception of guided black bear hunts and found that 40% of those surveyed had not formed an opinion on this issue (McMillan 2000). Concerned that a similar closure could occur in Alberta, APOS contacted Dr. Mark Boyce and offered to support a student that would conduct a study on the effects of hunting black bears. Although many funding organizations have supported this project, my thesis is a result of APOS making the initial decision to invest in scientific research.

2. Background

Black bears are generally solitary animals with home ranges of males overlapping over those of several females (Rogers 1987), and population numbers are regulated naturally through a combination of density-independent environmental factors and density-dependent social interactions (Bunnell and Tait 1981). Natality in a population is largely a function of the nutritional condition of female bears (Rogers 1976), while mortality and emigration are believed to be driven by the forced expulsion of subadults by resident adult male bears (Bunnell and Tait 1981). Cub mortality in hunted populations ranges between 25-41% and is affected by female nutritional condition, cannibalism, human interactions, behavior of the mother, and infanticide by males (Bunnell and Tait 1985, LeCount 1987, Elowe and Dodge 1989).

In general, black bear harvests are biased toward male bears (Beecham 1980; Schwartz and Franzmann 1991; Livaitis and Kane 1994). This is because females with young are protected in most jurisdictions, and males travel more extensively thus increasing the likelihood of encountering hunters (Bunnell and Tait 1985). Furthermore, black bears are particularly susceptible to human access in the landscape due to the practice of baiting, permitted throughout most of Canada and in areas outside of grizzly bear range in Alberta. In many areas of the province, twice as many black bears are hunted yearly than any other game species. Hunters create bait stations at regular intervals along access corridors to habituate bears thereby increasing hunter success and selectivity for large trophy males. Therefore, the level of access on the landscape directly influences the hunting pressure on bears, particularly adult males.

The difficulty in isolating the biological effects of hunting are the confounding effects of environmental conditions and the fact that the role of adult males in naturally regulated populations is not known (Miller 1990). This makes it difficult to make predictions on what the effect of removing adult dominant males might be and whether there are disproportionate effects beyond those of removing individuals from the population.

3. Objectives

My thesis is composed of 3 data chapters addressing the effects of hunting on black bears (Chapters 2-4) and an Appendix comprising a technical paper which describes equipment developed to capture bears for this project. My goal was to document the effects of trophy and sustained hunting on bear demographics, movement, and habitat selection. With this in mind, each chapter uses this information to also test explicit ecological hypotheses. This was possible because of the modified before-after control-impact (BACI) experimental design whereby hunting regimes were manipulated in 2 hunted and 1 unhunted study areas.

Specifically, Chapter 2 documents the differences in demographic parameters between areas with different hunting regimes. Differences observed were used to measure the influence of density on demographic parameters and test between competing hypotheses of infanticide in bears. Chapter 3 describes a test of the relative importance of food availability, population density, and infanticide avoidance in driving activity and movement patterns of females with cubs of the year. Lastly, Chapter 4 compares habitat selection patterns between males and females in each study area and tests for the occurrence of sexual segregation as a response to the threat of male infanticide.

Taken together, I believe these chapters provide new and valuable information to our understanding of bear social-dynamics. Within each Chapter, I make predictions of the effects of hunting and tie these results together in Chapter 5. My hope is that results provide managers with information to better predict the effects of hunting on bears and spawn future research to more accurately predict the effects of proposed management strategies.

4. Thesis organization

This thesis was written in paper format and manuscripts have been accepted or submitted for publication, therefore, I use we/our for co-authored papers. Status and authorship for each chapter is as follows:

Chapter 2 – Effects of hunting on demographic parameters of American black bears
Status: Published in Ursus 18:1-18
Authors: Sophie Czetwertynski, Mark Boyce, Fiona Schmiegelow

Chapter 3 - Determinants of early summer movements in female American black bears: the importance of habitat quality, population density, and infanticide avoidance.
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Author: Sophie Czetwertynski

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    - Flint Chapter
    - Stevens Point Chapter
    - Idaho Chapter
- Foundation for North American Wild Sheep (FNAWS)
    - Alberta Chapter
    - Eastern US Chapter
- Alberta Bowhunters Association
    - Rocky Mountain Longbow Association
    - Calgary Archers
    - Northern Bowhunters Association
    - Sherwood Park Archery Club
    - Brazeau Bowbenders
    - Strathmore Archery Club
    - Quinn Well Control (Des Quinn)
    - Southern Alberta Bowhunters Association
    - Game Country Archers
    - Prairie Transmission (Dale Collins)
    - Clearwater Archers Club
    - Grande Prairie "Concerned Bear Hunters Group"
    - Lloydminster and Area Archers Association
    - Kneehill Bowhunters
- Alberta Fish and Game Association (AFGA)
    - Whitecourt Chapter
    - Northeastern Alberta Chapter
    - Zone 6 Chapter
    - South Peace Chapter
    - Edmonton City Police Chapter
    - Sherwood Park Chapter
    - Rocky Mountain Chapter
    - Millet Chapter
    - Zone 4 Chapter
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Chapter 2: Effects of hunting on demographic parameters of American black bears

1. Introduction

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 (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 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, larger home ranges of males, and 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.

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, Figure 2-1) 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.

2. Study areas

2.1 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.

2.2 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.

2.3 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.

3. Methods

3.1 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 color 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.

3.2 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 (Figure 2-1), 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 was 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.

3.3 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.

3.4 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.

3.5 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.

3.6 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.

3.7 Population parameters

3.7.1 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.

3.7.2 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.

3.7.3 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.

4. Results

4.1 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.

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

4.3 Population structure

Bears in CLAWR were older than bears on 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 $U = 270$, $P = 0.070$; Figure 2-2). 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 $U = 188$, $P < 0.001$;

Figure 2-3). 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 ($\chi^2 = 1.45$, 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).

4.4 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 2002–2004 were ≥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 ≥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, $P = 0.581$).

4.5 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 ($F_{1,37} = 0.03$, $P = 0.858$). Similarly, we found no difference in BCI between solitary females ($F_{1,28} = 0.91$, $P = 0.347$), females with cubs ($F_{1,43} = 0.17$, $P = 0.687$), females with yearlings in the den ($F_{1,24} = 0.08$, $P = 0.777$), or yearlings ($F_{1,60} = 0.53$, $P = 0.470$). 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 2-1). 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.

4.6 Annual cub survival

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

4.7 Reproductive rate

Three-cub litters were more common in the unhunted CLAWR (71%, $n = 17$) than in the hunted Conklin area (44%, $n = 25$, $\chi^2 = 0.98$, $P = 0.045$; Figure 2-4). We found a correlation between the mass of females and their litter size ($F_{1,47} = 6.53$, $P = 0.014$). However, we found no effect of area ($F_{1,47} = 0.12$, $P = 0.728$) on litter size and no interaction of female mass and area ($F_{1,47} = 0.09$, $P = 0.762$). 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 ($n = 39$, $\chi^2 = 0.10$, $P = 0.002$; Figure 2-5), and most adult females produced cubs in alternate years; no reproductive synchrony was detected in the hunted Conklin area ($n = 55$, $\chi^2 = 0.82$, $P = 0.398$).

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

5. Discussion

5.1 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.

5.2 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.

5.3 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 2-2). 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.

6. 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 (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.

Table 2-1: 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

Table 2-2: 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

Figure 2-1: 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.

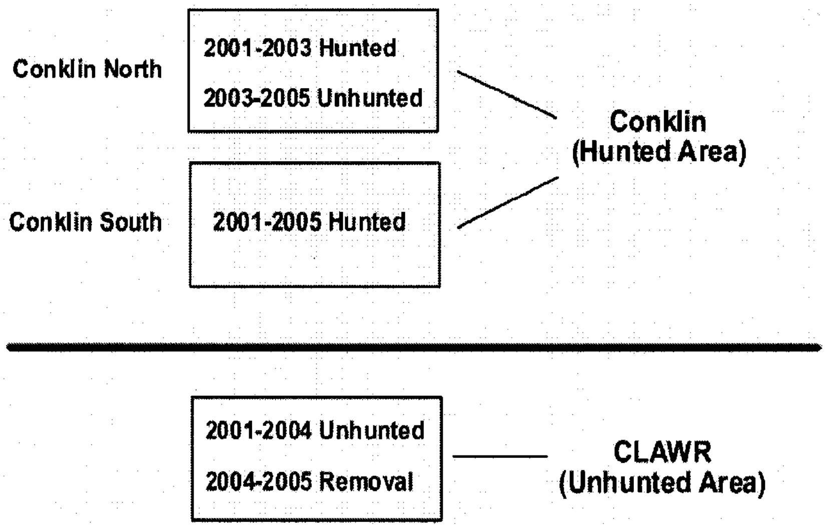


Figure 2-2: Age distribution of female black bears captured in the hunted Conklin (*n* = 38) and unhunted CLAWR (*n* = 20) areas in 2001, Alberta, Canada.

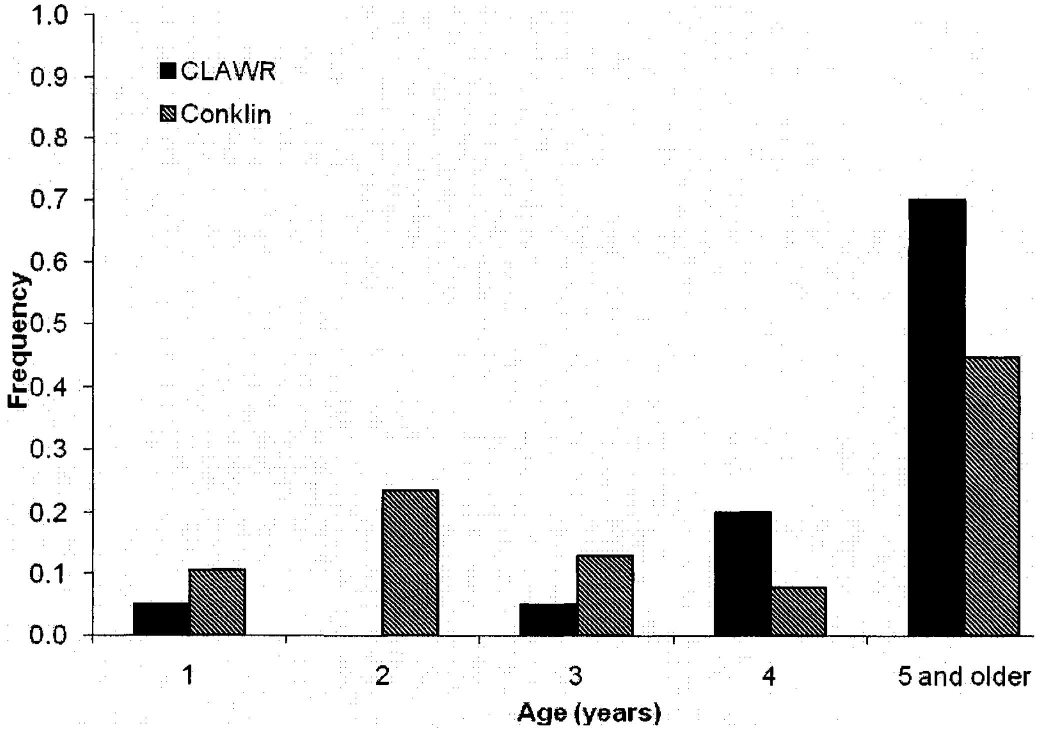


Figure 2-3: Age distribution of male black bears captured in the hunted Conklin (*n* = 51) and unhunted CLAWR (*n* = 17) areas in 2001, Alberta, Canada.

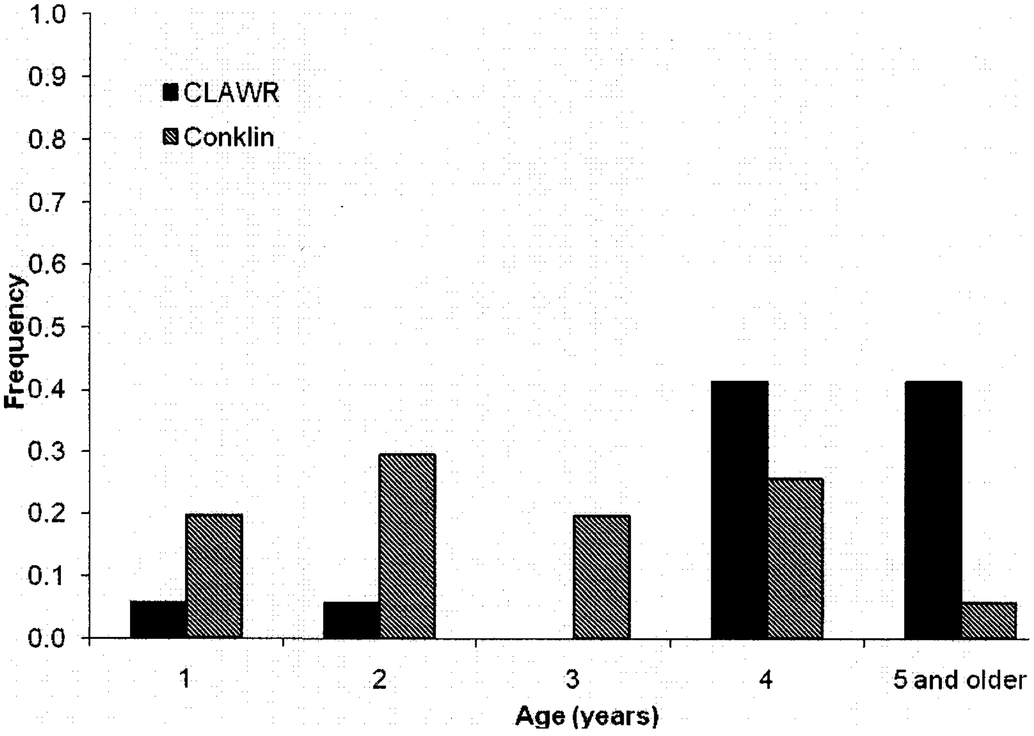


Figure 2-4: Distribution of litter sizes for the unhunted CLAWR area (2002–2004, *n* = 17) and the hunted Conklin area (CS 2002–2004 and CN 2002–2003, *n* = 25) for black bears, Alberta, Canada.

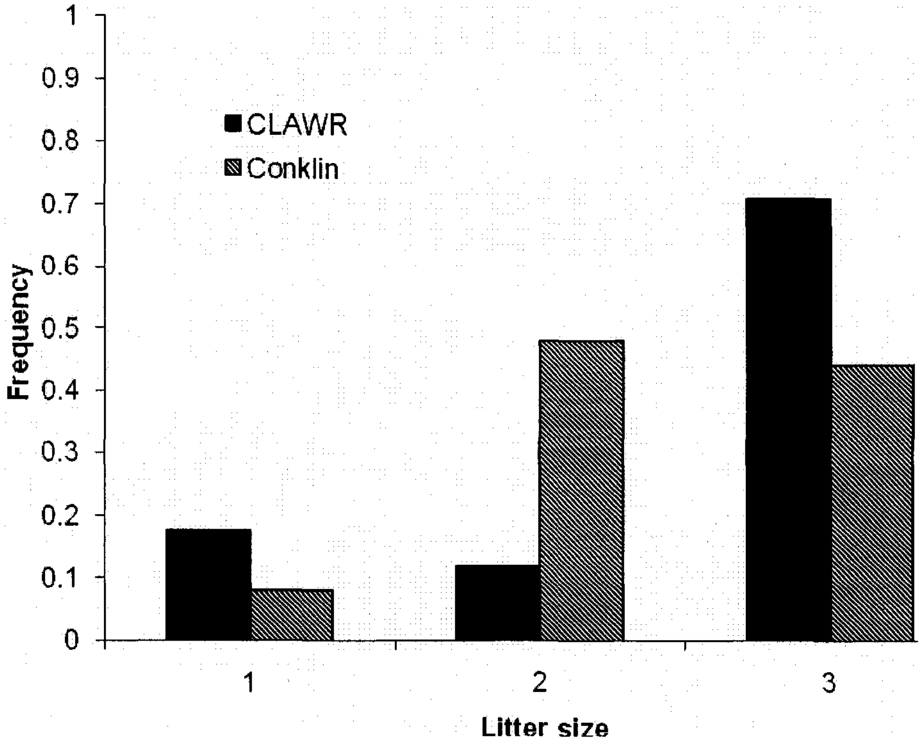
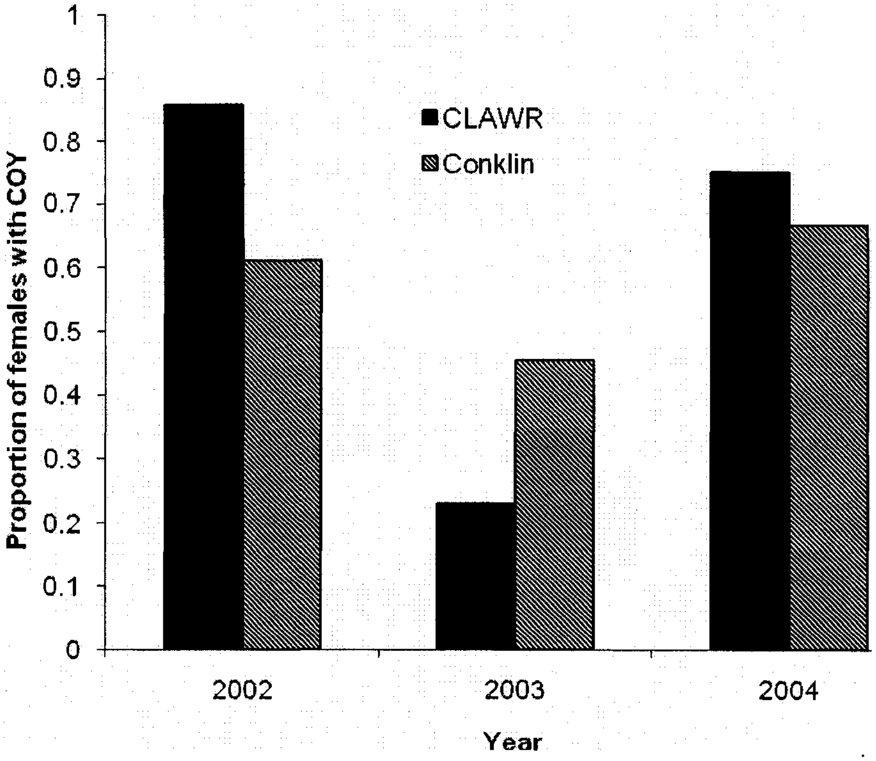


Figure 2-5: Annual proportion (2002–2004) of female black bears with cubs of the year compared to the number of females available to reproduce in the unhunted CLAWR (*n* = 39) and hunted Conklin areas (*n* = 55), Alberta, Canada.



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Chapter 3: Determinants of early summer movements in female American black bears: the importance of habitat quality, population density, and infanticide avoidance.

1. Introduction

At the individual level, mammalian movement patterns are considered most influenced by conspecific density and food availability (Clutton-Brock and Harvey 1978). In terms of spatial movement, studies on a variety of species have found home range size to be inversely correlated with conspecific density, resulting from increasing social interactions (Krebs 1971 – great tit Parus *major*; Kjellander et al. 2004 – roe deer *Capreolus capreolus*; Benson et al. 2006 – bobcat *Lynx rufus*) and also inversely related to habitat quality, because individuals are able to meet their requirements within a smaller area (Clutton-Brock and Harvey 1978; Powell et al. 1997 – black bears *Ursus americanus*; Herfindal et al. 2005 – Eurasian lynx *Lynx lynx*). Less is known about factors affecting the distances and daily activity patterns of animals, however, results are generally consistent with predictions of optimal foraging theory, where animals feed in a manor that is most efficient in terms of their survival and reproductive success (Schoener 1971 – see lit in Davidson 2001). For example, several studies have demonstrated a negative relationship between travel distance and food availability because animals are able to satisfy their nutritional requirements without extended searches (Stahl et al. 1988, Dussault et al. 2005; Kowalczyk et al. 2005). Similarly, activity patterns varied directly with population density as a response to food depletion (Massei et al. 1997; Moncorps et al. 1997) and increased social interactions (Pélabon and Komers 1997).

Although correlations of density and food availability with movement are reasonably documented, the relative influence of these factors in regulating behaviour is difficult to measure because a positive correlation between habitat quality and population density confounds most studies (Clutton-Brock and Harvey 1978; Don 1983; Massei et al. 1997). There are no examples of experimental studies on large carnivores separating these effects, however, a correlative study of bobcats compared the effects of density and food availability on home range size and found a stronger effect of density (Benson et al. 2006).

Female movement patterns in species with female parental care also are influenced by reproductive status. Specifically, females with offspring must meet their nutritional requirements while reducing potential threats to the survival of their young (Festa-Bianchet 1988; Poole et al. 2007). In species with no predators other than conspecifics, the threat of infanticide can be an important factor driving movement patterns, and is gaining attention in the primate literature (Janson 2000). Infanticide has a direct effect on a female's reproductive success and thus should exert significant selective pressure for females to evolve counter-measures (Hausfater 1984).

Black bears are a solitary species with a promiscuous mating system, extended female parental care, and documented infanticide predominantly by conspecific males (LeCount 1982, Garshelis 1994) but also females (LeCount 1987, Garshelis 1994). Infanticide has also been documented in brown (*Ursus arctos*, Miller et al. 2003), and polar bears (*Ursus maritimus*, Derocher and Wiig 1999), and most cub mortality occurs during the spring breeding season (Swenson et al. 1997; LeCount 1987) when cubs are most vulnerable and males may benefit from increased breeding opportunities by killing cubs and bringing a female into oestrus to sire their own cubs (termed sexually selected infanticide SSI; Hrdy 1979). Two forms of SSI have been proposed to explain patterns of infanticide in bears. The 'immigrant male' hypothesis originates from work in Scandinavia, where research suggests that hunting adult male bears results in an influx of new individuals and shifting of home ranges, creating a situation of increased encounters of males with females they were unlikely to have bred, thus increasing infanticide rates (Swenson et al. 1997; 2001; Swenson 2003). The 'mate recognition' hypothesis proposes that infanticide rates are a result of the age structure, sex ratio, and density of populations, whereby males are more likely to commit infanticide when there are few breeding opportunities (McLellan 2005).

There is considerable evidence that home ranges of female black and brown bears are a function of habitat quality (Lindzey and Meslow 1977; Garshelis and Pelton 1981; Powell et al. 1997; Koehler and Pierce 2003; McLoughlin et al. 2003; Moyer et al. 2007) and population density (Powell et al. 1997; Oli et al. 2002; Dahle and Swenson 2003). Recent work on North American brown and black bears with access to salmon streams suggests that the threat of infanticide by males influences female foraging behavior (Ben-

David et a. 2004; Peacock 2004; Rode et al. 2006) and therefore should be considered when designing management strategies (Nevin and Gilbert 2005). Furthermore, Scandinavian authors suggest that female brown bears with cubs restrict their movements during the breeding season to reduce the probability of encounter with infanticidal males (Dahle and Swenson 2003).

The "infanticide avoidance" hypothesis proposed by Dahle and Swenson (2003) to explain female movement is based on the observations that 1) females with cubs increased their range size after the post-mating season, and 2) females with cubs used smaller ranges than oestrus females and females with yearlings during the mating season. However, seasonal changes in home range use by bears have been extensively documented and attributed to changes in food availability and its distribution on the landscape throughout the year (Jonkel and Cowan 1971; Garshelis and Pelton 1981; Young and Ruff 1982; Moyer et al. 2007) and female movements may be restricted by their cubs (Lindzey and Meslow 1977). To date, no study has used an experimental approach to test the relative influence of food availability, population density, and infanticide on the spatial and temporal movement patterns of female bears with cubs.

I studied female black bears with cubs and compared seasonal home range size, interaction between neighboring bears, circadian activity patterns, and seasonal distances travelled using a modified BACI (before-after control-impact) design in 2 hunted and 1 nearby unhunted population in northeastern Alberta, Canada (Figure 3-1). I evaluated the relative importance of factors influencing movement in a series of 3 population comparisons: (1) between a lower-density hunted and unhunted population, (2) of a hunted population before and after an experimental closure of hunting, and (3) of an unhunted population before and after the experimental removal of adult males. A summary of hypotheses and predictions is provided in Table 3-1.

2. Methods

2.1 Unhunted study area (Cold Lake Air Weapons Range)

The Cold Lake Air Weapons Range (CLAWR) covers 11,600 km^2 and straddles the northeastern part of Alberta and northwestern part of 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 the CLAWR or unhunted area refers to this section. Hunting has been prohibited in the CLAWR since 1954. Based on mortality rates and an aged population structure, this population likely approached carrying capacity (Czetwertynski et al. 2007).

2.2 Hunted study area (Conklin)

The Conklin area (~6,000 km^2) was located just north of the CLAWR on crown (public) land. This area was 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 sufficiently far apart between study areas such that transboundary travel was minimal. I assumed that bears remained within the sites associated with the capture areas for the duration of the study. Bears could be legally hunted over bait in spring and fall and several outfitters operated guided hunts during spring (mid-April to end of May). Females with cubs of the year (referred to as cubs) were protected. The Conklin area has a lower density of bears and a lower proportion of adult males than the unhunted CLAWR because of an annual harvest (Czetwertynski et al. 2007).

2.3 CLAWR and Conklin Vegetation

Vegetation in the CLAWR and Conklin areas were relatively similar. The northern border of the CLAWR is adjacent to crown land which has not been transformed for agriculture or grazing and is thus an extension of the boreal mixed-wood forest in the CLAWR. Both areas consisted of rolling mixed-wood boreal forest interspersed with burned areas and wetlands. The area was composed of trembling aspen (*Populus tremuloides*), balsam poplar (*P. 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 jack pine (*Pinus banksiana*) were dispersed throughout the dry areas. The main difference between the two areas was the lack of forestry activities in the CLAWR. However, early seral stages were available in burned areas within the study area of the CLAWR. Additional details regarding these study areas are available in Czetwertynski et al. (2007).

2.4 Fieldwork

I captured bears using modified bucket traps (Lemieux and Czetwertynski 2006). Once restrained, bears were immobilized with tiletamine-zolazepam. A subset of captured bears was equipped with GPS (Global Positioning System 2200L programmed to acquire fixes hourly) radiocollars within each study area (Lotek Wireless Inc., Newmarket, Ontario, Canada).

Collared bears were located periodically throughout the summer using fixed-wing aircraft and extensive transects were flown during winter to locate dens. I visited dens of collared bears between mid-January and mid-March of each year to download GPS collar data and record reproduction. I rotated GPS collars on different individual bears annually and attempted to monitor 3 females with cubs in each Conklin area and 6 females with cubs in the unhunted CLAWR. I restricted this analysis to females who successfully raised at least 1 yearling (hereafter called females) thus eliminating potential bias from females who lost litters in the spring and were available for mating.

2.5 Study design

Study areas were selected relatively near to each other to control for the confounding effects of habitat quality often encountered when comparing remote populations (Bunnell and Tait 1981). The 2 Conklin study sites were hunted during the springs of 2001 and 2002 (Figure 3-1). However, outfitters agreed to close bait sites within the trapped area of CN during 2003 and 2004, thus significantly reducing hunting pressure and food supplementation in the area compared with previous years. The CS area remained hunted for the duration of the study. Trophy hunting in unhunted CLAWR was simulated by euthanizing collared male bears in January 2004 (Czetwertynski et al. 2007).

2.6 Seasons

I divided the spring and summer season into 2 sub-seasons to capture potential variation in activity patterns before and during the peak of the breeding season. The first season (termed spring season) extended from den emergence (beyond a 1-km radius around the den site movement was deemed independent of this point location) to June 14th when outfitters had ceased operating in the area for several weeks. The second season, referred to as the breeding season, extended from June 15th to July 14th and generally represents the peak of the breeding season (Garshelis and Hellgren 1994). The analysis was restricted to these 2 seasons for several reasons. First, animals can shift their home ranges throughout the year in response to food availability (Carsten and Neville 2006) and spring and early summer foods are predominantly in aspen stands, under pine stands, and along roads (Young and Ruff 1982), which are equally accessible to each bear throughout the patchy boreal landscape (forbs, grasses, poplar leaves, clover, insects). In late summer, bears feed predominantly on berry species (Young and Ruff 1982). Comparison of movements between seasons for individual bears would be confounded by the spatial distribution of burns and cutblocks on the landscape (Garshelis and Pelton 1981). Second, the threat of infanticide should be most pronounced during these seasons because females are receptive for breeding within 48 hours if they lose their cubs (Forstmeier and Weiss 2004). Third, bear hunting occurs predominantly in the spring and therefore any management implications would be targeted at this season.

2.7 Seasonal home range analysis

I calculated seasonal home ranges (HRs) of individual bears with 95% fixed kernel density estimates (Blundell et al. 2001) 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). I only included seasonal HRs in analyses when data were available for the entire season to standardize the sampling regime (Borger et al. 2006). I used all available locations 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 Gitzen and Millspaugh 2001). Therefore, I used the mean reference bandwidth calculated from each individual bear (Czetwertynski et al. 2007) to calculate the 95% fixed kernel density of bear seasonal home ranges for comparisons. I used a Mann-Whitney *U*-test to compare seasonal home-range size between hunted and unhunted areas and report medians with SD (calculated using the more conservative n – 1 in the denominator) and use a *P* value of 0.1.

2.8 Daily Activity patterns

I used location data from GPS collars programmed to take a fix every hour throughout the summer. To maintain consistency, I used only pairs of points that were taken at 1 hour intervals and distances between points with missing locations were omitted. Distance traveled within 1 hour was calculated as the Euclidean distance between the 2 points and distance values were grouped by time of day. Locations from different bears were merged to obtain population estimates and therefore weighted by the number of locations per bear. The distributions of distance values were highly skewed toward short distances. Therefore, I present median values to compare distance traveled throughout the day. I bootstrapped each hourly dataset 1000 times and used the sample size of each individual dataset as the bootstrap sample size. I used the bias corrected (BC) method, which adjusts for bias in the bootstrapped sampling distribution relative to the actual distribution, to compute 95% confidence intervals for each dataset (Haukoos and Lewis 2005). I considered hourly distance traveled by groups of bears different when 95% CI did not overlap (Johnson 1999).

2.9 Bi-weekly movements and interactions

I averaged hourly movement rates/day/female and retained only daily averages for which there were a minimum of 15 hourly bouts. 12 pairs of points were removed from the analysis as extreme values (> 1000 m). Distances were binned by 2 week periods from April 15th to July 14th. I used regression to evaluate the slope of the regression in each area.

I assessed spatial interactions between females during the breeding season by examining movement paths of bears with adjacent home ranges (Animal Movement extension in ArcMap 9.0, ESRI). In 2002, 1 pair of females with GPS collars had adjacent home ranges and 3 females in CLAWR had adjacent home ranges. In CLAWR, 2 collared females had adjacent home ranges in 2004 after the removal of males. Next, I used plots of Euclidean distances between these pairs of bears to determine if there were spatio-temporal interactions. For interaction plots, I retained only those data for which there was a simultaneous hourly location for each bear in the comparison.

3. Results

3.1 Seasonal home ranges

3.1.1 Between hunted Conklin and unhunted CLAWR

During the hunted season, I found no difference in the size of home ranges of hunted Conklin (34 km^2, range 5 – 94 km^2, SD = 12.04, n = 7 home ranges, n = 7,136 locations) and unhunted CLAWR females (16 km^2, range 6 – 31 km^2, SD = 5.28, n = 6 home ranges, n = 5,379 locations, mean h_{ref} = 0.28, P = 0.075). However, during the breeding season, CLAWR females had smaller home ranges (22 km^2, range 14 – 43 km^2, SD = 5.22, n = 6 home ranges, n = 3,259 locations) than hunted females in Conklin (87 km^2, range 15 – 136 km^2, SD = 13.43, n = 8 home ranges, n = 3,958 locations, mean h_{ref} = 0.28, P = 0.028).

3.1.2 Conklin before and after removal of bait sites

During the hunted season, I found no difference in the size of home ranges of females before (34 km^2, range 5 – 94 km^2, SD = 12.04, n = 7 home ranges, n = 7,136 locations) and after the closure of bait sites (40 km^2, range 32 – 143 km^2, SD = 34.49, n = 4 home ranges, n = 3,827 locations, mean h_{ref} = 0.28, P = 0.465). Similarly, I detected no difference in HR size during the breeding season before (87 km^2, range 15 – 136 km^2, SD = 13.43, n = 8 home ranges, n = 3,958 locations) and after the closure of baits (55 km^2, range 14 – 186 km^2, SD = 45.82, n = 4 home ranges, n = 2,255 locations, mean h_{ref} = 0.28, P = 0.715).

3.1.3 CLAWR before and after removal of males

During the hunted season, I found no difference in the size of home ranges of females before (16 km^2, range 6 – 31 km^2, SD = 5.28, n = 6 home ranges, n = 5,379 locations) and after the removal of males (22 km^2, range 10 – 44 km^2, SD = 4.26, n = 5 home ranges, n = 4,638 locations, mean h_{ref} = 0.28, P = 0.176). Similarly, I detected no difference in HR size during the breeding season before (22 km^2, range 14 – 43 km^2, SD = 5.22, n = 6 home ranges, n = 3,259 locations) and after the removal of males (18 km^2, range 9 – 21 km^2, SD = 3.28, n = 4 home ranges, n = 2,002 locations, mean h_{ref} = 0.28, P = 0.257).

3.2 Daily activity patterns

Females were diurnal in all study areas and during all seasons (Figure 3-2). Females in the hunted Conklin and unhunted CLAWR exhibited similar activity patterns during the spring (Figure 3-2 – a1) and breeding (Figure 3-2 – a2) seasons. The removal of bait sites did not affect female activity patterns in either the spring (Figure 3-2 – b1) or breeding (Figure 3-2 – b2) seasons. Females in the unhunted CLAWR showed no change in activity patterns after male removal during the spring (Figure 3-2– c1) or breeding season (Figure 3-2 – c2).

3.3 Bi-weekly movement and interaction

I found a positive correlation between the mean bi-weekly distance travelled and time (Figure 3-3) in Conklin females before ($\beta = 46.436$, $t(483) = 17.35$, $p < 0.001$) and after ($\beta = 49.358$, $t(171) = 9.32$, $p < 0.001$) the removal of bait sites. Similarly, CLAWR females also increased their distance travelled over time before ($\beta = 52.495$, $t(430) = 14.89$, $p < 0.001$) and after male removal ($\beta = 65.868$, $t(69) = 8.34$, $p < 0.001$).

Although the sample size for this analysis is extremely small and can be considered anecdotal, these data represent the most detailed information available to date on female-female interaction. Generally, females in hunted Conklin appeared less territorial than CLAWR females and had more encounters with neighbors (Figures 3-4 – 3-6). Conklin females F41 and F43 had 2 encounters lasting 10 and 34 hours (Figure 3-4). During the first encounter the bears remained within a 100 m radius whereas they travelled over 3 km during their second encounter. Both encounters ended with a rapid increase in distance between the bears. These females were within a distance where they would have detected each other (within 1 km) on 2 other occasions but quickly increased the distance between them. CLAWR females F18 and F118 never came within 0.5 km of each other while F118 and F15 had several very brief encounters later in the season followed a quick distancing from one another (Figure 3-5). The behavior of females did not change after the removal of males. Females F15 and F19 were within 0.5 km of each other on 2 occasions for only 2 consecutive GPS locations and each encounter ended in a fast increase in distance between them (Figure 3-6).

4. Discussion

4.1 Determinants of female spatial movements

The 'metabolic hypothesis' suggests that an animal's home range size is a function of the nutritional requirements of individuals (Clutton-Brock and Harvey 1978; McNab 1963). In this study, if food availability was the main factor, female seasonal home range sizes should be similar in all study areas before and after experimental manipulations because habitat quality was similar in all areas and spring foods, distributed throughout the landscape, were not a limiting factor (Table 3-1, A1-3). The 'infanticide avoidance hypothesis' predicts that females will reduce home range sizes to avoid encounters with infanticidal males when the risk of infanticide is high (Table 3-1, B-C). If the 'immigrant male' form was a driver was a driver of female movement, the threat should be greatest in hunted areas where the established social structure is disrupted and males are more likely to encounter females they have not bred. Therefore, as suggested by Dahle and Swenson (2003), I should observe smaller home ranges in hunted Conklin compared to unhunted CLAWR and a reduction in home range size in CLAWR after the removal of males (Table 3-1, B). In the case of the 'mate recognition' form, the male threat would be considered greater in the CLAWR where there were a greater proportion of large adult males in the population and cub mortality was higher compared to hunted Conklin. Therefore, if the threat of 'mate recognition' male infanticide was a driver of female spatial movements, I should have observed an increase in the size of home ranges of females after the removal of males from CLAWR and a reduction in home range size of Conklin females after the closure of bait sites because fewer males were harvested (Table 3-1, C).Lastly, the 'density-dependent hypothesis' predicts an inverse relationship between population density and home range size (Abramsky and Tracy 1980). If density were the main driver of female home range size, then I would expect larger home range sizes in lower-density hunted Conklin compared to unhunted CLAWR (Table 3-1, D), where the population is approaching carrying capacity (Czetwertynski et al. 2007). In addition, I would expect no change before and after experimental manipulations when density was not significantly affected.

Results are most consistent with a strong effect of density on the spatial extent of movements of females with cubs; female home ranges in lower-density Conklin were smaller than those in higher-density CLAWR by a factor of 2 during the spring season and a factor of 4 during the breeding season (Table 3-1, D1). These results are consistent with larger annual home range sizes of females in Conklin compared to CLAWR (Czetwertynski et al. 2007). Moreover, there was no change in the size of area used after the closure of bait sites in Conklin and removal of males in CLAWR during both seasons when density was not significantly affected (Table 3-1, D2-3).

A potential confounding factor in interpreting results with respect to the 'metabolic hypothesis' could be variation in the configuration of choice food patches between the Conklin and CLAWR areas, even though the general habitats were similar. Such differences could influence the spatial extent of the area used by females (Mitchell and Powell 2004). However, such a situation should be associated with higher movement rates of animals in the Conklin area where females had larger home ranges (Gehring and Swihart 2004). Results contradict this pattern because females with small (CLAWR) and large (Conklin) home ranges had similar movement patterns (Figure 3-2) and mean bi-weekly travel distances (Figure 3-3).

My results are not consistent with either the 'immigrant male' or the mate recognition' forms of the 'infanticide avoidance' hypothesis (Table 3-1, B-C). The only published account of range restriction in response to the threat of infanticide in areas without a concentrated food source is a study of brown bears in Scandinavia where authors compared home range sizes of bears before and after the mating season (Dahle and Swenson 2003). However, this seasonal correlation is confounded by the spatial distribution of choice foods throughout the later part of the summer when bear activity is focused on taking advantage of berries ripening (Dahle et al. 1998; Young and Ruff 1982). Dahle and Swenson (2003) argue that seasonal shifts in food availability do not affect their interpretation of results because non-dispersing 2-year-olds (not part of the breeding population) exhibited only a small change in range size . However, they did not differentiate between male and female 2-year-olds that show differences in home range size (Dahle et al. 1998) and more importantly did not acknowledge that subadults may not show behaviours representative of older more dominant individuals in the population. Differences in foraging behaviour associated with social dominance have been reported in a variety of taxa (Metcalfe 1986; Daily et al. 1994; Stahl et al. 2001, Hewitson et al.

2007) and in bears dominance at concentrated food sources is a function of body size (Herrero 1983, Gende and Quinn 2004). Consequently, there is no evidence that bear social behaviour should be different when choice foods are more dispersed. Therefore, comparisons of home range size in response to the threat of infanticide must be made within the same season to account for changes behavioural changes in response to food availability. It is likely that the confounding factor of food availability in the Dahle and Swenson study (2003) is the reason for the inconsistency with my results.

The motivation for larger home range sizes in the hunted Conklin area is unclear but consistent with the general pattern that reduced population densities lead to larger home ranges and less strict territorial structure (Sandell, 1989). One possible explanation for the larger home ranges in hunted Conklin could be that the female social structure is disrupted as a consequence of harvesting (Tuyttens and MacDonald 2000). This explanation does have some merit considering that females are not increasing their energy expenditure while travelling over greater spatial distances in Conklin. In general, Regardless of the mechanism for larger home ranges in hunted Conklin compared to unhunted CLAWR, all 3 predictions of the 'density-dependent' hypothesis are consistent with the data (Table 3-1, D) whereas this is not the case with the 'metabolic' and 'infanticide avoidance' hypotheses (Table 3-1, A-B-C). These results clearly demonstrate that density is the most important factor regulating home range size in female black bears with cubs.

4.2 Determinants of female activity patterns

Based on the predictions in Table 3-1, the 'food availability' hypothesis is best supported by the activity data (Table 3-1, A) followed by the 'density-dependent' hypothesis (Table 3-1, D). However, females in all study areas moved the same mean daily distance and had similar activity patterns, even though home range size was not consistent. These results differ from observations on other species where the distance travelled is positively correlated to the size of home ranges (Stahl et al. 1988, Kowalczyk et al. 2005). This suggests that interpreting activity patterns independently from the spatial extent within which they occur could be misleading, particularly in the unhunted CLAWR where females appear to be more territorial than hunted Conklin females (Figures 3-4; 3-6). If activity is considered relative to the spatial extent dictated by density, then activity per unit area (herein termed standardized activity) is a more accurate unit to compare temporal movements between areas.

Although the underlying reason for larger home ranges in lower-density Conklin is unclear, the smaller home ranges in high-density CLAWR should reflect seasonal requirements of females (Burt 1943). Therefore, if 'food availability' were the main driver of female standardized activity then activity patterns should be proportional to home range sizes. In terms of experimental comparisons, I would expect activity and mean distance travelled to be smaller in CLAWR compared to Conklin in proportion to the difference in home range sizes. Similarly, I should observe no change in activity patterns after manipulations in each area because the spatial extent used remained the same in each area. This hypothesis was not fully supported because females in higher-density CLAWR had greater standardized activity than females in lower-density CLAWR (Table 3-1, A1).

If the immigrant male form of the 'infanticide avoidance' hypothesis were the main driver of standardized activity, then standardized activity should be greater in unhunted CLAWR compared to hunted Conklin where the social structure has been affected. Because of the difference in home range size between areas, activity patterns and distance travelled in CLAWR would have to be at least equal to 1/2 or 1/4 times the activity in CLAWR during the spring and breeding seasons, respectively. Furthermore, I should have observed no difference in activity and movement patterns after the removal of bait sites whereas activity should decrease after the removal of males from CLAWR because of disruption to the social structure. This hypothesis was not strongly supported by the data because there was no change in standardized activity in CLAWR after the removal of males (Table 3-1, B3).

If the mate recognition form of the 'infanticide avoidance' hypothesis were the main driver of standardized activity, then standardized activity should be lower in unhunted CLAWR where there is a higher likelihood of encountering large infanticidal males compared to hunted Conklin. Because of the difference in home range size, activity in CLAWR would have to be lower than ½ and ¼ the activity in Conklin in the spring and breeding seasons to be consistent with this hypothesis. Furthermore, activity in Conklin should increase after the removal of bait sites and decrease in CLAWR after the removal of males in response to the change in the probability of encounter with infanticidal males. None of the 3 predictions of this hypothesis are supported by the data and therefore it is highly unlikely that infanticide avoidance regulates the standardized activity of female bears (Table 3-1, C).

My results were most consistent with a strong effect of density-dependence on the standardized activity of female bears whereby standardized activity should vary directly with population density. If the differences in home range size are taken into account, then activity patterns in higher-density CLAWR should be greater than ½ to ¼ of activity patterns in lower-density Conklin and there should be no change in activity patterns after manipulations. In fact, standardized activity was substantially greater in CLAWR compared to Conklin because activity patterns and distance travelled were similar whereas the spatial extent used by females in Conklin was greater than CLAWR. All 3 predictions of the 'density-dependent' hypothesis are met by the data and therefore best explain the observed patterns (Table 3-1, D).

4.3 Motivation for movement patterns

The effects of density can act on spatial and temporal patterns of species through social interactions (Pélabon and Komers 1997; Kjellander et al. 2004; Benson et al. 2006) or competition for food (Massei et al. 1997; Moncorps et al. 1997). In the case of female black bears, the increased standardized activity and observed territoriality in high-density CLAWR (Figures 3-4; 3-6) could be either a mechanism to protect resources (Roberts and Dunbar 2000) or offspring from conspecifics. Across taxa, territoriality in defence of food resources is rare unless they is centrally located or easily defendable (Wolff and Peterson 1998), whereas seasonal territoriality in females is a common strategy to protect young in species where females are infanticidal (Agrell et al. 1998; Ebensperger 1998; Wolff and Peterson 1998).

Although male bears are known to kill cubs and represent a threat, home ranges of male bears overlap those of several females, making them more unpredictable to respond to than neighbouring females. In bears, females have been reported to kill cubs (Garshelis 1994; Hessing and Aumiller 1994), appear to be more territorial towards unrelated female bears (Jonkel and Cowan 1971; Rogers 1987; Young and Ruff 1982; Stoen et al. 2005), and have areas of home range overlap that are smaller during the breeding season than during the summer (Horner and Powell 1990). Females can benefit from killing cubs of unrelated females (LeCount 1987; Garshelis 1994) and such competition should be most pronounced at very high densities. The lack of a response to the removal of males from CLAWR further reinforces the importance of female neighbours in regulating movement patterns. These results are also consistent with findings in red squirrels (*Sciurus vulgaris*) that density-dependent responses on demographic parameters vary more in response to the density of the same sex than to the opposite sex (Wauters et al. 2004). Therefore, results from this study suggest that female density could be a more important factor than total population density or male density in regulating movement patterns.

4.4 Implications for hunting

The determinants of space use described can be used to make predictions regarding the effects of hunting on movement patterns (Tuyttens and MacDonald 2000). Contrary to Scandinavian interpretations on brown bears, my results suggest that trophy hunting a low number of male black bears should have little effect on female movement patterns. Females in high-density populations should respond to the density of female neighbors and remain within small breeding home ranges and the probability of females encountering males would decrease or not be affected. More sustained hunting, where both male and female density is reduced and there are proportionally fewer adult males, may result in an increase in the size and overlap of female home ranges. This behavior should be taken into consideration because hunters may overestimate the actual numbers of females present on the landscape.

Table 3-1: Summary of hypotheses and predictions

Hypothesis	Comparison	Home range		Activity		Activity/Home range	
		Prediction	Supported	Prediction	Supported	Activity Prediction	Supported
A - Food availability and distribution hypothesis	1	No Difference	N	No Difference	Y	Conklin > CLAWR	N
	2	No Difference	Y	No Difference	Y	No Difference	Y
	3	No Difference	Y	No Difference	Y	No Difference	Y
B - Infanticide avoidance hypothesis - immigrant male form	1	Conklin < CLAWR	N	Conklin < CLAWR	N	Conklin <=CLAWR	Y
	2	No Difference	Y	No Difference	Y	No Difference	Y
	3	Before > After	N	Before > After	N	Before > After	N
C - Infanticide avoidance hypothesis - mate recognition form	1	Conklin > CLAWR	Y	Conklin > CLAWR	N	Conklin > CLAWR	N
	2	Before > After	N	Before > After	N	Before > After	N
	3	Before < After	N	Before < After	N	Before < After	N
D - Density-dependent hypothesis	1	Conklin > CLAWR	Y	Conklin < CLAWR	N	Conklin <=CLAWR	Y
	2	No Difference	Y	No Difference	Y	No Difference	Y
	3	No Difference	Y	No Difference	Y	No Difference	Y

Figure 3-1: Study design (2001–2005) depicting experimental closure of hunting in the Conklin North (CN) area and experimental removal of adult male bears in the Cold Lake Air Weapons Range (CLAWR), Alberta, Canada.

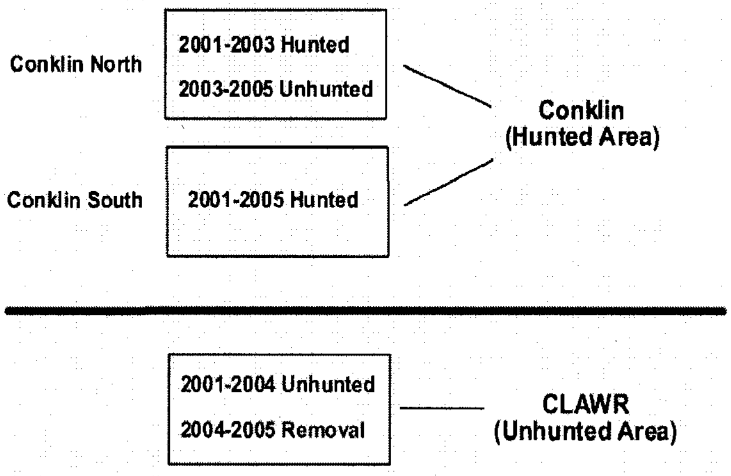


Figure 3-2: Daily activity patterns. Comparisons of median hourly distance travelled by females with cubs that survived to age 1 (a) before experimental manipulations in unhunted CLAWR and hunted Conklin (b) before and after removal of bait sites in hunted Conklin (c) before and after male removal in unhunted CLAWR during the (1) spring (den emergence beyond 1 km of den – June 14th) and (2) breeding (June 15th – July 14th) seasons, Alberta, Canada (2002 – 2004). Euclidean distances between hourly locations were calculated for each hour of the day. Confidence intervals represent bias corrected (BC) standard errors. Sample sizes for hourly distance bouts are presented in parentheses in the legends of individual graphs.

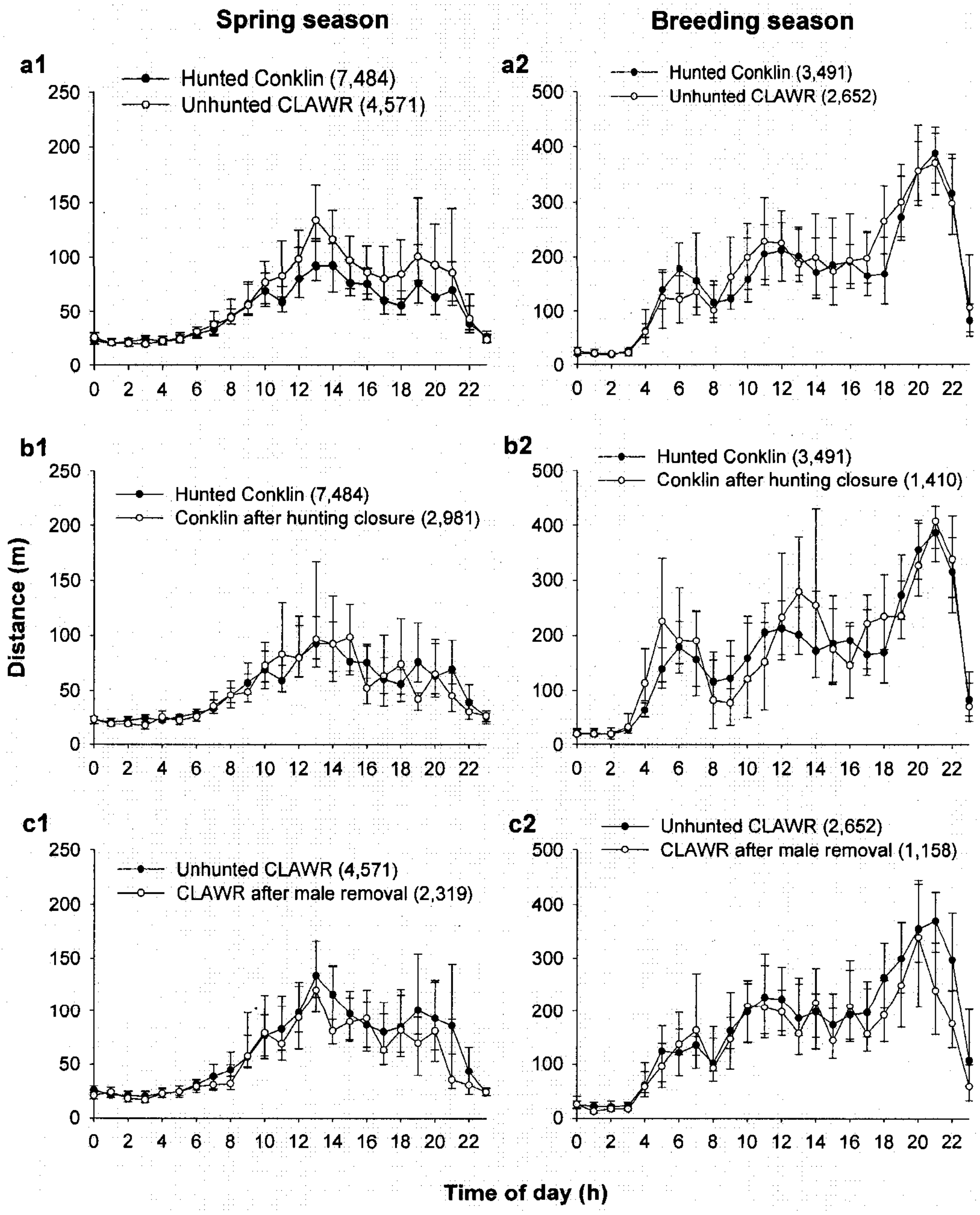


Figure 3-3: Seasonal distance travelled. Distance travelled by females with cubs that survived to age 1 in hunted Conklin (Conklin H, *n* = 426 days), unhunted CLAWR (CLAWR NH, *n* = 282 days), Conklin after bait removal (Conklin NH, *n* = 134 days), and CLAWR after male removal (CLAWR MR, *n* = 71 days) in Alberta, Canada (2002-2004). Each point represents the mean hourly movement rate/day/female with surviving cubs. Only days for which there were a minimum of 15 hourly bouts were retained for the analysis and 12 pairs of points were removed as extreme values (> 1000 m). Distances were binned by 2 week periods from April 15th to July 14th (groups 1-6).

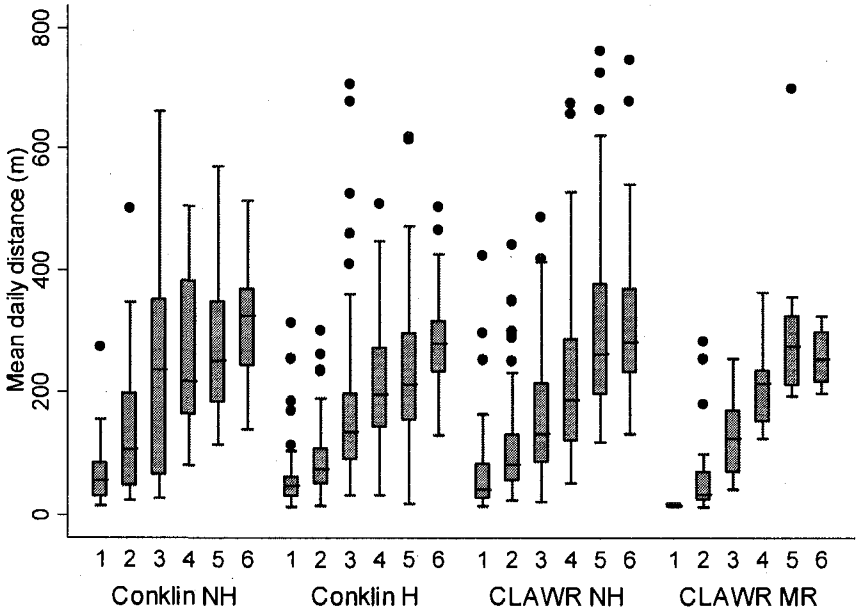


Figure 3-4: Unhunted CLAWR females. Locations and movement paths of CLAWR females (a) F18 (had 2 cubs that did not survive (timing of death is unknown, did not reproduce in 2003), (b) F118 (had 2 cubs that survived to age 1), and (c) F15 (had 3 cubs that survived to age 1) during the 2002 breeding season (June 15th to July 14th) in north-eastern Alberta, Canada. Hourly locations where only 1 of the 2 females was located were omitted. (d) Distances between females F18 and F118 throughout the breeding season (*n* = 400). (e) Distances between F118 and F15 (n = 379) throughout the breeding season.

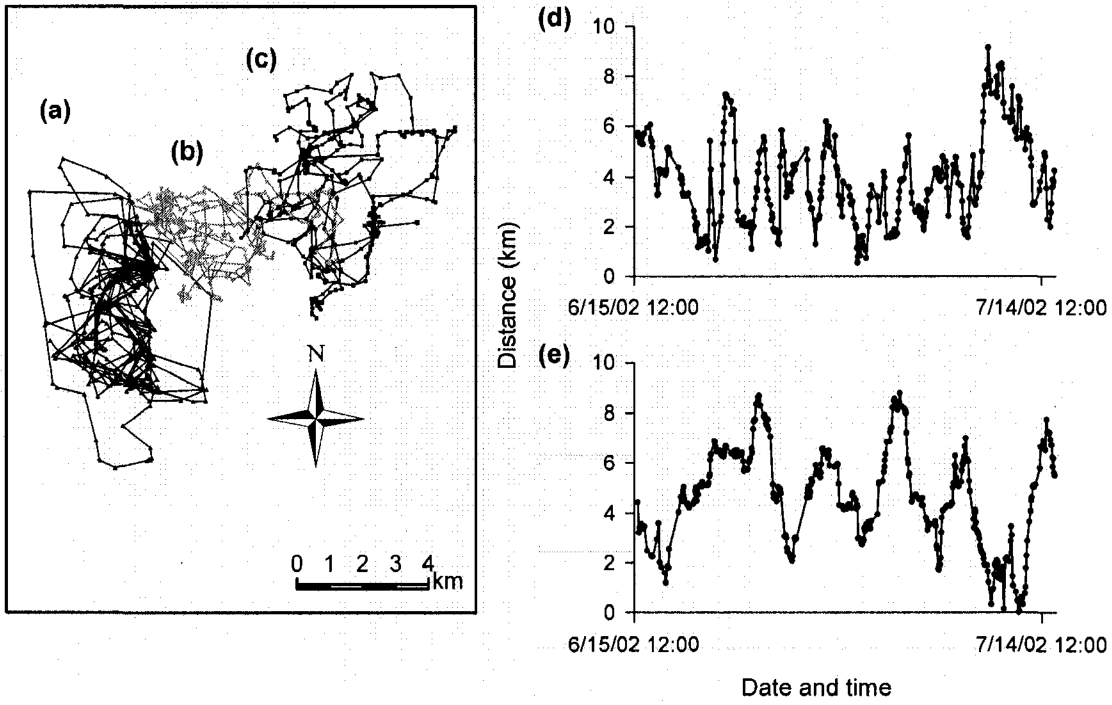


Figure 3-5: Hunted Conklin females with cubs. Locations and movement paths of Conklin females (a) F41 (had 1 cub that survived to age1) and (b) F43 (had 2 cubs that survived to age 1) during the 2002 breeding season (June 15th to July 14th) in north-eastern Alberta, Canada. (c) Distances between females F41 and F43 throughout the breeding season (*n* = 367). Hourly locations where only 1 of the 2 females was located were omitted.

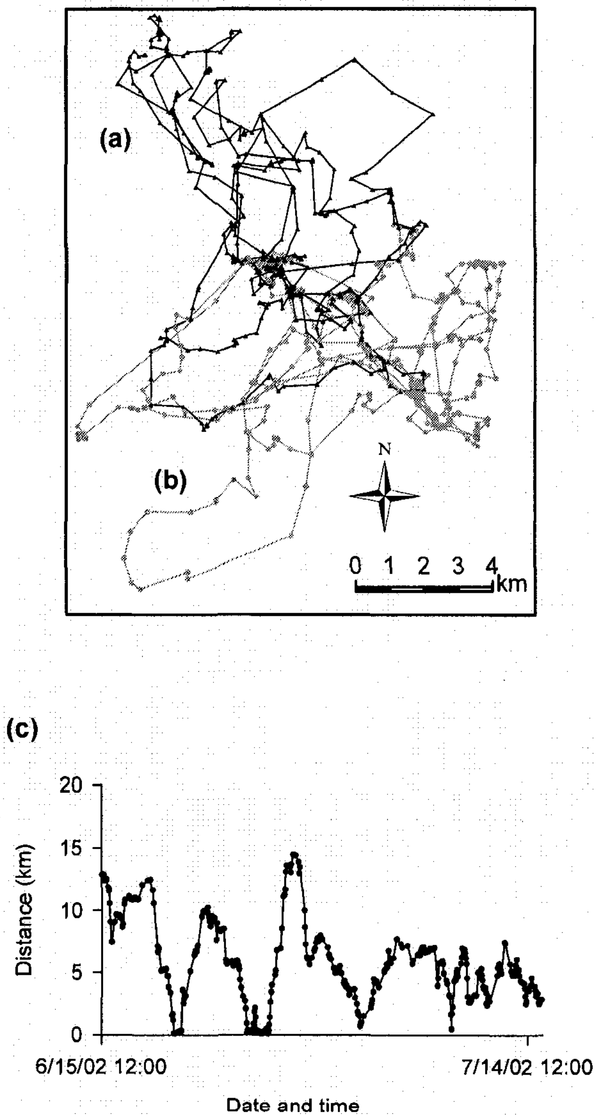
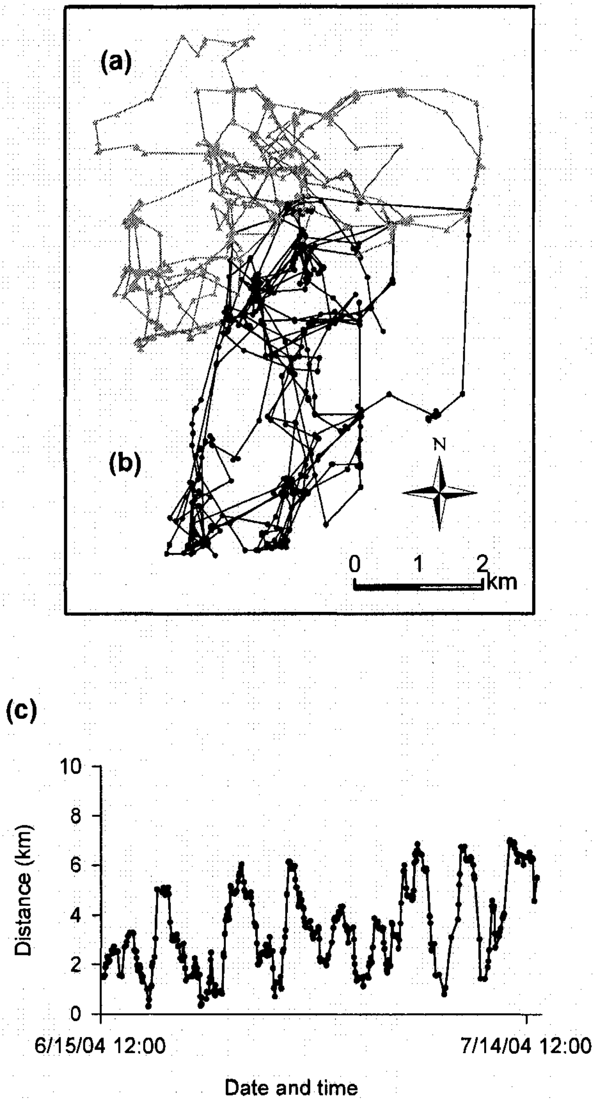


Figure 3-6: Unhunted CLAWR females after male removal. Locations and movement paths of Conklin females (a) F15 (had 3 cub and all survived to age 1) and (b) F19 (had 3 cubs that survived throughout the breeding season) during the 2004 breeding season (June 15th to July 14th) in north-eastern Alberta, Canada. (c) Distances between females F15 and F19 throughout the breeding season (*n* = 386). Hourly locations where only 1 of the 2 females was located were omitted.



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Chapter 4: Effects of hunting on sexual segregation and the threat of male infanticide in American black bears

1. Introduction

Selective hunting of large mammals can have consequences beyond the removal of individuals from the population including changes in space use, breeding system, sociality, and activity patterns (Tuyttens and Macdonald 2000, Frank and Woodroffe 2001, Milner et al. 2007). In some species, hunting adult males also can increase infanticide rates because of take-overs by new males who commit infanticide to breed with females and sire their own young (Arcese et al. 1997, Greene et al. 1998, Whitman et al. 2004), thus increasing their lifetime reproductive success (LRS). When the mechanism driving infanticide is well understood, harvest strategies of infanticidal species can be adapted to take such consequences into account and even reduce the impact of hunting on infanticide (Whitman et al. 2004, Loveridge et al. 2007). Sexually selected infanticide also has been demonstrated in bears (Bellemain et al. 2006b), a big game species where large trophy males are most targeted by hunters (Albert et al. 2001, Czetwertynski et al. 2007). Generally, the perturbation of social structures is not taken into account when managing solitary carnivores; demographic parameters are considered sufficient to set quotas and manage harvests sustainably (Miller et al. 2003, Czetwertynski et al. 2007). However, understanding if and how the threat of infanticide influences female habitat selection could provide information for more refined management strategies for bear populations.

Infanticide is difficult to observe in the wild but has been documented in black (*Ursus americanus*, LeCount 1987), brown (*U. arctos*, Miller et al. 2003), and polar bears (*U. maritimus*, Derocher and Wiig 1999, Amstrup et al. 2006). The most frequent cause of cub mortality is infanticide (LeCount 1987, Swenson et al. 1997, Swenson et al. 2001, Morner et al. 2005) and males most often are documented as the perpetrators (Jonkel and Cowan 1971, Lecount 1982, Bellemain et al. 2006b) although females also have been observed to kill cubs (Garshelis 1994, Hessing and Aumiller 1994). The relative importance of adult males as a threat to females is unclear (Czetwertynski et al. 2007) and is further confounded by the potential effects of hunting on the disruption of the social structure. Male home ranges are larger and overlap those of several females (Young and Ruff 1982, Czetwertynski et al. 2007) and during the spring breeding season, each sex employs a reproductive strategy to increase their reproductive output (Zeh and Zeh 2003). Specifically, adult males increase their LRS by breeding with multiple females (Zedrosser et al. 2007) while meeting their energy requirements. Similarly, lone adult females mate with multiple males to confuse paternity (Bellemain et al. 2006a, Bellemain et al. 2006b) and forage to meet nutritional demands of cub production. However, cubs remain with their mothers until they reach 1.5 to 3.5 years of age in black and brown bears (Schwartz et al. 2006, Czetwertynski et al. 2007). Therefore, unlike most large mammals where females are available for breeding annually, only a portion of female bears are receptive in the spring of any given year. Therefore, females with cubs must make foraging choices to meet the nutritional demands of lactation (Farley and Robbins 1995, Barboza 1997) and to protect their cubs from infanticide. Two competing hypotheses offer divergent predictions for the effects of disrupting established social structures on the threat of infanticide from adult males.

Research from Scandinavia claimed that hunting increases sexually selected infanticide rates because new immigrant males kill cubs that they did not sire so that they can breed with females (Swenson et al. 1997, Swenson et al. 2001). However, more recent work shows that resident bears also kill cubs (Bellemain et al. 2006b). This 'immigrant-male hypothesis' suggests that hunting increases cub mortality because of shifts in home ranges, and that resident males are more likely to come into contact and kill cubs of females they did not breed to bring these females into estrus so that they can sire their own cubs (Swenson 2003). A second hypothesis, termed the 'mate-recognition hypothesis' predicts that resident and immigrant males will kill cubs they were unlikely to have sired to increase their breeding opportunities (Mclellan 2005). Therefore, the density and sex ratio of populations will influence infanticide rates because they affect male searching efficiency for females (Mclellan 2005). Accordingly, studies of North American bear populations have consistently found higher cub survival rates in hunted populations reduced below carrying capacity (*K*) than in unhunted populations (Miller et al. 2003, Mclellan 2005, Schwartz et al. 2006, Czetwertynski et al. 2007). However, these hypotheses are based on comparisons of cub mortality rates between populations; an indirect measure of the threat of infanticide perceived by females with cubs. A more sensitive method to test these hypotheses is to compare if and how the threat of infanticide influences sexual segregation in areas with high and low cub mortality.

Sexual segregation is defined as the differential use of areas by males and females at specified spatial and temporal scales (Conradt 1998) and in ungulates is a common adaptive behavior to reduce the risk of predation on young when they are most vulnerable (Berger 1991, Bleich et al. 1997, Corti and Shackleton 2002, Ruckstuhl and Neuhaus 2002). In bears, many studies have documented segregation of females with cubs along salmon streams where they use less productive salmon spawning areas (Gende and Quinn 2004, Suring et al. 2006), spend less time foraging on streams (Ben-David et al. 2004, Nevin and Gilbert 2005a), and have lower catch rates (Gende and Quinn 2004) compared to other bears. These behaviors are in part a response to the perceived risk of infanticide from other bears (Rode et al. 2006) and carry considerable nutritional cost (Ben-David et al. 2004, Nevin and Gilbert 2005b). In areas without access to salmon, Wielgus and Bunnell (1995) found females with cubs to avoid berry-rich burn areas when male mortality was high but not when male mortality was low. Authors hypothesize that females avoided infanticidal immigrant males. To date, no study has documented sexual segregation in bears during the spring and early summer when most cub mortality occurs, (LeCount 1987, Elowe and Dodge 1989, Swenson et al. 1997), cubs are most vulnerable, and males benefit from sexually selected infanticide (SSI) by killing cubs, breeding with the female, and siring cubs the following year (Bellemain et al. 2006b). Furthermore, this period is of importance to management because it coincides with hunting seasons for black bears in many jurisdictions.

Therefore, in this study we address the following 3 questions. (1) Does sexual segregation vary in response to the threat of infanticide from adult males and, if yes, what changes in selection occur in response to various levels of threat? (2) Are patterns of habitat selection more consistent with the 'immigrant male' hypothesis or the 'mate recognition' hypothesis? (3) Can potential sex-specific habitat selection patterns have applications in habitat and harvest management strategies for bears?

2. Study design

We used a large-scale modified BACI (before-after-control-impact) design in 1 unhunted (Cold Lake Air Weapons Range, CLAWR) and 2 hunted (Conklin North, CN, and South, CS) study areas (Figure 4-1). The 2 Conklin study sites (high cub survival area) were hunted during spring 2001 and 2002. Outfitters agreed to close bait sites within the trapped area of CN during 2003 and 2004. The CS area was hunted for the duration of the study. The threat of male infanticide in CLAWR (low cub survival area) was manipulated 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 (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).

To minimize the potential confounding effects of social status (Sherry and Holmes 1989) and competition (Jacoby et al. 1999) on bear habitat selection, we use only females with cubs of the year where at least 1 cub was known to survive to the end of the breeding season beyond July 14th (herein called females) and conducted the study in a boreal area outside the current range of brown bears. Furthermore, to account for the effects of differences in density (Kie and Bowyer 1999) and sensitivity to human disturbance (Smith et al. 2005) on habitat selection in each of our study areas, we manipulated the potential threat of male infanticide in each area and compared female habitat selection before and after manipulations.

We divided the spring and summer season into 2 sub-seasons to capture potential variation in activity patterns before and during the peak of the breeding season. The first season (termed spring season) extended from den emergence (beyond a 1-km radius around the densite) to June 14th when outfitters ceased operating in the area. The second season, referred to as the breeding season, extended from June 15th to July 14th and represents the peak of the breeding season (Eiler et al. 1989, Garshelis and Hellgren 1994).

3. Study areas

3.1 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. 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 where there were 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 during 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. Shorter segments of road connected the MR to well pads to the east and west. Bear safety regulations were strictly enforced by Range Control personnel and non-compliance resulted in a 1 year ban from the range. Feeding bears along the MR was forbidden in CLAWR. Furthermore, vehicles were prohibited from stopping along roads to watch bears. 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 this study. The only harvest mortality of CLAWR bears occurred when bears traveled beyond the range to Crown and private lands.

3.2 Hunted area (Conklin)

The Conklin study area (~6,000 km^2) was north of CLAWR on Crown land, divided into 2 study sites north (CN) and south (CS) of Christina and Winefred Lakes. 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 the resident harvest to be negligible. Females with cubs of the year (cubs, hereafter) were protected.

3.3 CLAWR and Conklin vegetation and bear foods

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 (*P. balsamifera*), and white spruce (*Picea glauca*) at higher elevations. Black spruce (*P. 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.

Vegetation types with important bear foods common in both study areas include riparian corridors, aspen stands, and pine stands. Riparian areas represent one of the most important spring habitats for bears (Unsworth et al. 1989, Mclellan and Hovey 2001, Lyons et al. 2003). Common black bear foods in riparian areas include among others horsetails (*Equisetum arvense*), graminoids, and cow parsnip (*Heracleum lanatum*). Black bears are major predators of deer (*Odocoileus* spp.) and moose calves (Holcroft and Herrero 1991, Kunkel and Mech 1994) and riparian areas are selected for calving because of high-quality forage (willow, Bowyer et al. 1999) and visibility (Poole et al. 2007). Accordingly, grizzly bears selected wet forest sites when found feeding on ungulates (Munro et al. 2006). Therefore, riparian areas contained the greatest variety and quality of spring foods for bears and also could be used as travel corridors in spring when bears roam in search of mates (Amstrup and Beecham 1976). Next in order of importance are aspen stands which also contain many spring bear foods including wild sarsaparilla (*Aralia nudicaulis*), creamy peavine (*Lathyrus ochroleucus*), wild vetch (*Vicia americana*), and young aspen leaves. Lastly, understories of pine stands in our study area were often carpeted with bearberries (*Arctostaphylos uva-ursi*), a spring bear food

(Holcroft and Herrero 1991), because the fruits are preserved beneath the snow and available early in spring (Norment and Fuller 1997).

4. Methods

4.1 Fieldwork

We captured bears using modified bucket traps (Lemieux and Czetwertynski 2006) and L-83 ground snares (Jolicoeur and Lemieux 1992). Once restrained, bears were immobilized with tiletamine–zolazepam (Animal care #322104 University of Alberta) and a subset of captured bears was equipped with GPS 2200L radiocollars within each study area (Lotek Wireless Inc., Newmarket, Ontario, Canada). GPS collars were rotated between individuals during annual den visits (mid-January and mid-March) to increase the number of unique bears monitored. During den visits, we recorded mass, body measurements, reproduction, and cub survival (Czetwertynski et al. 2007).

4.2 GPS radiocollar data

GPS radiocollars were programmed to record hourly fixes throughout the summer (Table 4-1). We discarded early spring locations near den sites until 3 successive locations were beyond a 1 km radius. All data with PDOP values greater than 10 were individually inspected (D'eon and Delparte 2005). If the location was reasonable compared to locations before and after then it was retained for analysis. If individuals were monitored for more than 1 year, data from separate years were merged and all locations were assigned to that bear.

4.3 Identifying behaviors

Patterns of habitat selection are influenced by the activity in which the animals are engaged (Garshelis 2000). We thus split location data into either foraging or traveling points using a non-linear curve fitting procedure fit to a $\log_e$ transformed frequency distribution of movement rates (Sibly 1990, Johnson et al. 2002). We used this method to identify the scale criterion (r_c) which represents the break point between short and long movement rates (Johnson et al. 2002). Because bears exhibit a high degree of individual variation in movement patterns and females move progressively longer distances in the spring (Czetwertynski, unpublished data), we calculated a separate r_c value for each bear in each season.

4.4 Habitat characteristics

We used a GIS to obtain landscape covariates for all bear locations (ESRI ArcMap 9.0, Table 4-2) and generated separate maps for each year of the study to account for new burns and cutblocks. In the Conklin area, we used Alberta vegetation inventory (AVI, Timberline Forest Inventory Consultants 2004) maps to derive habitat covariates and updated recent burns with the historical spatial wildfire data from Alberta Sustainable Resource Development (http://www.srd.gov.ab.ca/wildfires/). We converted shapefiles to 30×30 m raster grids and generated a land-cover covariate based on the dominant tree species within each pixel (Table 4-2). A large proportion of the *other* category consisted of burns (65 and 60 % during the spring and breeding seasons). We did not consider this covariate separately because not all female bears had access to burns within their seasonal home range, and few spring foods were available in these areas. We calculated distance to water for bear locations using the Euclidean distance between points and the nearest water source extracted from AVI maps. Euclidean distance to nearest well sites and linear features (seismic lines, pipelines) were calculated from layers developed by IHS Energy Ltd. (Calgary, Alberta).

In CLAWR, where AVI data were not available, we used Alberta ground cover classification (AGCC; 25-m resolution raster, Earth Observation Systems Laboratory 2003) maps to derive a ground cover layer (Table 4-2). We overlaid the AGCC layer with updated historical spatial wildfire data from Alberta Sustainable Resource Development. This layer was not as detailed as AVI and the majority of conifer pixels were not differentiated by dominant tree species. Therefore, we merged the original AGCC categories into 4 biologically relevant classes that were available to each bear within their home range (conifer, deciduous, roads, other). Similarly to Conklin, a large proportion of the *other* category consisted of burns (62 and 78 % during the spring and breeding seasons). Although roads represented a small proportion of available habitat (2%), we chose to include it as a distinct category in this study area because roadside ditches were seeded with clover, a high protein food source for bears in the spring (Rode et al. 2001), and bears would regularly forage in these areas and were not disturbed by humans. The *road* class included roads and the cleared ditches on either side (100 m on either side of roads). We generated a distance to water category from water bodies extracted from the AGCC layer. Data on distance to anthropogenic features (well sites, seismic lines, pipelines) were obtained from EnCana (Calgary, Alberta) and merged with layers from HIS Energy Ltd.

4.5 Available habitats

We generated 100% MCPs of all available points within each study area and by season. Available habitats were classified based on the land-cover categories within each area (Table 4-2) and percentages were based on all available pixels within each habitat category. Water bodies were excluded before querying so that they did not represent points in the "other" category. Available habitats were used with marginal probabilities of bear use of land-cover categories as an aid to interpret the relative importance of changes in model covariates. For example, a significant change in selection for a habitat type might not be of great importance if that habitat category was rarely used.

4.6 Accounting for sexual dimorphism

Testing for sexual segregation as a response to infanticide in bears is confounded by sexual dimorphism (Isaac 2005) and lactation in females with cubs which can produce differences in nutritional requirements for each sex (McDonald 2002). Therefore, any differences between male and female habitat selection after den emergence could be a result of differences in nutritional requirements (Mooring et al. 2005) and not the threat of infanticide perceived by females. The relative influence of each sex as predators of ungulate calves is unclear; some studies report males responsible for the majority of kills (Boertje et al. 1988, Jacoby et al. 1999, Bertram and Vivion 2002, Zager and Beecham 2006) whereas others did not detect a difference between sexes (Hilderbrand et al. 1999, Bull et al. 2001). Therefore, to isolate the effects of the threat of male infanticide from potential differences in nutritional requirements, we compare sexual segregation by measuring the differences in male and female habitat section in areas with high and low cub mortality rates.

4.7 Modeling procedure

We assumed availability of habitat types to be similar in each area for males and females and used logistic regression to estimate coefficients for latent selection difference (LSD) functions (Appendix 1). The model has the form:

$$s(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k) \qquad (1)$$

where $s(x)$ represents the relative probability of the group coded as 1 occurring on the landscape compared to the group coded as 0 given a vector of predictor variables (x_i); the $\beta_i s$ represent corresponding selection coefficients. Coefficients represent the relative difference in selection between 2 groups and not the selection or use of a given habitat type (see Appendix 1). We specified the robust cluster option in STATA to estimate standard errors using the Huber-White sandwich estimators (White 1980). We grouped data by individual bears therefore assuming that observations were independent across clusters (between bears) but not within clusters (all data points associated with an individual bear) (Long and Freese 2003).

Because we wanted to make several different comparisons and considered all variables to be important, we used the full model for analyses. Linear predictor variables from GIS queries did not meet linearity assumptions for logistic regression in all models, therefore, we transformed them into categorical dummy variables. Cutoff points for each variable were determined biologically while accounting for error in GPS locations. Specifically, bears were considered to use ditches of main roads in CLAWR if they were within 100 m from the road (approximate distance of clover planted along roads, coded as 1), otherwise they were considered away from the road (coded as 0). Similarly, bears were considered in riparian areas (coded as 1) if they were within 100 m of a water feature (river, stream, lake). We chose this surrogate classification because it should best detect if bears use these corridors. We considered bears using anthropogenic features (coded as 1) if they were within 30 m of linear features (seismic lines, pipelines) or well sites.

We first compared male and female habitat selection within each area and season before manipulation. Secondly, we compared female habitat selection before and after manipulations in each area and season. We analyzed short-step foraging and long-step travelling points separately (Johnson et al. 2002). To isolate foraging sites from bedding sites (small-scale movements) we discarded locations before 07:00 and after 22:00 in the spring season and locations before 04:00 during the breeding season when bears were resting based on activity patterns (Czetwertynski, unpublished data).

5. Results

5.1 Conklin

The greatest difference between female and male habitat selection in hunted Conklin was in foraging selection for aspen stands (Table 4-3, Figure 4-2). During the spring and breeding seasons, the probability that bears selected aspen stands compared to spruce stands was ($e^{2.52}$) 12.43 and ($e^{1.47}$) 4.35 times higher for females compared to males (see Appendix for details on the interpretation of coefficients). This difference in selection for aspen stands also was significant for traveling locations but the difference was not as great as for foraging locations (3.90 and 2.32 times greater for females compared to males during the spring and breeding seasons). After the closure of bait sites (Table 4-4, Figure 4-2), there was no substantial change in female habitat selection for traveling locations. However, females were 17% as likely to forage in riparian areas in spring and 45% less likely during the breeding season after the closure of bait sites compared to before the closures. Furthermore, females were 39% as likely to forage in jack pine stands compared to spruce stands after the closure compared to before the closure of bait sites.

5.2 CLAWR

The greatest difference between female and male habitat selection in unhunted CLAWR was in foraging selection for riparian areas (Table 4-5, Figure 4-3). During the spring and breeding seasons, females were 19% and 33% as likely to select for riparian areas compared to males. Females also selected for riparian areas less for traveling than males during the spring (46% as likely) and breeding (52% as likely) seasons. After the removal of males (Table 4-6, Figure 4-3), females increased their selection for roads during spring. The probability of females selecting roadsides was 6.42 times greater for foraging and 5.05 times greater for traveling compared to selection for conifer stands. Later, during the breeding season, females were 4.14 times more likely to select for deciduous stands and 3.78 times more likely to be within 100 m of roads compared to conifer stands when foraging after the male removal compared to before the removal. Similarly, females also increased their selection for deciduous stands (2.92 times greater) and roadsides (3.10 times greater) compared to spruce stands for traveling after male removal. Furthermore, females also increased their foraging selection for riparian areas (2.22 times greater) but not their traveling selection after male removal.

6. Discussion

6.1 Linking the threat of infanticide, habitat selection, and sexual segregation

We found that lactating females adjusted their habitat selection in response to the probability of encountering a male and reduced their selection for highest-quality habitats as the threat of male infanticide increased. When the threat of infanticide was lowest (hunted Conklin), we detected no difference between males and females in selection for high-quality riparian areas. However, females segregated spatially from males and were up to 12 times more likely to be found in aspen stands compared to males. Cub survival in Conklin was high (83%, Czetwertynski et al. 2007) suggesting that this pattern in sexual segregation was an optimal trade-off for females to meet nutritional requirements and avoid the threat of infanticide when encounter rates with males were low.

At the opposite end of the spectrum, when the threat of infanticide was high (unhunted CLAWR cub survival = 66%, Czetwertynski et al. 2007), females selected for riparian areas less than males, particularly for foraging locations when they were up to 5 times less likely to occur than males. Reducing selection for such a food-rich habitat represents a substantial nutritional loss and is best explained as a strategy to avoid males in a high-density population. Furthermore, we detected no difference in selection between males and females for landcover classes. This is consistent with females spending more time avoiding males and less time foraging in preferred habitats (Steiner and Pfeiffer 2007). Females in CLAWR also would have more difficulty foraging in preferred habitats while avoiding males compared to Conklin females because of smaller female home ranges and thus fewer options of deciduous stands (Czetwertynski et al. 2007).

We assume that closures of hunting sites in north Conklin resulted in more males on the landscape compared to previous years and represent an intermediate threat level to CLAWR and Conklin before manipulations. Within riparian areas, sexual segregation increased because females decreased their foraging activities within these corridors. Furthermore, we detected a decrease in selection for jack pine stands but no change in selection for aspen compared to spruce stands. Reduced selection for jack pine stands by females suggests that females adapted to the increased threat by reducing their use of this habitat type this food source but this effect could not be confirmed experimentally. Unfortunately, vegetation maps in CLAWR did not separate conifer stands into pine and spruce so if such an effect occurred in CLAWR before male removal we could not detect it and thus also confirm its relative importance as a response to infanticide in Conklin. For example, the reduction in selection for jack pine could be a consequence of increased selection for other habitat types not detected in our analysis. The increased threat from males did not appear to be sufficient to affect female selection for aspen stands possibly because the probability of females encountering males was not as high as in unhunted CLAWR before male removal. Consequently, our results imply that at intermediate levels of threat from males, females were able to use inferior habitats to meet their nutritional requirements with little disturbance from males because cub survival rates did not change after the hunting closure (Czetwertynski et al. 2007)). The continued female selection of riparian areas for traveling but decreased selection for foraging in Conklin after the hunting closure suggests that females tried to forage in optimal habitats until they were displaced by males. This pattern also is consistent with results along salmon streams where males selected the best habitats and females made trade-offs by foraging in inferior habitats but reducing the threat of infanticide (Rode et al. 2006).

6.2 The 'immigrant male' versus 'mate recognition' hypotheses

The experimental removal of males from unhunted CLAWR offers new insight into the social dynamics of bears and the effects of hunting. Our results contradict the predictions of the 'immigrant male' hypothesis because females in unhunted CLAWR had the greatest difference in selection for riparian areas compared to males. This level of sexual segregation in a high-quality habitat is the opposite of what we would expect if males in an undisturbed population did not represent a threat. Furthermore, when males were removed from CLAWR females were twice as likely to select for riparian areas and significantly increased their selection for aspen stands. Females also increased their selection for roadside ditches and were up to 7 times more likely to be foraging along roads after male removal. Ditches in CLAWR were wide and densely seeded with clover. Captive spring foraging trials with grizzly bears have demonstrated that bears consistently choose clover over grasses; forbs are generally more digestible and higher in protein (Rode et al. 2001). Furthermore, adult females were able to gain weight even with no access to animal protein (Rode et al. 2001). Clover is a predictable food item in spring, probably one of the most efficient food sources (intake rate/search time) in CLAWR, and a dominant food item in the spring diets of free-ranging bears (Boileau et al. 1994, Mclellan and Hovey 1995, Munro et al. 2006). Increased road use by females after male removal also indicates that females were not avoiding these areas because of differences in sensitivity to human disturbance because human activity increased annually during the 4 year study. Females in hunted Conklin probably did not exhibit this behavior because clover was not as prevalent along roadsides and roadsides were risky. This increased selection for high-quality habitats by females after the removal of males in unhunted CLAWR is clear evidence that resident males in a bear population with a stable social structure are considered a threat by females.

This pattern of sexual segregation is consistent with the 'mate recognition' hypothesis (Mclellan 2005) whereby males in a high-density population would most increase their LRS by maximizing annual breeding opportunities because females are easily located by males that compete with neighbors with overlapping home ranges (Young and Ruff 1982). Therefore, habitat selection trade-offs made by females in an area were a direct response to the density of adult male bears and the probability of encountering them in preferred habitats. These results also strengthen the evidence against a potential delayed effect of increased infanticide rates from hunting as described in Scandinavian demographic results (Swenson et al. 1997) but which we could not measure in our study (Czetwertynski et al. 2007).

6.3 Conservation implications

Our location data were indirect evidence of behavior and did not allow us to differentiate between the immediate response of females to the presence of males and the risk involved in encountering a male in particular habitats (Bowyer 1987). Regardless, the realized differences in habitat selection offer unique landscape and hunting management opportunities to increase cub survival. Specifically, in areas where high quality spring habitats are patchy and predictable, females could anticipate where males concentrate and take their cubs elsewhere presuming that there are alternative places where females could meet the substantial energy demands associated with feeding a litter. Knowledge of area-specific spring and early summer habitat selection patterns for each sex could provide valuable information to predict the effects of landscape management regimes on sexual segregation and infanticide rates. For example, in boreal mixed-wood landscapes similar to our study areas, maintenance of intact riparian areas could provide not only high-quality food sources but also may concentrate males in these areas and make them more predictable to lactating females. Greater selection for aspen stands by females compared to males in Conklin after the closure of hunting sites when selection for foraging in riparian areas decreased suggests that aspen stands provided a reasonable alternative food source because cub survival rates were not affected (Czetwertynski et al. 2007).

In terms of hunting management, hunters generally target larger males. This preference has a smaller effect on population growth than killing females in a polygynous species, however, younger males and adult females are difficult to distinguish. Females with cubs are protected from harvest in most jurisdictions but are killed accidentally because they do not always travel with their cubs and/or bring them to bait sites. Although cub orphaning represents an extremely small portion annual cub deaths (<2% in Manitoba (Hristienko et al. 2004), it is an important consideration for the general public and was responsible in part for the closure of the spring bear hunt in Ontario, Canada in 1999 (Ontario Ministry of Natural Resources 1999). Therefore, educating hunters about sexual segregation and focusing effort in areas more likely to be selected by males could decrease the number of females in the harvest. Similarly, avoiding areas selected for by females may reduce the number of lactating females accidentally killed. In our study area, this would be accomplished by encouraging hunter effort in the vicinity (detection distance) of riparian areas and avoiding aspen stands.

Table 4-1: Number of bears and GPS radiolocations available for analysis in hunted Conklin and unhunted CLAWR, Alberta, Canada (2001-2004)

	Males		Females			
			Before Manipulations		After Manipulations	
Comparisons	Num. Males	Num. Loc.	Num. fem.	Num. loc.	Num. fem.	Num. loc.
CLAWR						
Spring - foraging	6	3499	6	2684	4	1759
Spring - travelling	6	3620	6	951	4	606
Breeding -foraging	6	1297	6	1270	3	787
Breeding - travelling	6	1640	6	1602	3	557
Conklin						
Spring - foraging	6	1820	7	3434	3	1398
Spring - travelling	6	1134	7	1107	3	506
Breeding -foraging	7	969	10	1665	3	455
Breeding - travelling	7	1158	10	2169	3	987

Table 4-2: Variables used to compare male and female black bear habitat selection in northeastern Alberta, Canada, 2001-2005.

Variable description	Variable code	Type	Range
CLAWR			
Land cover:			
Conifer (ref. category)	Conif	category	0 or 1
Deciduous	Decid	category	0 or 1
Within 100m of road	Road	category	0 or 1
Other	Other	category	0 or 1
Within 100 m of water source	Riparn	category	0 or 1
Within 30 m of well site	Well	category	0 or 1
Within 30 m of linear feature	Linear	category	0 or 1
Conklin			
Land cover:			
Spruce (ref. category)	Spruce	category	0 or 1
Larch	Larch	category	0 or 1
Jack pine	Jpine	category	0 or 1
Aspen	Aspen	category	0 or 1
Other	Other	category	0 or 1
Within 100 m of water source	Riparn	category	0 or 1
Within 30 m of well site	Well	category	0 or 1
Within 30 m of linear feature	Linear	category	0 or 1

Table 4-3: Estimated selection coefficients comparing male (coded as 0) and female (coded as 1) relative habitat selection during the spring (den emergence to June 14th) and breeding (June 15th to July 14th) seasons in hunted Conklin, Alberta, Canada (2001-2004). Models are based on foraging (movement rate $< r_c$) and travelling (movement rate $\geq r_c$) GPS radiotelemetry data from males and females with cubs where at least 1 cub survived to age 1. Resting locations were eliminated by only using locations from 7:00 to 22:00 inclusively during the spring season and locations after 3:00 during the breeding season.

	Spring Season						Breeding season					
Variable	Foraging			Travelling			Foraging			Travelling		
code	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*
Larch	0.512	0.584	0.381	0.160	0.396	0.686	0.100	0.368	0.786	0.011	0.289	0.971
Jpine	0.609	0.641	0.343	0.794	0.467	0.090	0.771	0.503	0.125	0.438	0.560	0.434
Aspen	2.519	0.384	<0.001	1.360	0.349	<0.001	1.474	0.426	0.001	0.837	0.333	0.012
Other	1.199	0.611	0.050	0.654	0.482	0.174	1.018	0.535	0.057	0.157	0.506	0.756
Riparn	0.694	0.639	0.278	0.084	0.390	0.830	-0.208	0.272	0.444	-0.359	0.239	0.132
Well	1.332	0.925	0.150	0.670	0.378	0.076	-0.157	0.592	0.791	-0.002	0.282	0.994
Linear	0.729	0.424	0.085	0.805	0.244	0.001	0.368	0.347	0.289	0.106	0.175	0.546

Table 4-4: Estimated selection coefficients comparing female relative habitat selection before (coded as 0) and after closure of bait sites (coded as 1) during the spring (den emergence to June 14th) and breeding (June 15th to July 14th) seasons in hunted Conklin, Alberta, Canada (2001-2004). Models are based on foraging (movement rate $< r_c$) and travelling (movement rate $\geq r_c$) GPS radiotelemetry data from males and females with cubs where at least 1 cub survived to age 1. Resting locations were eliminated by only using locations from 7:00 to 22:00 inclusively during the spring season and locations after 3:00 during the breeding season.

	Spring Season						Breeding season					
Variable	Foraging			Travelling			Foraging			Travelling		
code	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*
Larch	-0.078	0.624	0.901	0.178	0.347	0.609	0.752	0.581	0.196	0.172	0.620	0.781
Jpine	-0.732	0.489	0.134	-0.739	0.385	0.055	-0.944	0.424	0.026	-0.401	0.660	0.543
Aspen	-0.679	0.610	0.266	-0.955	0.632	0.131	-0.394	0.451	0.383	-0.192	0.486	0.694
Other	-0.785	0.449	0.080	-0.467	0.503	0.354	-0.105	0.777	0.893	-0.287	0.709	0.686
Riparn	-1.777	0.792	0.025	-0.641	0.407	0.115	-0.809	0.353	0.022	-0.090	0.303	0.767
Well	0.451	0.818	0.581	-0.039	0.643	0.952	-0.051	0.440	0.908	-0.316	0.285	0.268
Linear	-0.155	0.256	0.545	0.115	0.255	0.651	0.263	0.385	0.494	0.288	0.124	0.020

Table 4-5: Estimated selection coefficients comparing male (coded as 0) and female (coded as 1) relative habitat selection during the spring (den emergence to June 14th) and breeding (June 15th to July 14th) seasons in unhunted CLAWR, Alberta, Canada (2002-2004). Models are based on foraging (movement rate < r_c) and travelling (movement rate ≥ r_c) GPS radiotelemetry data from males and females with cubs where at least 1 cub survived to age 1. Resting locations were eliminated by only using locations from 7:00 to 22:00 inclusively during the spring season and locations after 3:00 during the breeding season.

	Spring Season						Breeding season					
Variable	Foraging			Travelling			Foraging			Travelling		
code	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*
Decid	0.967	0.659	0.142	-0.178	0.462	0.699	0.341	0.551	0.535	0.121	0.525	0.818
Road	0.215	0.750	0.774	-0.307	0.469	0.513	-0.209	0.607	0.730	0.278	0.499	0.577
Other	-0.870	0.483	0.072	-0.596	0.311	0.056	-0.196	0.263	0.456	-0.596	0.194	0.002
Riparn	-1.657	0.525	0.002	-0.774	0.305	0.011	-1.098	0.339	0.001	-0.647	0.247	0.009
Well	0.545	0.573	0.342	0.695	0.399	0.081	0.947	0.476	0.047	0.332	0.603	0.582
Linear	-0.243	0.223	0.276	-0.084	0.133	0.530	-0.483	0.214	0.024	-0.176	0.103	0.086

Table 4-6: Estimated selection coefficients comparing female relative habitat selection before (coded as 0) and after male removal (coded as 1) during the spring (den emergence to June 14th) and breeding (June 15th to July 14th) seasons in unhunted CLAWR, Alberta, Canada (2002-2004). Models are based on foraging (movement rate < r_c) and travelling (movement rate ≥ r_c) GPS radiotelemetry data from males and females with cubs where at least 1 cub survived to age 1. Resting locations were eliminated by only using locations from 7:00 to 22:00 inclusively during the spring season and locations after 3:00 during the breeding season.

	Spring Season						Breeding season					
Variable	Foraging			Travelling			Foraging			Travelling		
code	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*	Coef.	Std. Err.	*p*
Decid	0.039	0.687	0.955	0.704	0.464	0.129	1.416	0.447	0.002	1.074	0.486	0.027
Road	1.856	0.856	0.030	1.620	0.502	0.001	1.327	0.430	0.002	1.128	0.526	0.032
Other	0.733	0.293	0.012	0.142	0.286	0.621	0.542	0.326	0.097	0.560	0.276	0.043
Riparn	-0.544	0.489	0.266	-0.870	0.507	0.086	0.796	0.350	0.023	0.519	0.515	0.314
Well	-0.580	0.585	0.321	-0.727	0.493	0.140	-1.121	0.613	0.067	0.550	0.550	0.127
Linear	-0.463	0.281	0.099	-0.394	0.204	0.054	-0.003	0.298	0.993	-0.080	0.200	0.688

Figure 4-1: Study design (2001–2005) depicting experimental closure of hunting in the Conklin North (CN) area and experimental removal of adult male bears in the Cold Lake Air Weapons Range (CLAWR), Alberta, Canada.

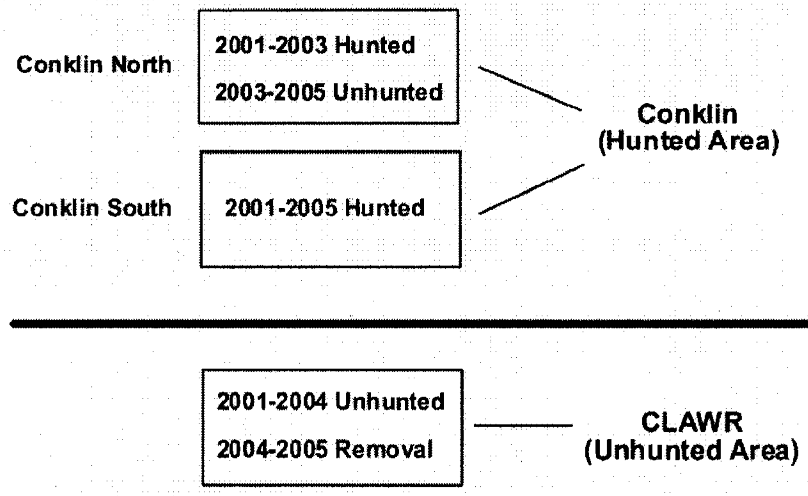
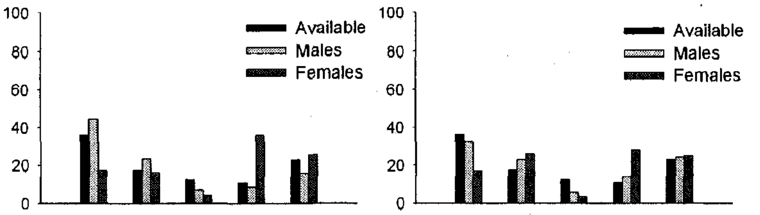


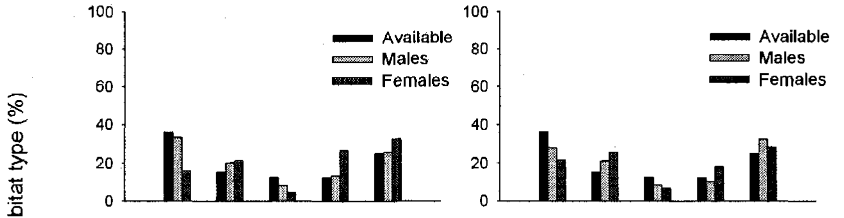
Figure 4-2: Marginal habitat selection during the spring (den emergence to June 14th) and breeding (June 15th to July 14th) seasons in Conklin, Alberta, Canada (2001-2004) for foraging (movement rate $< r_c$) and travelling (movement rate $\geq r_c$) GPS radiotelemetry locations from males and females with cubs where at least 1 cub survived to age 1. Resting locations were eliminated by only using locations from 7:00 to 22:00 inclusively during the spring season and locations after 3:00 during the breeding season. Available habitat was generated from 100% MCPs of all available points within the study area and by season.

Foraging **Travelling**

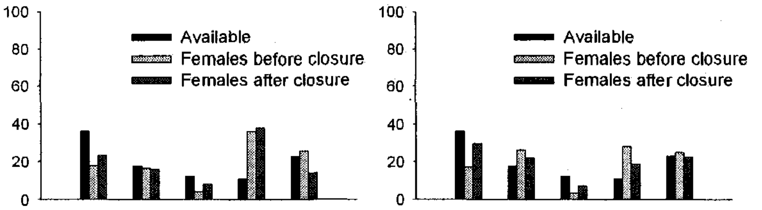
a) Hunting season before experimental manipulation



b) Breeding season before experimental manipulation



c) Hunting season experimental closure of bait sites



d) Breeding season experimental closure of bait sites

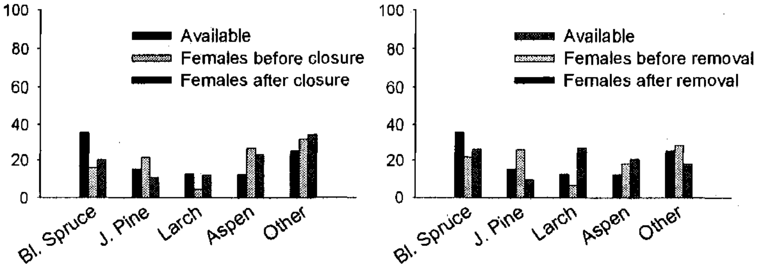
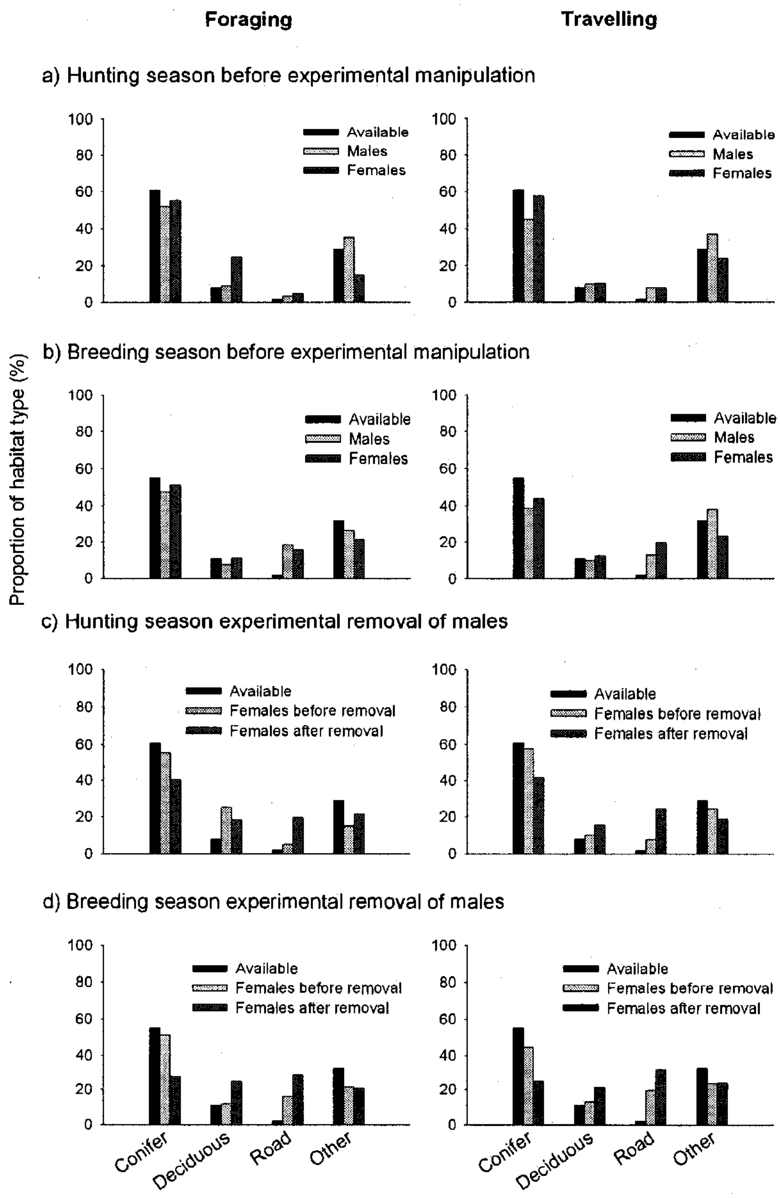


Figure 4-3: Marginal habitat selection during the spring (den emergence to June 14th) and breeding (June 15th to July 14th) seasons in CLAWR, Alberta, Canada (2002-2004) for foraging (movement rate < r_c) and travelling (movement rate $\geq r_c$) GPS radiotelemetry data from males and females with cubs where at least 1 cub survived to age 1. Resting locations were eliminated by only using locations from 7:00 to 22:00 inclusively during the spring season and locations after 3:00 during the breeding season. Available habitat was generated from 100% MCPs of all available points within the study area and by season.



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8. Appendix

8.1 Introduction

Comparison of selection patterns between groups are generally made by developing separate resource selection function (RSF) models for each group to be contrasted and then *qualitatively* comparing the direction, strength, and significance of estimated coefficients (Boyce et al. 2002, Hebblewhite et al. 2005, Mao et al. 2005). However, no method presently exists to *quantitatively* compare differences in RSFs.

In the following, we provide mathematical details on the concept, interpretation, and computation of the *quantitative* differences in selection between two groups such as males and females when we can assume that the available distribution is common to the two groups. Some previous studies have used logistic regression to compare use points of two groups (Fischer and Gates 2005, Mueller et al. 2004). However, these papers do not provide proper mathematical justification of their method. Furthermore, authors interpret coefficients in terms of odds-ratios whereas the correct interpretation should be in terms of probability ratios as shown below. The derivation here is based on the weighted distribution approach to Resource Selection Probability Function (RSPF) as developed in Lele and Keim (2006).

8.2 Latent Selection Difference functions

For pedagogical purposes, we will denote the two groups by Females (F) and Males (M). We assume that there are 'p' habitat covariates corresponding to each location. The collection of habitat covariates is denoted by $\underline{X} = (X_1, X_2, \ldots, X_p)$. Under the exponential resource selection probability function, the probability that a female will use the particular resource combination $\underline{x} = (x_1, x_2, \ldots, x_p)$ is given by:

$$\pi(x, \beta_F) = \exp(\beta_{0F} + \beta_{1F} x_1 + \cdots + \beta_{pF} x_p).$$

where the $\beta_i s$ represent corresponding selection coefficients. Similarly, probability that a male will use the particular resource combination $\underline{x} = (x_1, x_2, \ldots, x_p)$ is given by:

$$\pi(x, \beta_M) = \exp(\beta_{0M} + \beta_{1M} x_1 + \cdots + \beta_{pM} x_p).$$

The Latent Selection Difference Function (LSDF) is defined as the ratio of the probability that a particular resource combination will be used by a female versus a male when the available distribution is assumed to be common the two groups. Thus, we do not specify the exact form of the available distribution nor estimate it using a set of random points from the available distribution as was done in Lele and Keim (2006). The LSDF takes the form:

$$LSDF(\underline{x}, \beta_F, \beta_M) = \frac{\pi(\underline{x}, \beta_F)}{\pi(\underline{x}, \beta_M)} = \exp\{(\beta_{0F} - \beta_{0M}) + (\beta_{1F} - \beta_{1M})x_1 + \cdots + (\beta_{pF} - \beta_{pM})x_p\}$$

For the sake of simplicity, we use the notation: $\gamma_1 = (\beta_{1F} - \beta_{1M}), \cdots, \gamma_p = (\beta_{pF} - \beta_{pM})$.

These γ parameters can be estimated using only the 'used' GPS location data points from females and males.

8.3 Interpretation of the γ coefficients

We first start with the interpretation of the β coefficients in the exponential RSF. These coefficients tell us by how much the *probability* of selection, *not odds* of selection as sometimes interpreted in the literature (Hebblewhite et al. 2005), changes if the corresponding covariate changes by one unit. For example, an RSF with only the covariate distance to water (measured in meters) describes the probability of a bear using an area given its location to the nearest water source (i.e. selection for water). Let us suppose that the coefficient corresponding to 'distance to water' is -0.7. Then, the probability of selection reduces by 50% ($\exp(-0.7) = 0.496$) with every one meter increase in the distance from the water. This is known as relative risk in epidemiological literature (Rosner, 1994). In the case of LSD functions, we directly compute the difference in the β coefficients, namely $\gamma_1 = (\beta_{1F} - \beta_{1M}), \cdots, \gamma_p = (\beta_{pF} - \beta_{pM})$ between two resource selection functions without calculating the individual resource selection functions. Hence, the exponentiated coefficients, $\exp(\gamma_i), i = 1,2,...,p$ give us information on how the selection of one group *compares* to the reference group. This corresponds to the change in the RSF or equivalently, the difference in the relative risk. Here we provide the interpretation for 3 types of variables: (1) continuous variables, (2) categorical variables with 2 levels, and (3) categorical variables with more than 2 levels.

Continuing with the above example for continuous variables, we now compare the effect of distance to water on the selection of females versus males. Suppose, for males the $\beta_M = -0.2$ and for females $\beta_F = -0.9$. Then, $\gamma = \beta_F - \beta_M = -0.7$. The exponentiated γ coefficient, $\exp(-0.7) = 0.5$, is interpreted as 'with every one meter increase in the distance to water, relative risk of selection of such a habitat by females as compared to males is reduced by 50%. In the case of categorical variables with 2 levels (conifer (0) and deciduous (1)), $\gamma = \beta_F - \beta_M = -0.7$ would indicate that the relative risk of encountering a female compared to a male is 2 times less likely in deciduous stands compared to conifer stands. When a categorical variable has more than 2 levels, the interpretation is slightly different because the comparison is done in relation to a reference category (ratio) and is influenced by the other levels of the variable. For example, if a variable has 3 levels (spruce, aspen, and larch) and spruce is the reference category, then $\gamma = \beta_F - \beta_M = -0.7$ for aspen indicates that the relative risk of a female selecting for aspen stands compared to spruce stands is 2 times less likely than male selection. Coefficients from categorical variables with more than 2 levels should be interpreted with caution because significance could be a result of differences in the ratio of the reference category (between females and males) and not just due to the category of interest. Furthermore, biological relevance of significant covariates should be interpreted with information on use because significant differences in coefficients can occur even if certain habitat types are rarely used.

8.4 Estimation procedure

Step 1: Code one of the groups (e.g. females) as '1' and the other group (e.g. males) as '0'.

Step 2: Conduct a standard logistic regression analysis using any of the standard statistical packages such as STATA, SPSS or SAS.

Step 3: The estimates of the logistic regression coefficients are equivalent to the estimates of the parameters $\gamma_i, i = 1,2,\ldots, p$.

8.5 Statistical justification for the estimation procedure

Following the results of Gilbert et al. (1999) and Lele and Keim (2006), we can show that the above procedure yields maximum likelihood estimators for the non-intercept parameters $\beta_{iF} - \beta_{iM}, i = 1,2,\dots, p$. We assume that data are obtained under a use/available study design.

Let $X_{iM}, i = 1,2\dots,n$ denote the data set corresponding to the used points for males and $X_{iF}, i = 1,2\dots,m$ denote the data set corresponding to the used points for females. The likelihood function using the weighted distribution formulation described in Lele and Keim (2006) can be written as:

$$
\begin{aligned}
\prod_{i=1}^{n} f^{M}(x_{iM}) \prod_{j=1}^{m} f^{F}(x_{iF}) &= \prod_{i=1}^{n} \frac{\pi(x_{iM},\beta_M) f^{A}(x_{iM})}{P(\beta_M)} \prod_{j=1}^{m} \frac{\pi(x_{iM},\beta_F) f^{A}(x_{iM})}{P(\beta_F)} \\
&= \prod_{k=1}^{n} \frac{\dfrac{\pi(x_k,\beta_M) f^{A}(x_k)}{P(\beta_M)}}{\alpha \dfrac{\pi(x_k,\beta_M) f^{A}(x_k)}{P(\beta_M)} + (1-\alpha) \dfrac{\pi(x_k,\beta_F) f^{A}(x_k)}{P(\beta_F)}} \\
&\times \prod_{k=n+1}^{m+n} \frac{\dfrac{\pi(x_k,\beta_F) f^{A}(x_k)}{P(\beta_F)}}{\alpha \dfrac{\pi(x_k,\beta_M) f^{A}(x_k)}{P(\beta_M)} + (1-\alpha) \dfrac{\pi(x_k,\beta_F) f^{A}(x_k)}{P(\beta_F)}} \\
&\times \prod_{k=1}^{m+n} \alpha \frac{\pi(x_k,\beta_M) f^{A}(x_k)}{P(\beta_M)} + (1-\alpha) \frac{\pi(x_k,\beta_F) f^{A}(x_k)}{P(\beta_F)}
\end{aligned}
$$

The first term in the above product can be written as:

$$\prod_{k=1}^{n} \frac{\dfrac{\pi(x_k,\beta_M) f^A(x_k)}{P(\beta_M)}}{\alpha \dfrac{\pi(x_k,\beta_M) f^A(x_k)}{P(\beta_M)} + (1-\alpha)\dfrac{\pi(x_k,\beta_F) f^A(x_k)}{P(\beta_F)}} = \prod_{k=1}^{n} \frac{\dfrac{\pi(x_k,\beta_M)}{P(\beta_M)}}{\alpha \dfrac{\pi(x_k,\beta_M)}{P(\beta_M)} + (1-\alpha)\dfrac{\pi(x_k,\beta_F)}{P(\beta_F)}}$$

$$= \prod_{k=1}^{n} \frac{1}{1 + \dfrac{(1-\alpha)}{\alpha}\dfrac{P(\beta_M)}{P(\beta_F)}\dfrac{\pi(x_k,\beta_F)}{\pi(x_k,\beta_M)}}$$

$$= \prod_{k=1}^{n} \frac{1}{1+\exp(\gamma_0 + \gamma_1 x_{ik} + \cdots + \gamma_p x_{pk})}$$

Similarly the second term can be written as:

$$\prod_{k=n+1}^{n+m} \frac{\dfrac{\pi(x_k,\beta_F) f^A(x_k)}{P(\beta_F)}}{\alpha \dfrac{\pi(x_k,\beta_M) f^A(x_k)}{P(\beta_M)} + (1-\alpha)\dfrac{\pi(x_k,\beta_F) f^A(x_k)}{P(\beta_F)}} = \prod_{k=n+1}^{n+m} \frac{\dfrac{\pi(x_k,\beta_F)}{P(\beta_F)}}{\alpha \dfrac{\pi(x_k,\beta_M)}{P(\beta_M)} + (1-\alpha)\dfrac{\pi(x_k,\beta_F)}{P(\beta_F)}}$$

$$= \prod_{k=n+1}^{n+m} \frac{1}{1 + \dfrac{\alpha}{(1-\alpha)}\dfrac{P(\beta_F)}{P(\beta_M)}\dfrac{\pi(x_k,\beta_M)}{\pi(x_k,\beta_F)}}$$

$$= \prod_{k=n+1}^{n+m} \frac{1}{1+\exp\{-(\gamma_0 + \gamma_1 x_{ik} + \cdots + \gamma_p x_{pk})\}}$$

where $\gamma_0 = (\beta_{0M} - \beta_{0F}) + \log\{\frac{(1-\alpha)}{\alpha}\frac{P(\beta_M)}{P(\beta_F)}\}$, $P(\beta_M) = \int \pi(x_k,\beta_M) f^A(x_k) dx_k$ and

$P(\beta_F) = \int \pi(x_k,\beta_F) f^A(x_k) dx_k$.

To obtain the maximum partial likelihood estimators of the γ parameters, we only need to maximize the product of the first two terms in the full likelihood (Glibert et al. 1998). This can be achieved by using standard Logistic regression packages following the algorithm described earlier because the partial likelihood of the LSDF derived above is identical to the likelihood function of a logistic regression. Because of this relationship, as is the case with RSFs, other options such as case-control logistic and random-intercept logistic regression are not appropriate to estimate parameters for LSDFs. The intercept parameter obtained through this procedure is biologically meaningless and hence uninterpretable.

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Chapter 5: General Conclusion

1. Management implications of research results

The initial impetus for this research was the concern that hunting may indirectly increase cub mortality because of disruption to the male social structure and result in increased encounters of females with infanticidal males. Based on results from population comparisons, I found no evidence to support a strong effect of sexually selected infanticide (SSI) on bear demographics (Chapter 2). Furthermore, habitat selection results revealed that resident male bears in an unhunted population are considered a threat by adult females with cubs of the year and influence their spring and early summer resource selection (Chapter 4). Therefore, even if hunting did increase SSI, this effect was minimal compared to the density-dependent response of reducing a population below carrying capacity (K).

As predicted, cub mortality was higher in the unhunted population approaching K. Based on litter sizes and female body condition, my data is most consistent with the hypothesis that the majority of cub mortality is due to infanticide by either male or female bears (Chapters 2-4). Infanticide by bears has been widely reported in the literature (McLellan 1994, Miller et al. 2003) and generally males appear to be responsible for the majority of deaths (Lecount 1982, Garshelis 1994) but females also kill cubs (LeCount 1987, Garshelis 1994, Hessing and Aumiller 1994). Although the lack of an indirect effect of increased infanticide in response to hunting will be seen as a positive result by many hunters and managers, I hope that this result will not take away from the importance of considering other effects of harvest when managing hunted species.

The goal of this work was never to enter into a debate about the pros and cons of hunting, but to offer field-based scientific information for stakeholders to better understand the consequences of various management regimes. Generally, management plans are area-specific and have goals based on land designation (park, crown land, etc.) and public opinion (general public, anti-hunters, hunting community, First Nations). With this in mind, I present below the implications of my research based on the 3 most likely scenarios encountered by wildlife managers. I address management implications within the context of my research results. Therefore, readers should keep in mind that demographic responses presented are consistent with other North American bear research but proposed mechanisms are based on observed behavioral patterns and have not been replicated. Although I consider it responsible on my part to provide readers with this note of caution, I believe that that my results are reasonably substantiated to make this interpretation a starting point to understanding mechanisms of density dependence in bears and to further behavioral research and hypothesis-driven experimentation.

1.1 No harvest areas

Areas with no harvest are critical to understanding bear social dynamics, the natural regulation of populations, and as a baseline reference to untangling the effects of perturbations. Based on my results, density-dependent effects of demographic parameters affect bears similarly to other species (Fowler 1981, 1987). Specifically, at high densities approaching K, populations will have an older age structure and will exhibit higher cub mortality and a lower age of primiparity compared to populations in similar habitats where densities have been reduced (Chapter 2).

Although this demographic pattern is consistent with other research on brown bears in Alaska (Miller et al. 2003) and Yellowstone (Schwartz et al. 2006), the mechanism producing higher cub mortality rates and an older age of primiparity in populations approaching K is unclear. Although anecdotal, it appears that female competition could be responsible for the older age of primiparity. Female reproduction is determined by nutritional condition and habitat characteristics and male avoidance cannot explain why some females in the high density area were able to gain enough weight to reproduce while others did not (Chapter 2).

Similarly, female spatial movement patterns are most consistent with a response to the density of female neighbors (Chapter 3). My results show that females in an unhunted population approaching K have smaller home ranges and may be more territorial than females in a hunted population, particularly during the spring and early summer when most cub mortality occurs (Chapter 3). Therefore, cub survival rates may be further reduced in unhunted areas depending on the spatial configuration and availability of early summer foods. Situations where females with cubs cannot spatially segregate themselves from males within their home range and meet their nutritional requirements could further increase cub mortality rates (Chapter 4).

In areas where management goals are to increase population numbers it may be advisable to monitor sex-specific habitat use during the period when cubs are most vulnerable. Such an exercise may reveal potential habitat management possibilities that could increase sexual segregation and reduce cub and adult female mortality rates. Conversely, the removal of a small number of problem bears from high-density areas should have little or no effect on the demographic parameters of the remaining bear population.

1.2 Liberally hunted areas

I define liberally hunted areas as those where sustained hunting pressure has reduced male and female populations below K. In most jurisdictions, hunting pressure is directly related to demand and ease of accessibility because there are no limits placed on the number of permits sold, only on the number of bears per permit. Therefore, throughout most of Canada, liberally hunted areas would include most Crown land where access for motorized vehicles exists, particularly areas where baiting is permitted. Generally, the management goals for these areas are either to sustainably maximize hunting opportunities or to reduce bear numbers within the context of a predator control program.

A major difference between hunting management for bears and ungulates is the lack of sex- and age-specific harvest strategies for bears despite the fact that ursids have relatively low reproductive rates. Generally, the only restriction for permit holders is the protection of females with cubs (Williamson 2002). More specific hunting licenses are simply not feasible because of the difficulty in differentiating the sexes and estimating weight. Thus, the sex-ratio of hunted bears is entirely based on hunter selection and experience. This situation presents a challenge to managers because they are unable to set sex-specific quotas and sex-ratios in the harvest are not necessarily representative of the population (Kohlmann et al. 1999).

For areas managed primarily for harvest, managers generally seek strategies to maximize hunting opportunities while mitigating potential negative effects of hunting. Results from Chapter 2 show that bear populations below K can be managed with estimates of demographic parameters without accounting for potential indirect effects of removing individuals. However, results from demographic (Chapter 2) and movement analyses (Chapter 3) suggest that cub survival and potentially the age of primiparity may not show a density-dependent response unless female density is reduced.

In liberally hunted areas, female density will probably be reduced sufficiently to release reproductive parameters from density-dependent constraints even though hunters generally target trophy males (adult females unaccompanied by young are difficult to differentiate from males). For example, in Manitoba, females represented approximately 30% of the annual harvest and most were in their reproductive years (mean age = 7.06 years, Hristienko et al. 2004). Therefore, in the case of bears where managers cannot enforce sex and age hunting restrictions as in ungulates (antler and curl size), a more indirect approach is required. Estimates of reproductive parameters and approximations of bear densities should be sufficient to maintain bear numbers at target levels. However, more refined strategies could aim to increase productivity and should consider the potential longer-term evolutionary consequences of harvest.

In terms of productivity, given that female density will be reduced regardless of the hunting regime, management options should favor circumstances that reduce the number of highly productive older adult females in the harvest. Although females with cubs are protected in most jurisdictions, they are vulnerable and easily confused with adult males every other year on average. Therefore, the most selective harvest would only be possible in the spring when females are accompanied with cubs or yearlings on the verge of dispersal (or 2 and 3 year old cubs in brown bears) and hunters would have an increased likelihood of identifying adult females and could be encouraged not to hunt them. Refraining from hunting females with yearlings should be most stressed when they are accompanied with large litters. Some females may be genetically 'better' breeders (Swenson pers. comm.) and maintaining these individuals in the population should be highly encouraged.

From an evolutionary perspective, managers should implement harvest regimes that mimic natural mortality patterns (Milner et al. 2006) thus reducing the impact of sport hunting on game species (Festa-Bianchet 2003). However, encouraging hunters to target younger animals is not an option for most game species including bears where adult males are of highest economic value. A more feasible alternative would be to target the female segment of the population for such mitigating measures and encourage management options that would reduce the number of older females in the harvest. Beyond the advantages of productivity mentioned above is the possibility older mothers would be more typical of unperturbed populations where the age of primiparity and survival age are greater. In females, longevity is the most important factor influencing lifetime reproductive success (Bérubé et al. 1999) but harvest can create conditions where selection favors high maternal investment at the expense of maternal survival (Festa-Bianchet 2003, Proaktor et al. 2007). If the goal of wildlife management is to encourage policies that promote the expression of the full range of animals behavioral patterns (Singh and Kaumanns 2005), then creating conditions that would increase the mean age of females on the landscape should be a priority.

Reducing the number of adult females in the harvest would best be achieved by hunter education and promoting spring harvests when adult females are least likely to be confused with males. Although spring hunting is controversial because of the potential for cub orphaning when lactating females are accidentally killed (Ontario), Hristienko et al. (2004) showed that orphaning represents approximately 2% of annual cub mortalities. These accidental takes could further be reduced through hunter education by encouraging hunting sites in the best quality habitats where females are less likely to occur than males. Therefore, when debating the pros and cons of spring bear hunts, stakeholders should weight the advantages of reducing accidental orphaning over policies that would increase productivity and reduce the potential negative evolutionary consequences of harvests.

1.3 Trophy hunted areas

I define trophy hunted areas as those where hunting pressure is low and targeted at large trophy males leaving female density relatively untouched. This situation would be expected in more remote areas with limited access, particularly those where baiting is prohibited (lower success rate). In these areas, managers should expect an older high-density female population and an annual disruption/turnover of the male segment of the population.

The annual removal of a low number of males from a population should not have any indirect effects on reproduction and cub survival (Chapter 2). However, managers should keep in mind that these demographic parameters may be held at low levels because of the high density of animals and the increased likelihood of females encountering adult males (Chapter 3). Furthermore, potential habitat management schemes to increase sexual segregation and increase cub survival may not be as successful as in lower density areas because of the small spring and early summer home ranges of females (Chapter 4).

2. Suggested further research

A consistent pattern in my analyses of demographics, movement, and habitat selection is the apparent importance of female density and not necessarily population density in driving female reproduction (Chapter 2) and movement (Chapter 3) patterns. Given the promiscuous mating system and therefore sex-specific mechanisms to maximize fitness, it is not unreasonable to consider that demographic parameters may be influenced more by the density of the same sex than of the opposite sex. In fact, a long-term stud y of red squirrels (Sciurus vulgaris) found several demographic parameters to be dependent on the density of the same sex but not on the density of the other sex (Wauters et al. 2004). Therefore, I believe that comparisons where demographic parameters and movement patterns are examined with regard to within-sex density should be an important component of future bear research.

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Chapter 6: Appendix - Tube traps and rubber padded snares for capturing American black bears

1. Introduction

American black bears are most commonly captured using either culvert traps or Aldrich traps for foot snares. Culvert traps are ideal in high human-use areas because they protect the public and allow for the easy transport and relocation of problem bears. However, the large-scale use of these traps for research purposes in more remote areas is not practical for reasons of cost and mobility. The Aldridge trap addresses these issues and has proven a very popular and successful design for capturing bears in a diversity of field situations (Johnson and Pelton 1980). However, the Aldridge trap may have a relatively slow trigger depending on the dimensions of the spring which could increase the likelihood of toe captures and prevents the trap from being buried and hidden from the bear's view.

Rolland Lemieux designed the L-83 trap in 1983 to improve upon the Aldridge design (Jolicoeur and Lemieux 1984) and won the 1988 Ontario Trapper's Association Innovation prize. The L-83 is presently endorsed by the Quebec Trapper's Association. This trap has a more powerful spring and a long lever which reduces the number of toe captures. Also, the trap can be completely concealed with a substantial amount of vegetation without affecting the performance of the snare. When trapping in the boreal forest, the snare and trap can be covered with 10-20 cm of wet moss and not affect performance. Another advantage of the L-83 is the flexibility to use a larger diameter snare than is used with the Aldridge trap thus decreasing the likelihood of a large bear stepping on or beside the snare.

Both the Aldridge and L-83 traps have the disadvantage of being relatively unselective. Non-target species can set off the snare leaving it non-functional until it is reset. There is always the possibility of injuries when trapping which is of particular concern when non-target endangered species are present in the area. Reagan et al. (2002) designed a passively-triggered foot snare from PVC (polyvinyl chloride) pipe which reduced the capture of non-target species. However, the ratio of caught bears to triggered traps was only 0.20. This trap also requires digging a hole which could be problematic in certain study areas.

Most bear injuries are caused by the restraining mechanism (i.e. the snare linked to either a fixed attachment or drag) and not the trap (the mechanism that projects the snare). Snares can cause swelling and lacerations around the restrained area, and constant tugging by captured animals has the potential to cause fractures, muscle, tendon, nerve, and joint injuries. Public scrutiny concerned with the suffering of animals has placed increased pressure on the scientific community to continually improve capture methods and establish standards (Gilbert 1991). Our objective was to design a trap and restraining mechanism that would reduce the chance of injury and the capture of non-target species while not sacrificing efficiency. The RL04 is the latest in a series of bear traps and restraining mechanisms developed with these objectives in mind. Several prototypes were designed and tested before the development of the RL04 (Lemieux and Desrosiers 2001). However, these traps were built from plastic 20-L pails making them fragile and prone to destruction from captured bears. In this paper, we describe in detail the RL04 trap and accessories which we believe to be a significant improvement over previous designs in both performance and injury prevention.

2. Study area

We tested RL04 traps in 2 study areas in Canada. The first study area was located in the Cold Lake Air Weapons Range (CLAWR), a military zone operated by the Canadian Armed Forces in northeastern Alberta, and an adjacent area north of the CLAWR border (Conklin). Hunting and public access are prohibited in the CLAWR and all entry points to the area are monitored. Although logging operations are not permitted within the CLAWR, the oil and gas sector is very active and has constructed an extensive network of cutlines throughout the area. Most of this 5,100 km^2 landscape consists of mixed-wood boreal forest composed of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca,*), and balsam fir (*Abies balsamea*) at higher elevations. Black spruce (*Picea mariana*), tamarack (*Larix laricina*), and muskeg characterize lower elevations. Stands of jackpine (*Pinus banksiana*) are dispersed throughout the area where sandy soils are present. We captured bears in this area as part of a University of Alberta black bear study.

The second study area was located in the Laurentide Wildlife Reserve 100 km north of Quebec City, Quebec. The area trapped was located in the center of the reserve at 800 m of elevation. Forestry operations have been active in this area and have generated an extensive network of gravel logging roads. The forest is boreal, and cover is dominated by black spruce and balsam fir with trembling aspen regenerating in cutblocks. We captured bears in this area as part of a Quebec Ministry of Natural Resources, Wildlife, and Parks caribou study.

3. Methods

3.1 RL04 trap specifications

The body of the RL04 trap consists of a 51-cm long PVC pipe (Royal Seal PVC 12454 type PMS SDR35) with a 20-cm diameter (0.7-cm wall thickness) (Figure 6-1). To close one end of the pipe, we drilled three 6.4-cm steel-plated roofing screws equidistantly into the pipe 2.0 cm from the edge. Then, a circular piece of tight-fitting plywood was placed on the screws to seal the opening (Figure 6-1-A). Finally, we spread a thick layer of epoxy between the plywood and the end of the pipe to create a sturdy plug.

The trigger consists of a 2.54 x 1.27-cm wire screen (17 x 17-cm grid size) with rounded edges to fit within the pipe (Figure 6-1-B). We removed several mesh squares so bears could easily grab the trigger with their claws. We left 1 to 2 cm of space between the wire screen and the pipe wall to allow the screen to tilt easily within the pipe. A 7.3-cm long nail, bent at a 90° angle and welded to the top of the screen, served as the attachment point for the spring. Finally, we welded the mesh trigger to a hinge fastened to the inside of the pipe 8-cm from the plywood plug.

Once the trigger was installed, we used a jig saw to cut a series of slits in the pipe (Figure 6-2). The first slit, a 1.0 x 3.0-cm wide oval slit located above the bent nail, provides an entry point for the spring to connect to the nail of the trigger. The second slit, a 2-cm wide T-shaped incision cut at the open end of the pipe, along the same lengthwise axis as the first incision, enables the snare to link properly to the trigger (Figure 6-1-C).

The shorter section of the T-shape opening allows the snare to tighten within the pipe, while the longer section allows the bear to retract his restrained paw from the trap. The last set of slits are 2 narrow 10-cm long incisions cut 7.5-cm from the open edge of the pipe on either side of the T-shaped incision (Figure 6-1-D). The width of these slits is later adjusted to make a tight fit with the rubber pieces of the snare thus securing it tightly along the inside wall of the pipe and making it less visible to the bear. The last component of the RL04 trap is a 40-cm long and 1.5-cm wide spring to which we attached a 3.8-cm S-hook (Figure 6-1-E). The snare and S-hook connect to the nail of the trigger (Figure 6-1-F).

3.2 Restraining mechanism

The snare used in the RL04 trap was designed so that the expanded loop fit precisely within the PVC pipe and the extremity extended to the trigger device. A longer or shorter snare would prevent the trap from operating properly. The snare for the RL04 consists of 2 separate sections of wire (75.0 and 27.5 cm in length) joined by 0.635-cm galvanized-steel swivels with 386 kg of rupture strength (Figure 6-3). We used 0.20 cm swivels in our original snares, but after 2 of them were broken by captured bears, we replaced all swivels with the larger model described above, and none were broken in subsequent captures. The snare cable is 0.476 cm in diameter and constructed of 7x19 wire with 1900 kg of rupture strength. This cable is more rigid and frays less than the 7x7 aviation cable often used for snare assembly. All cables pieces were electrocut to prevent fraying from the extremities.

We used the Mikin BL02 (Figure 6-3 insert) on all bear snares. This lock is 5.5-cm long and made of 4-mm thick steel bent at a 110° angle with holes drilled at either end. The hole, in the shorter 2-cm arm of the lock, has a diameter slightly larger than the cable whereas the longer 2.5-cm arm has a larger hole. This design allows for a more rapid tightening of the snare. All rough edges and corners of these locks are rounded and polished to reduce chaffing and cuts to the limbs of restrained animals.

We assembled snares taking into account the natural curvature of the cable for the main loop of the snare (Figure 6-3). First, we bent the cable 8 cm from one end in the opposite direction of its natural curve. Next, we inserted a 1-cm long and 0.6-cm wide piece of rubber tubing followed by the BL02 lock using the larger of the 2 holes. A 3-cm aluminum sleeve closed the loop with the lock; the loose end of the cable was pushed completely within the sleeve to prevent cuts from the extremity of the cable. We polished the aluminum sleeve and covered it with rubber tubing to further reduce abrasions. Once completed, the elbow of the lock faced the outside of the snare. Then, we alternately strung 1-cm long rubber pieces of 0.50 and 0.60-cm diameter through the open end of the cable ending with a larger diameter piece which secured the snare within one of the slits in the trap (Figures 6-1 and 6-2). We used 19 rubber pieces for black bears to avoid skin contact with bare wire of the snare. Finally, we threaded the snare cable through the smaller hole of the BL02 lock and attached the cable to a swivel using a 3.0-cm long sleeve.

For the second part of the snare, we used the shorter 27.5-cm long cable (Figure 6-3). We attached one end of the cable to the swivel (described above) using a 3.0 cm long sleeve and attached a second swivel to the other end of the cable. We used a 0.635-cm long zinc-plated quick-link to connect the snare to the drag chain.

We custom designed drags from a 120-cm long and 17-mm thick steel rod twisted to take on the shape of an anchor (Figure 6-4). Once formed, the drag was 39-cm wide by 39-cm long and weighed 3 kg. The tips of the drag were cut diagonally and twisted to increase resistance when pulled through vegetation. We attached the drag to a 3-m of chain (0.635-cm diameter and 477 kg of resistance) with a quick-link. The length of the chain can be adjusted based on the density of vegetation in the trapping area; the longer the chain the faster the animal is likely to get tangled.

The last component of the restraining mechanism is a 35-cm long Mikin SA03 shock absorber (Figure 6-4 insert). We fastened one end of the shock absorber to the 3-m chain and drag. We fastened the other end to 30-cm of chain and the snare (Figure 6-4). The shock absorber is made of steel, has 18 coils, and has an external diameter of 3.66 cm. The design is closed at both ends to prevent bears from pulling it apart.

3.3 Installation

Installation of the RL04 trap requires 3 trees forming a tight triangle. Ideally, the pipe would fit snugly between 2 of the trees, and the back of the trap should have slight contact with the third tree (Figure 6-5). When a perfect fit could not be located in the area, we selected a tighter triangle of trees and thinned the front trees to fit the pipe. We nailed 2 pieces of wood (Figure 6-5-A) lateral to and 85 cm from the ground on either side of the 2 front trees. The pipe should fit between the trees with the T-incision facing up. Using 6.4-cm steel-plated roofing screws, we secured the pipe to each of the lateral pieces of wood and the 2 front trees. Next, we secured the pipe from above by nailing a third piece of wood (Figure 6-5-B) diagonally between the two front trees. We attached the spring to another piece of wood with a tie-rap and nailed the wood behind the 2 front trees 1.10 m above the pipe. To protect the spring and trigger from curious bears, we nailed 2 pieces of wood (Figure 6-5-C) across the 2 front trees above the pipe. A 20-cm space left between the trap and the lower piece of wood (Figure 6-5-D) permitted the snare to slide freely until it was fully tightened. Lastly, we covered the back of the trap with trees to encourage bears to visit the front end of the pipe (Figure 6-6). During trap installation, we placed bait bags (a mixture of sweet cookies, molasses, and honey in transparent 10 L bags each weighing approximately 1 kg) behind the mesh trigger and sprayed them with anis oil; sometimes, we placed an additional bait bag at the front of the trap (Figure 6-6). We sprayed seal blood and oil onto trees during daily trap visits to attract bears to the sites.

We activated the trap by first attaching the spring to the bent nail of the trigger (Figure 6-1-F). Next, we hung the quick-link in the snare end of the shock absorber on a nail placed 34 cm above the pipe on the left side of the front-right tree (Figure 6-5-E). This prevented the spring from having to lift the drag when tightening the snare. Lastly, we placed the snare inside the pipe with the rubber pieces squeezed into the long slits and connected the snare to the trigger with a #14 non-galvanized steel rod pressed into a 6-ure 8 (Figure 6-1-F). Thus, when a bear pulls on the screen, the nail is released from the S-hook activating the spring to tighten the snare around the bears paw.

In both study areas, when possible, we selected dense black spruce stands so bears would get tangled in shady and humid areas with little human activity. All traps were checked daily.

4. Results

Between 2001 and 2005, we trapped 304 bears in the CLAWR and Conklin areas in rubber-padded snares using a variety of bucket-type trap designs and L-83 traps. Injuries included 1 bear killed by another bear while in a snare and 12 bears (4%) with surface cuts smaller than 1 cm located where the lock rubbed against the paw. Snares were attached to drags unless there were tall trees in the surrounding area. In such circumstances, the restraining mechanism was tied around a large tree leaving just enough chain length to allow the shock-absorber to function properly. We did not measure the distances traveled by bears with drags, but we estimate the average distance to have been 10 m from the trap site. The longest distance any of the bears moved with the drags was approximately 20 m.

Bears were trapped in the CLAWR using the RL04 trap from September 1 to 10, 2004. Forty traps were set along a 40-km stretch of gravel road at approximately 1-km intervals alternating between the east and west side of the road. This area was previously trapped with plastic bucket traps (Lemieux and Desrosiers 2004) and L-83 traps (Jolicoeur and Lemieux 1984) in 2001 and 2002. Therefore, many of the bears in the area had been handled more than once. We trapped 11 bears including 6 bears captured in previous years. Nine bears were captured using the RL04 trap whereas 2 of the previously trapped bears were captured with the L-83 traps that were set after the RL04 traps had been ripped out from between the trees (Table 6-1). There were no capture-related injuries from either trap (i.e., cuts, broken teeth, etc.).

Trapping occurred in the Laurentide reserve from May 20th to June 5th, 2005 (session 1) and June 17 to 23, 2005 (session 2). During the first capture session 30 RL04 traps were set and 12 bears were captured; 2 were bears trapped the previous year with different trap designs, and 3 had been captured that spring. During the second capture session, we set 30 RL04 traps and captured 15 bears, 3 of which were bears captured that same year. The only visible injury observed during either capture session was minimal swelling of restrained paws.

In 2 instances, bears ripped RL04 traps out from between the trees to extract the bait and avoided being captured. In both cases, we verified that these were bears that had previously been captured, by capturing them the subsequent day using L-83 traps with a well camouflaged snare. None of the extracted RL04 traps had damage beyond claw marks, and all silicone plugs withstood the bear attacks. Due to the distance between the snare and the trigger, and the speed of the spring, all captured bears had snares tightened proximal to the metacarpal pad of the front paw. Except for these 2 instances, every triggering event of an RL04 resulted in capture of a bear.

5. Discussion

We found the RL04 trap to be very successful in capturing bears. Several bears previously captured in bucket sets were recaptured with the RL04, possibly because of the lack of a lid and a better camouflaged snare; lids with cut out holes were used in previous plastic bucket sets in both study areas (Lemieux and Desrosiers 2001). Similarly to the Reagan trap (Reagan et al. 2002), the RL04 prevented non-target species from triggering the traps due to either the height of the pipe in the tree (e.g., coyotes [*Canis latrans*], foxes [*Vulpes vulpes*], wolves [*C. lupus*]) or the resistance of the elastic on the mesh (e.g., squirrels [*Tamiasciurus hudsonicus*?, martens [*Martes americana*]). Small mammals are unlikely to be able to trigger the trap because it requires a strong tug to be activated. If this were to occur, the distance between the trigger and the snare is likely long enough to prevent the capture of animals such as martens and fisher. We did capture fishers (*M. pennanti*) around their waist with previous bucket designs, however the rubber-padded snares prevented suffocation and all were successfully released.

Another problem encountered with bucket-type designs is the capture of cubs by the neck. We captured 4 cubs by the neck with previous bucket designs because they were able to trigger them with their head. In these cases, the rubber-padded snares prevented strangulation and we were able to release the animals. Initial triggers used in some of our bucket designs were very sensitive and were activated when they were pushed. The mesh trigger in the RL04 trap requires a significant amount of force to be activated and needs to be pulled which is difficult for a bear to do with its teeth because of the mesh design (the trap will not be activated if the animal pushes on the mesh trigger). Bears are quite ingenious and our sample sizes are relatively small so we acknowledge that although we did not encounter such problems during our trapping sessions they may occur and further modifications may be required. However, we believe that this trap design significantly reduces the likelihood of trapping cubs by the neck. Furthermore, the use of rubber-padded snares should prevent strangulation for cubs managing to trigger the trap with their teeth. Larger bears are not able to trigger the trap with their head due to the distance between the mesh trigger and the trap opening (43 cm).

The fact that only bears could disturb the trap significantly increased the number of trap-nights that sets were operational for and reduced the amount of bait needed. Other advantages of the RL04 trap are simple assembly, low cost because a commercial trap is not required for the trigger, and the elimination of hind-foot captures. Hind-limbs have a smaller range of motion than fore-limbs and could potentially sustain more severe injuries if a bear is fighting to get free. Most importantly, the trigger is fast enough to tighten before the bear is able to retract its paw, yet gentle enough that a person can set off the trigger with a bare arm and not receive any bruising from the snare tightening.

We believe the use of rubber-padded snares was the most important innovation of the RL04. Snare-related injuries are best reduced my minimizing the time animals are restrained. However, bears trapped at night can spend many hours in a snare before being released and could benefit from any modification reducing the constriction and abrasiveness of the snare. The use of varying sizes of rubber pieces minimizes the surface area of the snare squeezing the paw of the bear and thus potentially reduces swelling. Only 4% of captured bears exhibited small 1-cm cuts due to contact with the lock of the snare (Figure 6-3, insert). All injured bears were captured with the L-83 which have more powerful springs to tighten the snare than do bucket sets and RL04 traps. We have no measurements comparing the swelling of paws with and without padding on the snares, however swelling appeared to be reduced compared to previous captures with bare-wire snares. In most cases, it was difficult to identify which foot had been restrained once the snare was removed. Having previously captured bears with non-padded snares, we found a substantial improvement in the condition of restrained paws in rubber-padded snares (cuts and chaffing). Initially, we had concerns about charging bears slipping out of the snares. However, after over 350 captures with padded snares this has never occurred. We would encourage all researchers and wildlife officials involved in black bear captures to experiment with this design.

Bears are extremely powerful animals, and when captured, have the potential to injure not only the restrained area but to inflict serious damage to limbs and joints (e.g., broken bones, dislocations, pulled muscles, nerve damage). We used drags at all trap sites unless there was a danger of bears climbing tall trees because we believe they offer several advantages over fixed-point attachments. Firstly, captured bears are able to travel away from the trap site thus leaving the installation intact and significantly reducing the time necessary to reset the trap. Secondly, bears can retreat away from the capture site which may reduce stress, particularly for animals trapped for the first time. In general, we found that bears restrained at the trap site caused more damage to the surrounding area than bears on drags. In fact, bears captured with drags were often found sleeping and only became destructive when discovered. Thirdly, drags can dampen the strain on the limbs of a bear by acting as a shock-absorber when tangled in the vegetation. The Mikin SA03 shock absorber can act either in consort with the drag or provide most of the elasticity when an animal is tangled. However, we did not specifically measure stress levels and have no data comparing injury rates between bears restrained with drags versus solid anchors so these comments are based only on personal observation. Lastly, when tying the restraining mechanism to a tree in areas with tall trees, the drag served as an additional safety restraint in case the bear were to fell the tree. Using only a fixed-point attachment was a concern in our boreal study areas where large diameter trees were rare. We acknowledge that the use of drags is a controversial issue and that many researchers prefer to use solid anchors as a safer alternative for capture crews, particularly where capturing grizzly bears (*Ursus arctos)* is a possibility. For this reason, we recommend that traps with drags be set in areas with low human use and only by experienced field staff as more precautions are necessary during trap visits.

We found the RL04 trap easy to install. Two people can build and set the trap in approximately 20 minutes once an appropriate trap site is located, less time than we required to set up a ground snare and build a cubby for the bear to approach the trap from the appropriate angle. Although we developed this trap for American black bears, it could be modified for any sized bear by adjusting the diameter of the PVC tube, the distance between trigger mesh and snare, and strengthening the snare components. It would also be possible to use this trap with scented lures instead of bait. We did not test using lures only with this trap design but would suggest placing small branches sprayed with lures behind the mesh trigger to create the illusion of bait; we have trapped several bears in other bucket trap designs using only anise oil and branches when bait was not available.

It is important for traps to keep evolving so as to minimize as much as possible potential injuries to bears and non-target species. We hope that these designs and some of the lessons we've learned may be of use to other researchers and that they will spawn further developments.

Table 6-1: Age, Sex, and weights of American black bears captured using the RL04 trap with rubber-padded snares in 3 trapping sessions in Quebec and Alberta, Canada.

	Bears from all areas combined	
	Males (n)	**Females (n)**
Total captures	20	18
Total unique bears	14	17
Mean weight (kg)	78 (14)	62 (17)
Range of weights (kg)	29-140 (14)	40-100 (17)
Mean age (yrs)	6 (14)	8 (12)
Range of Ages (yrs)	1-12 (14)	2 -24 (12)

Figure 6-1: The RL04 tube trap is constructed of PVC tubing closed at one end with plywood and epoxy (A). Bait is placed between the plug and a mesh trigger fastened to the tube with a hinge (B). The snare is fastened to the trigger and extends into the tube through a T-incision (C) where it is squeezed into slits (D). When a bear pulls on the trigger, the extended spring (E) shortens and tightens the snare.

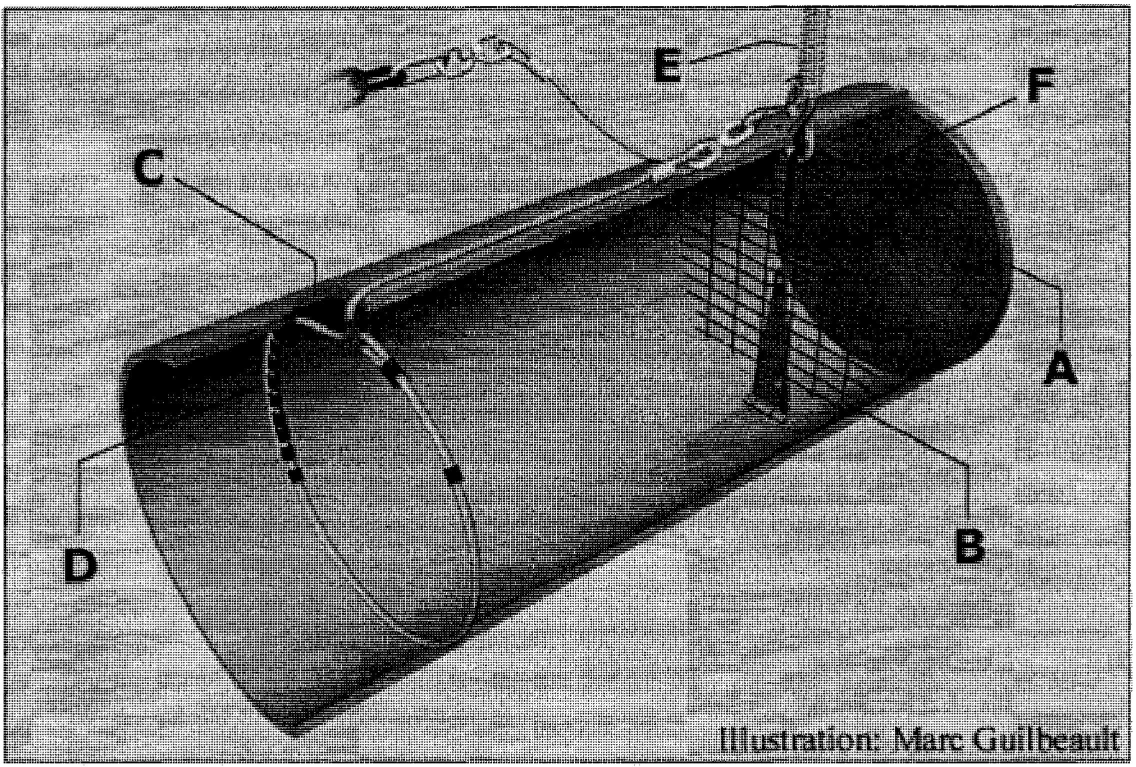

Figure 6-2: RL04 trap design measurements in cm.

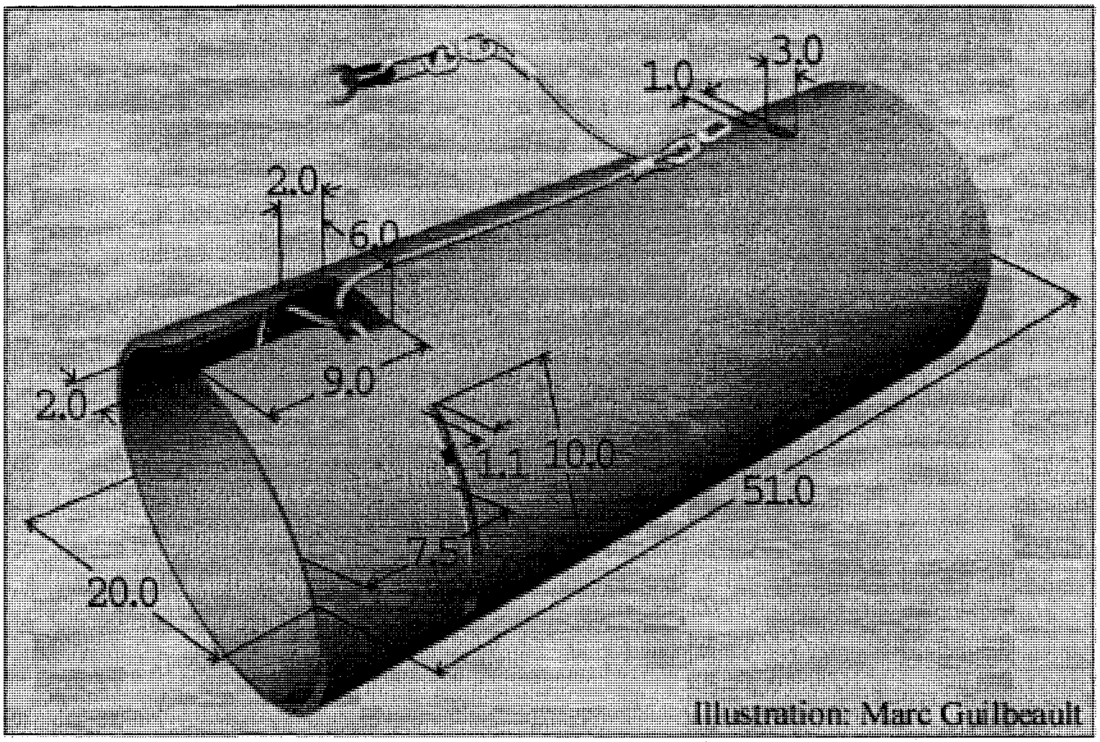

Figure 6-3: Rubber-padded snare used to capture bears with insert of the Mikin BL02 rounded lock. Snares are constructed of 0.476-cm diameter cable constructed of 7x19 wire with 1900 kg of rupture strength, 0.635-cm galvanized steel swivels with 386 kg of rupture strength, and 19 1-cm long rubber pieces of 0.5 and 0.6-cm diameter.

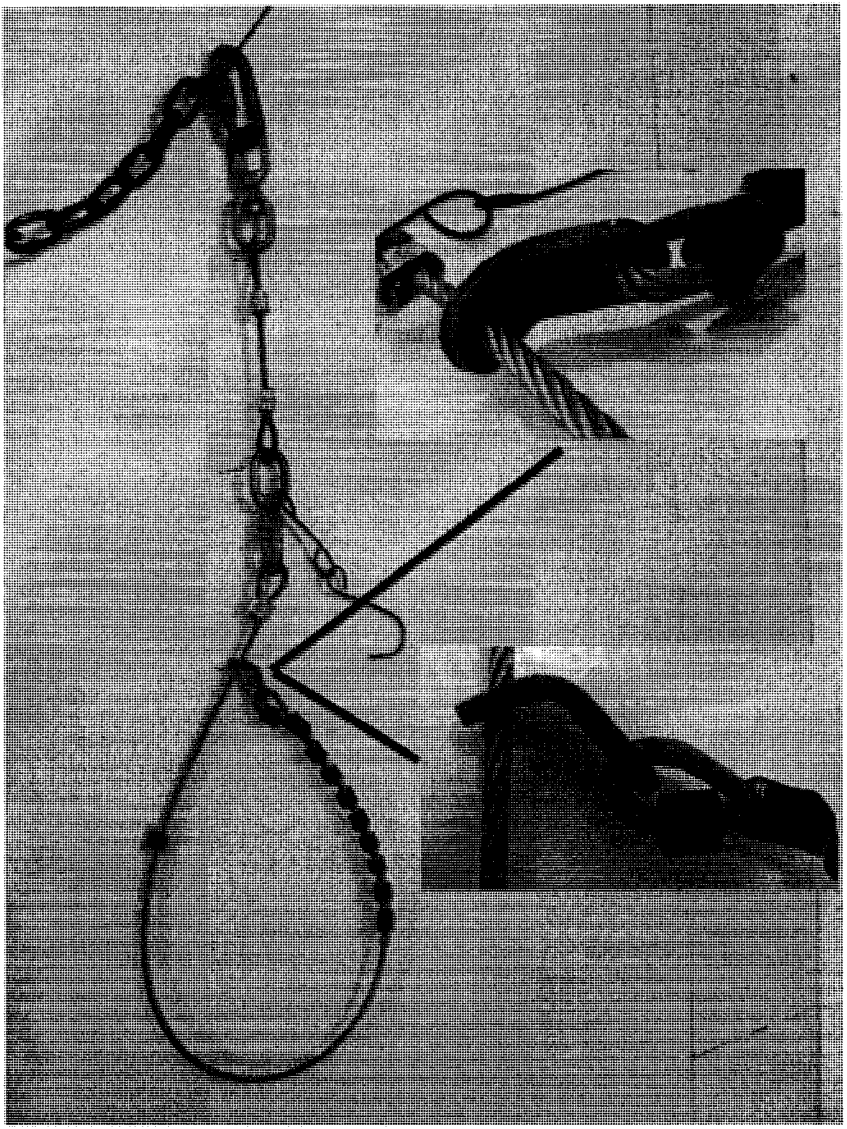

Figure 6-4: Components of the restraining mechanism include the rubber-padded snare attached to 30 cm of chain followed by the Mikin SA03 shock absorber (also in insert). The length of chain used between the shock absorber and drag depends on the density of surrounding vegetation (3 m shown here).

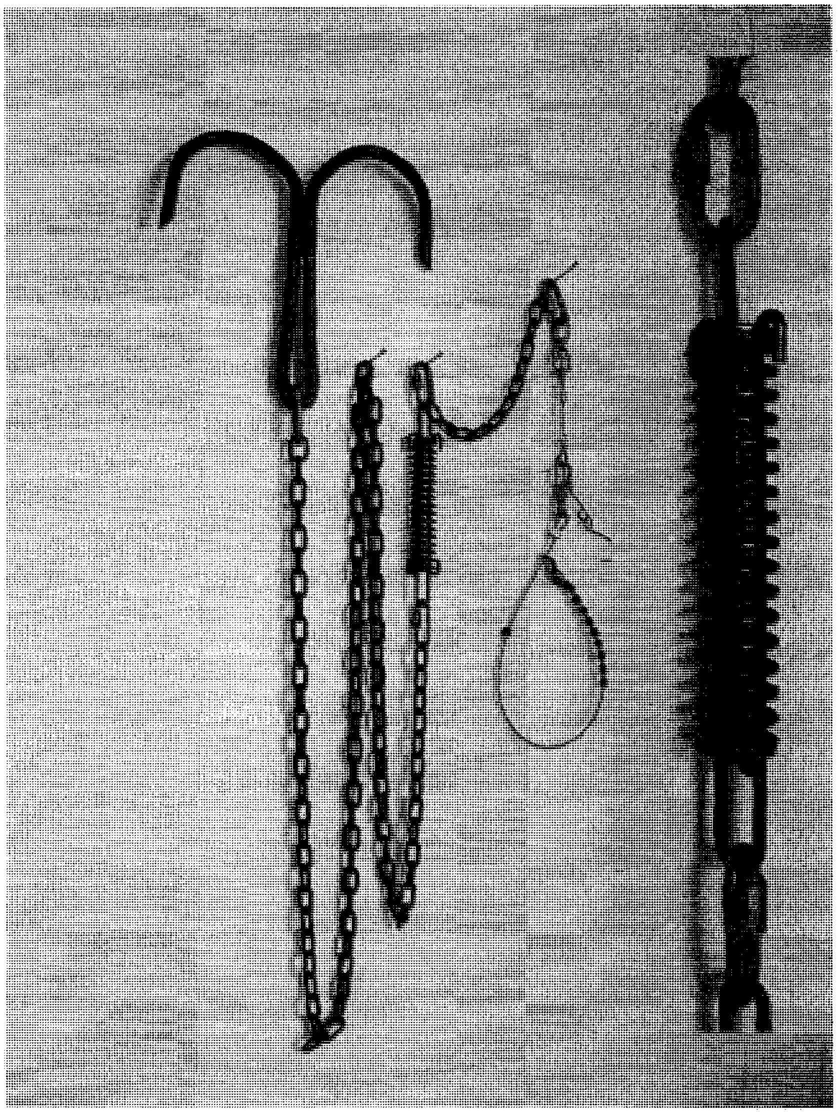

Figure 6-5: Skeleton installation of the RL04 trap between 3 trees forming a triangle. The tube trap is set 85 cm from the ground on 2 pieces of wood (A), screwed in place using 4-cm steel-plated roofing screws, and further solidified with a diagonal piece of wood (B). Two lateral pieces of wood (C) were nailed above the trap to protect the trigger and spring leaving a 20 cm gap to allow the snare to tighten (D). The quick link joining the snare to the chain hangs on a nail placed 34 cm above the pipe on the left side of the front-right tree (E) and prevents the spring from having to lift the drag when tightening the snare.

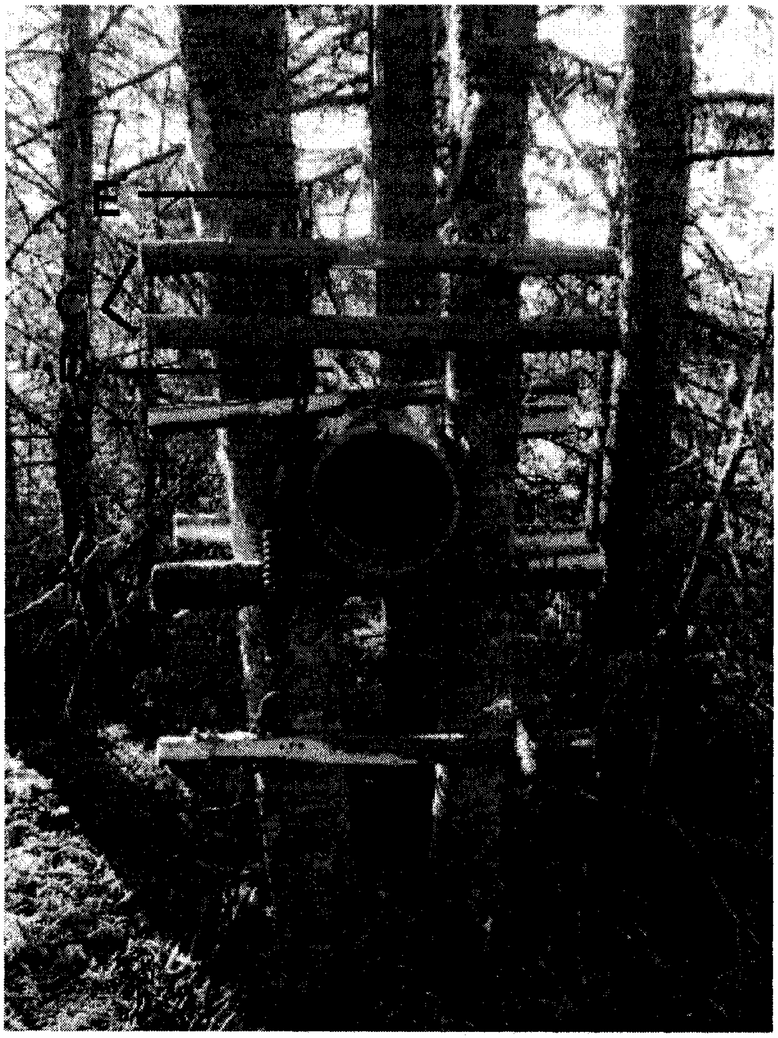

Figure 6-6: Completed installation of the RL04 trap. Dense vegetation placed around the trap and additional bait bags placed near the trap opening directed bears to the front of the trap.

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