Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival

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Abstract: Sexually selected infanticide (SSI) has been documented in some species with a mating system in which males have almost exclusive breeding rights with 1 or more females. When the dominant male is removed, the new male kills the offspring sired by the previous male to enable the mother to be bred earlier. It has been suggested that this immigrant male hypothesis of SSI operates in grizzly bears (*Ursus arctos*) and that removing dominant males by hunting results in high cub mortality due to killing by immigrant males, or in low reproductive rates because of a female counterstrategy of using suboptimal habitat to avoid potentially infanticidal immigrant males. I tested 2 predictions of the immigrant male hypothesis in a hunted area adjacent to protected areas with high densities of grizzly bears that could supply immigrant males. These predictions were not supported. Over 25 years, 134 grizzly bears were captured: most of the 77 male and 57 female grizzly bears were ≤3 years of age when first captured (54.5% and 52.6%, respectively), and 22.1% of the males and 19.3% of the females were 4–6 years of age when first captured. Similarities of these sex ratios suggest that there was not a substantially greater influx of subadult males than females into the hunted area. Cub survival to the end of the breeding season was high (0.93 or 0.95; $n = 87$), as was annual cub survival (0.85, $n = 81$); 15% of the 39 litters monitored for an entire year were completely lost. Yearling survival was 0.95 to the end of the breeding season, when SSI should cease. These results do not support the immigrant male hypothesis of SSI but suggest that grizzly bears either do not exhibit SSI, or that SSI exists in a different form. I propose a second hypothesis of how SSI may operate in bears. This mate recognition hypothesis of SSI is that males of any age may, if they are able, kill cubs that they believe they did not sire the previous year and try to mate with the mother. I use a simulation model to evaluate factors that may influence the existence and likely form of SSI in bears. Results of this study suggest that killing some adult males under a sustainable management regime does not decrease cub survival.

Key words: British Columbia, cannibalism, dispersal, grizzly bear, habitat selection, hunting, infanticide, Montana, mortality, survival rates, *Ursus arctos*

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Grizzly bears (*Ursus arctos*) are hunted over most of their >5,000,000 km^2 distribution in North America, yet the implications of hunting on populations remain controversial. In addition to the fundamental difficulty of estimating population abundance and a sustainable yield, the consequences of male-dominated harvest on the social structure of a population and resulting survival of cubs have not been resolved.

In the 1970s, researchers investigating the behavior of langurs (*Semnopithecus entellus*), a group-living primate, and African lions (*Panthera leo*), a group living carnivore, noted that when the dominant male in the group was replaced by an immigrant male, many of the offspring sired by the former male soon disappeared and their mothers came into estrus and mated with the new dominant male (Hrdy 1974, Bertram 1975). These species had extended maternal care of juveniles and a permanent harem mating system, so it was clearly genetically advantageous for the new dominant male to eliminate the unborn or unweaned offspring of the females in his harem and thereby advance their next estrus. These observations led to the theory of sexually selected infanticide (Hrdy 1977, 1979). Commonly stated requirements of SSI are that: (1) infanticidal males should not kill their own offspring, (2) death of

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the offspring should shorten the interbirth interval of the mother, and (3) infanticidal males should mate with the mother of the dead offspring and sire her next offspring (Hrdy 1979, Ebensperger 1998, Swenson 2003). For grizzly bears, additional requirements should likely include: (4) defence by the mother poses little risk to the infanticidal male, and (5) the male would obtain more breeding opportunities by killing juveniles and monitoring their mother until estrus (engaging in SSI) than by searching for other, unaccompanied females.

Shortly after the development of the SSI hypothesis, Stringham (1980, 1983) discussed 2 ways that SSI could operate in bears. He suggested that if adult males lived in a "territorial matrix", removing a resident male would allow an influx of other males, which could result in increased killing of resident offspring, much like was described in langurs and lions. Conversely, if grizzly bears were nomadic or hierarchical (non-territorial), natality and cub survival might be enhanced by the depletion of adult males that sometimes kill cubs, provided enough males remained to breed with females (Stringham 1980).

Subsequently, radiotelemetry studies demonstrated that grizzly bears did not live in a territorial matrix but typically have large home ranges that greatly overlap the ranges of conspecifics of both sexes (Craighead et al. 1995*a*, Mace and Waller 1997, Swenson 2003). Building on Stringham's (1980) work, McLellan (1994) suggested that SSI could operate in bears even though they are solitary and non-territorial, provided that males were able to distinguish their own offspring from others. He cited the suggestion of Hrdy (1977), who proposed that promiscuous mating behaviour of females may have evolved in part to confuse paternity and thereby reduce the number of males that may be infanticidal.

Thus, 2 potential forms of SSI, if it exists, have been proposed for grizzly bears and, of importance to managers, these 2 forms may have opposite effects on the rate of increase of hunted populations. The first form, which I refer to as the "immigrant male" hypothesis of SSI, is when resident adult males are replaced (usually after they are killed) by immigrant males that could not have sired cubs in the area so they kill cubs to advance the female's estrus and gain a breeding opportunity. This general form has been well documented in many group-living or territorial primates and carnivores where dominant males have near exclusive breeding rights with $\geq$1 female. The second form I call the "mate recognition" hypothesis and occurs when any male, including adult resident males, kill cubs to gain breeding opportunities with the mother. Although the mate recognition hypothesis of SSI would function best if males recognize their probable offspring (likely by recognizing the females with which they previously mated), mate recognition may not be essential (Craighead et al. 1995*b*). Among polygamous species, mate recognition has been shown in a variety of rodents (Mallory and Brooks 1978, Labov 1980, Huck et al. 1982), and individual recognition has been confirmed for at least 4 years in northern fur seals (*Callorhinus ursinus*; Insley 2000).

Since the mid 1990s, Wielgus and Bunnell (1995, 2000) and Swenson et al. (1997, 2001*a*) provided evidence that the immigrant male form of SSI operated in bears and the removal of adult males by hunting caused the rate of increase to decline. Although they did not document infanticide, Wielgus and Bunnell (1995, 2000) suggested that they detected a female counter-strategy to the immigrant male form of SSI that was costly in terms of reproductive output. They stated that hunting mortality of older males coincided with higher numbers of potentially infanticidal, immigrant males, that adult females avoided those males and their food-rich habitats, and that female reproduction appeared to suffer as a result (Wielgus and Bunnell 2000). Swenson et al. (1997, 2001*a*) also suggested that killing adult males can reduce population growth because immigrant males that replace the resident males may kill cubs, as predicted by the immigrant male form of the SSI hypothesis. Although recent evidence suggested that resident rather than immigrant males killed cubs, Swenson (2003) maintained that the immigrant male hypothesis of SSI still operated and postulated that resident males may realign their home ranges after another resident male is killed and thus function as immigrants. Again, of importance to managers and our understanding of the mechanism of SSI in bears, Swenson (2003) suggested cub mortality would increase in hunted populations.

Results presented by Miller et al. (2003) contrast the work of Wielgus and Bunnell (1995, 2000), Swenson et al. (1997, 2001*a*), and Swenson (2003). Miller et al. (2003) compared cub survival, litter size, and potential confounding factors between hunted and unhunted brown bear populations in high-density coastal and lower-density interior areas of Alaska and found that cub survival was greater in hunted populations. They also found that cub survival in one study area did not change when the sex ratio of the adult population shifted toward females because of increased male-biased harvest. Miller et al. (2003) stated that their results reversed what would be expected if male-biased hunting disrupted social structures leading to increased infanticide.

Because the effect of the 2 forms of SSI on the survival of cubs and yearlings may differ greatly in a hunted grizzly bear population, it is critical to evaluate and compare the validity of each form. My first objective was to test the immigrant male form of SSI, particularly the effect of grizzly bear hunting on cub and yearling survival, because this form of SSI was proposed by Wielgus and Bunnell (1995, 2000), Swenson et al. (1997, 2001*a*), and Swenson (2003). I tested this hypothesis by estimating grizzly bear population parameters in an area with a long history of male-biased hunting. The hunted area was immediately adjacent to the Waterton/Glacier International Peace Park, an area with a high density of grizzly bears that have been protected for decades (Gniadek and Kendall 1998). Under these distinct management regimes, the immigrant male hypothesis of SSI leads to 2 predictions. As suggested by Wielgus and Bunnell (1995, 2000), it first predicts a high immigration rate of potentially infanticidal males from the protected park into the hunted area, where many adult males have been killed. The second prediction of the immigrant male hypothesis of SSI—and most important from a management perspective—is that cub survival rates would be low in the hunted area or at least lower than in nearby areas where grizzly bears are not hunted. In particular, in the hunted area there would be a high loss of entire litters due to infanticide by immigrant males, and cub loss would be most common during the breeding season when SSI would most benefit the infanticidal male (Swenson et al. 1997, 2001*a*).

In addition to these predictions, the female counter-strategy to the immigrant male form of SSI, as described by Wielgus and Bunnell (1995, 2000), predicts that adult females in the hunted area would select different and inferior habitats than males to avoid potentially infanticidal males, and consequently have smaller litter sizes. McLellan and Hovey (2001*a*) recently tested the effects of sex, age class, and season on the selection of habitats and elevations by grizzly bears in the hunted area. Therefore, I do not re-analyze habitat selection here, but use results of that study to test this prediction.

Because of the apparent inconsistent expression of infanticide in grizzly bears (Swenson 2003), my second objective was to explore factors that may influence the natural selection of SSI in this species, and what form it may take under different conditions, by simulating trends in reproductive success of males that adopt different strategies. The first strategy that I investigated was SSI committed by males of various ages. Because grizzly bears are approximately 4–6 years of age when they disperse (Blanchard and Knight 1991, McLellan and Hovey 2001*b*), SSI by these age classes would more likely follow the immigrant male form of SSI, whereas older males would more likely follow the mate recognition form. The second strategy I investigated was that males do not kill cubs but simply search for estrous females.

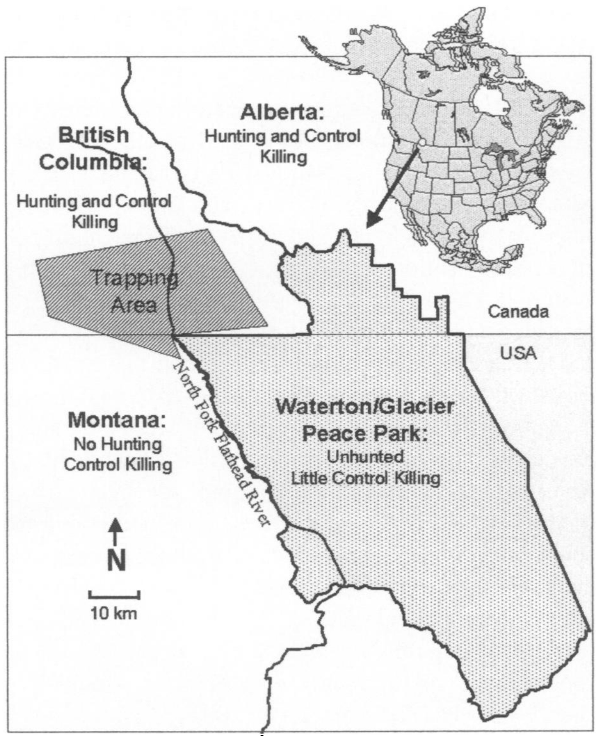

Fig. 1. Flathead study area in southeast British Columbia, Canada, and Montana, USA, showing the juxtaposition of hunted and protected areas and where bears were trapped, 1978–2003.

Study area

The study area consisted of 2 adjacent areas with different grizzly bear management objectives. The hunted area was mostly in the Canadian portion of the North Fork of the Flathead River drainage (Fig. 1) that flows from the extreme southeastern corner of British Columbia southward into the United States (49°N; 114°85′ W). In this portion of British Columbia, grizzly bears have been hunted for at least a century. In contrast, across the international border, the North Fork of the Flathead River forms the western boundary of Glacier

National Park (GNP), where strict management practices and enforcement have resulted in few grizzly bears being killed by people for many decades (Gniadek and Kendall 1998). The National Park has a high density of grizzly bears (Martinka 1974; K. Kendall, US Geological Survey, Glacier National Park, Montana, USA, personal communication, 2004) and should serve as a source of immigrants into the hunted area. Immediately east of the hunted area, grizzly bears within Waterton Lakes National Park (WLNP) are similarly protected and may also be a source of immigrant males.

There are no physical barriers between the 2 national parks and the hunted area. The western half of GNP is in the same 4–10 km wide valley of flat benches and rolling hills as the hunted area. The North Fork of the Flathead River and several major tributaries cross the international border between GNP and the hunted area. Although the continental divide separates WLNP from the hunted area, there are many forested passes. Radiocollared bears move freely among both parks and the hunted area (McLellan, unpublished data). Physical and vegetative characteristics of the study area have been published elsewhere (McLellan and Hovey 2001*a*).

Methods

Testing the immigrant male hypothesis

My first prediction of the immigrant male hypothesis of SSI is that hunting adult males in British Columbia would have disrupted the social stability of the population, resulting in an influx of young (4–6 year old), potentially infanticidal males from the adjacent, unhunted national parks. To test this prediction, I followed the method of Wielgus and Bunnell (1995, 2000) and used trapping records from the past 25 years in the hunted area, where most individuals have been captured (McLellan 1989, McLellan unpublished data). Due to their extensive movements, male grizzly bears of all ages are more often trapped than females; however, the predicted immigration of young males into the hunted area should result in a greater proportion of the males being 4–6 years of age when first captured (not previously captured before this age) compared with 4–6 year-old females that are more philopatric (Blanchard and Knight 1991, Mace and Waller 1998, McLellan and Hovey 2001*b*).

The second prediction of the immigrant male hypothesis is that cub mortality should be higher in the hunted than in nearby unhunted areas. In particular, there should be frequent whole litter loss during the breeding season in the hunted area. Because females in the study area, and throughout North America, most commonly have 3-year interbirth intervals (they are with cubs 1 year, yearlings the next, and then spend almost an entire year alone before giving birth again) it would be beneficial for infanticidal males to also kill yearlings up to the end of the breeding season. After that time, killing yearlings would not shorten a 3-year interbirth interval and therefore would not benefit infanticidal males.

I tested these 2 hypotheses using a long-term database of live-capture records and by monitoring the reproductive status of female grizzly bears. Between 1978 and 2003, bears were captured in foot snares, culvert traps, or darted from a helicopter outside of GNP and WLNP, across an area of approximately 650 km^2 in British Columbia or just south of the border in Montana. Bears were captured primarily in May, June, September, and October, but captures were recorded in all months of the bear-active season (Apr–Nov). Captured bears were ear-tagged, weighed, measured, and radiocollared, and those >1 year of age had a premolar removed and sectioned to estimate their age (Matson et al. 1993). The location of all radiocollared individuals was determined from fixed-wing aircraft at about 1-week intervals. High road density ($\approx$44 km/100 km^2) provided good access that also enabled most bears to be located from the ground every 1–10 days. Changes in litter-status of female bears were directly observed from aircraft or ground. Cubs no longer observed with their mother were assumed to have died. This assumption was also made for yearlings unless they were, through radiotelemetry or observation, known to be alive. Separation between mothers and yearlings during the breeding season does happen in the study area, so this assumption may lead to an inflated estimate of yearling mortality. Cub and yearling survival rates were estimated by the number that survived to the end of the period of interest, divided by number observed at the beginning of the period (Hovey and McLellan 1996, Mace and Waller 1998, Garshelis et al. 2005). Confidence limits, and other randomization tests deployed bootstrapping procedures using the Excel (Microsoft, Redmond, Washington, USA) addition POPTOOLS (Hood 2004).

Because there were no data on cub survival in GNP or WLNP, I compared cub survival rates in the hunted area with 2 other areas in the Rocky Mountains where grizzly bears are not hunted, although males and females die from other causes. Mace and Waller (1998) reported cub survival to be 0.77 ($n = 28$; 95% CI = 0.63–0.95) in the South Fork of the Flathead river drainage, Montana, centered approximately 200 km south of my North Fork of Flathead study area. Similarly, Garshelis et al. (2005)

reported cub survival rate of 0.79 ($n = 53$; 95% CI = 0.67–0.93) in and around Banff National Park and Kananaskis Country, Alberta, an area centered approximately 200 km north of my study.

Modeling sexually selected infanticide

Grizzly bears have a scramble competition polygamous mating system (Craighead et al. 1995*a,b*; Alcock 2001:382). Grizzly bear home ranges overlap extensively with conspecifics of both sexes, and male ranges are larger than those of females. Females are induced ovulators and may have 2 estrous periods of approximately 10 days, most frequently during the last 3 weeks of June (Craighead et al. 1995*a*). Males have 2 basic strategies: monopolize individual females by mate-guarding through their estrous period, or displace other males from breeding and add their gametes to those already deposited (Craighead et al. 1995*b*). When breeding females are scarce and widely distributed, males tend to locate one female to breed exclusively. However, when breeding females are more common, males travel widely to locate more females (Craighead et al. 1995*b*). In *Ursus* spp., body size of males is an important factor determining the outcome of fights over breeding females (Craighead et al. 1995*a,b*; Kovach and Powell 2003).

To explore factors that may influence the incidence of SSI, I estimated mating success under different scenarios using a model that mimics, in a simplistic way, the mating system of grizzly bears. The simulation model was built in Excel but incorporated the random number generator and Monte Carlo simulation features of POPTOOLS. The model used the body mass of bears (37 F, 59 M) captured in the Flathead and the upper Columbia River drainage (Apps et al. 2004), located 250 km north of the Flathead study area. I included 3-year-old male bears in the model because this is the age when males greatly expand their home ranges and begin to disperse (Mace and Waller 1998, Swenson et al. 1998, McLellan and Hovey 2001*b*). Three-year-old males are known to mate with adult females in Scandinavia (Swenson 2003). I classed bear ages as 3, 4, 5, 6–7, 8–9, 10–11, 12–17, and >17 years, which ensured >4 individuals per class. In the model, a focal male could adopt 1 of 2 strategies to obtain breeding opportunities. He could be infanticidal, kill cubs, and monitor the mother until receptive, or he could not kill the cubs and instead search for a breeding female.

I varied the following parameters in the model to test their implications on the success of the 2 strategies: (1) the proportional difference in body mass of the male relative to the mother that would enable it to kill cubs, (2) the mean and standard deviation (SD) of the time required for a female's physiological condition to change from a lactating mother to estrus, (3) the mean and SD of the time required to ensure a female is impregnated once receptive, (4) the mean number of adult (age >5 years) females in the focal male's breeding-season home range, (5) the mean interbirth interval of females, (6) the mean number of adult males in the focal male's breeding-season home range, and (7) the searching efficiency of males and estrous females. I modeled time required for a male to encounter a particular female in his range as a random number between 0 and the maximum time, which was an input variable and therefore reflected variation in search efficiency.

The model for infanticidal males proceeded as follows. A male was randomly selected from all males of a specific age class and, using a table of all females, was randomly matched with a female accompanied by cubs. If he did not meet the input size requirement to overcome female defense of her cubs, he did not mate (the model tracked the mass of all adult males and females). Alternatively, if he met the size requirement, he killed all her cubs. He then monitored the female (and did not search for another female) until she was receptive for mating and then impregnated her. This period was the sum of the time for the female to switch from being a lactating mother to being receptive and the time from receptivity to fertilization (both input variables). While the male monitored the female, all other males (the number being an input variable) who were not with other estrous females (derived from 2 input variables; the number of females and the breeding interval) would encounter the female, each with a probability governed by his independently selected searching efficiency (0 days to an input maximum). If any of the arriving males were larger than the infanticidal male, the smaller male was forced off and would not mate (Craighead et al. 1995*b*, Kovach and Powell 2003). If no larger males arrived before the female was bred, she was bred by the infanticidal male. Female mate choice could be incorporated in the model by extending the time between the death of her cubs and when she became pregnant or by increasing search efficiency and thus enabling encounters with more males. Further, an infanticidal male could be "discretionary" and not kill his own cubs if encountered, or "nondiscretionary" and kill his own cubs (only for bears >5 years of age; the probability of a male killing his own cubs was inversely proportional to the number of

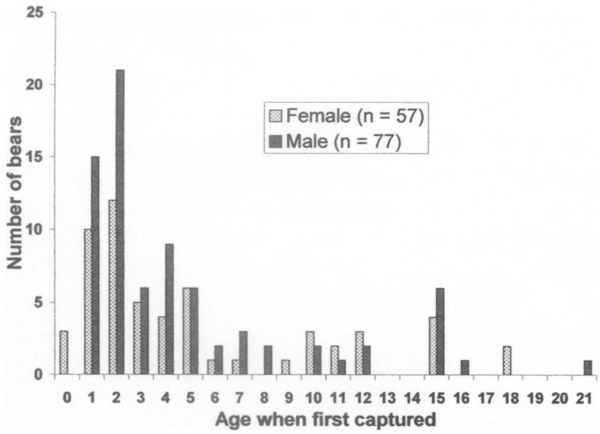

Fig. 2. Age distribution of male and female grizzly bears when first captured in the Flathead study area of British Columbia, Canada, and Montana, USA, 1978–2003.

adult males in the population) as well as those fathered by other males.

In the model, non-infanticidal males did not kill cubs but searched for other females until 1 was found. All other males also searched for these females. A non-infanticidal male was successful if he was the largest male to encounter the female within the time for her to become pregnant. The model only treated the multi-male interactions over 1 female (not multiple females over the entire breeding season). For each age class of males, I conducted 2,000 replicates of the model and recorded the success of both discretionary and non-discretionary infanticidal males and non-infanticidal males.

The objective of using the model was not to necessarily use true values for each parameter to determine which strategy performed best and thus should have been naturally selected for. Such use of the model would be presumptuous because true values are unknown for most parameters, values likely vary greatly within and among populations, and the model is simplistic. Instead, the model was used to explore how changes in the values of input variables may affect the success of males of various ages that adopt different mating strategies. Base scenario values for some parameters were selected because they were clear and simple (equal adult sex ratio, males had to be the same size or larger than the mother to successfully kill her cubs), and for other parameters base scenario values were selected from the often limited number of cases in the literature or through personal communication with research biologists. I then varied one input variable at a time, both lower and higher than the base scenario, to explore trends in reproductive success among males.

Results

Testing the immigrant male hypothesis

Between 1978 and 2000, 85 male and 45 female grizzly bears were killed by people in the 2 management units that included the hunted area. These units covered 2,815 km^2, resulting in annual kill densities of 1.37 males and 0.73 female bears/1,000 km^2. The mean and median age of harvested bears was 8.52 and 6, respectively, for males and 9.31 and 9, respectively, for females. In GNP, approximately 48 bears were killed between 1960 and 1994, giving an annual kill density of 0.33 bears of both sexes/1,000 km^2 (Gniadek and Kendall 1998). This annual kill density was reduced to 0.14 bears/1,000 km^2 during the 1990s (calculated from Gniadek and Kendall 1998), or 1/15th of the kill density in the hunted area.

In British Columbia and outside GNP in adjacent portions of Montana, 134 different grizzly bears were captured (77 M, 57 F). The ages of bears when first captured were similar for both sexes (randomization test $P = 0.38$; Fig. 2). When first captured, most male (54.6%) and female (52.6%) bears were $\leq$3 years old and 22.1% of the males and 19.3% of the females were 4–6 years of age. These capture records do not support the hypothesis that a substantial influx of potentially infanticidal, young males came into the area with hunting.

In the hunted area, 87 cubs were produced in 41 litters for an average litter size of 2.12 cubs/litter. In one case, I was uncertain whether the entire litter of 2 cubs died during or after the breeding season, so either 81 or 83 of 87 cubs survived for a survival rate of 0.93 (95% CI = 0.87–0.98) or 0.95 (95% CI = 0.91–0.99), and 38 or 39 of the 41 litters survived the breeding season (93% or 95%). In either case, there was high cub survival from den emergence to early July. The annual survival rate of individual cubs was 0.85 ($n = 81$; 95% CI = 0.78–0.93) and similarly, 33 of the 39 litters (85%) monitored for an entire year survived. The survival of cubs in the hunted area was not lower than the 0.79 ($P = 0.87$, 1-tail) in the Banff and Kananaskis area (Garshelis et al. 2005) or the 0.77 ($P = 0.76$, 1-tail) in the South Fork of the Flathead (Mace and Waller 1998). Fifty-six of 59 yearlings survived to the end of the breeding season for a survival rate of 0.95 (95% CI = 0.90–1.0), and none of the 28 litters of yearlings was entirely lost before the end of the breeding season. Equivalent data on yearling survival were not available from the other studies for

Table 1. Spring mass (x̄ and SD) of males by age class and the number of successful matings out of 100 (%) after 2,000 simulations for males adopting 1 of 3 strategies: (1) infanticidal but does not kill his own offspring (mate recognition), (2) infanticidal but may kill his own offspring and thus reduce reproductive success, and (3) searcher male that does not kill cubs but searches for an estrous female. NA = not applicable as it is unlikely that these young bears fathered existing litters.

		Age class of males (years)							
Model scenario	**Strategy**	**3**	**4**	**5**	**6–7**	**8–9**	**10–11**	**12–17**	**>17**
Mean spring mass (SD)		87.4 (17.3)	98.8 (31.7)	106.0 (37.9)	132.4 (40.8)	156.8 (68.7)	192.3 (27.3)	177.8 (24.7)	194.4 (37.8)
Base scenario	infanticidal	2.3	4.7	6.8	15.9	31.9	41.4	32.6	48.0
	indiscriminate	NA	NA	NA	7.8	23.3	32.6	22.3	39.9
	searcher	11.2	13.3	14.9	22.3	33.0	44.1	36.4	47.7
Cub death to estrus 2 days[a]	infanticidal	5.1	10.0	12.6	24.3	36.5	52.1	43.2	55.2
	indiscriminate	NA	NA	NA	16.1	28.8	42.6	34.6	46.9
	searcher	11.1	13.3	15.7	21.8	33.2	43.9	36.4	47.8
Cub death to estrus and time to impregnate 2 days[a]	infanticidal	11.1	18.3	22.1	36.0	45.4	63.9	58.2	66.4
	indiscriminate	NA	NA	NA	28.8	37.7	56.6	48.6	58.3
	searcher	24.5	25.7	27.2	31.4	36.5	43.8	41.0	45.3
Cub death to estrus 10 days[a]	infanticidal	0.3	1.3	2.2	8.7	24.9	29.3	18.7	38.0
	indiscriminate	NA	NA	NA	7.9	17.4	21.8	9.7	28.3
	searcher	10.9	13.6	15.3	21.7	33.4	43.5	36.5	48.1
5 adult males but 10 adult females[a]	infanticidal	18.9	29.1	32.6	44.7	48.8	67.6	64.6	69.1
	indiscriminate	NA	NA	NA	29.0	34.1	52.7	47.1	50.4
	searcher	66.6	69.0	70.1	75.9	80.4	87.2	84.5	88.1
10 adult males but 5 adult females[a]	infanticidal	1.7	3.6	5.7	14.1	29.1	37.0	27.2	44.5
	indiscriminate	NA	NA	NA	5.6	20.9	29.1	18.4	35.3
	searcher	3.4	4.4	4.9	7.3	14.4	17.6	13.7	20.8
Maximum 10 days to find breeding female[a]	infanticidal	0.3	0.8	1.5	6.8	23.4	25.1	14.1	34.1
	indiscriminate	NA	NA	NA	−1.4	15.7	17.6	5.3	25.2
	searcher	3.9	4.8	6.2	13.0	29.3	36.4	25.2	43.3
Maximum 30 days to find breeding female[a]	infanticidal	5.6	10.3	13.0	25.3	36.9	52.4	43.6	56.8
	indiscriminate	NA	NA	NA	16.6	29.9	43.9	35.0	48.4
	searcher	16.8	19.5	20.5	27.3	34.4	44.5	39.3	46.8

[a]Values of all other variables set to the base scenario.

comparisons. From these results, I conclude that cub and yearling survival was high and entire litter loss was low in the hunted area.

Modeling sexually selected infanticide

Base scenario. Adult females in the spring weighed an average of 99.9 kg (SD = 17.5). In the base scenario, males had to be the same size or larger than the female to kill her cubs (Table 1). The time for a female to change physiologically from lactating to estrus averaged 5 days (SD = 2) followed by an average of 5 days (SD = 2) to become pregnant. There was also an equal ratio of adult males to females, and it took between 0 and 20 days for each male that was not with another female to locate an estrous female. With these base inputs, most males that did not kill cubs but simply searched for females in estrus were reproductively more successful than males that did kill cubs (Table 1). The difference between the outcomes of the 2 strategies was greatest for younger, smaller bears, for which infanticide rarely generated successful breeding opportunities.

Time of estrus onset. With all input variables set to the base scenario but with shorter periods for females changing from lactating to estrus ($\bar{x}$ = 2 days; SD = 0.5) and being impregnated thereafter ($\bar{x}$ = 2 days later; SD = 0.5), older males were more successful by being infanticidal than by searching for estrous females. In this "quick estrus onset and impregnation" scenario, older, infanticidal males were more successful even if they could not determine if the cubs they were killing were their own. However, for bears <6 years of age, searching for an estrous female was a more successful strategy than being infanticidal, even when onset of estrus was quick (Table 1). In contrast, when onset of estrus was delayed ($\bar{x}$ = 10 days for a female to change from lactating to estrus), it was advantageous for males of all ages to search for another female; this advantage was particularly notable for young males (Table 1).

Sex ratio. If there were half as many adult males as adult females, it was better for males of all ages to not kill cubs but to search for estrous females. This scenario was the only one where young males had a high probability (65–70%) of siring offspring (but only among those who searched for estrous females). When there were half as many adult females as adult males, infanticide was a more successful strategy for all males, except for those ≤5 years of age when the 2 strategies resulted in similar success.

Mate searching efficiency. A reduced ability for males and estrous females to find each other also resulted in infanticide being a successful strategy for older males, but it remained less successful than searching for male bears ≤7 years old. With better searching efficiency, infanticide was less profitable.

Discussion

Testing the immigrant male hypothesis

Results of the Flathead study do not support the immigrant male hypothesis of SSI because neither of the 2 predictions were met. The area had been hunted for many years with more males shot than females, and it was immediately adjacent to unhunted areas. However, unlike results of Wielgus and Bunnell (1995, 2000), there was no indication of a substantial influx of subadult males to replace the killed male bears. Most bears of both sexes were ≤3 years of age when first captured and, although more males were 4–6 years old when first captured than females, there were, as expected, more males captured than females of all ages. These capture ratios, despite the higher mortality rate of males (McLellan et al. 1999), likely reflect the greater movements of males of all ages and thus greater trap encounter rates of males.

Because male grizzly bears disperse farther than females (Swenson et al. 1998, McLellan and Hovey 2001*b*, Proctor et al. 2004), the lack of an influx of young males is somewhat surprising. However, dispersal by both sexes of grizzly bears appears limited in distance and is a gradual process. After 50–60 years in Scandinavia, where brown bear populations have been rapidly growing, 99% of the males and females killed by hunters were within 80 km and 50 km, respectively, of source areas (Swenson et al. 1998). In the Flathead study area, males and females dispersed an average of only 30 km and 10 km, respectively. Using genetic analysis of 711 grizzly bears across a 100,000 km^2 area that included the Flathead study area, Proctor et al. (2004) found average dispersal distances of 41.9 km and 14.3 km for males and females, respectively. In addition to limited dispersal influencing the immigration of young males from the national parks, the Flathead hunted area has a high density and increasing population of grizzly bears (McLellan 1989, Hovey and McLellan 1996). The high density and production of young bears locally may have discouraged immigration from neighboring national parks.

The SSI prediction of high cub mortality and loss of entire litters, particularly during the breeding season, and high yearling mortality up to the end of the breeding season also was not supported. Cub survival was as high or higher in the Flathead hunted area than in either the unhunted South Fork of the Flathead or in the unhunted Banff and Kananaskis area. At 0.85, the point estimate of cub survival in the Flathead hunted area was higher than any of the 8 other published studies from North American ($\bar{x} = 0.61$, $n = 736$ cubs; Mace and Waller 1998, Miller et al. 2003, McLoughlin et al. 2003, Garshelis et al. 2005, Schwartz et al. 2005). Of these studies, only cub survival outside of Yellowstone National Park, but within the Yellowstone Grizzly Bear Recovery Zone, was similar at 0.82. Within Yellowstone National Park itself, cub survival was much lower at 0.49, likely reflecting a density effect (Schwartz et al. 2005).

There is, however, a potential bias in estimating cub survival because cubs could die before they are observed. This bias may be particularly problematic in more heavily forested areas, such as the Flathead area, where bears are sometimes difficult to observe. In the Flathead study area, however, all females had litters when they were expected (the spring following separation from their last litter) from 1979–1997 ($n = 36$ litters), so this bias was not a factor in estimating survival of entire litters for the first 18 years of study. The pattern of consistent reproduction ended in 1997 when some females, particularly some that were >20 years of age, failed to produce cubs when expected. The missed reproductive events later in the study may be due to a density effect as the population rapidly increased (Hovey and McLellan 1996). Additionally, there were major crop failures of huckleberry (*Vaccinium membranaceum*) in those years, and some old bears may have reached reproductive senescence (Schwartz et al. 2003). Results of this study demonstrate that infanticide, if it occurred, was rare despite the study area having a male-biased hunter harvest and being adjacent to a large unhunted area that could have supplied immigrant males.

Wielgus and Bunnell (1995, 2000) did not document infanticide in a hunted population of grizzly bears but suggested that they detected a female counterstrategy to the immigrant male form of SSI that was costly in terms of reproductive output. In an area with grizzly bear hunting, they found adult females to avoid potentially infanticidal, immigrant males and the food-rich habitats that they occupied and, consequently, that these females had small litters (Wielgus and Bunnell 2000). In the Flathead hunted area, sex and age class did not have a significant effect on habitat selection by grizzly bears (McLellan and Hovey 2001*a*). At 2.12 cubs, the average litter size in the hunted area was not small compared with the average of mean litter sizes from 26 studies across North America (2.068 cubs/litter, $n = 1{,}441$ litters; MacHutchon et al. 1993, McLellan 1994, McCann 1997, Case and Buckland 1998, Mace and Waller 1998, Wielgus and Bunnell 2000, McLoughlin et al. 2003, Miller et al. 2003, Garshelis et al. 2005) and larger (randomization test; $P = 0.003$) than the adjacent unhunted GNP which, between 1987 and 2002, had an average litter size of 1.80 ($n = 148$; US Fish and Wildlife Service, Missoula, Montana, USA, unpublished data).

Unlike the results of Wielgus and Bunnell (1995, 2000), adult females in the hunted area in this study did not avoid habitats preferred by males and they did not have small litters. However, the mechanism behind this prediction of Wielgus and Bunnell (1995, 2000) is unclear. If females with cubs or with yearlings up to the end of the breeding season avoid food-rich habitats where immigrant males are more often found, then decreasing body condition of the mother may result in elevated cub or yearling mortality. However, when mothers are with older yearlings or unaccompanied by offspring, they should make greater use of preferred habitat. After 1.5 years of using preferred habitat, the body condition of adult females should have recovered and their litters of new cubs should not be small.

Mattson et al. (1987) and McLellan and Shackleton (1988) noted that adult males were located farther away from roads than were adult females, particularly adult females with cubs. This result could be due to females avoiding habitats where adult males were present, which is consistent with both the immigrant male and mate recognition forms of SSI and the hypothesis that males may kill cubs for other reasons, such as predation.

Modeling sexually selected infanticide

Van Schaik (2000) developed a model to investigate decision rules of male primates. Van Schaik (2000) stated that his model assumes that a male has access to a particular female and will only kill infants upon assumption of his tenure as dominant male of the group. This model was designed for group-living primates and simply concluded that if infanticide shortens a female's interbirth interval and if the probability that the infanticidal male sires the female's next litter is greater than the probability that he sired the one he killed, infanticide benefits the male. Such a model is clearly too simple for bears that do not have a female defense polygamous (harem) mating system but rather a scramble competition polygamous system.

The model I developed has simplistic rules; however, it considers a scramble competition polygamous mating system. The primate model of van Schaik (2000) does not consider the ability of mothers to defend their young because males that live in a permanent group can wait for an opportune moment to kill dependent offspring and body size is not a significant factor (Janson and van Schaik 2000). Grizzly bears are solitary, so small males cannot easily wait for opportune moments to kill cubs, and female defense is undoubtedly important. Although this input variable could be changed, in the scenarios I presented, male bears had to be the same size or larger than the mother if they were to successfully kill her cubs. Some 3- and 4-year-old males are slightly larger than some adult females so, when randomly matched, these males successfully killed cubs. However, it is unlikely that a young male that was only slightly larger than a mother would be able to kill her cubs without significant risk. Miller et al. (2003) reported that all of the 19 bears seen attacking cubs on the Alaska Peninsula and Kodiak Island were adult males and of the 8 individuals of known age, the average age was 9.4 years and the youngest was 5 years. Similarly, 2 males known to have killed brown bear cubs in Scandinavia were 9 and 11 years of age and the youngest of 4 that were suspected of killing cubs was 6 years of age. It is probable that a male must be considerably larger than the mother to successfully kill her cubs without risk to himself. If so, even fewer young immigrant males than suggested by my model would benefit from the infanticidal strategy.

The group-living primate model of van Schaik (2000) also does not include details of female reproductive physiology but assumes that the time required for a female to change from lactating to estrus is short compared with the tenure of the new male. For primates, van Schaik (2000) stated that females usually return to receptivity within a month, but sometimes within 1 week or even 3 days. This variable is clearly important for bears or other species with a scramble competition polygamous mating system. If this period is long, not only may a larger or more dominant male encounter the female before she becomes fully receptive, but the infanticidal male may be much less efficient at finding other estrous females while he monitors the reproductive condition of the female whose cubs he killed.

It is likely that a reproductive strategy has evolved among female bears enabling them to advertise their availability for sufficient time to attract, if possible, competing suitors in an effort to become impregnated by the "best" male or males. Unlike a harem mating system, where much male–male competition occurs to obtain and maintain a harem before mating occurs, male–male competition among bears most often occurs during the female's estrous period (Craighead et al. 1995*a,b*; Kovach and Powell 2003). Consequently, it is unlikely that female bears will have evolved to become impregnated quickly after losing cubs.

The plasticity of reproduction in bears, such as occasional observations of female American black bears (*Ursus americanus*) breeding while raising cubs (LeCount 1983), makes estimating the period between litter loss and receptivity empirically problematic. I used 5 days in my base scenario and 2 and 10 days in other scenarios, but most of the scant evidence suggests that, on average, it is longer than 5 days. Captive female black bears bred 2 to 3 weeks after their cubs were removed (LeCount 1983), but the shortest time from cub removal to a mating event was 5 days for captive brown bears in Germany (Dathe 1961). In free-ranging conditions in Alaska, S. Miller (National Wildlife Federation, Missoula, Montana, USA, personal communication, 2004) observed a female almost daily after she became separated from her new cubs. She was first seen with a male 18 days later but was with him for <1 day and then with another male 3 days after that. In 2 other cases in Alaska, H. Reynolds (Alaska Department of Fish and Game, Fairbanks, Alaska, USA, personal communication, 2004) observed males in the company of females 9 to 11 days after the females had lost their cubs. Hessing and Aumiller (1994) reported that 4 days after a female's cubs were killed, a male bear (not the one that killed at least one of the cubs) followed the mother at a distance of 100 m, but after that observation, no males showed any interest in her. In Scandinavia, however, J. Swenson (Department of Ecology and Natural Resource Management, Agricultural University of Norway, Ås, Norway, personal communication, 2004) observed a female separate from her cub for only 12 hours but she gave birth the following winter.

Simulation results suggest that the sex ratio of adult bears is an important factor influencing the success of the different male strategies. If there are few adult males in the population (a typical condition when hunters remove more males than females), the searcher strategy by males is much more successful than infanticide. The results of the model were generally consistent with observations from the Flathead study and the 2 hunted study areas in Alaska (Miller et al. 2003). In those areas, hunters removed more males than females and cub survival was higher than in the unhunted control areas (Miller et al. 2003).

Although the model suggests that infanticide may become a less successful strategy when there are fewer males, not enough is known about the various parameters to determine a sex-ratio threshold beyond which SSI is unlikely to operate. Cub survival in the Susitna study area in Alaska did not change even after increased hunting shifted the sex ratio of adult bears from about 38% males to 20% males (Miller et al. 2003). Perhaps with only 38% males in the population, the searcher strategy already dominated male behavior, so a further reduction in sex ratio had no effect.

Rarely do hunters kill more female than male bears (Bunnell and Tait 1981, Miller et al. 2003), but this was the case in 1 of 2 black bear study areas in Arkansas (Clark and Smith 1994). Both populations were below carrying capacity and increasing, and body growth rates of females were among the highest in North America. In the study area where more females were killed than males, the sex ratio of bears ≥ 1 year of age was 1.44 males/female (26:18), the average litter size was 1.41 ($n = 17$), 4 of 13 cubs survived, and 6 of 8 entire litters were lost. In the study area where more males were killed than females, there was a net emigration of males (J. Clark, US Geological Survey, Knoxville, Tennessee, USA, personal communication, 2004), the sex ratio of bears ≥ 1 year of age was 0.64 males/female (27:42), the average litter size was 2.25 ($n = 20$), 18 of 20 cubs survived, and none of 8 litters was entirely lost. The results of Clark and Smith (1994) generally match those of the simulation model where infanticide (and low cub survival) was a more successful strategy when there were more males than females. However, Clark and Smith (1994) concluded that infanticide remained speculative in their study because other environmental variables may have contributed to differences between their populations.

The simulations also indicate that infanticide may become more profitable for males when their searching efficiency for estrous females decreases. This result suggests that SSI may be more prevalent in low-density populations, where bears have very large home ranges

Table 2. Summary of victims and killers in documented cases of intraspecific killing of grizzly or brown bears in North America. References: McLellan (1994); Clarkson and Liepins (1994); M. Gibeau, University of Calgary, Calgary, Alberta, Canada, personal communication, 2004; R. McCann, University of British Columbia, Vancouver, British Columbia, Canada, personal communication, 2003; S. Himmer, Bella Coola, British Columbia, Canada, personal communication, 2003; H. Reynolds, Alaska Department of Fish and Game, Fairbanks, Alaska, USA, personal communication, 2003; and B. McLellan, Revelstoke, British Columbia, Canada, unpublished data.

	Killer						
Victim	adult female	adult male	unknown adult	subadult male	unknown male	unknown	total
Adult female		16		1	2	7	26
Adult male		3				2	5
Subadult female		2				1	3
Subadult male		3				2	5
Unknown subadult		4					4
Yearling	1	4				3	8
Cub	7	13	4			12	36
Total	8	45	4	1	2	27	87

and travel widely in search of mates. If the area has few competing males and encountering an estrous female is relatively uncommon, then killing cubs and monitoring the mother as she returns to estrus may be a viable strategy.

Mate recognition hypothesis versus no sexually selected infanticide

Relative to the complex mating system and reproductive physiology of bears, the simulation model I developed is simplistic and was used only to explore trends in mating success with changing input variables. One consistent and somewhat obvious trend, however, is that if body mass is an important factor influencing whether a male can successfully kill cubs and influence male–male competition over estrous females, then older, larger males benefit more from being infanticidal than younger males. Observations in Alaska (Miller et al. 2003) and Scandinavia (Swenson 2003) suggest that large, older males kill cubs. In addition, if having multiple mates to confuse paternity is a female counter-strategy to SSI (McLellan 1994, Swenson 2003), it will only function if males can recognize females they mated with the previous 1 or 2 years. Having multiple mates, however, may also have evolved to encourage sperm competition. These observations and the results of the simulations suggest that if SSI does operate in bears, the mate recognition form is more likely than the immigrant male form. However, neither the results of the Flathead study or the simulations can differentiate between the role of mate recognition SSI and the alternative hypothesis that infanticide is due to other reasons, such as predation.

If infanticide is not sexually selected but indeed has another underlying cause, then bears of other age classes should be occasionally killed. In Scandinavia, Swenson et al. (2001*b*) found 13 cases of intraspecific predation in 668 bear-years of radiotracking, including an annual predation rate of 0.16 (6 of 38) for yearling females. In 11 studies in Idaho, Montana, British Columbia, and Alberta, 17 radiocollared subadult and adult grizzly bears died naturally (not killed by people), and the cause could be determined for 13 (McLellan et al. 1999; McLellan, unpublished data). Of these 13 deaths, 9 were killed by another bear and at least 7 were consumed. Eight of these 9 were adult females, but none were with cubs when killed and thus did not die defending their young. Information on intraspecific killings among grizzly bears in North American (McLellan 1994; McLellan, unpublished data) indicates that adult males do most of the killing and cubs are the most common victim (Table 2); however, males kill other age and sex classes and adult females also kill cubs.

Intraspecific killing that is not sexually selected appears relatively common among grizzly bears. It has also been documented that grizzly bears are particularly efficient predators of juveniles of a variety of large mammals (Larson et al. 1989, Gunther and Renkin 1990, Clarkson and Liepins 1993, Adams et al. 1995, Young and McCabe 1997, Bertram and Vivion 2002). This innate or learned predatory behavior may trigger adult males to focus particularly on grizzly bear cubs and yearlings. However, adult males and females that kill cubs do not always eat them (S. Miller, personal communication; McLellan, unpublished data, 2004), so the underlying cause may vary and, in some cases, may be sexually selected. The evolution of mate recognition SSI, if it exists, likely has its genetic roots in predatory behavior, therefore the 2 ultimate causes of infanticide (predatory and sexually selected) are both adaptive and may remain intertwined.

The mate recognition hypothesis: Scandinavia and Alberta

The results from the Flathead study and the SSI simulation model suggest that if SSI operates in grizzly bears, it would fit the mate recognition form, but not the immigrant male form as proposed by Wielgus and Bunnell (1995, 2000), Swenson et al. (1997, 2001*a*), and Swenson (2003). The mate recognition form of SSI generally fits the data presented by Miller et al. (2003), but does it fit the studies of Swenson et al. (1997, 2001*a*), (Swenson 2003), and Wielgus and Bunnell (1995, 2000)?

In Scandinavia, Swenson et al. (1997 and 2001*a*) compared cub survival rates between 2 distant populations (600 km apart) with different bear harvesting histories. The northern area (control area) had no adult males killed by hunters, whereas the southern area (treatment area) did have males killed (Swenson et al. 1997). Swenson et al. (1997, 2001*a*) concluded that the key factor in the relatively low cub survival in the southern treatment area was immigration of subadults following the death of 1 or more established adult males, and that resident males were not an important factor in the loss of cubs. Recently, however, genetic analysis of 2 males that killed cubs indicated that they were adult, resident males (Swenson 2003). Swenson (2003) maintained that killing resident adult males resulted in increased cub mortality.

In the Scandinavian study, 1 reason hunters did not kill any adult males in the northern control area was because there were very few, if any, there to kill. In the northern area, the probability of a male surviving from a yearling to adulthood (5 years) was 0.223, compared with 0.499 for the southern study area (Swenson et al. 2001*a*). Although there was little legal hunting, Swenson (2003) found evidence of considerable poaching of bears in the northern area (about 2.8× greater than the legal harvest). Swenson (2003) further suggested that the few males present in the northern control area were young, and most first bred successfully as 3-year-olds. The adult sex ratio in the northern area clearly favored females, thus males would be expected to adopt a searching strategy resulting in little or no infanticide and high cub survival. Also, the young male bears remaining in the northern area may have had difficulty killing cubs defended by their mother (Swenson et al. 2001*a*)

The southern area had adult males and some were shot by hunters. However, unlike hunted populations in North America, an equal number of females and males were shot in Scandinavia (Swenson et al. 1994). For example, between 1985 and 2001 only 16.4% of the bears legally harvested in the southern study area were ≥5-year-old males (Swenson 2003), whereas 47.8% of the bears legally killed by hunters in the Flathead were ≥5-year-old males. The hunted area in Scandinavia likely had a relatively even sex ratio of adults and thus, as the model suggests, infanticide by older males should be more common in the southern Scandinavian area than in heavily hunted North American populations.

The high cub survival (0.96) in the northern study area where there were few large, resident males because of high human-caused mortality, combined with the observation of Swenson (2003) that resident males killed cubs in the southern study area, supports the mate recognition form of SSI. It does not, however, preclude the alternative hypothesis that large bears kill small bears for reasons other than SSI; significantly more yearling females were killed by other bears (not SSI) in the southern Scandinavian study area, where adult males were relatively common, than the northern area, where adult males were rare (Swenson et al. 2001*b*).

Wielgus and Bunnell (1995, 2000) compared data from the dry, eastern slopes of the Rocky Mountains in the Kananaskis area of Alberta with data collected in the wet Selkirk Mountains in Idaho. Hunting was permitted in the Alberta study area only in the last 3 years of the 5-year study but it was not permitted in Idaho. Wielgus and Bunnell (1995, 2000) suggested that the hunting and consequent removal of adult males caused an influx of potentially infanticidal, young males; 9 3–7-year-old males were captured during the last 3 years of study. The authors suggested that the 4 adult females in Alberta used suboptimal habitat to avoid the males and consequently had small litters ($\bar{x} = 1.4$, $n = 5$). In Idaho, where there was no hunting (but 2 of 7 radiocollared adult males were killed by people; Wielgus et al. 1994), there was no apparent immigration of young males, adult females were not forced into suboptimal habitat, and females had 2.2 cubs/litter ($n = 10$).

For several reasons, the role and mechanisms of infanticide in the Alberta study is more speculative than in Scandinavia. First, infanticide was not detected and all cubs survived (Wielgus and Bunnell 1994). Second, as Miller et al. (2003) highlighted, samples sizes were very small and included related individuals (i.e., lacked independence). In addition, data for the main response variables were collected over the entire 5-year study when the treatment (hunting) began in year 3. Most (83%) of the telemetry data and all of the litter size data were obtained before most (3 of 5) of the adult males were killed. With much larger samples, Garshelis et al. (2005) found the reproductive rate of grizzly bears in the Banff and Kananaskis area remained among the lowest on the continent although hunting had been stopped in the area, and they suggested that nutritional factors, not hunting, was the cause of the low rate.

There are features of the Alberta study area, however, that may make SSI probable. The study occurred along the continental divide, and rugged mountains with relatively high grizzly bear densities (Boulanger 2001) are found immediately to the west, whereas prairies and ranchland with virtually no grizzly bears are found to the east. All female and 11 of 14 male grizzly bears were trapped within 10 km of the continental divide, and the home range of every radiocollared bear crossed this divide (Carr 1989). Perhaps because the study area was located along the edge of grizzly bear distribution, and because males have much larger home ranges than females, 17 male but only 6 female bears were captured. Although the trapping areas were of similar size, the 2.8 (M:F) ratio of captured bears in the Alberta study was significantly different from the 0.9 ratio (13 M:15 F) in the Idaho study (randomization test $P = 0.046$), and unlikely to be the same as the 1.28 (41 M:32 F) of independent bears in the Flathead study area (randomization test $P = 0.075$). The simulations of SSI suggested that as the sex ratio of the population shifts toward more males, infanticide becomes increasingly profitable because estrous females will be relatively rare. This interpretation leads to the hypothesis that along the fringes of occupied grizzly bear range, particularly where bear densities exhibit a marked gradient (high to low) over a short distance, the incidence of infanticide may be greater.

Management implications

Wielgus and Bunnell (1995, 2000), Swenson et al. (1997, 2001*a*), and Swenson (2003) suggested that the immigrant male hypothesis of SSI operates when grizzly bear hunting removes adult males. This hypothesis has significant implications for the management of hunted bear populations. For example, Swenson et al. (1997) suggested that removing 1 or 2 adult males over an area of 11,200 km^2 in a rapidly increasing population caused the 25–60 adult females to lose 11–25 cubs annually, and reduced the population growth rate (λ) by 3.4%. Conversely, if SSI does not operate, cub survival should increase once hunting reduces the population size below carrying capacity, as was reported by Miller et al. (2003).

The results of the Flathead study and the SSI simulation modeling did not support the immigrant male form of SSI but could not clearly differentiate between mate recognition SSI and the hypothesis that SSI does not operate in bears but that infanticide is rooted in other factors, such as predation. If mate recognition SSI occurs in grizzly bears, then the model suggests that its level of expression will depend on a variety of conditions. If there are very few adult males, such as in the northern Scandinavian population where males experienced high human-caused mortality, males should not kill cubs and monitor the mother until she becomes receptive, because doing so would cost them mating opportunities elsewhere. However, if hunting practices result in as many or more females being killed than males, such as in the southern Scandinavian brown bear population, SSI may be expressed because it is less likely that males would find estrous females that were not heavily contested for by other males. Similarly, on the edge of the bear's distribution, such as in the Alberta study area of Wielgus and Bunnell (1995, 2000), there may be, on average, more males than females due to males having larger ranges. There, infanticide may be more likely, although males would likely move to the portion of their range with more females during the mating season.

The model also suggests that if searching efficiency is low, perhaps due to a low density of bears, then infanticide may be profitable when a male encounters a female with cubs because the male may not otherwise encounter an estrous female. If infanticide is indeed greater on the edge of occupied grizzly bear habitat and where there is a low density of bears, then there are important implications for grizzly bear conservation. High adult female survival is not only important for continued reproduction, but also to keep the density of adult females high enough to reduce infanticide. Proponents of bear hunting may use this information to promote the harvest of males along the edge of grizzly bear distribution or in low-density populations. This strategy is not warranted because mate recognition SSI remains an untested hypothesis at this time and, more importantly, hunters also kill females.

If SSI operates in grizzly bears, it would only be one factor influencing cub survival. McLellan (1994), Miller et al. (2003), and Schwartz et al. (2005) presented data suggesting that unhunted populations at or near carrying capacity have reduced recruitment due to high cub mortality, smaller litters, longer intervals between litters, or a combination of these parameters. Hunting reduces the population size of grizzly bears and usually, at least in North America, also reduces the proportion of adult males. These hunted populations have greater recruitment than populations at carrying capacity. What remains unclear is the form of the relationship between population size with respect to carrying capacity and recruitment, and whether the relationship differs depending on the sex ratio of harvested bears. It is unlikely that this relationship is linear. Rather, it likely changes more rapidly near carrying capacity (Taylor et al. 1994). More uncertain are the implications of the sex ratio of the harvest. My results suggest that if more males are removed than females, cub survival will be greater than if the sex ratio of the harvest is equal or favors females. However, the form of relationship between the sex ratio of the living population and cub survival remains uncertain. The results of the Susitna experiment (Miller et al. 2003) suggest that removing more males does not affect recruitment once the sex ratio is <40% males.

Predictions of the mate recognition hypothesis of SSI may be tested in the important Scandinavian studies. If poaching can be curtailed in the northern study area, allowing the density of adult males to increase relative to that of females, then cub survival should decrease. Similarly, if, through regulation or education, hunters in the southern area can kill mostly adult males and not females, then cub survival should eventually increase. However, both of these populations have been rapidly increasing for many years (Swenson et al. 1997, 2001*a*), so density effects may eventually affect cub survival.

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