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11.

Implications of Sexually Selected Infanticide for the Hunting of Large Carnivores

Jon E. Swenson

When estimating sustainable harvest rates, wildlife managers are typically interested in population-level parameters, such as reproductive rates, survival rates, age distribution, sex ratios, density dependence, and the effect that hunting has on these parameters (Sutherland 2001). The potential effects of hunting on behavior, however, are usually not considered. As one might expect, hunting can affect wariness (Vosburgh and Irby 1998) and short-term habitat selection (Swenson 1982). In addition, effects of hunting on mating system and pair bonds have been documented. For example, pronghorn antelope (*Antilocapra americana*) may shift from resource-defense to harem-defense polygyny in response to a decline in the proportion of older males (Byers and Kitchen 1988). Also, killing male mallards (*Anas platyrhynchos*) after the pair bond has formed on the wintering area lowers subsequent reproduction by yearling females (Lercel et al. 1999). Greene et al. (1998) modeled the effects of hunting in relation to breeding behavior for some African mammals and concluded that the effect of harvest depends, in part, on the interaction between hunter selectivity and breeding system. They found that

for moderately polygynous ungulates, high-intensity hunting that focuses on either males or on adults of either sex has a greater effect on populations than hunting of all age and sex classes, and that monogamous and weakly polygynous species are particularly sensitive to hunting. In large carnivores, hunting dominant males can have a population effect through increased juvenile mortality due to sexually selected infanticide (SSI) following male turnover (Starfield, Furniss, and Smuts 1981; Swenson et al. 1997; Greene et al. 1998). In addition, decreased reproductive success has been reported when females choose less productive habitats to avoid potentially infanticidal males (Wielgus and Bunnell 1994, 2000).

In this chapter, I describe the SSI hypothesis and briefly summarize empirical evidence for SSI in many mammalian groups, including large carnivores, although SSI has been well described in many other groups of animals, including birds and invertebrates. I then focus on the evidence of SSI in large carnivores, particularly the lion (*Panthera leo*) in the Serengeti and the brown bear (*Ursus arctos*) in Scandinavia. I discuss the ramifications that SSI can potentially have for sport hunting of large carnivores and the controversy that this concept has generated.

Sexually Selected Infanticide

Infanticide is the killing of dependent offspring. A common formal definition is "any behavior that makes a direct and significant contribution to the immediate death of an embryo or newly hatched or born member of the perpetrator's own species" (Hrdy and Hausfater 1984). Hrdy (1979) classified the potential reasons for infanticide and concluded that infanticide can benefit the perpetrator if it is linked to competition for limited resources. When that limited resource is mates, the competition is intrasexual and the infanticide is termed sexually selected. The requirements of the SSI hypothesis are (1) infanticidal males should not kill offspring they have sired, (2) infanticide should shorten the interbirth period of the victimized females, and (3) infanticidal males should mate with the mother of the dead infant and sire her subsequent offspring (Ebensperger 1998). If loss of part or all of a litter will increase the size or survival of the subsequent litter, however, the interbirth period does not have to be shortened for SSI to occur (van Schaik 2000a). I limit my discussion about infanticide to SSI because it has the most direct implications for sport hunting of large carnivores.

Because infanticide reduces the fitness of the victim's parents, they are expected to evolve counterstrategies to prevent infanticide (Ebensperger 1998). For mothers, these may include (1) pregnancy termination to prevent additional investment on infants that would likely be killed (the Bruce effect), (2)

maternal aggression to protect the offspring, (3) female coalitions to repel infanticidal conspecifics, (4) avoidance of potentially infanticidal males, (5) promiscuity to confuse paternity and provide an incentive for males to tolerate the young, and (6) territoriality to keep potential intruders away from vulnerable infants (Ebensperger 1998). Behaviors consistent with these counterstrategies have been reported in various species of large carnivores (Craighead, Sumner, and Mitchell 1995; Craighead et al. 1995; Ebensperger 1998; Wielgus and Bunnell 1994, 1995, 2000; Logan and Sweanor 2001), although one would not necessarily expect to find all of these in every species showing SSI.

Patterns of Sexually Selected Infanticide in Mammals

A recent review revealed that various forms of infanticide have been observed in 91 species of wild or captive mammals (Ebensperger 1998). Van Schaik (2000a) investigated whether infanticide by males is concentrated in species with female life history patterns that are expected to promote SSI, especially long lactation (or any prolonged maternal care that delays conception) relative to gestation, because postpartum mating is unlikely given that it would produce two sets of young of different ages. Van Schaik (2000a) found that the gestation period is longer than lactation in most mammals. Species in which male infanticide has been documented, however, had significantly longer lactation:gestation ratios, as expected from the SSI hypothesis. The few species with short lactation and documented infanticide by males are rodents with large litters, where the loss of one litter either decreases the interbirth interval or increases the size of the next litter (Elwood and Ostermeyer 1984).

Van Schaik (2000a) found reports of infanticide in five taxonomic groups, all with lactation:gestation ratios greater than or equal to 1; primates, fissiped carnivores, odontocetid cetaceans, sciurognath rodents, and perissodactyls. In the other eight groups of nonvolant mammals examined, lactation:gestation ratios were significantly less than 1, and no deliberate infanticide by males had been recorded. The results of this analysis strongly support the SSI hypothesis and show that male infanticide is found primarily in three groups: primates, fissiped carnivores, and sciurognath rodents.

Another way to assess the importance of SSI is to determine whether females of species that are expected to show SSI also show counterstrategies against it. Van Noordwijk and van Schaik (2000) examined four predicted counterstrategies: (1) polyandrous preconception mating (leading to paternity confusion), (2) long mating periods (to promote polyandry), (3) postconception mating (which also confuses paternity because a male mates

with a female that is already pregnant), and (4) embryo abandonment in response to the arrival of potentially infanticidal males. They classified species as vulnerable if lactation lasts longer than gestation, reproduction is not strictly annual and seasonal, or implantation is facultatively delayed or the birth interval shortened after a lost litter. Females in vulnerable primate species mate polyandrously more often (62% of 47 species) than females of nonvulnerable species (9% of 11). In carnivores, 87% of 40 vulnerable species mate polyandrously compared with 58% of 26 nonvulnerable species. They found no clear pattern for length of mating periods or post-conception mating, but the latter is common among the vulnerable species in two of the most vulnerable orders, primates and carnivores. Although the data on embryo resorption or abortion are limited, especially for wild mammals, it is observed in many species in circumstances where subsequent infanticide is likely.

Primates are the best-studied group of mammals exhibiting male infanticide. Van Schaik (2000b) examined 54 cases of infanticide to see if they correspond with the predictions of SSI. He found that 85% of the cases of infanticide occurred after a reproductively able male became dominant; 94 to 98% of the infants were not killed by their father; 67 to 100% of the infants, depending on species, were killed at an age that would have shortened the time to their mother's next estrus; and, in 78% of the cases, the male gained mating access to the mother. These results are consistent with SSI. Recent DNA analyses have shown that male langur monkeys (*Presbytis entellus*) killed or attacked only infants they had not sired, and were the likely fathers of subsequent infants (Borries et al. 1999).

Packer and Pusey (1984) predicted that carnivores were more likely to exhibit infanticide than any other mammalian order. These studies provide strong theoretical and empirical support for the occurrence of SSI in carnivore species with female reproductive patterns that make them vulnerable for SSI.

Lions in the Serengeti

Among large carnivores, SSI has been best documented in lions, especially in a 24-year study in the Serengeti (Pusey and Packer 1994a). The presence of resident males in a pride deters infanticide by alien males. Virtually all cubs less than 9 months of age died after groups of males took over a pride of females. There was a clear benefit for the males to kill the cubs after a takeover because the time from cub death to conception is about 5 months, compared with 20 months from birth to conception when the cubs survive. Because the average tenure of a male coalition is only 24 months, the advantage is

obvious. Another advantage to the overtaking males is that the mothers terminate their alliance with the former males after their young die, and begin to cooperate with the new males to keep out other males (Pusey and Packer 1994a).

As expected, female lions show counterstrategies to infanticide (Pusey and Packer 1994a). McComb et al. (1993) documented that mother lions can identify the roars of potentially infanticidal males. When mothers heard roars of alien males, they stood up, grimaced or snarled, and stared in the direction of the roars. Most mothers then ran or walked with their cubs in the opposite direction. When meeting alien males, females with cubs threaten or attack them, and may be wounded or killed in the fighting (Pusey and Packer 1994a). Grouping by females appears to be an important defensive strategy; cubs of solitary females were more likely to be killed than cubs of groups of two or more females (Packer, Scheel, and Pusey 1990), even though the typical number of females in a crèche exceeds the optimal group size for female foraging efficiency (Packer, Scheel, and Pusey 1990) and crèche formation leads to milk theft by nonoffspring (Pusey and Packer 1994b). Also, alien males are more reluctant to approach playbacks of three females roaring in a chorus than single females roaring (Grinnell and McComb 1996). Pusey and Packer (1994a) concluded that risk of infanticide by males was an important factor influencing pride size.

Another counterstrategy to infanticide is attracting large male coalitions (Pusey and Packer 1994a). Because the length of tenure increases with coalition size, females associated with a large male coalition suffer lower rates of infanticide. Following takeover, females show heightened sexual activity but reduced fecundity for about 100 days. The heightened sexual activity of many estrus females that have lost their cubs encourages competition among coalitions, and the largest coalition eventually becomes resident in the pride. The reduced fecundity is thought to be a strategy to attract a larger male coalition before conceiving (Pusey and Packer 1994a). Delayed conception would lead to a higher female lifetime reproductive success if it increased the chance of attracting a large coalition by 30% (Packer and Pusey 1983a). Packer and Pusey (1983b) found that females also produced a higher proportion of sons in the first 300 days after a takeover. This was expected because the young males in the pride will then produce potentially larger male coalitions when they mature, increasing their chances of invading new prides.

The research in the Serengeti clearly shows SSI in lions. The three requirements of SSI were met and females showed five of the six counterstrategies. When the effect of SSI after male takeover is incorporated into harvesting models, several authors have shown that killing harem-holding males

reduced population growth rates (Starfield, Furniss, and Smuts 1981; Venter and Hopkins 1988; Starfield and Bleloch 1991; Greene et al. 1998). It is important to note, however, that the occurrence of SSI seems to vary among lion populations. The smaller parks of East Africa contain small isolated populations, and dispersing males suffer high mortality outside the protected areas. In these parks male takeovers apparently occur at a much lower frequency than in the Serengeti and there is only anecdotal evidence of infanticide (Packer and Pusey 1984). Also, cub:female ratios were not affected by removal of adult males in a lion population in Zambia, where the mortality rate of adult males was especially high (Yamazaki 1996). This apparently influenced the social organization, allowing males to copulate with females from several prides. I suggest that SSI would be lower in this situation, with uncertain paternity.

Brown Bears in Scandinavia

Bears are a likely candidate for SSI (Packer and Pusey 1984). Female reproductive intervals are 2.0 to 3.0 years in American black bears (*Ursus americanus*) (Garshelis 1994), 2.6 to 4.6 years in North American brown bears (McLellan 1994), and an average of 3.7 years in polar bears (*U. maritimus*) (Derocher and Taylor 1994). During the breeding season, captive female American black bears breed 2 to 3 weeks after their cubs are removed (LeCount 1983), but there is some evidence that black and brown bears in the wild may come into estrus within 2 to 4 days after losing their cubs (LeCount 1983, Hessing and Aumiller 1994). Evidently, a male has much to gain by killing cubs he has not fathered if he can sire the subsequent litter. Observed female counterstrategies include aggressive defense of young, and mothers may be killed or wounded in the fighting (McLellan 1994; Craighead, Sumner, and Mitchell 1995; Swenson, Dahle, and Sandegren 2001b); polyandry (Craighead, Sumner, and Mitchell 1995; Craighead et al. 1995); and avoidance of habitats frequented by males (Pearson 1975; Murie 1981; Mattson, Knight, and Blanchard 1987; McLellan and Shackleton 1988; Wielgus and Bunnell 1994, 1995, 2000).

It is well known that bear cubs, as well as older bears, including females, are killed by adult conspecifics of both sexes (Garshelis 1994, McLellan 1994). Killing of nonkin offspring by females may reduce competition for resources (Hrdy 1979, Lindzey et al. 1986). Although much conspecific predation is clearly not SSI, I will concentrate on male infanticide because it is most relevant to sport hunting.

Unlike lions, male brown bears are not associated with a harem, and neither sex is territorial. Bear home ranges overlap those of other bears of

both sexes (Mace and Waller 1997, McLellan and Hovey 2001). During the breeding season (mainly May and June), males and females usually remain together for several days to 3 weeks, although consortships can be as short as a few hours (Craighead, Hornocker, and Craighead 1969; Murie 1981; Herrero and Hamer 1997). Both sexes are promiscuous, with females mating with up to eight males in one season (Craighead, Sumner, and Mitchell 1995). Cubs stay with their mothers until they are 1 to 2 years old in Scandinavia (Swenson et al. 2001), but in North America few cubs leave as yearlings, and they can stay with their mother for up to 4 years (McLellan 1994).

Harvest of Adult Males and Cub Survival

The reported effects of hunting male bears on cub survival are equivocal. Some studies of brown and American black bears have reported a negative relationship between recruitment and density of adult males (McCullough 1981, Stringham 1983, Clark and Smith 1994), counter to the SSI hypothesis. The opposite effect has also been postulated, that increased hunting of adult males can increase cub mortality through SSI by immigrating males (Stringham 1980). Empirical evidence for SSI comes from one population of American black bears and a comparison of two populations of brown bears (LeCount 1987, Swenson et al. 1997). Miller (1990b) concluded that neither a positive nor a negative effect of killing adult males on cub survival has been adequately demonstrated.

My collaborators and I have been studying two populations of brown bear since 1984, one in northern Sweden (about 8000 km^2) and one in central Sweden–southeastern Norway (about 13,000 km^2); they are described in Bjärvall and Sandegren (1987). The study areas are about 600 km apart and are near the northern and southern edges of the species' range in Sweden. Both populations increased rapidly from 1984 to 1995, indicating they were below carrying capacity. The exponential rate of increase (r) was 0.13 in the north and 0.15 in the south (Sæther et al. 1998). Bear hunting was allowed during the autumn in both areas, but the northern area includes three national parks where hunting is forbidden. Hunting pressure has increased sevenfold since 1995 in the southern area. In the northern area, there is evidence of considerable poaching of bears, about 2.8 times greater than the legal harvest (Swenson and Sandegren 1999). Poaching is less important on the study area than in the surroundings, and it may restrict immigration to the study area (Swenson et al. 2001).

Swenson et al. (1997) examined data from 1985 to 1995 to test the following predictions of the SSI hypothesis: (1) premature loss of cubs would

shorten the interval to subsequent estrus, (2) cubs would disappear (presumably die) during the breeding season, (3) cub survival would be lower following the killing of adult (≥ 5 years) males in the south, where hunters killed males during the period from 1985 to 1995, and (4) cub survival would be high in the north, where no males had been killed by hunters. Unmarked cubs were monitored by following their radio-marked mothers. All the predictions were met (Swenson et al. 1997): (1) 8 of 10 females that lost all their cubs gave birth the next year, compared with none of 40 that kept their cubs; (2) 75% of the 20 cubs that disappeared did so during the breeding season; (3) survival of 74 cubs was significantly lower both 0.5 and 1.5 years after an adult male had been killed on the 11,200 km^2 study area in the south, but not 2.5 years after; and (4) cub survival was significantly lower in the south (0.72, $N = 74$) than in the north (0.98, $N = 50$). The time lags are not whole numbers because males were killed in the fall, and cub loss occurred the following spring.

We concluded that killing an adult male would disrupt the male social organization for 1.5 years and decreased the population growth rate (λ) by 3.4%. Killing an adult male in our southern study area led to a loss of recruitment equivalent to killing 0.5 to 1.0 adult females (Swenson et al. 1997). The time lag we recorded does not seem unreasonable for brown bears if the loss of cubs is primarily caused by infanticide by immigrating males that establish a home range on the study area after the death of a resident adult male. Bears are generally killed during the fall, when fattening for winter denning is important. The breeding season starts in the spring not long after den emergence and continues to midsummer. Thus there is a relatively short time for an immigrating male to become established in a vacancy from the dead adult male and to breed (Swenson et al. 2001). In addition, a young male will probably have difficulty killing defended young, but can become more effective with increasing age.

We have continued our research on SSI and reanalyzed our data using all adult male deaths, not just hunting kills, and extended the period to 1998. We changed the study area definition from a composite area containing all females with cubs for all years to an area containing the home ranges of females with cubs for each individual year. We made spatial and temporal comparisons to examine whether nutritional, social (SSI), or den disturbance factors best explained the observed variation in cub survival (Swenson et al. 2001). Cub survival was 0.96 in the north ($N = 78$) and 0.65 in the south ($N = 126$). The loss of cubs at both the spatial and the temporal levels of comparison was best explained by social factors.

Nutrition did not seem important because cub loss was greater in years when the mass of adult females and cubs was highest (Swenson et al. 1997,

2001). Disturbance was evaluated only in the south and explained some variation in cub survival. In the north, few adult males died and three adult males lost early in the study there were not replaced for many years, presumably due to little immigration of new males. In the south, five times as many males died annually. In years with recorded adult male mortality, an average of 20% died. The estimated number of adult males remained stable, presumably due to immigration. The number of adult males dying 1.5 years previously in the area containing all radio-marked females with cubs in a given year was correlated negatively with cub survival in the south. In the north, no factors correlated with temporal patterns of cub loss, but loss of adult males in these areas 0.5 to 1.5 years previously was the best explanatory variable among those tested. In the north, the few males present were young, and most first bred successfully as 3-year-olds, when they are possibly not large or experienced enough to kill cubs that are defended by their mothers. Swenson et al. (2001) concluded that immigrating males kill cubs, as predicted by the SSI hypothesis.

Identification of Infanticidal Bears

It is extremely difficult to observe infanticide or to identify the perpetrator. We have assumed that the perpetrators were primarily immigrant males based on the findings in many other studies of SSI, described earlier, and other evidence. Cub survival was high in the north during a period with no known adult mortality and little or no immigration, and in the south following years when no adult males were known to have died. An increase in the local density of subadult males has been associated with removing adult males in American black bears (Sargeant and Ruff 2001), and the 1.5-year time lag in increased cub mortality suggested that immigrating males could be responsible, as did the stable adult male numbers in spite of adult male mortality in the south. In our earlier analysis, we also found that cub mortality was elevated 0.5 year after the killing of an adult male (Swenson et al. 1997). We did not find this in the second analysis, but it included all dead adult males, not just hunter-kills, and the definition of the study area had been changed. Therefore, these two results are not directly comparable.

We have continued our investigations about this phenomenon, followed females with cubs intensively in 1998–1999, and expanded our studies using DNA fingerprinting. Here I will report some preliminary results. We collected tissue samples from the mother, the infanticidal male, and the killed cub(s) on four occasions. In all cases, DNA analyses revealed that the infanticidal male was not the father of the cubs he killed (E. Bellemain et al.

unpublished). Two infanticidal bears were marked adult resident males, 9 and 11 years old. Also, we observed males with mothers within a few days after cub loss and determined the father of the subsequent litter on six occasions. Four of these males (aged 6, 9, 12, 27 years) were marked and all were the father of the next litter. Two (aged 6 and 9) were unmarked at the time the female was observed with an unmarked male. Our DNA records suggest that one 6-year-old male was probably a first-time breeder, and the other a nonresident. Although we have no proof that these males killed the cubs, it is likely that they did. This shows clearly that the first male with a female just after she lost her cubs has a high probability of siring her next litter. Both of these findings are critical for the SSI hypothesis; the perpetrator is usually not the father of the cubs he kills, and he has a substantial chance to father the next litter. The DNA results also gave some limited support for the hypothesis that immigrants can be infanticidal. In addition, the only year we documented a 3-year-old male mating successfully in the south was 1.5 years after four adult males had been killed there.

These new preliminary results show clearly that resident adult males are also infanticidal in a manner consistent with SSI. Others have also reported that primarily large adult males kill cubs (Troyer and Hensel 1962, Murie 1981, Mattson, Knight, and Blanchard 1992; Olsen 1993; Hessing and Aumiller 1994; McLellan 1994). This is a major difference from the SSI observed in lions. An explanation may be that brown bears are not territorial, and home ranges of adult males overlap. Of course, SSI increases the fitness of a resident male as much, or more, than that of an immigrating male, and nothing in the SSI hypothesis requires that the species be territorial or social. How can we reconcile the relationship between the death of adult males and cub mortality with the evidence that resident males also are infanticidal? We have still not examined the possibilities, but one is that resident males may shift their home ranges after an adult male dies, bringing them into contact with new adult females.

We also looked at the bear-caused deaths of 13 subadult bears (1–4 years old) in relation to the death of adult males from 1984 to 1999 (Swenson, Dahle, and Sandegren 2001b). Most yearlings separated from their mothers in May. We found area differences in the rates of intraspecific predation only for yearling females, which was higher in the south (0.162, $N = 38$) than in the north (0, $N = 28$). Bears killed no subadult females older than yearlings, but males were killed as 1-, 2-, and 3-year-olds. Neither population density nor food abundance influenced rates of intraspecific predation on yearlings, but intraspecific predation on yearling females increased with the number of adult males that had died 2.5 years previously and when any adult male had died 1.5 years previously. Because the pattern for intraspecific predation on

TABLE 11.1. Effects of loss of at least one adult (≥ 5 years) male Scandinavian brown bear, with a 1.5-year time lag, on cub survival, yearling female survival, and population growth rate in the southern study area in Sweden.

	ADULT MALE DIED	NONE KNOWN DIED	SOURCE
Cub survival	0.55	0.92	Swenson et al. (2001)
Yearling female survival	0.70	0.85	Swenson, Dahl, and Sandegren (2001b)
Population growth (λ)	1.078	1.128	

The reproductive rate was increased to account for the shortened interlitter interval due to higher litter loss for the years following adult male death.

yearling females was similar to that for cubs, we speculated that infanticidal males might be prone to kill subadult bears, although this is clearly not SSI (Swenson, Dahle, and Sandegren 2001b). Intraspecific predation on subadults was highest during the breeding season, as it was for cubs and as reported by Mattson, Knight, and Blanchard (1992).

When I combined the results of our studies (Swenson, Dahle, and Sandegren 2001b; Swenson et al. 2001) and calculated population growth using a standard deterministic model (Ferson and Akçakaya 1990), I found that the loss of adult male(s) was associated with a 4.5% reduction in the population growth (Table 11.1).

We also had the opportunity to test whether an increase in harvesting adult male bears would increase cub mortality through SSI. Because the southern population showed a 16% annual growth rate from 1985 to 1995 (Sæther et al. 1998), harvest quotas were increased markedly. In Dalarna and Gävleborg counties the annual number of harvested bears increased sixfold after 1995, the annual number of harvested adult (≥ 5 years old) males increased 35-fold ($U = 6$, $p = 0.001$), and the total annual mortality of radio-marked adult males doubled ($z = 1.12$, $p = 0.26$), as did mortality of cubs accompanying radio-marked females ($z = 2.82$, $p = 0.005$). Thus the results supported the SSI hypothesis (Table 11.2).

We also studied females with cubs to determine whether they showed counterstrategies to infanticide, as would be expected if SSI were an important factor affecting female reproductive success (Agrell et al. 1998, Ebensperger 1998). We followed adult males and females with and without cubs intensively to determine whether the females with cubs exhibited any of the following counterstrategies to avoid meeting males: (1) avoiding males by (a) different activity

TABLE 11.2. Annual legal harvest of all brown bears and adult (≥ 5 years) males in Dalarna and Gävleborg Counties, Sweden, the total annual mortality of radio-marked adult male bears, and the annual mortality of cubs accompanying radio-marked females in the southern study area (1985–1995 and 1996–2001).

	1985–1995	1996–2001
Total number harvested annually	2.8 ± 0.74 (SE)	17.7 ± 2.33
Number adult males harvested annually	0.1 ± 0.09	3.5 ± 0.85
Adult male mortality	0.07 ± 0.04	0.14 ± 0.05
Cub mortality	0.28 ± 0.05	0.47 ± 0.04

SE: Standard Error

rhythms than males, (b) less movement during the breeding season, (c) different use of habitat, and (2) by mating promiscuously.

We found support for the hypothesized counterstrategies: (1a) During the breeding season, females with cubs were less active than males and females without cubs, and most active when adult males were least active (Myre 2000). (1b) Females with cubs moved less than either males or females without cubs during the breeding season (Zakrisson 2000). One could argue that this is because cubs restrict female movement, but home range sizes of females with cubs were negatively correlated with population density (Dahle and Swenson in press). Thus it is not only the cubs causing females to move less. (1c) Females with cubs used different habitats during the breeding season than those without cubs. Bed sites for females with cubs were located in areas with better visibility and large Scots pine (*Pinus sylvestris*) trees (Katajisto 2001, Kristoffersson 2003). We observed several cubs that avoided infanticide by climbing large pine trees (Fig. 11.1). Males killed cubs more often than expected in areas without large pine trees (Kristoffersson 2003). (2) Females mated promiscuously and several litters had mixed paternity (Bellemain 2001), as observed in Alaska (Craighead et al. 1995). During the breeding season, females have one or two estrus cycles of 16 to 27 days each (Craighead, Hornocker, and Craighead 1969). We have shown that the first male with the female often fathers the litter; it is therefore possible that dual estrus cycles are an example of postconception mating.

In conclusion, our results show that the three requirements for SSI are met in brown bears. Females with cubs showed three or four of the proposed counterstrategies: aggressive physical defense (Craighead, Sumner, and Mitchell 1995), avoiding males, promiscuity, and perhaps postconception mating. As far as we know, however, females do not use pregnancy block, group defense, or territoriality as counterstrategies.

FIG. 11.1. Attempted infanticide by an unmarked brown bear male on a cub in Sweden, 1999. The cub saved himself by staying at the top of the Scots pine tree. The male had already killed the cub's two siblings when the picture was taken. DNA from hairs collected from the tree revealed that he was not the father of the cubs. The cub may himself have been a product of sexually selected infanticide (SSI) because his mother lost her litter in 1998, and his father was observed with her just after the litter disappeared. (Photograph by Jonna Katajisto).

Evaluating the Evidence in Scandinavia and North America

Our recent research has strengthened our conclusion that SSI is an important factor in bear population dynamics. However, this does not mean that SSI is important in every population. Reviews of North American studies on black (Garshelis 1994), brown (McLellan 1994), and polar bears (Derocher and Taylor 1994) did not reveal conclusive evidence of SSI in any population. Infanticide was an important cause of cub mortality in one population of American black bears (LeCount 1987), but not in another (Elowe and Dodge 1989). In British Columbia, Hovey and McLellan (1996) found high cub survival in a hunted brown bear population adjacent to the unhunted Glacier National

Park, a potential source of immigrating males, and none of 44 cubs died during the breeding season (B. McLellan, 2002, pers. comm.). Miller (1990b) found no change in cub survival rates with increasing harvest rates of adult male brown bears in Alaska. However, there is not necessarily a linear relationship between the loss of adult males and cub mortality due to SSI (Swenson et al. 2001).

Is there a fundamental difference between Scandinavian and North American brown bear males? Perhaps we should remove some of the burden from the males because a high rate of infanticide also suggests that female counterstrategies are not functioning well (Janson and van Schaik 2000). What could inhibit these counterstrategies? North American and Scandinavian brown bears have very different histories. Humans tried to exterminate bears in Scandinavia with all available technology for hundreds of years, and almost succeeded (Swenson et al. 1995). This long history of persecution may have been an important selective force shaping life history strategies (Stearns 1992). After a long period with persistently high human-induced mortality rates and low density, it is not surprising that European brown bears are less aggressive toward humans (Swenson et al. 1999a), more nocturnal (Roth 1983), and more productive (Sæther et al. 1998) than North American brown bears. They are also poorer predators on adult moose (*Alces alces*) (Swenson, Dahle, and Sandegren 2001a). Lowered aggressiveness and increased productivity, perhaps as a trade-off against body growth, may make European brown bear females less able than North American females to defend their cubs from infanticidal males. This may not have been a problem in low-density, heavily hunted populations, but may be a problem in the present higher-density populations.

In contrast to Europe, brown bears in North America were exterminated rapidly after European immigrants arrived; they survived only in inaccessible areas, primarily in the north. In southwestern North America, for example, the brown bear was exterminated about 60 years after the first European settlement (Brown 1985). I am making essentially the same arguments regarding the effect of long-term heavy hunting pressure on the selection for life history traits that Festa-Bianchet discusses in chapter 12. An in-depth comparison of behavioral differences between European and North American brown bears may provide important insight into the mechanisms of SSI, the factors affecting the effectiveness of counterstrategies, and, ultimately, the implications for managing hunting of brown bears.

Evidence from Large Solitary Cats

There is also evidence of SSI in several species of large, territorial, nonsocial cats. Logan and Sweanor (2001) found that male cougars (*Puma concolor*) caused 44% of all kitten mortalities, but females killed no kittens; infanticidal

males were "apparently" not the fathers of the kittens they killed; and in 13 cases resident males, including 3 cases of known sires, associated safely with females with kittens. Two males that killed and ate entire litters subsequently sired litters with the mother of the killed kittens. The loss of newborns to 2-month-old kittens may accelerate breeding access to females by 8 to 10 months. Logan and Sweanor (2001) also found several counterstrategies among females with kittens: aggressive defense, avoidance of other cougars, and perhaps "pseudoestrus." Spreadbury et al. (1996) reported that two young kittens were killed by two different transient males. Ross and Jalkotzy (1992) recorded high kitten survival (97%) with a stable male population. Later, with a high turnover in adult males due to trophy hunting, the kitten survival rate declined (I. Ross, 2002, pers. comm.).

Leopard (*Panthera pardus*) males have also been documented siring the subsequent litter after killing kittens (Bailey 1993). A suggestion of SSI has also been reported in tigers (*P. tigris*). Smith and McDougal (1991) estimated 90% cub survival and no infanticide when resident males were stable, but 33% cub survival and much infanticide when new males were taking over the territories of former residents.

Although these results are not conclusive, they are consistent with SSI. They also strengthen the case for SSI in nonsocial carnivores.

The Controversy

Although there are few critics of SSI among behavioral ecologists, it is a very controversial hypothesis, especially among some anthropologists who view infanticide as maladaptive or aberrant (Sommer 2000). In a more extreme criticism of SSI in lions, Dagg (1999) stated that the SSI hypothesis "resonates with Western culture in which many people accept male dominance and aggression and condone in part the control of female sexuality by men." For other reasons, the SSI hypothesis is also controversial among some North American wildlife biologists (Wielgus and Bunnell 2000), although some North American wildlife biologists have proposed its existence (Stringham 1980, LeCount 1987). SSI is also a controversial issue in hunting of cougars, where some managers apparently believe that harvesting males increases kitten survival (I. Ross, 2002, pers. comm.), just as some do for bears (Miller 1990b). Researchers have also speculated that harvesting males may increase juvenile mortality through SSI in cougars (Ross and Jalkotzy 1992; Murphy, Ross, and Hornocker 1999; Logan and Sweanor 2001) and wolverines (*Gulo gulo*) (Landa et al. 2000).

Some critics of SSI in bears believe that SSI should not be expected in nonsocial and nonterritorial species. The SSI hypothesis is not specific to any social organization, and the large number of species exhibiting SSI also

argues against it being restricted to any specific social organization. The evidence of SSI in solitary cats supports this. Our preliminary DNA-based results suggest that the pattern of SSI in nonterritorial species may differ from that in territorial species. In nonterritorial species, infanticide by resident males that are not the father to the young may be more common. Such behavior would be hindered in territorial species, where the male has a more exclusive access to the females in his territory. SSI is also easier to observe in social species. In an intensively studied red howler monkey (*Alouatta seniculus*) population, the infant mortality rate was 200 times greater within 1 month after a male status change than during nonchange periods of the same groups. However, less than 5% of the suspected infant killings by newly dominant males were observed (Crockett and Sekulic 1984). Also, infanticide was observed only seven times in the Serengeti and Ngorongoro Crater in Tanzania during intensive studies on lions between 1966 and 1982, but circumstantial evidence suggested that infanticide occurred almost every time a new coalition of males took over a pride (Packer and Pusey 1984).

Paradigm shifts always take time in science in general and in wildlife management in particular, and many wildlife managers remain skeptical. Conservatism was evident in a report that rejected SSI as a possible biological consequence of hunting brown bears, because only one study had suggested it, whereas others showed no clear trend, even though no study had clearly rejected it (British Columbia Ministry of Environment, Lands and Parks 1995). It is well known that many large carnivores can only sustain quite low levels of human-induced mortality, and that adult females are particularly sensitive (Knight and Eberhardt 1985, Miller 1990a). As a consequence, some agencies encourage large carnivore hunters to select males (e.g., Smith 1991).

Wildlife research is usually not optimal to document SSI because it involves marking many animals and monitoring them relatively infrequently to obtain rates of mortality and reproduction. Intensive, individual-based studies are the exception, rather than the rule. It is perhaps not surprising that behavioral ecologists, who work more intensively with their study animals, find evidence of SSI, rather than wildlife biologists. It is very difficult to observe infanticide in wild mammals and many conclusions are based on patterns in relation to hypotheses being examined, including our conclusions regarding SSI in brown bears.

Conclusions and Recommendations

How should managers react to the possibility of SSI in populations that they manage? The SSI hypothesis clearly predicts that many large carnivores should show SSI, but is that enough to accept it for management purposes? A

rodent that was expected to show infanticide did not (Ebensperger 2001). Should managers just ignore these hypotheses for now? I would argue that they should not. The review and tests of the SSI hypothesis in addition to the evidence of its existence in lions, brown bears, and some large solitary cats strongly suggest that SSI should be considered when managing harvest of large carnivores. Also, various estimates of the effects of SSI on population growth are large enough to have consequences for management. Given the controversy among researchers, however, it is not surprising that many managers are unsure about SSI.

Male infanticide has been observed in the wild in a context that is consistent with SSI in many species of large carnivores that are commonly exploited by humans: spotted hyena (*Crocuta crocuta*), cougar, Canada lynx (*Lynx canadensis*), bobcat (*L. rufus*), lion, leopard, tiger, American black bear, brown bear, and polar bear (van Schaik 2000). I would add the wolverine. Although it is a seasonal breeder and most adult females mate every year (Magoun 1985), only 40 to 60% of the females raise cubs each year (Landa et al. 1998), and infanticide is a common cause of cub death in some years (Persson et al. in press). If the killing of cubs in 1 year increases the probability of successfully rearing cubs the following year, SSI would be adaptive, as has been suggested in a captive population of another seasonal breeder, the red deer (*Cervus elaphus*) (Bartos and Madlafousek 1994).

The ramifications for hunting are more difficult to predict. Because SSI is associated with the turnover of adult resident males, hunting should have a greater impact on the level of SSI in species in which hunters can distinguish the sexes in the field, such as lions and cougars (and somewhat for bears, Smith 1991). However, hunting should have an effect on SSI whenever it reduces the survival rate of adult males, as it does for brown bears (McLellan et al. 1999). The death of 20% of the adult male brown bears reduced population growth rate by 4.5% (from 1.13 to 1.08) in the local area, and the hunting death of a male reduced population growth by 3.4% (Swenson et al. 1997). Using a very different approach, Wielgus et al. (2001) estimated that a grizzly bear population could experience a 5.7% reduction in growth if females avoided productive habitats frequented by potentially infanticidal males that immigrated after resident adult males were killed. Actual infanticide was not included in their model. Models of lion population dynamics have also showed reduced population growth when adult males are killed (Starfield, Furniss, and Smuts 1981; Venter and Hopkins 1988; Starfield and Bleloch 1991; Greene et al. 1998).

It appears that some populations of lions, brown bears, American black bears, and probably other large carnivores are more susceptible to losses of young than others. Also, in some species both resident adults and immigrants

can be expected to exhibit SSI. If many ecological and environmental factors affect the expression of SSI, it will be difficult for a manager to predict the effects of killing adult males in a given population. Obviously, we need more research on SSI in hunted large carnivores, particularly to allow us to predict when SSI should be expected.

Generally, too little is known about the effects of hunting on the behavior of hunted species. Festa-Bianchet (chapter 12) discusses the effects of hunting in terms of selection pressure on life history traits, and notes that there is little research in this important area. This applies equally well to effects on social organization and mating systems. I searched the last 5 years of the *Journal of Wildlife Management* and *Behavioral Ecology* for articles on this subject. I found that no papers in *Behavioral Ecology* and only 0.7% of the species-oriented papers in the *Journal of Wildlife Management* were on the behavioral effects of hunting (Table 11.3). Who will study the effects of hunting on animal behavior, if not behavioral ecologists or wildlife biologists? I reiterate Festa-Bianchet's (chapter 12) ethical concerns about manipulating the morphology and behavior of hunted species by hunting. Is it ethically right to allow hunting when we do not understand its consequences? One could counter that it is usually necessary to hunt large carnivores where the landscape is human-dominated and tolerance to depredations caused by large carnivores is low, but that does not release us from our ethical obligation to understand what we are doing to these species when we hunt them.

Now, back to the manager. A biologist responsible for managing the hunting of large carnivores can either ignore SSI until it has been conclusively demonstrated, or assume a population consequence of harvesting adult males unless SSI has been documented not to occur in a species and area. I recommend the latter, which follows the precautionary principle, and which I believe is only good management procedure. Just as harvesting should be more conservative when population estimates are uncertain (Tufto et al. 1999), it should also be more conservative when the effects of hunting are

TABLE 11.3. Articles published in the *Journal of Wildlife Management* and in *Behavioral Ecology* (1996–2000) that examined the effects of hunting on behavior.

	JWM	BE
Number of articles	698	439
Species-oriented articles:	651	386
about commonly exploited species	65%	10%
effects of hunting reported	3.6%	0.7%
behavioral effects of hunting reported	0.7%	0

uncertain because of factors such as SSI (Boyce, Sinclair, and White 1999; Anthony and Blumstein 2000).

Summary

Sexually selected infanticide (SSI) can occur when a male, who is not the father of a dependent young, may gain increased mating success by killing the young. It is promoted by disruption of the male social organization by killing resident adult males, thus allowing new males into an area or perhaps allowing other resident males to realign their home ranges. It has a solid and well-documented theoretical basis and should be expected in many species of large carnivores. SSI has been well documented in one population of lions, strongly indicated in brown bears in Sweden, and suggested for cougars, leopards, tigers, American black bears, and wolverines. Estimates of the effects of SSI following killing adult males on population growth (3.4–5.7% reductions in *r*) are large enough to have consequences for management. In species exhibiting SSI, hunting adult males can promote it. According to the precautionary principle, we should consider SSI when managing the hunting of large carnivores. Because there may be geographical or population differences in the occurrence of SSI, however, much more research is required before we can reliably apply knowledge of SSI to carnivore hunting management. The effects of hunting on the behavior of the hunted animals should receive increased attention from behavioral ecologists and wildlife biologists.

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