

Mating Strategies in Relation to Sexually Selected Infanticide in a Non-Social Carnivore: the Brown Bear

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Abstract

Based on the sexually selected infanticide (SSI) hypothesis, infanticide can be an adaptive mating strategy for males, but this is rarely documented in non-social mammals. This phenomenon should not benefit females, so one would expect females to evolve mating counter strategies in order to protect their infants from infanticidal males. Cases of SSI are extremely difficult to document in the field, especially for non-social species. Using field observations and genetic methods, we describe mating strategies employed by both sexes of brown bears (*Ursus arctos*) in relation to SSI. We present evidence for the first time suggesting that infanticide is an adaptive male mating strategy in this non-social carnivore, as all requirements for SSI are fulfilled (1) infanticide shortens the time to the mother's next estrus, (2) the perpetrator is not the father of the killed infants, and (3) putative perpetrators sire the next litter. Moreover, all infanticide cases occurred during the mating season. We expected that primarily immigrant males were infanticidal, as in social species. However, we found that resident adult males commonly committed infanticide. Perhaps they recognize females they have mated with previously. Moreover, we used DNA-based parentage testing to demonstrate a minimum of 14.5% of multiple paternities (up to 28% for litters with at least three young). Female promiscuity to confuse paternity may be an adaptive counter strategy to avoid infanticide.

Introduction

The concept of sexual selection, as first proposed by Darwin (1871), predicts that the fundamental reproductive asymmetries between males and females give rise to a conflict between sexes. Male reproductive success tends to be limited primarily by access to mates, whereas female reproductive success is usually limited by access to resources. Infanticide, the killing of dependent young by conspecifics, is a well-known phenomenon among animals and can be regarded as a component of this intersexual conflict (Hrdy 1979; Hrdy & Hausfater 1984). Sexually

selected infanticide (SSI) refers to competition for breeding opportunities and is more prevalent in polygynous mating systems. Three prerequisites are needed to consider infanticide as sexually selected: (1) infanticide shortens the time to the mother's next estrus, which consequently increases the infanticidal male's own opportunity to breed, (2) the perpetrator is not the father of the infants he kills, and (3) perpetrators have a higher probability of siring the female's next litter (Hrdy & Hausfater 1984).

The known cases of infanticide by male mammals are remarkably concentrated in a few orders and have mainly been described in social species, parti-

cularly among primates (Van Schaik & Janson 2000a) and carnivores (Packer & Pusey 1983). Most tests of SSI have been laboratory experiments with small mammals for which paternity was manipulated (Agrell et al. 1998). In the field, patterns of infanticide commensurate with SSI have been observed (Van Schaik & Janson 2000b), but very few studies show strong supporting evidence for the two latter prerequisites, as they require the knowledge of paternity. Despite these difficulties, infanticide is now widely recognized as an adaptive behavioral strategy to increase the fitness of the perpetrator (Van Schaik & Janson 2000b).

In social mammals, the perpetrator is often assumed not to be the father of the killed infant when it was not with the group when the infant was conceived. However, only two studies of primates demonstrated genetically that male attackers were not related to the infant victim, and that they were likely to sire the female's next litter (Borries et al. 1999; Soltis et al. 2000). Concerning non-social carnivores, infanticide has been documented in some large solitary cats (Smith & McDougal 1991; Bailey 1993; Logan & Sweanor 2001) and bears (reviewed in Taylor 1994), but those studies lacked supporting evidence for SSI, as paternity is extremely difficult to document in the wild. Ebensperger (1998) and Janson & van Schaik (2000) stressed the importance for future studies to obtain paternity estimates in order to assess the reproductive benefits to infanticidal males.

As infanticide is rarely of net benefit to females, one would expect females to evolve counterstrategies to defend their infants against infanticidal males. Many studies have examined females' anti-infanticidal behaviors (see Agrell et al. 1998 for a review). Mating with multiple males was hypothesized by Hrdy (1979) to be a female counterstrategy to forestall infanticide by manipulating information available to males about paternity. This hypothesis is gaining increasing theoretical support, however, the genetic consequences of multi-male mating require further investigations (Wolff & MacDonald 2004).

We studied wild Scandinavian brown bears (*Ursus arctos*), to determine mating strategies employed by both sexes in relation to infanticide. Brown bears are non-social carnivores with overlapping home ranges. The mating season occurs from mid May to early July. (Curry Lindahl 1972; Dahle & Swenson 2003a). Males and females remain together for a period that ranges from few hours to several days. Some males copulate and leave the female shortly thereafter and some may consort for up to 2 wk

(Herrero & Hamer 1977; Craighead et al. 1995a). Both males and females mate promiscuously, with females mating with up to eight males in a mating season (Craighead et al. 1995a) and both sexes roam to mate, increasing their range sizes during the mating season (Dahle & Swenson 2003a). Implantation is delayed until Nov. (Renfree & Calaby 1981) and females give birth to one to four small cubs in Jan., while still hibernating in dens, after 6–8 wk of gestation (Pasitschniak-Arts 1993). There is no paternal care. After birth, the young remain with the mother for 1.5–4.5 yr before they separate (Dahle & Swenson 2003b) and females do not mate while caring for their young (Swenson et al. 1994). Thus the minimum birth interval between successful litters is 2 yr. The long lactation period of bears decreases the availability of fertile females in this species. As female bears become receptive again within 2–4 d after losing an unweaned cub, during the breeding season, the long period of infant dependency (Haysen 1984) may serve to increase the advantage to male bears from eliminating unweaned infants. Infanticide has been reported in several bear studies (Troyer & Hensel 1962; Nagy et al. 1983; Taylor 1994; Craighead et al. 1995a), and Swenson et al. (1997, 2001) concluded that SSI was one of the most important factors affecting cub survival in the Scandinavian brown bear population.

Here, we use a combination of field observations of Scandinavian brown bears and molecular genetic methods to study whether infanticide might be an adaptive mating strategy for males in a non-social carnivore. As other strategies in relation to infanticide have been reported elsewhere (Swenson 2003), we choose here to concentrate our analyses on mating strategies in relation to infanticide. Specifically, we test the three predictions required for infanticide to be considered as sexually selected (see above). We also predict that infanticide occurs during the mating season and that primarily immigrant males would commit infanticide. Finally, we use DNA-based parentage testing to determine the proportion of multiple paternities in this population and test the hypothesis that female promiscuity to confuse paternity is an adaptive counter strategy to avoid infanticide.

Materials and Methods

Studied Populations

The study areas were in northern Sweden (67°N, 18°E; 8000 km²) and central Sweden to south-eastern

Norway (61°N, 18°E; 13 000 km²; Bjärvall & Sandegren 1987; Swenson et al. 1998). In the southern study area, the elevation ranges from about 200 m in the south-eastern part to about 1000 m in the western part at the Norwegian border, but only a minor part of the area is above timberline, which is at about 750 m. Lakes and bogs are common, but most of the hilly landscape is covered with intensively managed coniferous forest, dominated by Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*). The northern study area is dominated by mountains that rise to over 2000 m in the west and elevations are below 300 m in the east. Northern boreal coniferous forest dominates, but there are extensive subalpine birch (*Betula pubescens*) forests. The two study populations belong to separate mitochondrial lineages (Taberlet et al. 1995), however there is high genetic diversity based on nuclear DNA revealing that there has been an extensive gene flow throughout the entire bear population (Waits et al. 2000). On average, bears are active from Apr. to Nov., reflecting the length of the snow-free period, which is about a month shorter in the northern study area (Sandegren & Swenson 1997).

We used radio-telemetry for long-term monitoring of adult bears, locating them at least every 1 or 2 wk. Totally, radio-tracking encompassed 849 bear-years (a bear-year reflects an individual bear followed for 12 mo). Twenty-four adult females were followed intensively (almost continuously) during 1998 and 1999. Other bears were followed intensively for varying periods in other years. Bears, including yearlings accompanying radio-collared females, were captured by immobilizing them from helicopters in the spring. During capture, a skin biopsy was taken from the inner part of an ear for genetic analyses. In addition, we recorded standard zoological data, e.g. weight and body measurements and removed a first premolar tooth to determine the age (to year), by counting annuli from a thin, stained slice of the root when viewed microscopically (Matson et al. 1993). Adult bears were fitted a collar mounted with a transmitter (Telonics Model 500, 260 g and Telonics Model 600, 480 g; Telonics Inc., Mesa, Arizona, USA). Radio-collars of subadult, growing bears, were fitted with cotton spacers designed to break away after about 20 mo. Collars of adult fully grown bears were replaced every second or third year.

In the north, virtually 100% of the adult bears were radio-marked; in the south, it was about 80% of the adult females and 50% of the adult males (Swenson et al. 2001). In addition, tissue samples, sex and age were obtained from all bears reported to be killed or

found dead in and near the study areas. We documented the disappearance of cubs-of-the-year accompanying radio-marked females during 1988–2001 and assumed that cubs that disappeared had died. We observed a family group as soon as possible after den emergence, again in late Jun. to early Jul. (end of the mating season) and again before they entered the den, in autumn. The date of cub loss was estimated when the female was observed with and without cubs within a maximum of 5 d. The site of infanticide was documented based on the remains of a cub or cubs or an observation (see Swenson et al. 2001 for more details). Males were documented or suspected of committing the infanticide either from direct observations or from genetic evidence using samples (feces, hairs or remains of dead bears) found at the site of infanticide. We define a resident as an individual that used an area overlapping the infanticide site during the mating season, both the year before and the year of infanticide.

DNA Extractions and Typing

Hairs were preserved dry, feces and tissues were preserved in 95% alcohol until the DNA extraction. DNA extractions from bear tissues were carried out using the QIAamp Tissue Kit (Qiagen GmbH, Hilden, Germany) involving overnight digestion with proteinase K. DNA extractions from bear hairs were performed using the Chelex method as described by Walsh et al. (1991) in a room dedicated to processing ancient samples, hairs and feces. Tubes without tissues or hairs were treated in the same way in order to check for exogenous DNA contaminations.

Microsatellites primers described in Paetkau & Strobeck (1994); Paetkau et al. (1995) and Taberlet et al. (1997) were amplified using polymerase chain reaction. Eighteen microsatellite loci were amplified for tissue samples (G1A, G1D, G10B, G10C, G10L, G10P, G10X, G10H, G10O, G10J, cloned from an American brown bear DNA library and Mu05, Mu10, Mu15, Mu23, Mu50, Mu51, Mu59, Mu61, cloned from a European brown bear DNA library). The probabilities of identity (PI; Paetkau & Strobeck 1994; PIsibs; Waits et al. 2000) were low: $PI = 3.1 \times 10^{-17}$ and $PIsibs = 2.4 \times 10^{-7}$. The nine most discriminant loci, i.e. loci with the lowest PI, were chosen to be amplified for the hair and feces samples (G1A, G10C, G1D, G10P, G10X, Mu10, Mu51, Mu59, Mu61). Those nine loci allowed us to identify an individual unambiguously ($PI = 5.1 \times 10^{-9}$ and $PIsibs = 3.6 \times 10^{-4}$) and determine its parentage with a high probability. One primer of each pair was synthesized with a fluorescent

dye group (6-FAM, TET or HEX) on the 5' end to allow detection and sizing of fragments on an ABI Prism 377 DNA sequencer (Applied Biosystems, Foster City, California, USA). The amplification and analysis of microsatellites was carried out following the protocol described in Waits et al. (2000). For feces or hair samples and for each microsatellite, the amplifications were repeated eight times (multiple tubes approach, Taberlet et al. 1996), using the newly defined 'multiplex pre-amplification' approach (Piggott et al. 2004). For sex identification, we used the SRY primers described in Bellemain & Taberlet (2004). The gels were analyzed using GENESCAN version 2 and GENOTYPER version 1.1 software packages (Applied Biosystems, Foster City, California, USA).

Parentage Analysis

Based on the multilocus genotypes of mothers, young and males, we analyzed paternity of cubs we consider may have been killed by known male brown bears or born to a female the year after probable infanticide using the software PARENTE (Cercueil et al. 2002). A set of 550 Scandinavian brown bear genotypes (Waits et al. 2000; E. Bellemain, J.E. Swenson & P. Taberlet, unpubl. data) was used to determine the parents of the killed cubs. The genotypes of the cubs were compared with the genotype of the suspected infanticidal male and the number of exclusions or allelic incompatibilities (number of loci for which the male could not have given any allele to the cub) was counted. Paternity probabilities (when the mother is known) were calculated using the software PARENTE, taking into account the allelic frequencies, the error rate and the sampling rate of the population (see the program documentation for more details).

We used the same data set of 550 Scandinavian brown bear genotypes, including 69 litters, to docu-

ment multiple paternities in this population. We examined litters of two or more young with known mother-offspring relationships. Paternity analyses allowed us to detect multiple paternities when two different fathers were identified in the same litter or when a male was a probable father for only a part of the litter. When no father was identified for the whole litter, we compared the genotypes of the mother with those of her offspring and were able to deduce a multiple paternity when more than two different paternal alleles were identified in the offspring genotypes. This method only worked for litters of three cubs or more.

Results

Cub mortality averages 35% annually in the southern study area and 4% in the northern study area (Swenson et al. 2001). A study examining nutritional, social (SSI), and den disturbance factors found that the patterns of cub mortality were best explained by social factors in both populations (Swenson et al. 2001). Cub loss was not influenced by poorer female condition nor by female size or age (Swenson et al. 1997, 2001; A. Zedrosser, pers. comm.) The difference in the infanticide rate between the two populations might be explained by a lower adult male mortality and an extremely low immigration rate in the northern study area (Swenson et al. 2001). Mothers that lost all cubs ($n = 44$) had their next litter more than 1 yr earlier than those with surviving cubs ($n = 119$) [1.09 ± 0.29 (SD) yr vs. 2.22 ± 0.47 (SD) yr, respectively, $U = 42.5$, $p = 0.000$].

We obtained precise field data from only eight cases of infanticide (seven from the south and one from the north population; Table 1). In seven cases, the male was observed with the mother shortly after

Table 1: Documented and suspected cases of infanticide in Scandinavian brown bears

Case	Mother	Litter size	Date for loss of cubs ^a	Date the male was first seen with the female	Determination of the infanticidal male ^b
1	W9308	4 cubs	2 cubs, 16 May 1996 2 cubs, \approx 24 May 1996	16 May 1996 24 May 1996	Unmarked male observed with the mother Marked male W8807 observed with the mother
2	W9404	2 cubs	2 cubs, \approx 15 Jun. 1997	15 Jun. 1997	Marked male W9311 located with the mother
3	W8905	1 cub	1 cub, \approx 23 May 1998	27 May 1998	Marked male W8607 located with the mother
4	W9307	1 cub	1 cub, \approx 24 Jun. 1998	24 Jun. 1998	Marked male W9301 observed with the mother
5	W8905	3 cubs	1 cub, 25 May 1999	25 May 1999	Marked male W9807 located at the site, tissues available
6	W9307	3 cubs	2 cubs, 9 Jun. 1999	9 Jun. 1999	Hairs collected, unmarked male observed attacking cubs
7	W9615	1 cub	1 cub, 18 Jul. 2000	18 Jul. 2000	Cub remains collected, marked male W9921 located at the site
8	BD07	\geq 2 cubs	\geq 2 cubs, \approx 8 Jun. 2000	8 Jun. 2000	Feces, bones collected

^aWhen the date is given, we know the exact date, if it is given with ' \approx ', the loss occurred within 2 d of this date.

^bObservation, location or/and collection of samples at the infanticide site, shortly after the cub disappeared.

the cub loss (Table 1) and was considered to be a putative infanticidal male. In cases 5–8, tissues, hairs, feces or bone samples were found at the site of infanticide, allowing us to identify the probable infanticidal male genetically. In two cases (5 and 8), the female was killed during the infanticidal attack, consequently, there was no subsequent litter. In one especially interesting case (8), one of the three fecal samples found at the infanticide site contained a bone that could be identified as a cub's skull bone (Natural History Museum of Geneva). The cub's genotype, as identified from the bone sample, was also found in the three separate male fecal samples among other alleles, i.e. several loci showed four different alleles (i.e. two from the cub and two from the male). Food passes quickly through a brown bear's digestive system; taking 9–13 h, depending on diet (Pritchard & Robbins 1990). All four known infanticidal males were excluded as fathers of the killed cubs by two or more microsatellite DNA loci (cases 5–8 in Table 2). The other four males observed with a female shortly after her cubs disappeared (putative infanticidal males) were all the fathers of the subsequent litters (cases 1–4 in Table 2).

Overall, infanticidal and putative infanticidal males consisted of six residents, one probable non-resident and one with unknown status (Table 2). The unmarked male in case 8 was considered to be a probable non-resident because virtually 100% of the adult bears are marked in this area, but this male had not been captured by 2003.

Multiple paternities were common in these populations. It was found in 14.5% of 69 litters with at

Table 3: Multiple paternity in litters of Scandinavian brown bears

Litter size	Study area	No. of litters	No. and proportion with multiple paternity
2	North	16	0 (0%)
	South	21	1 (4.7%)
≥3	North	12	5 (42%)
	South	20	4 (20%)

least two young and in 28% of 32 litters with at least three young (Table 3). Although anecdotal, the three litters that suffered infanticide and had known paternity of all cubs were all single paternity litters.

Discussion

The SSI Hypothesis

For the first time for a large non-social carnivore, we present evidence suggesting that the three requirements of the SSI hypothesis are met in brown bears: the perpetrator is not the father of the infants it kills, it has a high probability of siring the next litter (Hrdy & Hausfater 1984) and infanticide shortens the time to the mother's next estrus, increasing the infanticidal male's own opportunity to mate with the mother (Hrdy & Hausfater 1984). Moreover, all infanticide cases occurred during the mating season, which gives further support to the SSI hypothesis, as SSI would not occur outside this time and other forms of infanticide would not be so restricted in time. Although our sample sizes were small, we

Table 2: Paternity analysis of Scandinavian brown bear cubs killed or probably killed by male bears

Case	Mother	Putative infanticidal male (1–4); infanticidal male (cases 5–8)			Father of the killed litter		Father of the next year's litter	
		ID (age)	No. of loci exclusions	Male's status ^a	ID (age)	Paternal probability	ID	Paternal probability
1	W9308	W8807 (12)	b	R	b		W8807	>0.98
2	W9404	W9311 (6)	b	R	b		W9311	>0.95
3	W8905	W8607 (27)	b	R	b		W8607	>0.99
4	W9307	W9301 (9)	b	R	b		W9301	>0.99
5	W8905	W9807 (11)	6/18	R	W8607 (28)	>0.99	c	
6	W9307	Unmarked ^d	4/9	U	W9301 (10)	>0.99	b	
7	W9615	W9921 (9)	7/18	R	Unmarked ^e	>0.99	b	
8	BD07	Unmarked ^f	2/9	NR	BD88 (8)	>0.99	c	

^aR, resident, NR, non-resident; U, unknown.

^bNo cub sample available for genetic analysis.

^cMother was killed during the infanticidal attack.

^dIdentified from DNA in hair (age unknown).

^eNo paternity identified among sampled males.

^fIdentified from feces DNA with cub remains in an area where almost 100% of the resident adult males were radio-marked.

Note: 'Unmarked' refers to a non-radio-collared bear.

suggest that infanticide is an adaptive male mating strategy in this non-social carnivore.

Several alternative explanations have been proposed to explain infanticidal behavior by males (Van Schaik & Janson 2000a); however, they do not seem appropriate in this case. The competition for resources hypothesis predicts that males kill infants to make more resources available to their kin and descendants, although this is controversial (Broom et al. 2004). The cannibalism hypothesis states that males kill infants to consume them as food. We reject those two first hypotheses, as resources in terms of food and space did not seem to be limited in the rapidly growing and expanding Scandinavian bear populations (Swenson et al. 1998; Sæther et al. 1998). The social pathology hypothesis, associated with abrupt social change, considers infanticide as a maladaptive social behavior (Dolhinow 1977), and the incidental infanticide hypothesis assumes that infants are killed as a by-product of male–female aggression. Neither hypothesis is supported because infanticidal males were not related to the infants that they killed. Moreover, infanticidal males can actively pursue the cubs in the trees to kill them (J. Katajisto, pers. comm). Cub loss in brown bears can also be explained by nutritional factors and den disturbance, however, this would not explain the preponderance of male killers, and Swenson et al. (2001) concluded that cub loss in Scandinavia was best explained by social factors (SSI), both at spatial and temporal levels.

Mating Strategies in Relation to SSI

By committing infanticide during the mating season and causing the females to return to sexual receptivity, males can stop their new mating partner from investing in the offspring of other males and also maximize their own fitness. Although the four males siring litters after infanticide were not confirmed to have killed the cubs, they were all with the mother immediately following the infanticide. That they all were subsequent fathers of the next litter supports the SSI hypothesis, because it shows that the first male with a female after losing its cubs can sire the next litter.

In cases where females were killed (2/8), and where females suffer sequential infanticides, i.e. in 2 yr in a row (2/8), the benefit for the infanticidal male is harder to evaluate. The percentage of females killed during the infanticide (2/8), in this study, is surely an overestimate, as these circumstances made it easy to obtain the DNA from every

individual involved. In our data set, only three females with cubs were killed by conspecifics during 138 bear-years. It is well documented that females fight vigorously to defend their cubs from males (Craighead et al. 1995a). We propose that females are killed as an accident in such a fight. Male bears provide no paternal care. Consequently, the perpetrators cannot prevent other males from killing their cubs. Moreover, they cannot predict whether or not their cubs will be killed the following year, especially because cub loss seems to be related to disruption of male social organization (Swenson et al. 1997), which is not under the bears' control. However, the risk of the cubs being killed by another infanticidal male is <35%, as this total cub mortality rate includes other mortality factors. This rate is also much lower in years following years with low adult male mortality (Swenson et al. 1997, 2001).

It is rarely a net benefit for the female to have its infant(s) killed, although it might have a slight gain if it loses a single cub and has a high probability of producing more young the next year (Tait 1980). The major cost associated with infanticide is the loss of fitness by the victimized female. Consequently, females are likely to have evolved counterstrategies that reduce the risk of infanticide. Multi-male mating has often been suggested as an effective counterstrategy that can be employed by females to confuse paternity, causing males to treat infants as though they were their own offspring (Hrdy 1979). Field observations show that females mate promiscuously (Craighead et al. 1995a). In addition, mixed paternities were demonstrated genetically in one-third of the litters in Alaskan brown bears (Craighead et al. 1995a) and in one case in American black bears (*Ursus americanus*) (Schenk & Kovacs 1995). In our large genetic database, we have documented a minimum of 14.5% multiple paternity litters in the Scandinavian brown bear, although this is certainly an underestimation. The value using litters of three or more young was 28%, which is also an underestimate. Thus multi-male mating resulting in mixed paternities appears to be common in this species. By mating with many males, female bears may confuse paternity assessment by those males. In support of this, the three litters with completely known parents that suffered infanticide were all single paternity litters. Other hypotheses could also explain multiple mating by females (see Jennions & Petrie 2000 for a review), for instance multi-male mating might allow females to increase the genetic diversity of their offspring, although this is controversial (Yasui 1998). We suggest that multi-male mating is an adaptive

female reproductive counterstrategy to infanticide, as predicted by the SSI hypothesis.

Infanticide in Non-Social Carnivores

In social mammals, immigrant males, i.e. males entering the group, kill offspring (e.g. Borries 1997; Janson & van Schaik 2000) and there is no reason to expect this phenomenon not to occur in non-social carnivores. Bears are not strongly territorial but have home ranges that overlap those of other bears of the same and opposite sex (Mace & Waller 1997; McLellan & Hovey 2001). Infanticide has been reported to occur after adult male bears die, with the interpretation that the death of a resident adult male allowed immigrant males to establish themselves and commit SSI (Swenson et al. 1997, 2001). This hypothesis is controversial (Sommer 2000), including among bear biologists (Wielgus & Bunnell 2000; Miller et al. 2003). Craighead et al. (1995b) viewed infanticide in brown bears as a foraging strategy rather than a mating strategy, because they did not observe that males mated with mothers of killed young. Our results indicate that SSI by resident adult males in non-social carnivores also can be natural part of the species repertoire. The SSI hypothesis does not require that the species is social or territorial, and a resident male can increase his reproductive success through SSI as much as a non-resident male. This implies that resident males are able to differentiate their own progeny from unrelated cubs. The assessment of paternity likelihood could be based on mating history: males tend not to kill infants of females they have copulated with (Hrdy & Hausfater 1984; Soltis et al. 2000). Thus, females may mate promiscuously in order to confuse paternities. In social mammals, this mechanism of recognition is usually not speculated upon, as infanticidal males were formerly not a member of the group and thus unrelated to the killed infants.

Conclusion

This study illustrates male–female conflict in reproductive strategies (Chapman et al. 2003). If mating strategies have developed in both sexes in relation to SSI, then this phenomenon might be one of the underlying mechanisms determining mating systems in species with SSI (Wolff & MacDonald 2004). Our results suggest that SSI is not restricted to social mammals and not only immigrant males kill infants. SSI has not been documented before in field studies of non-social mammals, probably because it is diffi-

cult to document, even in social mammals (Packer & Pusey 1984), and is much more so in non-social mammals. Most studies of non-social mammals generally do not have enough intensive observation effort to document cases of infanticide. In our field study, one of the largest for large carnivores, about 100 individuals have been radio-tracked each year and many were followed intensively in some years. Although infanticide has been documented as the major cause of cub mortality, it is very hard to get this type of data, and we obtained precise data on only eight cases during 1996–2000. However, this sample size could be considered as very good given the constraints of the species (solitary, secretive, low density and living in dense forest) and the phenomenon (cub loss occurred on average about once per 1000 km² per year on our southern study area). Consequently, documenting infanticide and determining the perpetrator and its relationship to the killed infant is a monumental task. In fact, in the classic 12-yr behavioral and ecological study of grizzly bears in Yellowstone, Craighead et al. (1995a) never observed infanticide, although it did occur.

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