

## REVIEW

### The mating system of the brown bear *Ursus arctos*

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## ABSTRACT

1. Research on mating systems and reproductive strategies is valuable for providing ethological knowledge, important for the management and conservation of a species, and in a broader sense, important for biodiversity conservation.
2. We reviewed the literature to document the mating system of the brown bear *Ursus arctos*. We determined that many aspects of the reproduction of the brown bear remain unclear, including (i) biological aspects, such as hormone and oestrous cycling, sperm competition, mate choice, sexually selected infanticide, etc. and (ii) human impacts on the mating system, occurring when humans alter population size and structure, through, for example, hunting or habitat degradation.
3. We considered three mating system classification frameworks from the literature (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003) and applied various brown bear populations to them. We did this (i) to document the plasticity of the mating system of the brown bear, and (ii) to find commonalities among the reported mating system classifications in order to provide a general and common classification of the brown bear's mating system.

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4. The mating system of the brown bear can, in general, be classed as 'polygamous'. Subclassifications can nevertheless be valuable on smaller spatial scales.
5. Within the polygamous mating system of the brown bear, biological aspects and human impacts can influence reproductive strategies at the individual and population level. Mating system classification frameworks often lack a common terminology, which contributes to the variety of published classifications of the mating system of the brown bear.

**Keywords:** female mate choice, male-male competition, polygamy, reproductive strategies, sexual selection

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## INTRODUCTION

An animal species' mating system refers to the general behavioural strategies employed in obtaining mates, and includes features such as number of mates, manner of mate acquisition, characteristics of association and parental care (Emlen & Oring 1977). Mating systems and strategies are driven by the strength of sexual selection, which in turn is determined by male-male competition and female mate choice (Shuster & Wade 2003, Shuster 2009). Over 90% of mammalian species are polygynous, and the energetic investments in gametes and rearing offspring are typically larger for females than for males, especially in the absence of paternal care (Orians 1969, Trivers 1972, Clutton-Brock 1989, Andersson 1994, Shuster & Wade 2003). Mate selection is thus a much more important decision for females than for the rather indiscriminate males (Orians 1969, Trivers 1972). For females, mate choice should be based on expressions of male genetic quality, such as size, fighting skills or weaponry, in order to optimize individual fitness (Orians 1969, Andersson 1994, Arnold & Duvall 1994). Because receptive females are generally considered to be the limiting resource in reproduction, males face intra-sexual competition for mates (Trivers 1972, Emlen & Oring 1977, Arnold & Duvall 1994, Shuster & Wade 2003). Male reproductive success is often found to be proportional to the number of mates or copulations, and shows considerable variance as a consequence of intra-sexual competition for females, whereas female reproductive success generally varies less (Bateman 1948, Trivers 1972, Andersson 1994, Shuster & Wade 2003, Shuster 2009). Although there is a large body of literature on sexual selection and mating system theory, no universal agreement exists on terminology and mating system classification (Andersson 1994). Knowledge of mating systems not only has ethological value, but is important for species-specific conservation and management, and for biodiversity conservation in general (Berger 1996, Palermo et al. 2007).

Brown bears *Ursus arctos* have been the subject of intensive research (see, e.g. Pasitschniak-Arts 1993, Craighead et al. 1995a, Servheen et al. 1999, Swenson et al. 2000, Schwartz et al. 2003b, Kaczensky et al. 2004, Garshelis 2009) and substantial knowledge on their biology and life history has been gained over the last decades. However, many aspects of the reproductive biology of the brown bear remain poorly documented. The literature suggests that there is variation in the brown bear's mating system, reproductive strategies, and reproductive parameters; their mating system has been described as polygamous (Pasitschniak-Arts 1993, Zedrosser et al. 2009), promiscuous (Swenson et al. 2001a, b, Schwartz et al. 2003b, Bellemain et al.

2006a, b), scramble competition polygamous (Dahle & Swenson 2003c, McLellan 2005) and contest competition polygamous (Zedrosser et al. 2007a). Both the lack of a common mating-system terminology and the apparent variation in the mating system of the brown bear probably contribute to the large variety of mating system classifications assigned to this species.

In this paper we summarize and review the literature on brown bear reproductive behaviour and biology, and classify the mating system of the brown bear, based on three existing mating system classification frameworks. Emlen and Oring (1977) and Clutton-Brock (1989) provide two widely accepted theoretical classification frameworks based on the spatiotemporal clustering of resources, which include reproductive partners. Shuster and Wade (2003) provide a more recent classification framework based on the statistical quantification of the strength of sexual selection and the evolution of mating systems.

### **ECOLOGY AND SOCIAL ORGANIZATION**

The brown bear is one of the eight species of bears and one of the six members of the genus *Ursus* (Schwartz et al. 2003b). It is a holarctic omnivorous member of the Carnivora and the most widespread species of Ursidae (Pasitschniak-Arts 1993, Schwartz et al. 2003b). Brown bears occupy a large variety of habitats, ranging from treeless arctic tundra, grasslands, boreal forest, to coastal, mountainous and desert habitats, reflecting their adaptive nature (Swenson et al. 2000, Schwartz et al. 2003b). Human presence is the most important factor determining the distribution of brown bears in their historical range (Kaczensky et al. 2006); it alters their ecology and behaviour, such as habitat selection and circadian rhythms (Pasitschniak-Arts 1993, Swenson 1999, Klinka & Reimchen 2002, Ciarniello et al. 2007, Nellemann et al. 2007). The brown bear is currently listed globally as a species of least concern, which has stable or increasing population sizes in North America, northern Asia, and northern and central Europe (Anonymous 2008). However, southern Europe and Asia harbour several small, isolated and critically endangered populations (Swenson et al. 2000, Anonymous 2008).

Brown bears are sexually dimorphic: males are 1.2–2.2 times larger than females (Lefranc et al. 1987, Jakubiec 1993, Schwartz et al. 2003b, Swenson et al. 2007). Body size varies geographically and seasonally, and is related to local food supply (Hilderbrandt et al. 1999, Meiri et al. 2007, Garshelis 2009). Brown bears generally reach 95% of their asymptotical size at nine and 14 years of age for females and males, respectively (Kingsley et al. 1983, Swenson et al. 2007). Growth rates, however, depend on food conditions and population densities, and thus show variation among populations (Kingsley et al. 1988, Zedrosser et al. 2006, Zedrosser et al. 2007a). Adult body mass ranges from 80kg to over 600kg; the largest individuals are found in coastal Alaskan populations with access to seasonal salmon runs (Hilderbrandt et al. 1999, Schwartz et al. 2003b).

Brown bears are considered to be solitary and non-territorial (Craighead et al. 1995a, Dahle & Swenson 2003a, b, c, Bellemain et al. 2006a). This implies that social interactions and consorting is limited to the breeding season only, and that they have home ranges instead of strict territories (Schenk & Kovacs 1995, Hawkins & Racey 2009). However, Støen et al. (2005) showed evidence of territoriality in female brown bears in a Scandinavian population: related females apparently excluded unrelated females from common areas. Home range sizes and bear densities vary according to

geographical range and food supply, and overlap both inter-sexually and intra-sexually: male home ranges are large and overlap with the home ranges of several females (Hilderbrandt et al. 1999, McLoughlin et al. 2000, McLellan & Hovey 2001, Dahle & Swenson 2003c, Støen et al. 2005). Annual home range sizes range between 24–2434 km<sup>2</sup> and 115–8171 km<sup>2</sup> for females and males, respectively (McLoughlin et al. 2000). Population densities range between an estimated 1.2 individuals/1000 km<sup>2</sup> in a Russian population (Chestin et al. 1992), and 551 individuals/1000 km<sup>2</sup> in an Alaskan population (Miller et al. 1997, McLoughlin et al. 2000). Within populations, seasonal home range sizes vary according to age and sex, population density, reproductive status during the mating season, and the occurrence of temporally available congregated foods (e.g. salmon, garbage, army cutworm moths *Euxoa auxiliaris*; Craighead et al. 1995a, Dahle & Swenson 2003c, Preatoni et al. 2005, Rode et al. 2006, Bellemain et al. 2006a).

Natal dispersal is typically male biased (Støen et al. 2005), and is considered to be a mechanism to avoid inbreeding (Bellemain et al. 2006b, Zedrosser et al. 2007b). Up to 92% and 46% of subadult males and females, respectively, were found to disperse in Scandinavia. Maximum dispersal distances were 467 km and 90 km for males and females, respectively (Støen et al. 2006a). In southwestern Canada, natal dispersal occurs less often and over shorter distances, averaging 49.1 km for males and 14.3 km for females (McLellan & Hovey 2001, Proctor et al. 2004, McLellan 2005). Similarly to some ungulate species (Clutton-Brock et al. 1982, Poteaux et al. 2009), philopatry of female brown bears can lead to the formation of matrilineal assemblages, in which genetic relatedness is spatially autocorrelated (Støen et al. 2005, Poteaux et al. 2009). The formation of matrilineal assemblages can alter fitness parameters (Ishikawa et al. 2003, Dalerum et al. 2006), such as reproductive success and survival (Støen et al. 2005). Støen et al. (2006b) and Ordiz et al. (2008) suggested that sociality in female brown bears may be more pronounced than generally acknowledged.

## REPRODUCTIVE PHYSIOLOGY

Reproductive seasonality probably evolved through natural selection to optimize juvenile survival rates as an adaptation to adverse environmental conditions (Baker 1938, Bronson 1985). Seasons and their climate are signalled by photoperiod (Spady et al. 2007). Photoperiod, regulates the status of reproductive hormones, which also can be modified by social factors, metabolic state and nutrition (McMillin et al. 1976, Palmer et al. 1988, Tsubota et al. 1998, Spady et al. 2007). The variance in photoperiod over geographical ranges therefore may explain the corresponding variance in breeding seasonality within a species, such as the brown bear (Fernández-Gil et al. 2006, Spady et al. 2007). The mating season of the brown bear lasts for approximately 2.5 months, from late spring to early summer (Craighead et al. 1995a, White et al. 1998, Schwartz et al. 2003b, Dahle & Swenson 2003c, Spady et al. 2007). Captive brown bears in the Southern Hemisphere show a 6-month shift in mating behaviour compared with their northern counterparts (Spady et al. 2007). Autumn reproductive behaviour and copulation have been reported anecdotally in wild brown bears in coastal British Columbia, Canada (Nevin & Gilbert 2005), Kamchatka, Russia (Vaisfeld & Chestin 1993) and Hokkaido, Japan (Kohira & Mori 2010).

The oestrous cycle of female brown bears remains poorly understood, and most studies have been carried out on bears in captivity (Schwarzenberger 2007). Research on reproductive behaviour in captive female brown bears has shown that concen-

trations of faecal estradiol are elevated during oestrus, and progesterone levels appear to increase after the oestrus period (Mano et al. 2002, Ishikawa et al. 2003, Dehnhard et al. 2006). Observational studies from the wild suggest that oestrus lasts for between 1 and 50 days (Craighead et al. 1995a, Ishikawa et al. 2003).

Female brown bears have delayed implantation (Mano et al. 2002, Schwartz et al. 2003b). The fertilized ova remain dormant in the uterus for about five months, prior to implantation in November–December. The hormone prolactin, which is controlled by photoperiod, is important in reactivating *corpora lutea* (Spady et al. 2007). Dehnhard et al. (2006) observed a sharp increase in faecal progesterone levels in captive fertilized female brown bears in December, coinciding with the approximate moment of implantation.

Induced ovulation occurs in female American black bears *Ursus americanus* (Boone et al. 2004) and may occur in polar bears *Ursus maritimus* (Rosing-Asvid et al. 2002) and brown bears (Hamer & Herrero 1990, Craighead et al. 1995a, McLellan 2005, Bellemain et al. 2006b). The oestrus period of captive unmated female brown bears separated from males lasts longer than that of their mated counterparts, suggesting that copulation may terminate oestrus (Ishikawa et al. 2003). Ishikawa et al. (2003) also described sexual behaviour, such as intra-sexual mounting, presenting and masturbation in captive unmated female brown bears during the breeding season. The variation in duration and timing of oestrous is large, both between females and within females, over years (Pasitschniak-Arts 1993, Craighead et al. 1995a, Spady et al. 2007). This variation, which might be related to the mechanism of induced ovulation, results in some level of reproductive asynchrony (Ims 1990), a prerequisite for the potential of sexual selection (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003).

Because brown bears have delayed implantation, each *corpus luteum* becomes dormant following ovulation and luteal progesterone secretion stops. This may allow females to re-enter oestrus (Spady et al. 2007). Craighead et al. (1995b) reported seasonal polyoestrous in female brown bears, in which two cycles were separated by four to 18 days of sexual inactivity. Stenhouse et al. (2005) suggested that polyoestry is common in free-living female brown bears, because 51% of the reproducing females that they monitored engaged in more than one male-female association per breeding season. Polyoestrous cycling facilitates the development of different sets of ova, and thereby increases the potential of these to be fertilized by different males (Pasitschniak-Arts 1993, Craighead et al. 1995b, Schwartz et al. 2003b, Spady et al. 2007). Multiple paternity occurs relatively frequently in brown bears (Bellemain et al. 2006b). In Scandinavian populations, in 14.5 and 28% of the litters with  $\geq 2$  and  $\geq 3$  young, respectively, young were sired by different fathers (Bellemain et al. 2006a, b).

Brown bear females show lactational anoestrus (Dahle & Swenson 2003b, Spady et al. 2007). Females that lose offspring by either death or family break-up can enter oestrus already after 2–7 days (Swenson 2003, McLellan 2005, Bellemain et al. 2006a, Swenson & Haroldson 2008). Pseudo-oestrus also occurs in brown bears (Ishikawa et al. 2003). Pseudopregnancy and spontaneous ovulation have been shown to occur in other bear species, and may occur in the brown bear as well (Mano et al. 2002).

Male brown bears show a circannual rhythm in reproductive behaviour and testis development (White et al. 1998, Spady et al. 2007). The males' annual reproductive period encompasses the receptive period of female brown bears, lasts for 4–5 months, and varies among individuals (Erickson et al. 1968). Male testis size corre-

lates with seasonal variation in serum testosterone levels and sperm production (Gomendio et al. 2006). Testis mass during the mating season is up to twice that during hibernation in adult male bears (McMillin et al. 1976). Testis size, that is, mass, length and diameter, is also positively correlated with age, body mass and body length (White et al. 1998). Spady et al. (2007) distinguished four phases in the annual testis cycle: (i) quiescence, characterized by no mating or spermatogenesis; (ii) recrudescence, characterized by increasing testis size and the preparation for mating and spermatogenesis; (iii) peak testicular function during the mating season and (iv) regression, when testis function diminishes after the mating season. Testicle mass increases linearly with age, at least until the age of 14.4 years (White et al. 1998).

## LIFE HISTORY

Brown bears reproduce slowly. They are long lived, reach sexual maturity relatively late, and have prolonged reproductive cycles (Pasitschniak-Arts 1993). Cubs are born during winter denning, between January and March, after a gestation period of approximately 6–8 weeks (Schwartz et al. 2003b). The short *in utero* developmental phase after delayed implantation is probably a mechanism to preserve female muscle mass and proteins during hibernation, by switching to milk production (Ramsay & Dunbrack 1986, Hissa 1997). Sex ratio at birth usually is assumed to be 50:50. In some populations, however, male-biased sex ratios in newborns have been reported (55–59% males; Craighead et al. 1974, Knight & Eberhardt 1985). This sex bias is assumed to compensate for greater male than female cub mortality, because of the more bold and curious nature of male cubs, which may result in more accidents and predation (Schwartz et al. 2003b). The sex ratio of 1326 newborn brown bears in captivity in North America was unbiased (51% males; Anonymous 1993).

Neonates are highly altricial and weigh between 350g and 500g, depending on litter size and maternal condition (Couturier 1954); paternal care is absent (Dahle & Swenson 2003a). Lactation lasts for 1.5 to 2.5 years, and peaks around midsummer in the first year of life of the cubs (Farley & Robbins 1995, Craighead et al. 1995a).

Reproductive parameters, such as average age of primiparity, mean litter size, mean litter interval, mean age of first weaning (Kovach et al. 2006), and reproductive rate, vary among populations (Ferguson & McLoughlin 2000, Nawaz et al. 2008; Table 1). The earliest ages of primiparity recorded were three years, in Austria (Zedrosser et al. 2004) and Croatia (Frkovic et al. 2001). Average ages of primiparity range from 5.2 to 10.3 years in a highly productive Swedish population and in a high latitude population in Denali National Park, Alaska, respectively (Swenson et al. 2001b, Miller et al. 2003, Zedrosser et al. 2009). Kovach et al. (2006) argue that the mean age of first weaning, though not often reported in the literature, is a more appropriate demographic parameter than mean age of primiparity. Litter sizes typically range from one to three cubs and may be positively correlated with the number of female copulations (Jakubiec 1993, Pasitschniak-Arts 1993, Craighead et al. 1995a, Schwartz et al. 2003b). Litters comprising four cubs are uncommon (Schwartz et al. 2003b); Vaisfeld and Chestin (1993) reported one case of five brown bear cubs in a litter under natural conditions in Karelia, Russia. Litters of up to six cubs have been observed in captivity (Laikre et al. 1996) and under natural conditions (Pazetnov & Pazetnov 2005). Mean inter-birth intervals show considerable variation among populations, depending on offspring survival and environmental and geographical conditions, and range from 2.4 to 5.7 years (Nawaz et al. 2008). Maternal care continues

Table 1. Reproductive parameters of 34 brown bear populations in North America, Europe and Asia

Population	Lat. (°N)	AP	MLS	MLI	RR	AFW	CS	Ref.
<b>Europe</b>								
Central Sweden	61	5.2	2.3	2.4	0.96	117	0.65–0.83	Sæther et al. (1998)
Northern Sweden	67	5.4	2.4	2.6	0.92	120	0.96	Sæther et al. (1998)
Croatia	45	2.39				128		Frkovic et al. (2001)
Cantabrian Mountains, Spain	43	5.3	2.3	3.3	0.7			Wiegand et al. (1998)
<b>Asia</b>								
Deosai National Park, Pakistan	34	8.25	1.33	5.7	0.23	73	0.94	Nawaz et al. (2008)
Hokkaido, Japan	44	1.8	2.3–3		0.6	103	0.45	Mano et al. (2002), Kohira et al. (2009)
<b>North America</b>								
Anderson Horton Rivers, Canada	69	6	2.27	4.9	0.78*			Case and Buckland (1998)
Kugluktuk, Canada	66	8.7	2.26	3.3	0.87*	164	0.81	Clarkson and Liepins (1994)
Tuktoyaktuk, Canada	69	6.4	2.3	3.3	0.7	124		McLoughlin et al. (2000), McLellan (1994)
Northern Yukon, Canada	68	7	2	4	0.5	116		McLoughlin et al. (2000), McLellan (1994), Lefranc et al. (1987)
Kluane National Park, Canada	61	7.8	1.59	3.1	0.51	121		Bunnell and Tait (1981)
Mackenzie Mountains, Canada	64	8	1.8	3.8	0.47	110		Case and Buckland (1998), McLoughlin et al. (2000), McLellan (1994)
Selkirk Mountains, Canada	48	7.3	2.22	3	0.74			Wielgus and Bunnell (1995)
Banff-Kanan, Canada	51	6.7	1.8	4.4	0.41		0.91	Garshelis et al. (2005)
North Flathead, Canada	49	6.1	2.2	3.1	0.42*	114	0.87	McLoughlin et al. (2000), McLellan (1994)
Jasper National Park, Canada	53	6	2			129		McLoughlin et al. (2000), Lefranc et al. (1987)
Western Brooks Range, USA	69	7.9	1.98	4.1	0.48	117	0.56	McLoughlin et al. (2000), McLellan (1994), Lefranc et al. (1987)
Eastern Brooks Range, USA	70	9.6	1.78	4.2	0.42	108		McLoughlin et al. (2000), McLellan (1994), Lefranc et al. (1987)
NW Alaska, USA	69	6.1	2.17	3.9	0.66*	132		McLoughlin et al. (2000), McLellan (1994), Lefranc et al. (1987)
Katmai National Park, USA	58	7.2	2.06	5.6	0.37	207	0.34	McLoughlin et al. (2000), Case and Buckland (1998)
Kodiak Island, USA	57	6.7	2.23	4.6	0.48	202		Sellers and Aumiller (1994)
Kuskokwim Mountains, USA	63	6.3	1.9	4.5	0.42	170		McLoughlin et al. (2000), Lefranc et al. (1987)
Nelchina Basin, USA	62	5.6	2.1	3.2	0.88*	144		Van Daele et al. (2001)
Black Lake, USA	56	6.3	2.57	3	0.86	256	0.57	McLoughlin et al. (2000), Lefranc et al. (1987)
McNeil River, USA	58	6.8	2.24	3.9	0.57	160		Lefranc et al. (1987)
Admiralty Island, USA	57	8	1.84	3.9	0.47	168		Sellers and Miller (1999)
Alaska Range, USA	65	6.2	2.2	4	0.51*	154		McLoughlin et al. (2000), McLellan (1994), Lefranc et al. (1987)
Southeastern USA	62	7.2	2	2.6	0.77		0.58	McLoughlin et al. (2000), Lefranc et al. (1987)
Cabinet-Yaak, USA	48	6.6	2.1	3	0.7		0.88	Kovach et al. (2006)
Swan Mountains, USA	48	6.6	1.6	3	0.53		0.79	Wakkinen and Kasworm (2004)
East Front, Montana, USA	47	6	2.14	2.6	0.82	125	0.86	Mace and Waller (1998)
Greater Yellowstone Ecosystem 1983–2002, USA	44	5.81	2	2.78	0.64*		0.64	McLellan (1994), Aune et al. (1994)
Yellowstone National Park 1959–1970, USA	44	5.7	2.2	3.2	0.69	152	0.74	Schwartz et al. (2006)
Yellowstone National Park 1975–1989, USA	44	5.7	1.9	2.6	0.73	134	0.85	Craighead et al. (1974) Stringham (1990)

Lat. (°N), latitude of the study area in degrees North; AP, age of average female primiparity (years); MLS, mean litter size; MLI, mean litter interval (years); RR, reproductive rate (MLS/MLI); AFW, average female body mass (kg; corrected according to McLellan 1994); CS, annual cub survival probability.  
\*RR was not calculated as MLS/MLI, but taken from the literature. Empty cells indicate no information was available in the literature.

for, on average, between 1.4 and 3.5 years in most brown bear populations (McLellan 1994), but was reported to continue for up to 4.5 years in a high-alpine low-production population in South Asia (Nawaz et al. 2008). Reproductive rate, that is, the average number of offspring raised per adult female per year, varies from 0.23 to 0.96 in a high-altitude population in Deosai National Park in Pakistan and a Scandinavian population, respectively (Sæther et al. 1998, Swenson et al. 2001b, Swenson et al. 2007, Nawaz et al. 2008).

Female reproductive maturation and senescence was modelled by Schwartz et al. (2003a), based on the litter production of 4756 radio-collared female brown bears from 20 study areas. Inflection points in fertility occurred at the ages of four to five, and 28–29 years. Females in their prime, between nine and 20 years old, were estimated to produce most offspring (Schwartz et al. 2003a). No female older than 29 years gave birth (Van Daele et al. 2001), and the oldest observed free-ranging female was 34 years old. The oldest captive female brown bear was 42 years old (Schwartz et al. 2003a). Thus, post-reproductive survival is limited. Post-weaning maternal care is advantageous for the offspring in brown bears (Dahle & Swenson 2003a), but is not necessary for their survival (Swenson et al. 1998); therefore, according to the senescence theory (Williams 1957), there is no selective advantage of long-term survival after losing reproductive ability (Schwartz et al. 2003a).

The average age of reaching sexual maturity in male brown bears was estimated to be 5.5 years in continental North America (White et al. 1998). The youngest males observed to be reproductively successful were 3.5 years old in a Swedish population (Zedrosser et al. 2007a). Age at sexual maturity in male brown bears is related to nutritional factors and varies between ecoregions (White et al. 1998, Schwartz et al. 2003b). Older and larger males generally have higher annual reproductive success (Zedrosser et al. 2007a) than younger, smaller males. Size and age are correlated with dominance and experience, and probably reflect genetic superiority (Trivers 1972, Shuster & Wade 2003, Isaac 2005, Bellemain et al. 2006b, Zedrosser et al. 2007a). The oldest males observed in captivity and in the wild were 50 and 30 years old, respectively, but no male older than 27 years has been documented to be reproductively successful (Schwartz et al. 2003a, Zedrosser et al. 2007a).

Cub mortality in brown bears varies among populations and is typically higher than mortality in other age classes. Kovach et al. (2006) reported annual cub mortality in southwestern Alaska to average 2.8%, whereas, in Denali National Park in Alaska, annual cub mortality can reach 66% (Miller et al. 2003). Mano et al. (2002) report neonate mortality and mortality before the breeding season to be low. In two Swedish populations, primiparous females were more likely to lose cubs than multiparous females (Zedrosser et al. 2009). Infanticide is considered to be a major cause of death among brown bear cubs, at least in some populations. Resource competition, exploitation, social pathology and male reproductive strategy (Hrdy 1979) may explain infanticide in brown bears (Swenson et al. 1997, McLellan 2005, Bellemain et al. 2006a, b, Fernández-Gil et al. 2010). Most cub mortality occurs during the breeding season, and about 80% of conspecific killing is carried out by adult males (Schwartz et al. 2003b). Females in poor body condition may abandon their dependent offspring as an adaptive maternal strategy. This allows them to re-enter oestrus during the ongoing breeding season, and produce offspring with potentially higher survival rates (Tait 1980).



## REPRODUCTIVE BEHAVIOUR

In brown bears, reproductive individuals of both sexes mate a variable number of times with a variable number of partners during a given mating season (Pasitschniak-Arts 1993). Females typically mate with three to four males during a breeding season, although females have been observed to mate with up to 20 partners (Craighead et al. 1995a). Males show more variation, and mate with between one and eight females per breeding season, although many males do not obtain any matings (Craighead et al. 1995a). Aggression and sexual harassment occur rarely within a reproducing pair (Craighead et al. 1995a, Fernández-Gil et al. 2006). Pairs typically travel together while the male monitors the female's oestrous status, which is believed to be signalled by pheromones, by smelling her genitalia (Clevenger et al. 1992, Craighead et al. 1995a). Pairs tend to copulate several times, and successful copulations last from less than one minute to one hour (Clevenger et al. 1992, Craighead et al. 1995a, Fernández-Gil et al. 2006). Male vigour, female receptivity and competing males may influence copulation duration (Craighead et al. 1995a, Schwartz et al. 2003b). Consorting lasts from less than a day to several weeks (Herrero & Hamer 1977, Craighead et al. 1995a, Swenson 2003). Reproductive associations are generally comprised of one male and one female bear, but associations with two or more females per male, or more than two males per female, are not uncommon (Sparrowe 1968, Stenhouse et al. 2005, Fernández-Gil et al. 2006). Fernández-Gil (pers. com.) reported an association comprised of two adult males and three adult females in the Cantabrian Mountains, Spain. Home range sizes of reproductive individuals tend to increase during the breeding season; both sexes roam to mate (Glenn et al. 1976, Swenson et al. 2000, Dahle & Swenson 2003c, Stenhouse et al. 2005), and track each other, probably by using scent cues (Green & Mattson 2003, Dahle & Swenson 2003c).

The use of specific mating areas of four to 125 ha has been described in a small brown bear population in Spain (Fernández-Gil et al. 2006). Some of these areas have been used for up to five consecutive years, and up to seven different adult brown bears have been observed there in a 24-hour period (Fernández-Gil et al. 2006). Solitary species in low-density populations can show reduced reproductive success as a consequence of difficulties in finding mates (Stephens et al. 1999), by the Allee effect (Allee et al. 1949). Fernández-Gil et al. (2006) suggest that specific mating areas facilitate meeting and reproducing, and thereby counteract aspects of the Allee effect. Repeated use of mating areas by brown bears, albeit over shorter time periods, has also been observed in the Rocky Mountains, Canada (Hamer & Herrero 1990).

Social hierarchies can develop in highly clustered bear populations at food congregations (e.g. the former Yellowstone Trout and Rabbit Creek garbage dumps in Yellowstone National Park, USA), and here, male bears may monopolize reproductive females to some extent by displacing subordinate males from breeding attempts (Stonorov & Stokes 1972, Craighead et al. 1995a). Craighead et al. (1995a) suggested that male dominance hierarchies at these congregations depend on size and mass, but also on aggressiveness and willingness to fight. Craighead et al. (1995a) distinguished four hierarchy classes in the Yellowstone Ecosystem food congregations, where up to 80 bears congregated at a time: (i) alpha male, (ii) beta males, (iii) contenders and (iv) non-contenders; and showed that the dominance hierarchy was highly variable and unpredictable from year to year. No relationship was found between frequency of copulation and dominance status, however. Subordinate

males obtained copulations, but predominantly with females late in the oestrus cycle, or when dominant individuals were preoccupied in aggressive interactions (Craighead et al. 1995a).

Long-term sequestering of single females by single males has been observed on mountain ridges in the Rocky Mountains (Hamer & Herrero 1990, Brady & Hamer 1992). Similar behaviour has been documented in low-density populations of polar bears, where males sequestered females on cliffs, in small bays or on small island plateaus (Ramsay & Stirling 1986, Zeyl et al. 2009). Hamer and Herrero (1990) and Herrero and Hamer (1977) suggested that this behaviour assures paternity for the sequestering male, as long as he sequesters the female during her entire oestrus and mates successfully with her.

Females with dependent offspring have been reported to avoid prime bear habitat both spatially and temporally, and even select for areas with relatively high human presence (McLellan 1994, Wielgus & Bunnell 1995, Craighead et al. 1995a, Swenson 2003, Kaczensky et al. 2006, Rode et al. 2006). However, Fernández-Gil et al. (2010) suggested that habitat fragmentation and human disturbance could influence the ability of females with cubs to avoid adult males and sexually selected infanticide. Habitat segregation as a female anti-infanticide strategy also has been reported for a range of other species, mainly primates, rodents and carnivores (Hrdy 1979, Ebensperger 1998).

#### **MALE–MALE COMPETITION**

Trivers (1972) distinguished three main types of male–male competition. Besides direct precopulatory contest, competition can continue within the female's reproductive tract (sperm competition), and after females have given birth (by sexually selected infanticide).

Male–male competition for access to receptive females based on the outcomes of aggressive physical encounters is referred to as contest competition, and is considered a driving force in the evolution of sexual dimorphism and polygynous mating systems (Strier 2000, Radespiel et al. 2001). Aggressive behaviour and fights form the basis of loose and dynamic dominance hierarchies in male brown bears (Sparrowe 1968, Craighead et al. 1995a), and antagonistic encounters vary greatly in duration, intensity, and final outcome (Craighead et al. 1995a). Individuals can be severely injured during fights (Craighead et al. 1995a, Fernández-Gil pers. com.), and the inflicted wounds can be lethal, especially for smaller individuals (Craighead et al. 1995a). Body size, age, experience, condition and aggression (and signs of this, such as scars and wounds) are considered to be determinants of male dominance status (Craighead et al. 1995a, Fagen & Fagen 1996, Zedrosser et al. 2007a). Craighead et al. (1995a) found that all dominant males in Yellowstone National Park ranged between the ages of 12 and 17 years. Zedrosser et al. (2007a) found that the annual reproductive success of male Scandinavian brown bears was positively correlated with both age and body size. However, the importance of both variables varied between populations and was related to population density and composition: body size was apparently most important in populations with a highly male-biased operational sex ratio. Also, outbred males appeared to have a relatively high annual reproductive success (Zedrosser et al. 2007a), which is consistent with the mate choice theory based on heterozygosity (Brown 1997). Scramble competition, the competitive searching for mates, may be a complementary or alternative male mating strategy to

contest competition when receptive females are spaced widely and unpredictably (Strier 2000, Radespiel et al. 2001).

Sperm competition has been documented in a range of species with mating systems characterized by female promiscuity, and is considered a strong force in shaping sexual selection (Trivers 1972, Dixson & Anderson 2004, Gomendio et al. 2006). Conclusive evidence of the occurrence of sperm competition does not exist in ursids, but it may occur in brown bears (Dahle and Swenson 2003c, Bellemain et al. 2006b, Zedrosser et al. 2007a), American black bears (Schenk & Kovacs 1995) and polar bears (Dyck et al. 2004).

Sexually selected infanticide is an adaptive male mating strategy (Darwin 1871) in which males kill the unrelated, dependent offspring of conspecifics, thereby shortening the victimized female's time interval to the next oestrus (Hrdy 1979). This offers the perpetrator a higher probability of siring offspring, either directly by mating with the victimized female after she re-enters oestrus (Trivers 1972, Hrdy 1979, Janson & Van Schaik 2000, Swenson 2003), or indirectly by reducing intra-male competition through lowering the typically male-biased operational sex ratio (McLellan 2005). Slowly reproducing species with long maternal care are especially prone to this type of behaviour (Van Schaik 2000). Sexually selected infanticide may be a population-regulating mechanism in some brown bear populations (Ordiz et al. 2008, Fernández-Gil et al. 2010), and can be facilitated by the removal of dominant males and by the subsequent influx of immigrant males (Swenson et al. 1997). The importance of sexually selected infanticide as a population regulatory factor is dynamic, and can vary within a species (Hrdy 1979, Janson & Van Schaik 2000, Swenson 2003).

Sexually selected infanticide in the brown bear has been documented in two Scandinavian (Swenson et al. 1997, Bellemain et al. 2006a) and one Spanish population (Fernández-Gil et al. 2010), and has been suggested to occur in populations in British Columbia, Canada and in the Central Pyrenees of France and Spain (Wielgus et al. 2001, Chapron et al. 2009). Support for the sexually selected infanticide hypothesis has been reported for other ursids as well, that is, the American black bear (Wielgus & Bunnell 1995) and the polar bear (Taylor et al. 1985). Many researchers do not accept that infanticide in bears is sexually selected (McLellan 2005, Garshelis 2009), but ascribe infanticide to reducing prospective and immediate resource competition, or to intra-specific predation (Craighead et al. 1995a, Derocher & Wiig 1999, Miller et al. 2003, Garshelis 2009). McLellan (2005) argued that sexually selected infanticide did not occur in brown bears, but that, if it were to occur, it should follow his proposed 'mate recognition hypothesis' of sexually selected infanticide. This states that all males, irrespective of age, should kill conspecific offspring that they have not sired, given the opportunity (McLellan 2005).

Because female lifetime reproductive success can be reduced through infanticide, females have evolved counterstrategies against this behaviour (Hrdy 1979, Swenson 2003). Ebensperger (1998) summarized six female counterstrategies to infanticide: (i) pregnancy termination, (ii) maternal aggression, (iii) group defence, (iv) avoidance of infanticidal individuals, both in space and in time, (v) promiscuity and (vi) territoriality. Of these strategies, ii–v have been reported in brown bears [e.g. (ii) McLellan 2005, Fernández-Gil et al. 2010; (iii) Craighead et al. 1995a; (iv) Dahle and Swenson 2003c, Ben-David et al. 2004, Rode et al. 2006 and (v) Craighead et al. 1995b, Swenson et al. 2001b, Bellemain et al. 2006a, b].

## FEMALE MATE CHOICE

Female brown bears are promiscuous, and control mating acts and partners to some extent (Craighead et al. 1995a, Fernández-Gil et al. 2006). Females have been observed initiating mating on some occasions (Fernández-Gil et al. 2006), and both sexes show roam-to-mate behaviour (Dahle & Swenson 2003c). McLellan (2005) suggested that females signal their receptivity to attract the best or most dominant males. In most species, females tend to be the more selective sex in relation to mate choice, because of their higher investment in gametes (Darwin 1871, Clutton-Brock 1989). To optimize reproductive success, females should therefore select for high-quality males. Age and morphological traits, such as body size, weaponry and signs of aggression or willingness to fight, are considered to reflect male quality (Andersson 1994). The apparent success of larger, older or more aggressive male brown bears might be explained, in part, by female choice for these traits as signs of genetic quality.

Infanticide, in whatever form, is common in brown bears (Craighead et al. 1995a, Swenson et al. 1997, Garshelis 2009), and promiscuity by females is generally acknowledged to be an aid in countering infanticide by males through paternity confusion, either directly by mate recognition or indirectly by multiple paternity (Ebensperger 1998). Bellemain et al. (2006b) suggested a mating strategy dilemma for female brown bears in a population exhibiting sexually selected infanticide, where females have to choose between mating with the phenotypically best male, or with nearby males that they are likely to encounter in the future (suggesting promiscuity as a strategy to counter infanticide by males). Bellemain et al. (2006b) found that the oldest, largest and most heterozygous of all nearby males had the highest chance of becoming the father of the female's next offspring. Promiscuous mating by females has potential benefits such as the assurance of fertilization (Wilson et al. 1997), sperm competition (Stockley & Purvis 1993), and selection of the most compatible partner and his sperm (Gray 1997).

Støen et al. (2006b) and Ordiz et al. (2008) found that age at primiparity was affected by social factors in a matrilineally organized Scandinavian brown bear population: females that were not living in a matrilineal assemblage were younger at primiparity. In addition, females were reproductively suppressed when in the vicinity (home range centroids <10km apart) of another female with cubs of the year (Ordiz et al. 2008). This results in a spatially and temporally oscillating female reproductive asynchrony, thereby offering higher mate availability to females (Ims 1990, Ordiz et al. 2008).

## MATING SYSTEM CLASSIFICATION

The classical works of Emlen and Oring (1977) and Clutton-Brock (1989) considered mating system research in an ecological context of spatiotemporally distributed resources, including receptive females, and the potential of mate detection, monopolization and reproduction (Apollonio et al. 2000). Even with the lack of agreement on terminology and classification, the frameworks are generally accepted and are often used as a starting point in mating system studies (Andersson 1994, Shuster & Wade 2003). Shuster and Wade (2003) provided a key to identify the detailed mating system of a species, based on the spatiotemporal distribution of sexually receptive females, the variance in reproductive success within and between both sexes as a measure of the strength of sexual selection, and a number of

evolutionary traits, such as sperm competition, female copying, sexual dimorphism, paternal care, sexual conflicts and potential alternative mating strategies. The key requires preclassification in one of 12 major classes of mating system. These are: sedentary pairs, iterant pairs, mass mating, polygamy, male dominance, social pairs, mating swarms, leks, feeding sites, nesting sites with female care, nesting sites with male care and polyandrogyny (Shuster & Wade 2003).

Various authors have classified the mating system of the brown bear differently, that is, as polygamy (Pasitschniak-Arts 1993, Zedrosser et al. 2009), promiscuity (Swenson et al. 2001b, Schwartz et al. 2003b, Bellemain et al. 2006a, b), scramble competition polygamy (Dahle & Swenson 2003c, McLellan 2005) and contest competition polygamy (Schwartz et al. 2003b). The variation in descriptions of the mating system may have been caused by differences in the spatiotemporal availability of receptive mates within and among populations (Emlen & Oring 1977, Herrero & Hamer 1977, Clutton-Brock 1989), by plasticity in the sense of Shuster and Wade (2003), that is, alternative mating strategies, or by the lack of consistent terminology, as pointed out by Andersson (1994) and Shuster and Wade (2003).

Based on the framework of Emlen and Oring (1977), the mating system of the brown bear can be classified as polygynous or polyandrous, because individuals of both sexes frequently gain access to multiple mates (Table 2). Using the classification system of Clutton-Brock (1989), both sexes can be considered promiscuous in brown bears, where promiscuity is defined as males attempting to mate with any receptive female, and females mating with several males in successive breeding attempts (Table 2). Clutton-Brock (1989) associated mating systems with four main forms of mate guarding: (i) the defence of individual females during part or all of their period of receptivity; (ii) the defence of feeding territories that overlap the ranges of individual females or groups of females partly or completely; (iii) the defence of particular groups of females, either during the mating season or throughout the year without defence of any fixed area and (iv) the defence of dispersed or clustered mating territories within a portion of females' ranges (Clutton-Brock 1989). Only mate guarding form (i) occurs in the brown bear. It encompasses the 'sequestering' strategy and the 'roving male' strategy, in which females range widely and are solitarily and unpredictably distributed at low population densities, and males range widely in search of oestrous females, consorting with them and defending them against other males (e.g. Dahle & Swenson 2003a, b, c, McLellan 2005). Mate guarding form (i) also is applicable to the reproductive behaviour that bears exhibit around clumped food resources, such as spawning salmon (e.g. Sellers & Aumiller 1994) or garbage dumps (e.g. Craighead et al. 1995a). Around clumped food resources, males develop a dominance hierarchy (Craighead et al. 1995a), which may be used to obtain access to receptive females also visiting these food resources. Subdominant males may gain access to receptive females through a satellite strategy (Table 2).

Shuster and Wade (2003) defined a given mating system as polygamous if both sexes had variable numbers of mates, and if male and female mating success was approximately equal; they defined a mating system as polygynandrous if male mating success was more variable than female mating success. Both definitions seem to apply to the mating system of the brown bear (Table 2). Evidence from North America (Craighead et al. 1995a) and Scandinavia (Zedrosser et al. 2007a), however, suggests that variation in reproductive success in males is more pronounced than in females. This implies that, according to Shuster and Wade (2003), polygynandry best

**Table 2.** Mating system classification of the brown bear according to the frameworks of Emlen and Oring (1977), Clutton-Brock (1989) and Shuster and Wade (2003)

SW		Detailed		Interpretation	Example populations
EO	CB	Main	Detailed		
Polygyny/ polyandry* [promiscuity, polygamy]	Promiscuity Roving males, mate guarding form (i)** Stonorov and Stokes (1972)	Polygamy***	Polygamy/cursorial polygyny or polygamy [scramble competition]	Highly mobile males during the breeding season, males search for and attempt to mate with several females. Both sexes may mate a variable number of times with a variable number of mates during a breeding season (Dahle and Swenson 2003c, Bellemain et al. 2006a, Swenson et al. 2000, Craighead et al. 1995b, Green and Mattson 2003, Stonorov and Stokes 1972). Males may also sequester, defend and attempt to mate with individual receptive females. This may occur sequentially during a breeding season. This sequestering may be at the expense of females' reproductive interests and feeding opportunities (Brady and Hamer 1992, Hamer and Herrero 1990, Herrero and Hamer 1977).	Waterton Lakes National Park, Canada (Brady and Hamer 1992) Banff National Park, Canada (Hamer and Herrero 1990, Herrero and Hamer 1977) North and South Sweden (Dahle and Swenson 2003c, Bellemain et al. 2006a, Swenson et al. 2000) Greater Yellowstone Ecosystem, USA, after garbage dump closures, USA (Craighead et al. 1995b, Green and Mattson 2003) Alaska, USA (Stonorov and Stokes 1972) Cantabrian Mountains, Spain (Fernández-Gil et al. 2006) Banff National Park, Canada (Herrero and Hamer 1977)
		Male dominance	Polygamy/polygamy (possible convergence to leks) [contest competition]	Both sexes may mate a variable number of times with a variable number of mates during a breeding season. Mating areas may develop, i.e. groups, with >1 male, when population densities are very low (Herrero and Hamer 1977).	
			Dominance polygynandry	In populations where individuals of both sexes aggregate at food congregations (Craighead et al. 1995b, Craighead et al. 1974), dominance hierarchies may develop. Subdominant males may gain access to receptive females through a satellite strategy.	Greater Yellowstone Ecosystem, USA, before garbage dump closures (1968-71; Craighead et al. 1995b, Craighead et al. 1974).

EO, Emlen and Oring; CB, Clutton-Brock; SW, Shuster and Wade. 'Main' and 'Detailed' represent the main and detailed mating system classes according to SW.

For the classification according to Shuster and Wade (2003), we assumed that reproductive success in both sexes differed between individuals, and both yes/no options of sperm competition and female copying were considered.

\*Includes female defence polygyny. \*\*Mate guarding form (i) implies guarding individual females during their receptive period. \*\*\*Polygamy is, according to Shuster and Wade (2003), characterized by plasticity, and thereby includes both guarding and roving male mating strategies. 'Possible convergence to leks' here implies that durable mating areas may develop, and not classical leks in the strict sense of the term. Alternative terminology in the literature is indicated within square brackets [ ].

describes the mating system of the brown bear. Based on the identification key by Shuster and Wade (2003), the mating system of the brown bear can be described as male dominance (dominance polygynandry), polygamy, cursorial polygyny or polygamy, or as polygamy with possible convergence to leks (not classical leks, but mating areas; Shuster & Wade 2003; Table 2). There is no evidence of bears using leks in the same way as black grouse *Tetrao tetrix* (Alatalo et al. 1991) or fallow deer *Dama dama* (Apollonio et al. 1992), that is, (i) males display in locations without resources required by females, (ii) the locations of leks may shift between years and (iii) females frequent leks for mating purposes only and leave afterwards to raise offspring on their own (Shuster & Wade 2003). However, there is evidence from Europe and North America that bears sometimes use mating areas (Herrero & Hamer 1977, Hamer & Herrero 1990, Fernández-Gil et al. 2006).

In summary, variation in reproductive behaviour of the brown bear is related to the spatiotemporal clustering of individuals, as in other species (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003). Brown bears may aggregate during the breeding season at abundant and predictable food resources (e.g. Craighead et al. 1995a), or from a reproductive perspective, perhaps to counter difficulties in finding mates (e.g. Fernández-Gil et al. 2006). In populations that do not aggregate during the breeding season, the strategies of sequestering and defending a few females (e.g. Herrero & Hamer 1977), or searching out and attempting to mate with several receptive females (e.g. Dahle & Swenson 2003c), might be chosen by individual males depending on their dominance level and personality (Craighead et al. 1995a, Fagen & Fagen 1996), and on the population density, which may affect male black bear mating strategies (Costello et al. 2009).

The spatiotemporal distribution of receptive females is one of the most important factors shaping the mating system of a species (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003). In species without paternal care, such as the brown bear, the spatiotemporal distribution of the availability of food is probably the most important factor determining the size and spacing of female home ranges (Clutton-Brock & Harvey 1978). Resources are probably too dispersed, and home ranges too large, to be actively defended by either female or male brown bears. Therefore, the benefits of territoriality, such as resource reliability (Waser & Homewood 1979), are probably diminished in brown bears. Because paternal care is absent, males may increase their reproductive success, that is, the number of offspring they produce, by attempting to mate and reproduce with several females. The operational sex ratio in the brown bear is, at least in unhunted populations, heavily male biased, due to long inter-litter intervals (Pasitschniak-Arts 1993), asynchrony in female oestrous cycling (Craighead et al. 1995a, Spady et al. 2007) and female-induced reproductive suppression (Ordiz et al. 2008). A high potential for sexual selection is expected in species with a polygamous mating system and a male-biased operational sex ratio (Emlen & Oring 1977, Shuster & Wade 2003), and thus in the brown bear. This is reflected in the large size dimorphism between male and female brown bears, probably as a result of intense male-male competition for receptive females.

## CONCLUSIONS

The commonality among the mating system classifications applied to the brown bear is that individuals may mate a variable number of times with a variable

number of mates, and are thus polygamous in the broadest sense of the term. We therefore suggest that the brown bear's mating system should generally be classed as 'polygamous', but stress the need for research on the brown bear's reproductive biology at smaller spatial scales (e.g. at the population level). Within a polygamous mating system, at the species level, individual brown bears seem to show plasticity regarding mating strategies, based on geographical and ecosystem characteristics, as well as individual and sex-specific behaviour. Most classification frameworks focus mainly on male reproductive behaviour and strategies, because males generally show more variation in reproductive success than females. This approach might underestimate the role of females in shaping the mating system of a species (Reynolds 1996).

Many aspects of brown bear reproductive biology remain poorly understood. From a physiological perspective, these aspects include sperm competition, female reproductive cycles and hormone status, and the roles of olfaction in reproduction and kin recognition. These aspects affect aspects of reproductive behaviour, including sexually selected infanticide, mate selection and male mating strategies, which need further attention.

Brown bear populations worldwide are influenced by humans, through hunting, recreational activities, habitat degradation, etc. (Swenson 1999, Weisberg & Bugmann 2003, Bischof & Zedrosser 2009). These human influences can have direct demographical effects, which are generally known or acknowledged (e.g. hunting). In addition, indirect demographic effects may occur (Anthony & Blumstein 2000), that is, those that affect population growth rates, because of an altered population structure (Bischof et al. 2009), as well as evolutionary and habitat effects (Allendorf & Hard 2009). Human impacts on the reproductive behaviour and mating system of the brown bear remain unclear, and may differ among populations. This is illustrated by the following example: removing brown bear males from some populations in British Columbia and Alberta, Canada and Montana and Alaska, United States, appeared to have no effect, or even a positive effect, on cub survival and infanticide was not considered to be a major cause of cub mortality (Miller et al. 2003, McLellan 2005). The opposite appears to be true in a population around Kananaskis, Alberta and in two Scandinavian populations, where the removal of adult males disrupted an established social structure by provoking an influx of potentially infanticidal, immigrant, males, thereby lowering cub survival through sexually selected infanticide (Swenson et al. 1997, Swenson 1999, Wielgus et al. 2001, Bellemain et al. 2006a, b).

Human impacts may have contributed to some of the reported variation in the mating behaviour of the brown bear. Alteration of the social structure of a population, and potential effects on the population's reproductive parameters, should be considered when planning reintroduction programmes, defining hunting quotas and their selectivity, and instigating other management measures, such as the translocation of nuisance individuals. To understand more fully the plasticity of the mating system of the brown bear, research is needed at local and regional levels.

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