

Observations of mixed-aged litters in brown bears

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Abstract: We report on 3 cases of mixed-aged litters (young born in different years) in brown bears (*Ursus arctos*); in 1 instance the cub-of-the-year (hereafter called cubs) died in the den. Two cases occurred in Sweden after mothers were separated from their young during the breeding season. In one, the mother was separated from the accompanying cub for at least 12.5 hours and possibly up to 3.3 days, and later possibly separated for 4 days. In the other, the mother was separated from her yearling at least 3 times for 1–14, 1–6 and 1–6 days. She was with a male during the first separation. Specific events that produced the mixed-aged litter observed in Greater Yellowstone Ecosystem were unknown and our interpretation is based on estimates of ages of accompanying young from photographs. The observation of only 2 mixed-aged litters, after den emergence, from a sample of 406 observed cub litters accompanying radiomarked females confirms the rarity of this phenomenon. The mechanism apparently includes a short separation of mother and young, and, in the case of cubs, the mother must mate while lactating. Better understanding of the physiological mechanisms that allow mixed-age litters would help us in the debate about the occurrence of sexually selected infanticide in bears.

Key words: brown bear, mixed-aged litters, Sweden, *Ursus arctos*, Yellowstone

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On rare occasions mixed-aged litters (young born in different years) in brown bears (*Ursus arctos*) and

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American black bears (*U. americanus*) have been reported in the literature. Stroganov (1962) reported that hunters in Siberia talked of mixed-aged litters of brown bears and that they called the older sibling a “pestun,” thinking that it acted as a “nurse” for its younger siblings. He agreed with other Russian scientists that the existence of these “pestuni” had not been documented scientifically, and that the phenomenon probably was a hunter’s tale. Norikov (1956:95) also reported mixed-age litters in the USSR, but wrote that “the reports are contradictory.” Nevertheless, mixed-aged litters in North American brown bears have been reported in the scientific literature (Erickson 1964, Dean et al. 1992), and co-denning by unrelated or mixed-age assemblages of young have been reported in American black bears (Schwartz et al. 1987). Here, we report 3 cases of mixed-aged litters in brown bears, 2 in Sweden and 1 in the Greater Yellowstone Ecosystem (GYE) in the United States. For descriptions of our study areas and methods, we refer to Arnemo et al. (2006) and Zedrosser et al. (2006) for Scandinavia and to Schwartz et al. (2006) for the GYE. We did not capture any of the cubs observed in the wild for verification of maternity.

Observations of mixed-aged litters

Case 1. Female W8904 emerged from her den in the southern study area of the Scandinavian Brown Bear Research Project (SBBRP) with 2 cubs, her third litter, in spring 1993 when she was 6 years old. She had lost previous litters born in 1991 and 1992. In 1993, she lost 1 of the cubs during the spring breeding season and entered a den in the autumn with the surviving cub. In spring 1994, she and her yearling were captured to change her radiocollar and collar the male yearling (W9401). We documented 3 short-term separations during 1994. The first instance was on 27 May, when radio relocations indicated that the mother was with W9303, a 5-year-old male, and that W9401 was 9.5 km away. W9401 had been relocated with his mother on 21 May and they were seen together again on 4 June, indicating a separation of 1–14 days. This was unusual, because yearlings usually separate permanently from their mother in this population, often when the mother is with a male during the breeding season (Swenson et al. 1994, Dahle and Swenson 2003). In the second

instance, the mother and yearling were relocated together on 17 July, but on 20 July 1994 a field technician with long experience judged them to be separated when he radiolocated them 4 times that day (0730, 0900, 1000, 1030) (K.-A. Olander, SBBRP, Älvdalen, Sweden, personal communication, 1994). They were relatively close, however, as is common when yearlings are in the process of separating from their mothers (Dahle and Swenson 2003). Three days later, on 23 July, they were together again, indicating a separation of 1–6 days. In the last instance, W9804 and W9401 were radiolocated together on 30 July, were 860 m apart on 3 August, and were together again on 5 August, also a separation of 1–6 days. We do not know of other instances when W9401 was away from his mother in 1994 and he denned with her. Upon examining their den (1 Apr 1995), we found the carcass of an intact male cub weighing 1.3 kg. A necropsy carried out at the National Veterinary Institute of Sweden indicated that the cub had died of malnutrition and that there were no signs of aggression toward the cub. Had the cub lived, W8904 could have been followed by a mixed-age litter (a cub and a 2-year-old) during the spring until the older offspring separated. Bear W9401, now a 2-year-old, separated from its mother during the breeding season.

Case 2. Female W9307, also in the southern study area of the SBBRP, had 3 cubs in her third litter in 1999, when she was 6 years old. She had lost all cubs in her 2 previous litters, in 1997 and 1998. At 2155 on 6 June 1999, an adult male bear was seen climbing a Scots pine (*Pinus sylvestris*) tree after 1 of her cubs; she was nearby (picture in Swenson 2003:183). We learned later that he had already killed the other 2 cubs. The male was last seen at 0100 (7 Jun). From 2330 W9307's transmitter signals were checked every 10 minutes. She was passive until 0020, when she became active, and at 0030 she moved away from the vicinity of the tree with the cub and out of our sight; the signals indicated that she was moving from where her cub was at 0100 (J. Katajisto, Wiebke Neumann, et al., SBBRB, unpublished data). At 0510 on 7 June, W9307 was 3.5 km from the site and at 0630 the cub was still in the tree. At 0820 she began to move directly toward the site where she left the cub. While moving, she was observed alone at 1055 and 1105. At 1325, after an absence of about 12.5 hours, she arrived at the site where we last saw the cub 7 hours earlier. We kept our distance to not

disturb their reunion, but returned at 1430 and confirmed that the cub was not in the tree. Because W9309 returned directly to the site where she left the cub, and we know that it was still there 7 hours before she arrived, we assume that she reunited with her cub shortly after 1325. We saw W9307 with the cub on 10 June, at 0945, and again on 14 June. Thus, it is possible, although improbable, that she had been separated from the cub for as long as 3.3 days. Another unusual incidence regarding this female also occurred in 1999, when she might have been away from her cub for 4 days. From 16 July at 1610 to 17 July at 2132 she moved 13.9 km north, to an area she had not been located earlier or later that year. She was last located there on 19 July at 1500. She was not found on 20 July, but on 21 July at 1700 she was back in her usual area, about 14 km from the location on 19 July. We tried to observe her during this period, but we were not able to determine if she was with the cub or any other bear due to dense cover. She was observed with her cub on 22 July. These movements were noteworthy because females with cubs in this area move an average of 1.6 km daily, and 97.5% of all daily movements are <2.2 km (Zakrisson 2001). Bear W9307 denned with the cub. When she and her male yearling (W0017) were immobilized on 27 April 2000, we observed a cub in the tree at the site. A few days later, an observation of a female bear with 2 offspring, 1 large and 1 small, 1 km from the immobilization site was reported to us. We observed female W9307, yearling W0017, and the cub on 5 and 13 May (Fig. 1). The cub was not seen after 13 May, and W0017 separated from W9307 on 6 or 7 June.

Case 3. Female 349 was observed in Yellowstone National Park with 2 cubs of similar size during an aerial telemetry flight on 24 May 2005, when she was 11 years old. On 2 August 2005 she was observed briefly from the air at a timbered site, but no cubs were seen. She was not observed again during 2005. During the spring and summer of 2006, female 349 was observed during telemetry flights on 8 occasions (28 Apr; 30 May; 18 Jun; 10, 24, and 27 Jul; 3 and 27 Aug). On 28 April 2006, she was at her den site with at least 2 cubs, although the pilot indicated that 3 offspring might have been present. During 6 subsequent observations from 30 May through 3 August, 3 offspring were observed and the pilots commented on the difference in size among the offspring. A photograph taken on 24 July (Fig. 2) clearly shows a larger offspring, which was similar in



Fig. 1. Female brown bear W9307 with 1 cub and 1 yearling (W0017), Sweden, May 2000. Photograph by S. Widstrand.

size to typical yearlings in the GYE, and 2 smaller offspring, which were typical cub size. On 27 August only the larger offspring, presumably a yearling, was observed with 349. The 2 cubs were absent and presumed dead.

Discussion

We have observed 253 cub litters accompanying radiomarked female brown bears in Scandinavia during 1988–2006, and 153 in the GYE during 1975–2006. Observations of only 3 mixed-aged litters (only 2 outside dens) in 406 observed cub litters (0.5%) confirms the rarity of this phenomenon. That mixed-age litters are an unusual event is also supported by the comments of Russian biologists, who did not believe hunters' reports about this phenomenon (Norikov 1956, Stroganov 1962). All of the younger members of these mixed-age litters were known or suspected to have died during their first year of life, which would also contribute to it rarely being observed. Other reported observations of mixed-aged litters in brown bears include a single cub and 2 ≥ 1.5 -year-old young in Alaska (Erickson 1964), a single cub and an adopted yearling in Yellowstone National Park (Craighead et al. 1969), a single cub

and a 2.5- or 3.5-year-old young in Denali National Park, Alaska, and 2 cubs and 2 yearlings in the same litter at McNeal River, Alaska (Dean et al. 1992). In the latter 2 cases, all the young were observed to nurse from the female they accompanied (Dean et al. 1992).

One possible explanation for our second and third observations is adoption, which has been documented in brown bears (Erickson and Miller 1963, Glenn et al. 1976, Wilk et al. 1988, Barnes and Smith 1993, Craighead et al. 1995), American black bears (Benson and Chamberlain 2006), and polar bears (*U. maritimus*; Atkinson et al. 1996, Derocher and Wiig 1999, Lunn et al. 2000). Craighead et al. (1995) documented 9 cases of adoption in brown bears and reported that most orphaned offspring were adopted during 1959–1970 in Yellowstone National Park, when bears were concentrated at garbage dumps. Natural adoption seems to occur primarily where bears congregate at abundant food sources (Dean et al. 1992) and may occur as the result of errors or mistakes made by females with young following the confusion and stress caused by confrontations with other bears (Erickson and Miller 1963).

We consider adoption to be improbable in our cases. In Scandinavia, where brown bears do not



Fig. 2. Female grizzly bear 349 and 3 young, Yellowstone National Park, 24 Jul 2006. Note differences in size and coloration among young. Photograph by pilot Steve Ard.

congregate, all 314 yearlings captured with a female in the spring were shown genetically to be the offspring of that female (Bellemain et al. 2006a). In Pennsylvania, Alt (1984) did not observe a single instance of natural adoption in a 10-year study (1974–83) of American black bears that did not congregate at food sources. Similarly, brown bears in the GYE do not congregate to the extent that they did prior to closures of open-pit dumps, where bears had interacted for generations (Meagher and Phillips 1983, Schullery 1992). Additionally, we observed the mixed-age litters early in the year (Apr and May), making adoption even more unlikely.

It is also possible that the mothers could have mated while with their young were still at their side, even though female bears do not normally breed while accompanied by dependent young (Craighead et al. 1969, Herrero and Hamer 1977, Murie 1981, Dahle and Swenson 2003). However, in all 3 cases we observed short-term separations (Sweden) or suspected a separation (GYE). In case 1, we documented 3 separations of a yearling for 1–14 days in June, when the mother was with an adult male, 1–6 days in

July, and 1–6 days in early August. Yearlings commonly separate permanently from their mothers in southern Scandinavia, but rarely rejoin them as in this case. In case 2, the female was separated from the cub for a minimum of 12.5 hours in June, although it could have been up to 3.3 days, and perhaps was separated for 4 days in mid-July. The breeding season in Sweden is concentrated to early May through late June, with a few observations of males and females together in mid-July (Dahle and Swenson 2003). For case 3, the female was observed too infrequently and briefly in 2005 to ascertain with certainty if, or for how long, she may have been separated from her cubs, although during one observation no cubs were seen.

There are few observations of times between separations from cubs and breeding in brown bears (McLellan 2005), although the shortest time it has been documented in captivity was 5 days (Dathe 1961). McLellan (2005) reported observations of 3 wild female brown bears in Alaska that were first seen with males 9, 11, and 18 days after being separated from their cubs. These observational

sequences, like ours, were not continuous. Nevertheless, observations of long intervals from cub separation to mating are not relevant to the formation of mixed-age litters, because any cubs undergoing such long separations would likely die before the mother returned to them. In the cases reported by McLellan (2005), no mention was made of the fate of the cubs. Breeding after short periods of separation from cubs also has been observed in wild American black bears. Erickson et al. (1964) reported that a wild female in Michigan produced young the year after he had withheld cubs from her for 2 days, but he did not mention any mixed-age litter. LeCount (1983) reported 2 cases of female American black bears that were only periodically seen with their cubs during observations in the breeding season in Arizona. In both cases, the mothers bred while with cubs, but the cubs in both litters apparently died. Forced short-term separation of a mother and her litter has been used in zoos to produce consecutive litters of American black bears (Baker 1904, 1912).

Thus, we conclude that the most likely explanation for the mixed-age litters we observed is that the mothers mated during short separations from their young. We documented this in case 1, involving the yearling young. In many field studies of bears, females with cubs are captured with snares or culvert traps and are separated from their cubs, rarely for periods >24 hours. However, the cubs almost always stay near and reunite with their mother after she is released (M. Haroldson, unpublished data.). Furthermore, these mothers do not mate with males while they are captured. Thus, we would not expect this to contribute to mixed-age litters. In fact, the study in the GYE uses these types of captures, whereas the study in Scandinavia uses only captures from helicopters, in which the mothers and yearlings are captured together, all immobilized, and wake up together. Our observations did not suggest a greater frequency of mixed-age litters in the GYE.

One observation from Sweden and the observations of mixed-age litters from the literature provide information about how quickly female brown bears can come into estrus after being separated from their cubs. This is important when evaluating the likelihood that sexually selected infanticide (SSI) might occur in brown bears, which is a controversial subject (Swenson et al. 1997, 2001; Miller et al. 2003; Swenson 2003; McLellan 2005; Bellemain et al. 2006b). McLellan (2005) varied several parameters

thought to influence the probability of SSI in brown bears in a model and suggested that older males would be more successful by being infanticidal than by searching for estrous females when the time from loss of cubs to impregnation was 4 days. However, he concluded, based the evidence (see above), that it was unlikely that female brown bears had evolved to come into estrus that quickly after losing cubs. He estimated that this time was more likely about 10 days (3–7 days to change physiologically from lactating to estrus and another 3–7 days to become pregnant). This might be an overestimate, or at least some females can come into estrus much more quickly. It appears that female brown and American black bears are capable of mating while still lactating, because some successfully raised cubs following impregnation. In addition, 14 lone adult females captured during the breeding season in Sweden were both lactating (milk could be expressed) and estrous (swollen vulva); 1 was killed that year and the other 13 produced cubs the following year (J.E. Swenson, unpublished data). Mating while still lactating is essential for mixed-age litters of cubs and yearlings to occur.

The estrus cycle of bears is poorly understood, but knowledge about it is necessary to better understand specifically how mixed-age litters can occur and the mating system in bears generally. The duration of estrus is unknown for the American black bear and poorly documented for the brown bear (Craighead et al. 1995, Ishikawa et al. 2002), although it is known that brown bears can have 2 estrus periods within a breeding season, separated by 4–18 days (Craighead et al. 1995). Factors determining the length of estrus in bears are also unknown (Boone et al. 2004), and estrus physiology even may vary among bear species, because the species require specific methods for detecting estrus and monitoring pregnancy (Knauf 2005). Bears are induced ovulators, but can occasionally exhibit spontaneous ovulation, and have delayed implantation (Sato et al. 2001, Boone et al. 2004). Brown bears do not seem to have the rapid increase in estradiol concentrations for 1–2 days during estrus (the estrogen surge) that is common in most mammals (Ishikawa et al. 2002), although Tsubota et al. (1998) found elevated serum estradiol levels in American black bears before and during estrus. Larivière and Ferguson (2003) suggested that induced ovulation in carnivores evolved through sexual selection as a reproductive strategy beneficial for males and females. The physiology of the estrus

cycle in bears may have been under a similar selection. We encourage more research on the reproductive physiology of bears to allow us to better understand their mating system and reproductive ecology. In addition, DNA analyses of mothers and all young of mixed-aged litters, when possible, would also help us understand the phenomenon of mixed-age litters.

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Literature cited

- ALT, G.L. 1984. Cub adoption in the black bear. *Journal of Mammalogy* 65:511–512.
- ARNEMO, J.M., P. AHLQVIST, R. ANDERSEN, F. BERNTSEN, G. ERICSSON, J. ODDEN, S. BRUNBERG, P. SEGERSTRÖM, AND J.E. SWENSON. 2006. Risk of anaesthetic mortality in large free-ranging mammals: experiences from Scandinavia. *Wildlife Biology* 12:109–113.
- ATKINSON, S.N., M.R.L. CATTET, S.C. POLSHCHUK, AND M.A. RAMSAY. 1996. A case of offspring adoption in free-ranging polar bears (*Ursus maritimus*). *Arctic* 49:94–96.
- BAKER, A.B. 1904. Further notes on the breeding of the American black bear in captivity. *Smithsonian Miscellaneous Collections* 59:1–4.
- . 1912. A notable success in the breeding of black bears. *Smithsonian Miscellaneous Collections* 45: 175–179.
- BARNES, V.G., JR., AND R.B. SMITH. 1993. Cub adoption by brown bears, *Ursus arctos middendorffi*, on Kodiak Island, Alaska. *Canadian Field-Naturalist* 107:365–367.
- BELLEMAIN, E., J.E. SWENSON, AND P. TABERLET. 2006b. Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. *Ethology* 112:1–9.
- , A. ZEDROSSER, S. MANEL, L.P. WAITS, P. TABERLET, AND J.E. SWENSON. 2006a. The dilemma of female mating selection in the brown bear, a species with sexually selected infanticide. *Proceedings of the Royal Society B* 273:283–291.
- BENSON, J.F., AND M.J. CHAMBERLAIN. 2006. Cub adoption by a translocated Louisiana black bear. *Ursus* 17:178–181.
- BOONE, W.R., B.B. KECK, J.C. CATLIN, K.J. CASEY, E.T. BOONE, P.S. DYE, R.J. SCHUETT, T. TSUBOTA, AND J.C. BAHR. 2004. Evidence that bears are induced ovulators. *Theriogenology* 61:1163–1169.
- CRAIGHEAD, J.J., M.G. HORNOCKER, AND F.C. CRAIGHEAD. 1969. Reproductive biology of young female grizzly bears. *Journal of Reproduction and Fertility. Supplement* 6: 447–475.
- , J.S. SUMNER, AND J.A. MITCHELL. 1995. The grizzly bears of Yellowstone, their ecology in the Yellowstone Ecosystem, 1959–1992. Island Press, Washington, DC, USA.
- DAHLE, B., AND J.E. SWENSON. 2003. Family break-up in brown bears: are young forced to leave? *Journal of Mammalogy* 84:536–540.
- DATHE, V.H. 1961. Beobachtungen zur Fortpflanzungsbiologie des Braunbären, *Ursus arctos* L. *Der Zoologische Garten* 25:235–269. (In German.)
- DEAN, F.C., R. MCINTYRE, AND R.A. SELLERS. 1992. Additional mixed-age brown bear, *Ursus arctos*, associations in Alaska. *Canadian Field-Naturalist* 106:257–259.
- DEROCHER, A.E., AND O. WIIG. 1999. Observation of adoption in polar bear (*Ursus maritimus*). *Arctic* 52: 413–415.
- ERICKSON, A.W., AND L.H. MILLER. 1963. Cub adoption in the brown bear. *Journal of Mammalogy* 44:584–585.
- . 1964. A mixed-age litter of brown bear cubs. *Journal of Mammalogy* 45:312–313.
- , J.E. NELLOR, AND G.A. PETRIDES. 1964. The black bear in Michigan. Michigan State University, Agricultural Experiment Station, Research Bulletin 4, East Lansing, Michigan, USA.
- GLENN, L.P., J.W. LENTFER, J.B. FARO, AND L.H. MILLER. 1976. Reproductive biology of female brown bears (*Ursus arctos*), McNeil River, Alaska. *International Conference on Bear Research and Management* 3:381–390.

- HERRERO, S., AND D. HAMER. 1977. Courtship and copulation of a pair of grizzly bears, with comments on reproductive plasticity and strategy. *Journal of Mammalogy* 58:441–444.
- ISHIKAWA, A., S. KIKUCHI, S. KATAGIRI, H. SAKAMOTO, AND Y. TAKAHASHI. 2002. Efficiency of fecal steroid hormone measurements for assessing reproductive function in the Hokkaido brown bear (*Ursus arctos yesoensis*). *Japanese Journal of Veterinary Research* 50:17–27.
- KNAUF, T. 2005. Vergleichende Studien zur Reproduktionsbiologie bei Großbären. Dissertation, Fachbereich Veterinärmedizin, Freie Universität Berlin, Germany. (In German.)
- LARIVIÈRE, S., AND S.H. FERGUSON. 2003. Evolution of induced ovulation in North American carnivores. *Journal of Mammalogy* 84:937–947.
- LECOUNT, A.L. 1983. Evidence of wild black bears breeding while raising cubs. *Journal of Wildlife Management* 47:264–268.
- LUNN, N.J., D. PAETKAU, W. CALVERT, S. ATKINSON, M. TAYLOR, AND C. STROBECK. 2000. Cub adoption by polar bears (*Ursus maritimus*): determining relatedness with microsatellite markers. *Journal of Zoology* 251:23–30.
- MCLELLAN, B. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16:141–156.
- MEAGHER, M.M., AND J.R. PHILLIPS. 1983. Restoration of natural populations of grizzly and black bears in Yellowstone National Park. *International Conference on Bear Research and Management* 5:152–158.
- MILLER, S.D., R.A. SELLERS, AND J.A. KEAY. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* 14:130–152.
- MURIE, A. 1981. The grizzlies of Mount McKinley. US Department of the Interior, National Park Service, Scientific Monograph Series No. 14. Washington, DC, USA.
- NORIKOV, G.A. 1956. Carnivorous mammals of the fauna of the USSR. Keys to the fauna of the USSR No. 62. Zoological Institute of the Academy of Sciences of the USSR, Izdatel'stvo Akademii Nauk USSR, Moscow. (Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, 1962.)
- SATO, M., T. TSUBOTA, G. WATANABE, K. TAYA, T. MURASE, I. KITA, AND T. KUDO. 2001. Changes in sex steroids, gonadotropins, prolactin, and inhibin in pregnant and nonpregnant Japanese black bears (*Ursus thibetanus japonicus*). *Biology of Reproduction* 65:1006–1013.
- SCHULLERY, P. 1992. The bears of Yellowstone. High Plains Publishing Company, Incorporated, Worland, Wyoming, USA.
- SCHWARTZ, C.C., S.D. MILLER, AND A.W. FRANZMANN. 1987. Denning ecology of three black bear populations in Alaska. *International Conference on Bear Research and Management* 7:281–291.
- , M.A. HAROLDSON, AND S. CHERRY. 2006. Study area and methods for collecting and analyzing demographic data on the Yellowstone grizzly bear. Pages 9–16 in C.C. Schwartz, M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, D. Moody, and C. Servheen, editors. *Temporal, spatial, and environmental influences on the demographics of the Yellowstone grizzly bear*. *Wildlife Monographs* 161.
- STROGANOV, S.U. 1962. Carnivorous mammals of Siberia. Biological Institute, Siberian Branch, Academy of Sciences of the USSR, Izdatel'stvo Adademii Nauk USSR, Moscow. (Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, 1969.)
- SWENSON, J.E., F. SANDEGREN, A. BJÄRVALL, A. SÖDERBERG, P. WABAKKEN, AND R. FRANZÉN. 1994. Size trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation* 70:9–17.
- , ———, A. SÖDERBERG, A. BJÄRVALL, R. FRANZÉN, AND P. WABAKKEN. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450–451.
- , ———, S. BRUNBERG, AND P. SEGERSTRÖM. 2001. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80.
- . 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, DC, USA.
- TSUBOTA, T., L. HOWELL-SKALLA, W.R. BOONE, D.L. GARSHELIS, AND J.M. BAHR. 1998. Serum progesterone, oestradiol, luteinizing hormone and prolactin profiles in the female black bear (*Ursus americanus*). *Animal Reproduction Science* 53:107–118.
- WILK, R.J., J.W. SOLBERG, V.D. BERNS, AND P.A. SELLERS. 1988. Brown bear, *Ursus arctos*, with six young. *Canadian Field-Naturalist* 102:541–543.
- ZAKRISSON, C. 2001. Do brown bear (*Ursus arctos*) females with cubs alter their movement pattern in order to avoid infanticidal males? Examenarbete (MS thesis), Swedish University of Agricultural Sciences, Umeå, Sweden.
- ZEDROSSER, A., B. DAHLE, AND J.E. SWENSON. 2006. Population density and food conditions determine adult female size in brown bears. *Journal of Mammalogy* 87:510–518.

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