

Research Article

Genetic evidence for multiple paternity in the Asiatic black bear population reintroduced in South Korea

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ABSTRACT

Background: Multiple paternity in mammals results from multiple mating between males and females during a single season and may be facilitated by reproductive characteristics such as repeated estrus and ovulation in females. Although multiple paternity has been documented in several bear species using molecular approaches, little is known about occurrence of multiple paternity in wild Asiatic black bears. To better understand their breeding ecology, this study examined multiple paternity in a reintroduced population of wild bears in South Korea using molecular parentage analysis.

Results: A pedigree of wild-born cubs and their biological parents was constructed using genotyping data from 20 microsatellite markers. Parentage analysis revealed multiple paternity in three independent litters: two litters born to females F-18 and F-27 in 2012 and one litter born to female F-23 in 2014. Each litter was sired by two different male bears. Multiple paternity was detected in 15.8% of the litters with two cubs identified in this study.

Conclusion: This study provides molecular evidence of multiple paternity in wild Asiatic black bears in South Korea. Further studies incorporating additional genetic data and spatial analyses across the entire population will help elucidate breeding patterns and reproductive ecology and provide valuable information for the conservation and management of the threatened Asiatic black bear.

Keywords: Asiatic black bear, multiple paternity, parentage, pedigree

INTRODUCTION

Information on mating systems and reproductive biology is essential for understanding the behavioral ecology of wildlife and developing effective conservation and management strategies. Mammals exhibit a wide range of mating systems, including monogamy, polygyny, polyandry, and polygynandry (Stockley, 2003; Steyaert et al., 2012; Dobson et al., 2018). In many mammalian species, individuals may mate with multiple partners within a single breeding season. Multiple paternity, which occurs when offspring within a single litter are sired by more than one male, is a consequence of female mating with multiple males. This reproductive strategy increases genetic diversity among offspring and reduces genetic relatedness among siblings within a litter. Such effects may enhance the fitness of wildlife populations in changing environments (Charmanter et al., 2004; Arnett et al., 2008; Bennett and Hale, 2014; Gayet et al., 2016; Ammerman et al., 2019). Previous studies have suggested that the occurrence of multiple paternity may be influenced by several ecological factors, including population density and sex ratio (Baker et al., 1999; Say et al., 1999; Burton, 2002; Kokko and Rankin, 2006; Ishibashi and Saitoh, 2008).

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Bears have complex mating behaviors, and females may mate with multiple males during a single breeding season (Craighead et al., 1995; Bellemain et al., 2006; Zeyl et al., 2009; Shimozuru et al., 2019). In several bear species, adult males generally have larger home ranges than females, and the spatial overlap between male and female home ranges, together with increased male mobility during the breeding season, may facilitate encounters with potential mates (Dahle and Swenson, 2003; Koehler and Pierce, 2003). Both male and female bears may mate with multiple partners, with estimates ranging from three to eight mating partners during a single breeding season in some populations (Craighead et al., 1995; Schenk and Kovacs, 1995; McLellan and Hovey, 2001). Female bears generally show not only repeated estrous and ovulatory events during a breeding season, but also exhibit delayed implantation in which embryonic development is temporarily suspended before implantation in the uterus, allowing reproduction to be synchronized with seasonal conditions and maternal energy requirements associated with hibernation (Wimsatt, 1963; Sato et al., 2001; Chang et al., 2011; Huang et al., 2012; Steyaert et al., 2012; Himelright et al., 2014). The combination of multiple mating, repeated reproductive events, and delayed implantation may provide opportunities for multiple paternity in bears (Craighead et al., 1995; Bellemain et al., 2006; Spady et al., 2007; Chang et al., 2011; Himelright et al., 2014). Molecular evidence of multiple paternity has been documented in several bear species, including the American black bear (*Ursus americanus*), brown bear (*U. arctos*), polar bear (*U. maritimus*) and Japanese black bear (*U. thibetanus japonicus*) (Schenk and Kovacs, 1995; Kovach and Powell, 2003; Bellemain et al., 2006; Zeyl et al., 2009; Yamamoto et al., 2012; Shimozuru et al., 2019).

During the twentieth century, Asiatic black bear (*U. thibetanus ussuricus*) populations in South Korea declined substantially, along with those of other large carnivores, including tigers, leopards, and wolves. This decline was associated with extensive hunting under the policy of exterminating harmful wild animals during the Japanese colonial period (1910–1945), the Korean War (1950–1953), and subsequent industrialization and habitat changes (Kim et al., 2011; Hyun et al., 2022). These historical pressures contributed to severe population declines and increased the risk of local extinction for several native carnivore species. In response, a restoration project for the Asiatic black bear was initiated in South Korea in 2004. Since then, the population has increased through the release of bears reintroduced from overseas and those bred in captivity, as well as through natural reproduction in the wild (Lee and Jeong, 2009; Kim et al., 2011; Hyun et al., 2022).

Despite the progress of the Asiatic black bear restoration project, information on the reproductive ecology of the population, particularly the occurrence of multiple paternity, remains limited. Understanding multiple paternity can provide valuable insights into mating patterns and reproductive dynamics and contribute to the genetic management of this population. Therefore, this study investigated the occurrence of multiple paternity in the wild population of Asiatic black bears in Jirisan National Park and its surrounding areas, South Korea, using parentage analysis based on microsatellite genotypes.

MATERIALS AND METHODS

Animal samples and DNA extraction

A total of 122 Asiatic black bears were used in this study. Of these, 52 bears (28 females and 24 males) had been reintroduced from overseas populations in northeastern China, the Russian Far East, and North Korea. The remaining 70 bears consisted of nine bears born in breeding facilities and 61 individuals born in the wild. Samples of blood ($n = 140$), tissue ($n = 5$), hairs ($n = 68$), and feces ($n = 21$) were collected from bears captured in the wild in Jirisan National Park and its surrounding areas, South Korea, between March 2012 and December 2025. In addition, blood samples from 52 reintroduced Asiatic black bears were included in the genetic analyses. Genomic DNA was extracted from blood and tissue samples using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), from hair samples using the QIAamp DNA Micro Kit (Qiagen, Hilden, Germany), and from fecal samples using the QIAamp PowerFecal DNA Kit (Qiagen, Hilden, Germany). DNA concentration and purity were assessed using a DS-11 UV/Vis Spectrophotometer (DeNovix, USA). The extracted DNA was used as a

template for polymerase chain reaction (PCR).

Microsatellite genotyping

Twenty microsatellite markers previously reported for Asiatic black bears by Myung et al. (2025) were used for pedigree reconstruction. The markers were fluorescently labeled at the 5' ends with FAM, VIC, NED, or PET dyes to enable multiplex PCR and subsequent genotyping. PCR amplification was performed using a Mastercycler Nexus Gradient thermal cycler (Eppendorf, Germany) in a 10- μ L reaction volume containing Multiplex PCR Mix (Qiagen, Hilden, Germany), following the PCR conditions described by Myung et al. (2025). The amplified PCR products were separated using an ABI Prism 3730XL DNA Analyzer (Applied Biosystems, Foster City, CA, USA), and allele sizes were determined using GeneMapper software (Applied Biosystems, Foster City, CA, USA). To minimize genotyping errors, each sample was genotyped at least three times.

Detecting multiple paternity

Individual bears were identified using multilocus genotypes based on 20 microsatellite loci by Identity test using CERVUS version 3.0.6 (Kalinowski et al., 2007), and samples sharing the identical genotypes at all loci genotyped were considered to be the same individual. Parentage analysis was conducted to assign candidate parents to each offspring using CERVUS. Adult bears older than three years were considered potential parents, resulting in 54 candidate mothers and 63 candidate fathers. Parentage assignments were evaluated using the likelihood-based approach implemented in CERVUS, and parent-offspring trios were accepted when the assignment confidence level exceeded 95%. A pedigree was subsequently constructed based on the parentage analysis results. Multiple paternity was identified when offspring within the same litter were assigned to different biological fathers in a single breeding season.

RESULTS AND DISCUSSION

Based on the microsatellite genotypes, a pedigree was constructed for nine bears born in breeding facilities and 61 wild-born cubs and their parents from 51 litters in the Asiatic black bear population (Figure 1). The pedigree revealed complex mating patterns, including monogamy, polygyny, and polyandry. Multiple paternity was identified in three independent litters with two cubs in a single breeding season (Figure 2). These cases involved offspring of females F-18 and F-27 in 2012 and female F-23 in 2014. Female F-18 produced two cubs, M-42 and M-55, in 2012, which were assigned to different fathers, M-02 and M-19, respectively (Figure 2A). Similarly, female F-27 produced two cubs, M-1203 and M-1204, in 2012, which were assigned to M-02 and M-19, respectively (Figure 2B). The third case involved female F-23, which produced two cubs, F-58 and F-59, in 2014, assigned to different fathers, M-14 and M-30, respectively (Figure 2C).

In this study, molecular parentage analysis identified three cases of multiple paternity in the reintroduced Asiatic black bear population in South Korea. Multiple paternity has also been documented in several other bear species, including American black bears (Schenk and Kovacs, 1995; Kovach and Powell, 2003), brown bears (Bellemain et al., 2006; Shimozuru et al., 2019), polar bears (Zeyl et al., 2009), and Japanese black bears (Yamamoto et al., 2012). These findings indicate that multiple paternity occurs across several bear species. The occurrence of multiple paternity varies considerably among mammals. Previous studies have reported low or absent multiple paternity in some species, such as wolverines and white-toothed shrews, whereas high frequencies have been documented in species such as honey possums and Mexican ground squirrels (Bouteiller and Perrin, 2000; Wooller et al., 2000; Hedmark et al., 2007; Schwanz et al., 2016). This variation suggests that multiple paternity may be influenced by differences in mating systems, reproductive biology, and ecological conditions among species. In bears, multiple paternity has been associated with multiple mating during the breeding season, which generally extends from spring to summer or autumn depending on the species, as well as with reproductive characteristics such as delayed implantation (Craighead et al., 1995; Sato

et al., 2001; Spady et al., 2007; Chang et al., 2011; Steyaert et al., 2012). Multiple mating may increase the number of potential sires within a litter and thereby increase genetic diversity among siblings. Consequently, multiple paternity may reduce genetic relatedness among littermates and increase within-litter genetic diversity (Arnett et al., 2008; Ammerman et al., 2019). Such genetic variation may potentially contribute to offspring fitness and population adaptability under changing environments (Charmantier et al., 2004; Bennett and Hale, 2013; Gayet et al., 2016). These potential benefits may be particularly relevant to threatened populations, such as the Asiatic black bear, in which maintaining genetic diversity is an important component of conservation and population management (Gladstone, 1979; Walker, 1980; Schenk and Kovacs, 1995).

Multiple paternity was detected in three of the 19 litters with two cubs, corresponding to an occurrence rate of 15.8%. This rate is within the range reported for other bear populations, including Scandinavian brown bears (14.5%; Bellemain et al., 2006) and Japanese black bears (14.6–17.1%; Shimozuru et al., 2019). In Arctic grizzly bears, multiple paternity was reported in approximately one-third of known litters containing two or more cubs (Craighead et al., 1995). In polar bears, multiple paternity was detected in two of 29 litters containing two or more cubs (6.9%; Zeyl et al., 2009). Differences in the reported occurrence rates among bear populations may reflect variation in reproductive behavior, ecological conditions, population characteristics, and sampling or analytical methods. Previous studies have suggested that the occurrence of multiple paternity may be associated with ecological and demographic factors, including population density and sex ratio (Baker et al., 1999; Say et al., 1999; Burton, 2002; Kokko and Rankin, 2006; Ishibashi and Saitoh, 2008). For example, in swift foxes, mating systems have been reported to vary with population density, with polygyny observed in high-density groups and monogamy in low-density areas (Kamler et al., 2004). These findings suggest that population density may influence mating opportunities and reproductive strategies, although the relationship may differ among species. The occurrence rate of multiple paternity observed in the present study was comparable to those reported in several other bear populations. However, the current sample size and the limited number of multiple-paternity cases do not allow us to determine whether population density, sex ratio, habitat area, or mating competition influence the occurrence of multiple paternity in the South Korean Asiatic black bear population. Further studies incorporating larger sample sizes and long-term ecological monitoring are therefore needed to investigate the potential relationships between multiple paternity and ecological or demographic factors in this population.

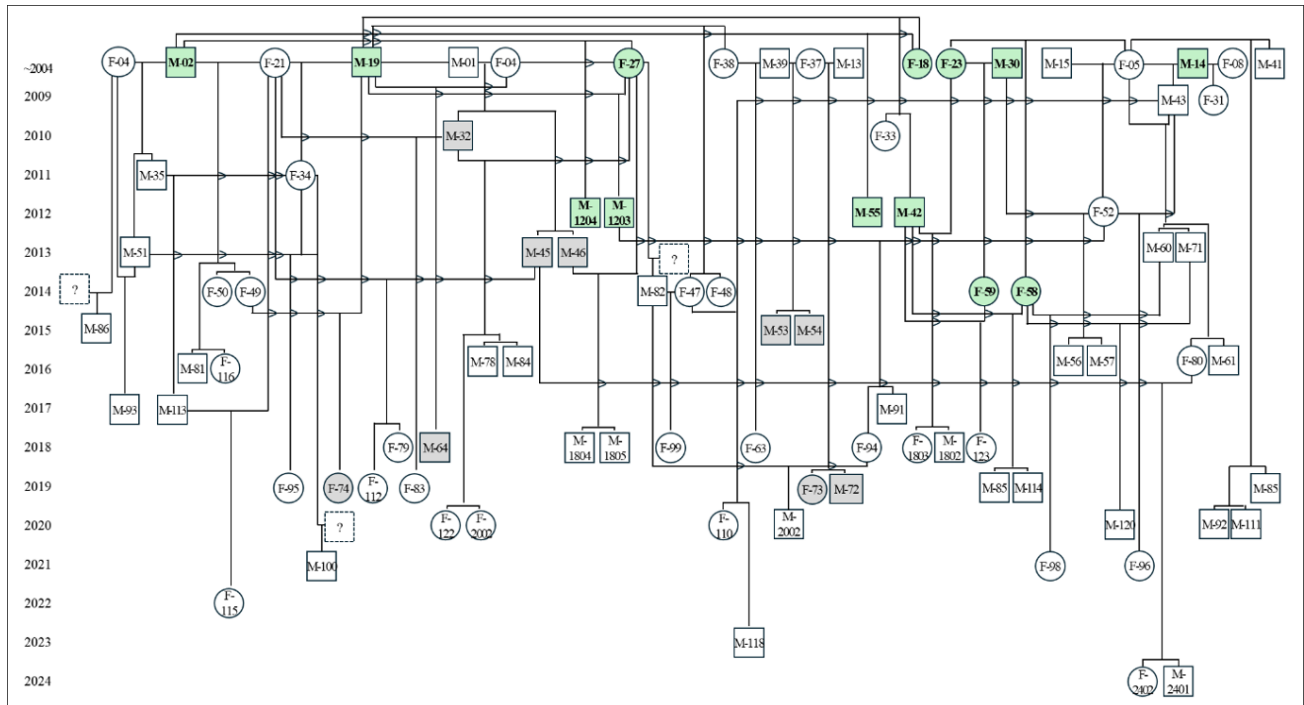


Figure 1. Pedigree of the reintroduced Asiatic black bear population in South Korea. The pedigree illustrates the relationships between bear cubs and their parents, as determined by parentage analysis using microsatellite genotypes. Squares and circles represent males and females, respectively. Gray symbols indicate cubs born in captivity through human-assisted reproduction. Green symbols with bold labels indicate cubs and their parents involved in multiple paternity cases. The squares marked with a question mark in a dotted line represent unidentified father bears. Numbers along the left margin indicate the estimated birth years of the bears. Thirty-three reintroduced bears that had produced no offspring were excluded from the pedigree illustration.

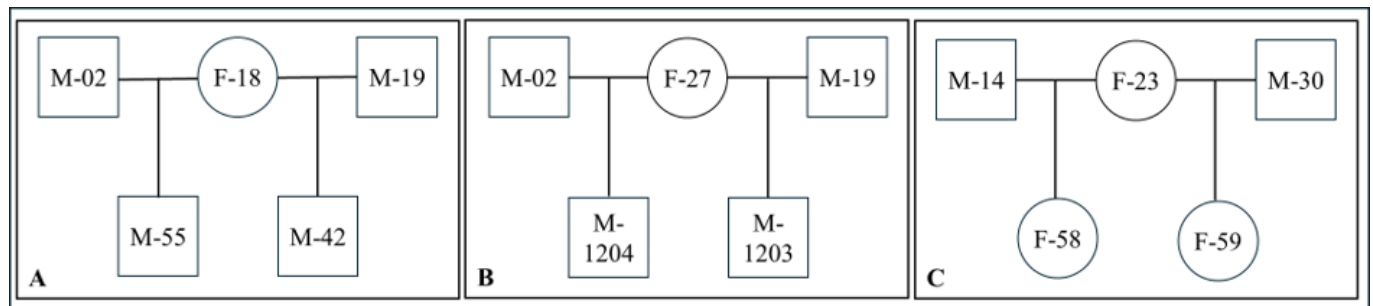


Figure 2. Pedigrees illustrating multiple paternity cases identified in the wild Asiatic black bear population. The parents of wild-born cubs were assigned through parentage analysis using microsatellite genotypes. (A) The family of female F-18, whose two cubs (M-42 and M-55), born in 2012, were sired by M-02 and M-19. (B) The family of female F-27, whose two cubs (M-1203 and M-1204), born in 2012, were sired by M-02 and M-19. (C) The family of female F-23, whose two cubs (F-58 and F-59), born in 2014, were sired by M-14 and M-30.

CONCLUSION

Although the ecological and evolutionary significance of multiple paternity is not yet fully understood, previous studies have suggested that its occurrence in mammals may be influenced by the population density, anthropogenic mortality and other ecological factors during the breeding season. In the present study, multiple paternity was detected in three litters with two cubs in the Asiatic black bear population in

South Korea. The relatively large wild population, which comprised over 90 bears as of August 2026, together with limited habitat availability and potential mating competition, may influence mating opportunities and reproductive patterns in this population. However, the present study does not provide sufficient evidence to establish a direct relationship between these factors and the occurrence of multiple paternity. Further research involving larger sample sizes and additional field data is therefore needed to clarify the ecological and demographic factors associated with multiple paternity. To our knowledge, this study provides the first molecular evidence of multiple paternity in the Asiatic black bear population in South Korea. Further studies integrating genetic, spatial, and ecological data will be essential to elucidate the relationships between reproductive patterns, population characteristics, and environmental conditions. The findings of this study provide valuable baseline information for understanding the reproductive ecology of wild Asiatic black bears and may contribute to the development of effective habitat and population management strategies and conservation policies aimed at establishing a genetically viable and self-sustaining population beyond the restoration phase.

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AUTHOR CONTRIBUTION

Conceptualization: Myung CH, Kim TW, Lim HT, Han SH. Data curation: Myung CH, Kim TW. Formal analysis: Kim TW, Lee SH, Yang DH, Han SH. Methodology: Myung CH, Kim TW, Han SH. Writing – original draft: Myung CH, Kim TW. Writing – review & editing: Han SH, Lim HT. Supervision: Han SH. Funding acquisition: Han SH, Lee SH, Yang DH. All authors read and approved the final manuscript.

CONFLICT OF INTERESTS

No potential conflict of interest relevant to this article is reported.

ETHICAL STATEMENT

Ethical approval for the study was granted by the Institutional Animal Care and Use Committee of the National Park Institute for Wildlife Conservation (NPIWC-R-20260223-1). All animal procedures complied with the NPIWC Guidelines for the Care and Use of Animals and adhered to the ethical standards set by the committees.

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USE OF ARTIFICIAL INTELLIGENCE

We did not use generative artificial intelligence tools in the creation of this manuscript. All research, writing, and revisions are our own work.

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