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Long-term video and genetic data yield insights into complex sociality of a solitary large carnivore

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ABSTRACT

American black bears (*Ursus americanus*) may be more social than currently understood. We used long-term video and genetic data to evaluate social interactions among wild, independent-aged black bear on a conservation property in western Montana, USA. We used multinomial logistic regression to evaluate predictions about male-male interactions within the context of individual fitness, female-female interactions within the context of inclusive fitness, and male-female interactions within the context of female counterstrategies to infanticide. Overall, our findings challenged the assumption that independent-aged bears interact only during the mating season or when concentrated feeding sites are present. We documented 169 interaction events by at least 66 bear pairs, 92 (54%) of which occurred outside of the peak mating season and in the absence of concentrated feeding sites. The probability that male-male pairs engaged in play and other non-agonistic behaviours was higher than that for female-female pairs. Conversely, the probability that female-female pairs engaged in chase behaviour was higher than that for male-male and male-female pairs. We documented evidence of female mate choice, female resource defense, sexually selected infanticide (SSI), and female counterstrategies to avoid SSI. Our findings improve our understanding of ursid ethology and underscore the complexity of ursid sociality.

1. Introduction

Understanding the behaviour of wildlife species that are solitary in nature is important to wildlife conservation and management (Gosling, 2003; Stenhouse et al., 2005). Ursids are generally considered solitary, except during the mother-offspring relationship, during mating season, and when individuals occasionally congregate at large, concentrated feeding sites (e.g., dumps, streams or rivers with spawning fish; Herrero, 1983; Stirling and Derocher, 1990; Pelton, 2003). After family break-up and outside of the mating season, however, bears do not live in a social vacuum (Noyce and Garshelis, 2014). For example, bears use chemical signaling (e.g., scent marking and scent investigation) to communicate with each other (Rogers, 1987; Clapham et al., 2012, 2014; Sato et al., 2014; Taylor et al., 2015), even outside of the mating season (Clapham et al., 2012, 2014).

Bears may also socially interact in ways beyond chemical signaling, but observing behavioural interactions among large terrestrial carnivores like wild bears is challenging owing to their wary, cryptic nature and relatively large spatial requirements (Balme et al., 2010). Thus, direct observation of wild bear interactions is rare and tends to occur at concentrated food sources (Egbert and Stokes, 1976; Latour, 1981; Rogers, 1987; Fagen and Fagen, 2009; Clapham and Kitchin, 2016). Other bear behaviours such as resource and habitat selection (Northrup et al., 2012; Duquette et al., 2017; Zeller et al., 2019; Bowersock et al., 2021), home range overlap (Jonkel and Cowan, 1971; Rogers, 1987; Powell et al., 1997), and dispersal (Schwartz and Franzmann, 1992; Costello, 2010) have been evaluated using data from collared bears. However, collar data alone cannot be used to infer the type of interaction behaviours that may occur among bears (Stenhouse et al., 2005). For example, two collared bears that share the same space may engage in various interactions, including aggressive fighting, mating, playing, foraging, and walking.

Video cameras installed in areas frequented by wildlife can provide opportunities to document behavioural interactions among wild

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individuals (Bloomquist and Nielsen, 2009). For black bears, studies have used relatively short-term (1–2 years) camera data to evaluate wild bear behaviour at supplemental feeding stations (Nolte et al., 2001), outside den sites (Bridges et al., 2004; Miller et al., 2017), along seismic lines (Tigner et al., 2014), and at rub trees (Clapham et al., 2012; Taylor et al., 2015). No study to date has used long-term video data to evaluate behavioural interactions among wild ursids. Such information would improve our understanding of ursid social dynamics.

This study aimed to document and evaluate behavioural interactions among wild, independent-aged American black bears (*Ursus americanus*) using long-term (11 years) video and genetic data. How independent-aged bears interact with each other may depend on the sex of the interacting bears. For example, individual fitness and season may influence interactions among male-male pairs. Male black bears maximize lifetime reproductive success through polygyny (Trivers, 1972), and their reproductive strategies may include resource holding of estrus females and fighting other males for females (Costello et al., 2009). Thus, competition, aggression, and fighting among ursid males can be intense during the mating season (Latour, 1981; Derocher et al., 2010), evidenced by fresh lacerations, wounds, and scars observed on live-captured American black bear males (Beecham, 1980; LeCount, 1982; Garshelis and Hellgren, 1994; Costello et al., 2009). Therefore, we predicted that male-male interactions during the mating season would include aggressive behaviours.

Ursid males communicate via chemical signaling, with more frequent scent marking in the mating season for some bear populations (Rogers, 1987; Sato et al., 2014; Taylor et al., 2015). Chemical signaling and investigation during the mating season may function to communicate competitive ability among males (Clapham et al., 2012), which may increase male fitness by reducing the rate of aggressive, costly interactions between male competitors. Few male-male physical interactions in the mating season would indicate the importance of chemical signaling for avoidance of aggressive interactions around estrus females.

Outside the mating season, ursid males may engage in non-agonistic behaviours, including social play. Male polar bears (*U. maritimus*; Latour, 1981), brown bears (*U. arctos*; Clapham and Kitchin, 2016) and American black bears (Rogers, 1987) were observed play fighting during non-competitive seasons. Possible functional explanations for social play among male ursids include refining fighting skills in a non-aggressive way (Fagen, 1981; Pellis and Pellis, 1998), refining social interaction skills (Latour, 1981), self-assessment (Thompson, 1998), and opponent assessment (Clapham and Kitchin, 2016; Fagen and Fagen, 2009). Successful opponent assessment during social play could help males avoid serious injury or death from superior conspecifics when opponents meet during the mating season (Clutton-Brock et al., 1979), positively affecting individual fitness. Thus, we predicted that male-male interactions during the non-mating season would include social play and other non-agonistic behaviours.

Behavioural interactions among female black bears may be influenced by inclusive fitness, encompassing individual fitness (survival and reproduction) and indirect fitness (gene transmission by non-descendent kin; Hamilton, 1964). Matrilineal relatedness is common in black bear populations due to limited dispersal of female offspring (Elowe and Dodge, 1989; Powell et al., 1997; Costello, 2010). Even after independence, female offspring share space with their mothers (Jonkel and Cowan, 1971; Rogers, 1987; Schwartz and Franzmann, 1992), benefiting from familiarity with foraging and security areas in their natal home ranges (Waser and Jones, 1983). Therefore, we predicted that female-female interactions would be primarily non-agonistic and more frequent than male-male interactions.

Behaviours between independent-aged males and females are primarily driven by mating, leading us to predict that most male-female interactions would occur during the mating season. However, the extent of adult female interaction with adult males may also depend on whether females have cubs-of-the-year (COY). Studies of grizzly bears (*U. a. horribilis*; Mattson et al., 1992; Olson, 1993; Hessing and Aumiller, 1994; Dean et al., 1986; Davoli et al., 2018; Ballesteros et al., 2021) and American black bears (LeCount, 1987; Davis and Harestad, 1996) documented infanticide by adult males. Female counterstrategies to sexually selected infanticide include aggressive defense of young (Kolenosky and Strathearn, 1987; McLellan, 1994; Swenson, 2003) and avoidance of areas frequented by adult males (Pearson, 1975; Mattson et al., 1987; Wielgus and Bunnell, 1994, 1995, 2000). Therefore, we predicted that adult females with COY would either not interact with males at all or, if they did, exhibit aggressive behaviour toward them.

2. Methods

2.1. Study site

Our study was conducted on MPG Ranch (46°42′26″N, 114°00′16″W), a 6,191-ha conservation property located in the Northern Sapphire Mountains in western Montana, USA (Fig. 1). Large, concentrated feeding sites (e.g., dumpsters, streams with spawning fish) do not exist on the Ranch. However, ungulate carcasses are occasionally available because elk (*Cervus canadensis*), deer (*Odocoileus hemionus*, *O. virginianus*), and mountain lions (*Puma concolor*) are abundant on our study site. The elevation ranges from 966 to 1833 m. Dominant tree species on the eastern and northern portions of the study site include Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), subalpine fir (*Abies lasiocarpa*), and quaking aspen (*Populus tremuloides*). The southern and western portions of the study site consist primarily of open, grass-covered slopes with narrow deciduous woody draws that lead to bottomland riparian cover in the Bitterroot River floodplain (Durham et al., 2017). Deer and elk hunting occurs on MPG Ranch, but black bear hunting is prohibited on the Ranch and on ~ 4000 ha of adjoining private lands. Black bear hunting is permitted on nearby lands held in block management by The Nature Conservancy and on nearby public and private lands.

2.2. Video data

We used the following video camera systems to observe and document bears and their behaviours: Stealth Cam model STC-DVIRHD, Stealth Cam model STC-G42NG (Grand Prairie, Texas, USA), Bushnell model 1197678 (Overland Park, Kansas, USA), Reconyx XR6 UltraFire (Grand Prairie, Texas, USA), and Browning models 8FHD-P and BTC-7A (Morgan, Utah, USA). During 2011, we placed video cameras at 26 stations to determine which areas were most frequented by bears. We added video cameras and video camera stations and adjusted the location of some video camera stations during 2012–2016 to maximize the detection of black bears. We removed unproductive video camera stations in 2017 and 2018. During 2018–2021, the number (n = 88) and placement of video camera stations were consistent. A station was defined as one or more video cameras aimed at one unique feature, such as a water source (pond, stock tank, creek), rub feature (rub post, rub tree), wildlife trail, gated gravel road, thicket, open forest, carcass, and apple trees. We often placed multiple video cameras at different angles at a single station to maximize individual identification (Karanth and Nichols, 1998; Rich et al., 2014). We placed cameras ~0.3–1.0 m off the ground to view black bear characteristics such as chest blazes, facial features (e.g., eyebrows, moustaches, ear notches, relative ear size, head and snout shape, snout scars), genitals, and other body traits (e.g., body size, coat color, bare spots).

Cameras recorded for 1-min intervals at up to 60 frames per second, were motion-activated, and were operational 24 h per day. We checked all video cameras every 2–3 weeks during the summers of 2011–2014 and replaced camera batteries at least four times annually. During 2015–2021, we checked cameras and replaced camera batteries every six weeks from March to November, annually.

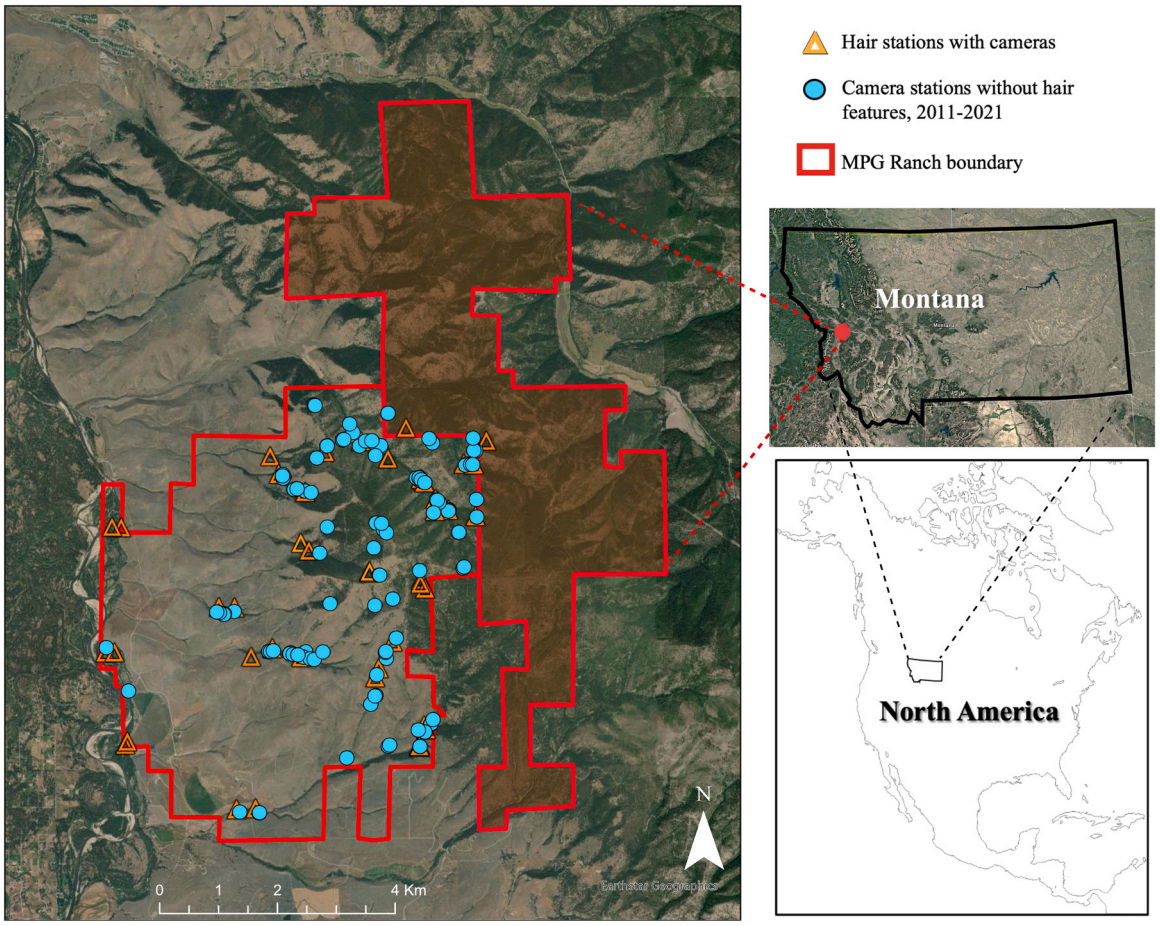

Fig. 1. MPG Ranch, a 6,191-ha conservation property in the Northern Sapphire Mountains in western Montana. The unshaded and shaded portions of MPG Ranch were purchased in 2009 and 2016, respectively.

2.3. Hair stations, DNA analyses, and ancillary data

In addition to collecting video data, we installed hair collection stations (Mulders et al., 2007; Kendall et al., 2009; Ramsey et al., 2019) to determine individual genetic identity, maternity, and paternity (Reynolds-Hogland et al., 2022a). During 2013–2021, we collected >1300 bear hair samples at 36 rub trees and rub posts. Detailed methods of genetic analyses, conducted by the National Genomics Center for Wildlife and Fish Conservation (Missoula, MT), are provided in Ramsey et al. (2019).

As part of our broader black bear research program, we began live-trapping black bears in 2020. During 2020–2021, we live-captured 30 black bears using cage traps that were modified with remote photography and remotely triggered trap doors (Seward et al., 2022). We fitted bears that weighed ≥ 25 kg with GPS collars that bore unique symbols, which we used to help identify individuals during video captures. To help differentiate males from females during video-captures, females received one ear tag in the right ear and males received one ear tag in the left ear. We pulled a premolar to determine age using cementum annuli (Willey, 1974; McLaughlin et al., 1990). We also installed three trail cameras at each cage trap location to document bear behaviours near traps. Although we collected GPS data for 24 collared bears during 2020–2021, we did not include an evaluation of GPS data for this paper because we wanted to maximize the sample size of GPS data before analyzing them. GPS data will be accumulated to January, 2025, when we will evaluate GPS data to test hypotheses about bear sociality developed here.

2.4. Identifying individuals

We meticulously scrutinized every second of each video. The vast majority of bears on our study site had unique traits (e.g., collars with unique symbols, chest blazes, distinct coat patterns, eyebrow colors, ear notches, relative ear sizes, profile snout shapes, snout and head shapes, snout moustaches, snout scars and lines, snout colors, temporalis and masseter sizes, and bare spots and scars), which we used to help identify individuals (Ramsey et al., 2019; Reynolds-Hogland et al., 2022a, 2022b; Reynolds-Hogland et al., 2023). We also linked visual markers of individuals with their genetic identifications, following Ramsey et al. (2019).

We video-captured known individuals frequently and regularly, which aided individual identification. For example, 46 individuals on our study site were video-captured >100 times, and 20 were video-captured >500 times (Reynolds-Hogland et al., 2022a). Regular video-captures allowed us to track gradual changes (e.g., body growth as bears aged, changes in temporary marks like wounds), which minimizes misidentification error associated with camera data due to changes in natural marks (Yoshizaki et al., 2009). We previously conducted a blind test and demonstrated a 97% individual identification accuracy rate using video data (Reynolds-Hogland et al., 2022a).

We classified individual bears into four age classes: cub (<1 year old), yearling (1–2 years old), subadult (2–4 years old), and adult (≥ 5 years old; Hebblewhite et al., 2003, Obbard and Howe, 2008). When an individual was video-captured across multiple years, we updated the individual's age classification accordingly. For example, a bear classified as a yearling during year x was classified as a subadult during year $x+1$.

2.5. Classifying interaction events

We defined an interaction event as a video, or series of videos, where two or more independent-aged bears were recorded together in the same frame at the same time. If Bear *x* and Bear *y* were video-captured together at different camera stations over multiple hours, we counted the interaction as one event unless we video-captured Bear *x* or Bear *y* by themselves at any camera station during that period. This definition may have under-represented the sample size of interaction events. We defined the duration of each interaction event as the time between the beginning of the first video-capture of a bear pair interacting together and the end of the last video-capture of the bear pair interacting together.

We assessed bear behaviour during each interaction event. We documented the following bear pair interaction behaviours: bears sniffing each other (Fig. 2A) or a rub feature (Fig. 2B), rubbing a rub feature, one bear chasing another bear (Fig. 2C), mating (Fig. 2D), swimming, drinking (Fig. 2E), foraging, walking together (Fig. 2F), and social playing (Fig. 2G). For some interaction events that occurred in water, bears both swam and played. We classified those interaction events as play behaviour.

Play behaviours were characterized by non-agonistic, physical interactions such as inhibited wrestling, swatting, boxing, or thrashing (Latour, 1981) without vocalization (Henry and Herrero, 1974; Latour, 1981; Clapham and Kitchin, 2016). Aggressive behaviour was defined as interactions characterized by agonistic actions such as unrestrained biting, wounding, and clawing or an interaction where one or both bears chuffed (Latour, 1981). Chase events (i.e., when one bear chased another bear) can be part of social play or aggressive behaviour (Henry and Herrero, 1974), depending on the bear pair and the social context. For one chase event, we video-documented the beginning of the chase event from multiple angles, which provided sufficient information to determine that an 8-year-old female aggressively chased a distantly related, independent yearling female. For all other chase events, the chase behaviour began off camera so we only observed one bear being chased by another bear. Therefore, we classified chase behaviours as chase interactions without further qualifying whether those interactions were social play or aggressive.

Fig. 2. Examples of American black bear (*Ursus americanus*) pair interaction types: A) sniffing each other, B) sniffing a rub feature, C) chasing behaviour, D) mating, E) swimming or drinking, F) walking together, and, G) playing.

2.6. Mating season

We defined the mating season as the period between late May through early August (Jonkel and Cowan, 1971; Foresman, 2012). If an interaction event occurred during May 24-August 7, then we classified it as a mating season event. We defined the peak mating season as the period between mid-June through mid-July (Jonkel and Cowan, 1971; Rogers, 1987, Eiler, 1989). If an interaction event occurred during June 13-July 18, then we classified it as a peak mating season event.

2.7. Camera station location type and year

We installed camera stations at the following types of locations: rub features, gated gravel roads, wildlife trails, water sources (creek pool, stock ponds), thickets, and forested areas. In addition, we installed one camera station near two productive apple trees in 2011 and added a second camera at that same station in 2013. We also installed one camera station at a carcass in 2015. That camera station remained in place and active, even after the carcass was gone, through September, 2016. The number of camera stations were not equal among all camera station location types and among all years. Therefore, we calculated a weighted interaction event value for each camera location type (# interaction events/# camera stations at each location type) for each year. We used ANOVA to evaluate if the weighted interaction event value differed by camera station location type. We also used ANOVA to evaluate if the number of unweighted interaction events differed by year.

2.8. Modeling approach

To evaluate most predictions about social interactions, we used multinomial logistic regression to assess the relative effects of intrinsic and extrinsic factors on bear pair interaction event type. We grouped bear pair interaction events into three types: play, chase, and other non-agonistic behaviours. Other non-agonistic behaviours included walking, foraging, drinking, sniffing a rub feature, sniffing the other bear, rubbing a rub feature, lounging, swimming, and mating. Aggressive behaviour was not included as a bear pair interaction event type because no interaction events included unrestrained biting, wounding, clawing, or chuffing.

For multinomial logistic regression models, we included only the interaction events for which we knew the identity of all interacting bears. All but two interaction events included two bears. One interaction event included three males (two subadults and one adult) and one interaction event included two adult males and one adult female. For multinomial logistic regression models, we considered the male-male-male interaction event a male-male event and we considered the male-male-female interaction event a male-female interaction event. We evaluated the effects of the following intrinsic factors on bear pair interaction type: pair sex (male-male, female-female, male-female) and pair age (adult/adult, subadult/adult, adult/yearling, etc.). We did not include bear pair relatedness as an intrinsic factor because seven interacting bears did not leave hair on rub features, so we could not determine their genetic relatedness with other bears. We evaluated the following extrinsic factors on bear pair interaction type: mating season, peak mating season, year, and camera station location type. We considered all combinations of factors (e.g., pair sex*year) and considered the intercept-only model to be the null model. We used Akaike's information criterion with an adjustment for small sample size (AIC_c; Akaike 1973) to rank models in terms of their ability to explain the data. Models with Δ AIC_c values < 2.0 were considered to have substantial support (Burnham and Anderson, 2002). We evaluated Akaike weights for each model. We estimated the probability of each interaction behaviour type using the beta estimates that were included in the top-ranked model. We estimated 95% confidence intervals around estimated probabilities using 2000 iterations and bootstrapping. We used Program R version 3.1.2 (R Core Team, 2016) for all statistical analyses.

2.9. Ethical note

This work was part of our long-term research on wild black bear behaviour and demography. All documentation of bear behaviours were based on video data collected from non-invasive trail cameras installed on a private conservation property. Most genetic identities of individuals were based on hair samples that bears left at rub trees and rub posts located in view of camera stations. To minimize our presence on the landscape, one field technician visited camera and hair stations every two or three weeks during 2011–2014 and every six weeks during 2015–2021. During 2020–2021, we expanded our research program by live-trapping and collaring black bears. Our trapping, handling, and collaring methods were approved by the Montana Fish Wildlife and Parks (MFWP) Institutional Animal Care and Use Committee (IACUC No. FWP02–2020). Our procedures were conducted under Montana Fish Wildlife and Parks Scientific Collecting Permits 2020–5-W and 2021–14-W-01. To capture bears, we used cage traps that were modified with motion-activated remote photography. We monitored cage traps constantly via remote photography. When a bear was captured, cameras sent photos in real-time via email to researchers so that bears could be handled quickly. Thus, bear confinement time in traps was minimized, which helped minimize bear stress. With bear welfare in mind, we also created cage trap doors that could be released remotely. If a previously captured bear was recaptured, we immediately remotely released that bear without immobilization. The use of cage traps over foot-hold snares also increased bear welfare by minimizing the frequency and severity of trap-related injuries. For example, trap-related injuries from bear studies that used foot-hold snares included fractures, amputations, lacerations and other injuries to tendons, muscles, joints, and nerves. Trap injuries resulting from the use of our cage traps were minimal and included only slight injuries to some bear's claws. We minimized bear pain during handling by ear tagging only one ear (instead of both ears) and we used a numbing agent prior to extracting a tooth. Bears were handled efficiently, their vital rates were monitored throughout the handling, and bears were released at the site of capture.

3. Results

During 2011–2021, we collected 35 697 1-minute videos of an estimated 115 unique black bears (66 M: 35 F: 14 Unknown gender; Table A1). Two or more individuals were observed in the video frame simultaneously in 557 (2%) videos, representing 169 events. We were able to identify both or all three interacting individuals in 136 interaction events (Fig. 3). For 24 interaction events, we could determine the identification of one interacting bear, but the other individual was not identifiable because the bear was too far from the video camera, obstructed by darkness, or part of the bear was not in view (Fig. 4). For nine interaction events, we were unable to determine the identity of both interacting individuals (Fig. 4).

Based on the 136 interaction events for which we were able to identify all interacting individuals, we documented 66 bear pairs (Table A2) made up of 40 different bears. We observed 23 male-male pairs that interacted 39 times, seven female-female pairs that interacted 10 times, and 34 male-female pairs that interacted 85 times. Also, one group of three males interacted once, and one group of two males and one female interacted once.

No male-male interaction events included aggressive or chase behaviours. Of the 40 interaction events that included 2 or 3 males, 19 included social play. Most ($n = 9$) female-female interaction events included chase behaviour. In addition, four interaction events between an adult female and an unidentified individual included chase behaviour (Fig. 4). Most male-female interaction events included other non-agonistic behaviours (Fig. 3).

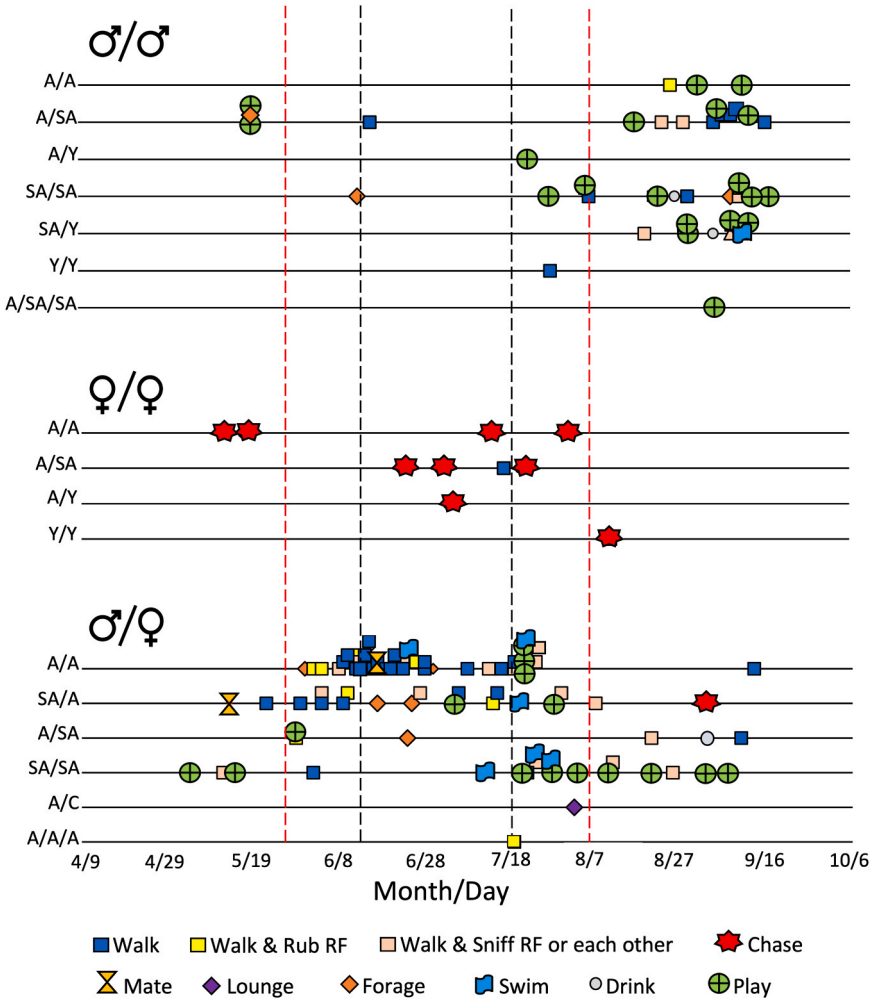

Fig. 3. Behavioural interaction events between American black bear (*Ursus americanus*) pairs or groups for which the identity of all interacting bears in each event is known, by pair sex (male-male, female-female, male-female), interaction type, and date on a conservation property in western Montana, 2011–2021. A = adult. SA = subadult. Y = yearling. C = cub. Black dotted lines indicate peak mating season. Red dotted lines indicate mating season.

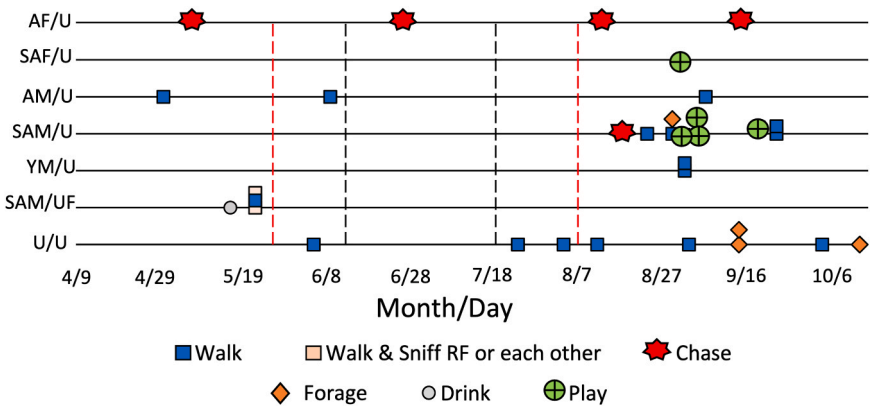

Fig. 4. Behavioural interaction events between American black bear (*Ursus americanus*) pairs or groups for which the identity of at least one interacting bear in each event is unknown, by pair sex, interaction type, and date on a conservation property in western Montana, 2011–2021. A = adult. SA = subadult. Y = yearling. M = male. F = female. Black dotted lines indicate peak mating season. Red dotted lines indicate mating season.

Overall, the interaction event duration was the longest for male-female pairs (Fig. A1). Seventeen male-female interaction events lasted > 40 min, and 12 of those male-female interaction events lasted > 500 min. Eight male-male interaction events lasted > 40 min, and six male-male interaction events lasted > 500 min. All female-female interaction events lasted between 1 and 3 min.

3.1. Camera station location type and year

The weighted interaction event value did not differ by camera station

location type (P = 0.46). The unweighted value of interaction events differed by year (P = 0.007). The number of interaction events was highest during 2016, 2018, and 2021 and lowest during 2011, 2012, and 2017 (Table A1).

3.2. Modeling approach

Only one model of bear pair interaction event type had a Δ AIC_c < 2.00. The top-ranked model included pair sex and peak mating season (Table 1). The AIC_c weight for the top-ranked model was 0.98, compared to 0.02 for the second-ranked model. The null model ranked very low, as did models with the effects of year, mating season, and camera station location type.

3.2.1. Male-male interactions

Most male-male interactions occurred during the non-mating season (Fig. 3). Seven of 40 male-male interaction events occurred during the mating season, and only two occurred during the peak mating season. During the non-peak mating season, males equally engaged in play and other non-agonistic behaviours (Table 2). During the non-peak mating season, the probability that male-male interaction events included chase behaviour (π = 0.00; Table 2) was significantly lower than the probability that male-male interaction events involved play (π = 0.48; 95% CI: 0.35, 0.61) or other non-agonistic behaviour (π = 0.52; 95% CI: 0.39, 0.65). We observed only two male-male interaction events during the peak mating season, so the sample size was too small to provide reliable probability estimates. However, both male-male interaction events during the peak mating season included other non-agonistic behaviours–One male-male pair foraged together and the other male-male pair walked together (Fig. 3).

3.2.2. Female-female interactions

Seven of 10 female-female interaction events occurred during the mating season, and five occurred during the peak mating season (Fig. 3). During the peak mating season, the probability that female-female pairs engaged in chase behaviour (π = 0.80; 95% CI: 0.37, 1.00; Table 2) was higher than the probability that female-female pairs engaged in play behaviour (π = 0.00; 95% CI: 0.00, 0.00). During the non-peak mating season, the probability that female-female pairs engaged in chase behaviour (π = 1.00; 95% CI: 0.94, 1.00) was higher than the probability that female-female pairs engaged in other non-agonistic (π = 0.00; 95% CI: 0.00, 0.04) or play behaviours (π = 0.00; 95% CI: 0.00, 0.04). The probablity that female-female pairs engaged in chase behaviour was significantly higher than the probablity that male-male pairs engaged in chase behaviour during any time (Table 2).

For eight of nine female-female interaction events that included chase behaviour (Fig. 3), and for all four interaction events between a female and an unidentified bear that included chase behaviour (Fig. 4), the chaser was an adult female. Three female-female interaction events that included chase behaviour occurred when the adult female chaser had a cub or dependent yearling at heel (Table 3).

Table 1
Model rankings of bear pair interaction type (Chase, Play, Other non-agonistic) for American black bears (*Ursus americanus*) on a conservation property in western Montana, 2011–2021. Only the top 4 models and the Null model are presented. Peak MS = Peak Mating Season. ω = AIC_c model weight. k = number of estimable parameters. Deviance = measure of model fit.

Model	AIC_c	Δ AIC_c	ω	Model Likelihood	*k*	Deviance
Pair sex + Peak MS	153.59	0.00	0.98	1.00	3	133.41
Pair sex * Peak MS	161.49	7.90	0.02	0.02	4	133.18
Pair sex	166.55	12.96	0.00	0.00	2	150.46
Pair sex + Peak MS + Pair age	170.27	16.68	0.00	0.00	4	121.96
Null	222.42	68.83	0.00	0.00	1	218.39

3.2.3. Male-female interactions

Seventy of 86 male-female interaction events occurred during the mating season, and 37 occurred during the peak mating season (Fig. 3). Male-female pairs engaged in other non-agonistic behaviours significantly more than they engaged in chase or play behaviours during both the peak mating season and the non-peak mating season (Table 2). Adult females generally did not interact with males during years when females had COY (Table 4). There were three exceptions: 1) adult female F7 chased subadult male M30 in 2018 when F7 had 2 COY, 2) adult female F6 was followed by adult male M16 on July 19, 2019 and July 21, 2019, the same year that F6 had one COY, who disappeared on July 21, 2019, and, 3) adult female F2 interacted with two adult males during 2016 when F2 had one COY, which died due to cub abandonment during 2016 (video documentation of cub abandonment provided in Reynolds-Hogland et al., 2022a).

Fifteen male-female pairs (44%) interacted multiple times within a single year, while 12 pairs (35%) interacted across multiple years (Table A3). Some males interacted with specific females over multiple years and sired offspring with them. For example, male M2 interacted with four females over time and fathered nine offspring with three of those females (Table A3). Additionally, certain adult females interacted with multiple adult males during the same mating season (Table A3).

Nine male-male pairs interacted together more than once within a single year, but only two male-male pairs interacted across multiple years. Only one female-female pair interacted more than once during a single year, and only one female-female pair interacted multiple times across multiple years. Most male-male pairs (93%) were genetically unrelated, and all female-female pairs were genetically related (Fig. A2).

4. Discussion

Our data challenged the assumption that independent-aged bears do not interact with conspecifics outside of the mating season or when large, concentrated feeding sites are absent. We documented 92 bear pair interaction events (38 male-male; 5 female-female; 49 male-female) outside of the peak mating season and 52 black bear pair interaction events (33 male-male; 3 female-female; 16 male-female) outside of the mating season (Fig. 3), even though large, concentrated feeding sites did not exist on our study site. Moreover, all black bear interaction events that we documented occurred in front of camera stations that were not food-baited.

4.1. Male-male interactions

We documented no aggressive behaviours between male-male pairs during our study. Instead, males drank, foraged, swam, calmly investigated rub features and each other, engaged in social play, and walked together. Only two male-male interaction events occurred during the peak mating season, evidence that chemical signaling was likely a primary communication mechanism for males during the mating season on our study site. Ursids have specialized glands that play important roles in chemical communication (Morehouse et al., 2021). For instance, brown bear anal gland secretions contain chemical signals related to sex (Jojola, 2011; Rosell et al., 2011). Both polar and brown bears possess pedal scent glands, which contain compounds likely involved in communication within their respective species (Owen et al., 2014; Sergiel et al., 2017). Female giant panda (*Ailuropoda melanoleuca*) secretions convey information about age class, sex, and individual identity (Liu et al., 2005; Hagey et al., 2003). Considering these findings, it is reasonable to conclude that the American black bear pedal and anal glands also communicate information about age, sex, and individual identity.

Chemical signals communicate information at a low cost (Allen et al., 2016), which may be most important during the mating season for male

Table 2
Probability estimates for bear pair interaction types (Chase, Play, Other non-agonistic) based on the top-ranked model. π = estimated probability. n = number of interacting pairs. Number of interaction events are in parentheses. LCI = Lower 95% Confidence interval. UCI = Upper 95% Confidence interval.

Bear Pair	n	π Chase	L CI	U CI	π Play	L CI	U CI	π Other	LCI	UCI
M/M Peak MS	2 (2)	–	–	–	–	–	–	–	–	–
M/M Non-peak MS	25 (38)	0.00	0.00	0.00	0.48	0.35	0.61	0.52	0.39	0.65
F/F Peak MS	4 (5)	0.80	0.37	1.00	0.00	0.00	0.00	0.20	0.00	0.63
F/F Non-peak MS	5 (5)	1.00	0.94	1.00	0.00	0.00	0.04	0.00	0.00	0.04
M/F Peak MS	16 (33)	0.00	0.00	0.00	0.03	0.00	0.05	0.97	0.94	1.00
M/F Non-peak MS	29 (53)	0.02	0.00	0.05	0.29	0.18	0.40	0.69	0.58	0.80

Table 3
Interaction events between female-female American black bear (*Ursus americanus*) pairs, with information about whether event occurred during the mating season (MS), the relationship between the two interacting bears, the behaviour that occurred between the two interacting bears, which bear chased the other, and whether interacting females had dependent young at heel during the interaction event, on a conservation property in western Montana, 2011–2021. M-OFF = Mother-offspring relationship. COY = cub-of-the-year. Sibs = Siblings. Y = dependent yearling.

	Age		Age						Dependent
Bear 1	Bear 1	Bear 2	Bear 2	Date	MS	Relationship	Behaviour	Chaser	young at heel
F4	12	F6	7	5/13/2018	N	M-OFF	Chase	F4	F4 had Y
F11	7	F6	10	5/17/2021	N	Cousins	Chase	F11	F6 had Y
F2	6	F6	5	7/13/2016	Y	Cousins	Chase	F2	F2 had COY
F2	8	F16	1	7/4/2018	Y	Distant	Chase	F2	No
F2	8	F6	7	7/31/2018	Y	Cousins	Chase	F2	No
F6	5	F11	2	6/23/2016	Y	Cousins	Chase	F6	No
F6	5	F11	2	7/2/2016	Y	Cousins	Chase	F6	No
F6	9	F16	3	7/21/2020	Y	M-OFF	Chase	F6	F6 had COY
F22	1	F20	1	8/11/2020	N	Sibs	Chase	F22	No
F1	11	F2	3	7/17/2013	Y	M-OFF	Walk	NA	No

Table 4
Years during which female American black bears (*Ursus americanus*) had one or more cubs-of-the-year (COY) and years during which we video-documented females interacting with males on a conservation property in western Montana, 2011–2021.

Female	Years female had COY	Years female was documented interacting with males
F1	2010, 2014	2011, 2013, 2015, 2016
F3	2010, 2012	NA
F4	2011, 2013, 2015, 2017, 2019	2012, 2014, 2016, 2018, 2020, 2021
F7	2016, **2018** * , 2020	2014, **2018** * , 2021
F6	2017, **2019** * *, 2020	2013, 2014, 2016, 2018, **2019** * *, 2021
F11	2019	2016, 2017, 2018, 2021
F9	2019, 2021	2018, 2020
F15	2021	2018, 2019, 2020
F2	2014, **2016** * ** , 2017, 2019, 2021	2012, 2013, 2015, **2016** * ** , 2018, 2020

*Adult female chased male, both COY survived first year
* *Adult female lost COY during COY's first year
* **Adult female with COY through July 18, 2016, then adult female abandoned COY

black bears. Female black bears exhibit asynchronous estrus (Erickson et al., 1964; Garshelis and Hellgren, 1994), so males roam widely during the mating season to find estrus females (Costello et al., 2009; Rogers, 1987). Thus, the mating season becomes energetically demanding for males, where time is of the essence. Engaging in aggressive encounters with other males during this period consumes valuable energy and time that could be used for finding and mating with receptive females. Scent marking allows for communication of dominance and competitive ability among cohorts (Clapham et al., 2012, 2014) without the need for direct, sometimes costly interactions (Mills et al., 1980).

In grizzly and black bear populations near concentrated food sources, male ursids vocally displayed and aggressively fought with conspecifics (Hornocker, 1962; Herrero, 1983), and cannibalism has been reported among male ursids (Tietje, . et al., 1986; Davis and Harestad, 1996; Garrison et al., 2007). Also, evidence of male aggression was observed in live-captured male black bears (Beecham, 1980; LeCount, 1982; Garshelis and Hellgren, 1994; Costello et al., 2009). We did not document aggressive behaviours or cannibalism among males, but we did observe wounds on two adult males and two subadult males that we live-captured during 2020–2021. Also, 10 adult and seven subadult males had facial scars visible on video, which may have resulted from aggressive behaviour by conspecifics. It is also possible that females inflicted some scars on males during mating, resource holding, or when females with COY defended dependent young. Our camera network did not cover the entire study area, so aggressive interactions between male-male pairs might have occurred outside of the camera network that we did not detect.

Outside the peak mating season, male-male pairs were equally likely to play or engage in other non-agonistic behaviours. Our findings regarding the timing of play behaviour corroborate observational research that documented social play outside the mating season by male polar bears (Latour, 1981) and male brown bears (Clapham and Kitchin, 2016). Studies reported ursid play behaviour occurs when bears congregate near abundant food sources. For example, brown bears played together near tidal marshes (Clapham and Kitchin, 2016) and near salmon streams during runs (Egbert and Stokes, 1976; Fagen and Fagen, 2009). Also, non-littermate black bears played together at trash dumps (Rogers, 1987). Here and in Latour (1981), male bears played with conspecifics when abundant, concentrated feeding sites were absent. We also documented male-male pairs walking, investigating rub features, and foraging together during the non-peak mating season. This finding supports work by LeCount (1980), who documented seven occasions of male-male pairs traveling together. Noyce and Garshelis (2014) also reported male black bears followed each other and concluded that their chemical signaling likely transmitted knowledge of foraging areas.

4.2. Female-female interactions

Contrary to our prediction, female-female interactions were less frequent than male-male interactions. We recorded only 10 female-female interactions over 11 years, compared to 40 male-male

interactions over the same time period. This may be partially explained by the sex ratio of our video-capture data, which was skewed toward males. Black bear studies similarly reported a male-biased sex ratio of individuals that were physically captured (Hellgren and Vaughan, 1989; Kasworm and Thier, 1994; Sargeant and Ruff, 2001; Koehler and Pierce, 2005), likely owing to differences in space use between genders (Jonkel and Cowan, 1971). The paucity of female-female interaction events that we observed may also indicate that independent-aged females on our study site primarily relied on chemical signaling to communicate with conspecifics. Over half of all females video-captured on our camera network rubbed or investigated rub features (Reynolds-Hogland et al., 2022b), indicating both males and females used chemical communication.

Nine of 10 female-female interaction events, and interactions involving adult females and unidentified bears (n = 4; Fig. 3), involved chase behaviour. Except for one instance involving yearling siblings, all female chasers were adults. In one event, an 8-year-old female (F2) aggressively chased a distantly related, independent yearling (F16). The reproductive status of the female chasers and the timing of chase events offer insights into potential motives. During three chase events, the adult female chaser had a cub or dependent yearling (Table 3), suggesting protection of their young or defense of resources and space. Four of the remaining five female-female chase events occurred during the mating season when adult females may have been locating and mating with males.

Competition among males is well-documented in polygynous mammals (Bergeron et al., 2008; Spillmann et al., 2016), including ursids (Derocher et al., 2010). However, competition among females can also be important when older, dominant females defend resources such as food, space, and mating opportunities against younger, subordinate females (Mitani, 2009). Here, all female chasers were adults, and four had visible scars on their faces. Ancillary video data from our broader black bear research program documented extremely aggressive behaviour by an adult female toward an unrelated subadult female in a cage trap in 2021. The adult female, who was outside the cage trap, charged the female inside, loudly vocalized for four seconds, stomped on the top of the cage trap, and marked nearby bushes and trees (video available: https://mpgcloud.egnyte.com/dl/1I5UfidCiD). If the captured female had been able to flee, she would likely have fled when the aggressive female approached. Although the artificial setting may have influenced this specific encounter, our combined data suggest the occurrence of female resource defense. These findings support research on territorial behaviour in collared female black bears in Arkansas (Clark, 1991) and Alberta (Young and Ruff, 1982). In contrast, studies in Massachusetts, North Carolina, and Ontario did not observe territoriality among collared female black bears (Elowe and Dodge, 1989; Powell et al., 1997; Schenk et al., 1998).

The chase behaviours by female-female pairs suggest territoriality, but some chases could be part of social play. However, if female chase behaviour was playful, we expected to observe other social play behaviours (e.g., playful swats, stances, and wrestling) among female-female pairs. We observed adult and subadult females engage in these social play behaviours with adult and subadult males during 15 interaction events (Fig. 3). However, we confirmed no social play behaviours between adult and/or subadult female-female pairs.

We predicted female-female pairs would engage in non-agonistic behaviours, given that females in black bear populations often exhibit kin-related spatial structure (Darwin, 1859; Haldane, 1932; Støen et al., 2005). Yet, adult females chased their daughters and cousins, suggesting density-dependent mechanisms at play. As a wildlife population increases, finite resources become less available and intraspecific competition increases (Smith, 1992; Lebreton and Gimenez, 2013). The black bear population on our study site was increasing throughout the study (Reynolds-Hogland et al., 2022b). In 2011, we video-captured 11 individual black bears, three were adult females. By 2013, we video-captured 20 individuals, three were adult females. At the end of our study in 2021, we video-captured 41 individuals, eight were adult females. All female-female interaction events that included chase behaviours occurred during 2016–2021, when the number of individual bears and the number of adult females video-captured was ≥ 25 and $\geq$ five, respectively. This suggests increased competition as resources became scarcer.

4.3. Male-female interactions

Unsurprisingly, most male-female interaction events occurred during the mating season. Several male-female interaction events lasted over multiple consecutive days during the mating season, indicating possible female holding/guarding by males (Emlen and Oring, 1977). Also, video cameras aimed at cage traps during the mating season during 2020–2021 documented five cases where an adult male visited and stayed near traps in which an adult female was captured (P.W. Ramsey, *unpublished data*). Mate guarding by males has been reported for birds (Møller and Birkhead, 1991; Krokene et al., 1996), reptiles (Ancona et al., 2010), fish (Alonzo and Warner, 2000; Yokoi et al., 2016), insects (Bennett et al., 2012), primates (Van Belle et al., 2009; Girard-Buttoz et al., 2014; Setchell et al., 2016; Rebout et al., 2017), and mongoose (*Mungus mungo*; Nichols et al., 2010). Less is known about mate guarding by male American black bears, however grizzly bear (Craighead et al., 1969; Herrero and Hamer, 1977; Stenhouse et al., 2005) and polar bear (Wiig et al., 1992; Derocher et al., 2010; Stirling et al., 2016) studies showed male-female pair bonds during the mating season lasted from a few hours up to weeks. Also, male polar bears have been observed herding estrus females (Ramsay and Stirling, 1986; Wiig et al., 1992; Derocher et al., 2010; Stirling et al., 2016) and fighting with or chasing away males who attempted to compete for pair-bonded females (Stirling et al., 2016).

We documented 15 male-female pairs interacting multiple times within a single year (Table A3). Stenhouse et al. (2005) similarly reported 30 collared male-female brown bear pairs associated within 500 m more than once during a single year. It may be that males assess the reproductive status of females during multiple male-female interactions.

Alternatively, or in addition, females may assess male quality during multiple male-female interactions. Female mate choice is widely recognized in birds (Chaine and Lyon, 2008; Wells et al., 2016), primates (Robinson, 1982; Silk and Boyd, 1983; Janson, 1984), and other mammals (Isaac, 2005; LaDue et al., 2022), but it is poorly understood in ursids. On our study site, we documented adult females interacting with multiple males during a single mating season, and those females subsequently bore offspring sired by only one of the males with whom they interacted. For example, we documented female F4 interacting with males M2 and M3 during the 2012 and 2016 mating seasons. Female F4 bore two cubs in 2013, both sired by M2. Female F4 also bore two cubs in 2017, one was sired by M2 the other by M6. We could not confirm whether female F4 was in estrus when we documented her interactions with M2 and M3, but she interacted with both males within one day in 2012 and two days in 2016.

Similarly, we documented female F2 interacting with three males (M2, M6, and M17) during the 2015 mating season. Female F2 bore a cub in 2016 sired by male M2. That cub was abandoned during the summer of 2016 and died. We documented female F2 again interacting with the same three males (M2, M6, and M17) during the mating season in 2016, and F2 subsequently bore three cubs in 2017, at least one of which was genetically confirmed to be sired by M2. Adult female black bears may interact with multiple males before and during the relatively extended mating season but only mate with their choice of suitor/s during each female's limited estrus period.

As expected, adult females with COY generally avoided interactions with males. Out of 86 male-female interaction events, only five involved an adult female with COY. Two of these events occurred in the 2019 mating season, where male M16 walked behind female F6 who had one

COY, which subsequently disappeared.

By analyzing the chronological sequence of video captures, we observed that F6 and her COY were seen together last on July 12th. On July 19th and 21st, we documented M16 walking behind F6. Visual observation suggested that F6 was in estrus on July 21st when M16 followed her. At 16:50 on the same day, we captured the last video of F6′s COY alone. Female F6 was documented alone on 34 occasions between July 23rd and November 29th, 2019. In 2020, F6 gave birth to one cub, genetically confirmed to be fathered by M16.

The disappearance of F6′s COY could be attributed to sexually selected infanticide (SSI), where males kill offspring to increase their breeding opportunities (Hrdy, 1979; Bellemain et al., 2006). We observed F6 in apparent estrus on July 21, 2019, a few hours before the last sighting of her COY. This suggests that F6′s COY was alive when M16 was following F16 during estrus. While SSI appears to involve the killing of offspring to induce estrus in females (Davoli et al., 2018), LeCount (1983) documented cases of female black bears mating while still caring for COYs. These females gave birth to new litters the following year without yearlings present. Therefore, it is possible that F6 was in estrus on July 21, 2019, while having a COY, and it is plausible that M16 killed F6′s COY as part of the mating process in 2019.

Three criteria must be met for infanticide to be considered sexually selected: (1) the killing of offspring shortens the interbirth period, (2) the infanticidal male has a higher probability of mating with the dead infant's mother, and, ultimately siring her subsequent offspring, and, (3) the infanticidal male is not the father of the infant/s he kills (Ebensperger, 1998; Bellemain et al., 2006). The interbirth period for American black bears is generally two years (Powell et al., 1997), which was shortened for F6 in 2019 after we documented her interacting with M16 in the mating season. Also, M16 sired F6′s offspring in 2020. Thus, the first two criteria of SSI were met for at least this case. We did not collect genetic data from F6′s COY in 2019, so we do not know his paternity to evaluate criterion #3. However, older (> 7 years old; Costello et al., 2009) and larger (Kovach and Powell, 2003) male black bears sire the most offspring and M16 was a young male (< 7 years old) in 2018 when F6 mated to produce her COY in 2019. Thus, M16 likely did not sire cubs in 2018 and, therefore, would have no reason to not kill cubs in 2019.

The natural history of ursids make them likely candidates for SSI (Packer and Pusey, 1984). Yet, we found only one study that implied SSI in a black bear population (LeCount, 1987) and one study (three papers) that reported probable SSI in a brown bear population (Bellemain et al., 2006; Swenson et al., 1997; Swenson et al., 2001). Regarding the latter, authors described four cases of likely SSI in a brown bear population in Sweden, based on methods similar to those that we used. They used field observations of male-female-COY interactions in the mating season and paternity of offspring sired the following year. Black bear studies have reported infanticide by adult males (Hellgren and Vaughan, 1989; Davis and Harestad, 1996; Garrison et al., 2007), but those authors indicated cub killings were likely motivated by nutritional benefit or the motivation was not specified.

Regarding the disappearance of F6′s COY, it is also possible that F6 abandoned her COY sometime in summer-fall 2019, and that F6′s COY died due to reasons unrelated to M16. Theoretically, cub abandonment can be a reproductive strategy for females, particularly for females with only one COY that have a good chance of producing multiple cubs in their next litter (Tait, 1980). Also, cub abandonment may benefit mothers who are in relatively poor condition when a mother cannot provide nutrition to ensure COY survival. We previously video-documented one case of cub abandonment on our study site–Bear F2 abandoned her 7-month-old COY during the 2016 mating season (Reynolds-Hogland et al., 2022a). Subsequently, F2 bore three cubs in 2017.

Notably, the documentation of F2′s abandoned COY in 2016 also provided video data of an adult male interacting with an unrelated COY in the mating season. Male M6 approached the abandoned COY in view of a video camera station. Male M6 was not the genetic father of this COY, yet M6 did not act aggressively toward the COY. Male M6 looked at the COY and then left the area. The COY later died alone in view of a video camera station. Thus, at least one adult male on our study site did not kill a COY when presented with the opportunity. This finding supports black bear research that reported no evidence of infanticide (Elowe and Dodge, 1989).

If infanticide occurred on our study site, it was rare. Estimated cub survival on our study site from 2013 to 2019 was 86% (Reynolds-Hogland et al., 2022b), indicating most cubs survived their first year. The limited occurrence of infanticide we found may be partially explained by possible female counterstrategies to infanticide, which include: (1) maternal aggression, (2) avoidance of infanticidal males, (3) promiscuity to confuse paternity, and (4) territoriality to keep potential infanticidal males away (Ebensperger et al., 1998). On our study site, we documented one adult female (F7) chasing a subadult male (M30) when F7 had two COYs. This behavioural interaction appeared to be maternal aggression. Notably, both of F7′s COYs survived their first year. Also, most females with COY on our study site were not observed interacting with males, indicating females with COY may have avoided males. Those same females did interact with males in years when females did not have COY. Regarding counterstrategy # 3, we genetically confirmed multiple paternity for one litter on our study site (Reynolds-Hogland et al., 2022a), which supported findings of multiple paternity in other black bear populations (Kovach and Powell, 2003; Costello et al., 2009; Ombrello et al., 2016).

In summary, ursids are generally considered solitary. However, we documented behavioural interactions among wild, independent-aged black bears outside of the mating season and in the absence of large, concentrated feeding sites. Social interaction type varied by sex and season, underscoring the complexity of ursid sociality. Our findings provided insights into evolutionary processes such as resource defense, female mate choice, counterstrategies to SSI, and resource holding. Similar to Stenhouse et al. (2005), our findings have implications for analyses of habitat selection, which assume that space used by ursids is habitat-based and individual bears used space independently.

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CRediT authorship contribution statement

Melissa J. Reynolds-Hogland: Conceptualization (equal), Data curation (equal), Formal analysis (equal), Investigation (equal), Methodology (equal), Project administration (equal), Software (equal), Supervision (equal), Validation (lead), Visualization (equal), Writing – original draft (lead), Writing – review & editing (equal). **Carly Brooks:** Conceptualization (equal), Data curation (equal), Formal analysis (equal), Investigation (equal), Methodology (equal), Validation (equal), Visualization (equal), Writing – original draft (supporting), Writing – review & editing (equal). **Alan B. Ramsey:** Conceptualization (equal), Data curation (equal), Funding acquisition (supporting), Investigation (equal), Methodology (equal), Project administration (lead), Resources (supporting), Supervision (lead), Validation (equal), Visualization (equal), Writing – original draft (supporting), Writing – review & editing (equal). **John. S. Hogland:** Conceptualization (equal), Data curation (supporting), Formal analysis (equal), Investigation (equal), Methodology (equal), Software (equal), Validation (equal), Writing – original draft (supporting), Writing – review & editing (equal). **Kristine L. Pilgrim:** Conceptualization (equal), Data curation (supporting), Formal analysis (equal), Investigation (equal), Methodology (equal), Software (equal), Validation (equal), Writing – original draft (supporting), Writing – review & editing (equal). **Cory Engkjer:** Conceptualization (supporting), Data curation (equal), Formal analysis (equal), Investigation (equal), Methodology (equal), Software (equal), Validation (equal), Writing – original draft (supporting), Writing – review & editing (equal).

Philip W. Ramsey: Conceptualization (equal), Funding acquisition (lead), Investigation (equal), Project administration (lead), Resources (lead), Supervision (lead), Validation (equal), Visualization (equal), Writing – original draft (supporting), Writing – review & editing (equal).

Declaration of Competing Interest

The authors declare no competing interests.

Data availability

Data are provided as supporting material.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2023.104972.

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