

Cannibalism in bears

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Abstract: Bears are the largest terrestrial carnivores, and most bear species can be characterized as opportunistic omnivores. An infrequent foraging tactic for bears is cannibalism, where a bear consumes a conspecific individual, either through scavenging or following intraspecific predation. Although several reports of cannibalism events are known, no attempt has been made so far to gather the available information to analyze for general patterns. We therefore performed a systematic literature review to understand patterns of cannibalism in bears. We documented 39 studies detailing 198 cannibalism events. We only found evidence of cannibalism in 4 of the 8 bear species, with more events reported for polar bears (*Ursus maritimus*; $n = 107$, 54.0%) than for all other species combined. Cannibalism was most frequently associated with infanticide ($n = 66$, 33.3%) and conspecific strife ($n = 30$, 15.2%), both of which were more frequent among males than females. The most common apparent reason for cannibalism among predators is to increase fitness (i.e., eating a conspecific increases nutrition, whereas killing reduces competition for resources), but is also often linked to sexually selected infanticide in bears. Cannibalism most often appears to be an opportunistic consumption of an available carcass and not directly connected with the primary cause of death. As such, cannibalism in bears may be more casual and opportunistic than a behavior that evolved as a life history strategy.

Key words: bear, behavior, cannibalism, foraging ecology, infanticide, mortality, nutritional ecology, predation, scavenging, sexually selected infanticide

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Cannibalism, where an animal consumes a conspecific individual, is found throughout the animal kingdom (Allen et al. 2020, Gómez et al. 2021). It is primarily believed to increase fitness (i.e., consuming provides nutrition, whereas killing reduces immediate and future competition for food and other resources; Gómez et al. 2021). However, consumption of conspecifics can come with a cost in a form of parasite transmission, which is the reason that carnivores generally avoid consuming the carcasses of other carnivores, especially their own species (Moleón et al. 2017). There can be many reasons and motivations for instances of cannibalism, and these can vary by species and season (Allen et al. 2020, Gómez et al. 2021). It is therefore important to understand the different types of cannibalism and why they occur among different species.

Cannibalism tends to be associated with 1 of 5 forms (Table 1; Allen et al. 2020). The first distinction is to separate the consumption of a conspecific that was killed by the individual consuming it (predation) from consumption of a conspecific that died of another cause (scavenging). For cannibalism resulting from predation, we distinguish among several types that vary in respect to the age and relatedness of the consumer and victim: conspecific strife (killing of an adult), siblicide (killing of a sibling), filicide (killing of one's dependent young), and (nonfamilial) infanticide (full definitions provided in Table 1). Conspecific strife is the only type of predation-caused cannibalism involving adults as a victim but is typically less common than other types of cannibalism, potentially as a result of the difficulty and risks associated with killing a competitor that is similar in size and strength (Gómez et al. 2021). In most predators, intraspecific predation is more commonly focused on dependent young, which are easier to kill than adults. Killing of nonrelated young (i.e., nonfamilial infanticide) is typically one of the most common forms of cannibalism, allowing an individual to both feed on a young animal as a resource and also reduce future competition for resources for the individual and their progeny (Hrdy 1979). In some groups, such as raptors, siblicide (the killing and eating of siblings) and filicide (the killing and eating of dependent young by

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Table 1. Categorization and definitions for types of cannibalism, with respect to the mortality cause.

Type of cannibalism	Source of the carcass	Definition
Scavenging	Scavenging	Consumption of a conspecific that died of other causes (i.e., not killed by the individual consuming it).
Conspecific strife	Predation	The killing and eating of an adult conspecific.
Siblicide	Predation	The killing and eating of sibling(s), usually while dependent young.
Filicide	Predation	The killing and eating of dependent young by parents.
(Nonfamilial) infanticide	Predation	The killing and eating of unrelated dependent young by conspecifics.

parents) can be common and often revolves around brood success, with the weaker individuals being killed and fed upon to increase the survival of siblings, especially in years with lower food availability (Bechard 1983, Allen et al. 2020).

Cannibalism has been observed many times in bears, but it is an infrequent foraging tactic and the reasons for cannibalism are unclear. Most bear species are opportunistic omnivores that forage on a variety of food sources, including carrion (Mattson 1997, Narita et al. 2006, Bojarska and Selva 2012). Bears are also known to be one of the most effective terrestrial scavengers (Krofel et al. 2012, Inagaki et al. 2020) and therefore it is not surprising that they also consume dead conspecifics found while foraging, despite the risk of disease or parasite transmission. Beside scavenging, some bear species, most notably the polar bear (*Ursus maritimus*), are also known as effective predators capable of subduing large prey (Derocher et al. 2000, 2002; Ordiz et al. 2020). These characteristics also give them the ability to kill conspecifics, especially when they are smaller than the attacker. However, not all intraspecific killing results in consumption of the victim, suggesting that motivations for killing are not always connected with obtaining of food. Among the most commonly cited reasons for intraspecific killing among bears is sexually selected infanticide, where male bears kill (and sometimes consume) cubs that are not their own in order to increase mating opportunities (Hrdy 1979, Swenson et al. 1997, Bellemain et al. 2006). Sexually selected infanticide is a frequent behavior in bears that has led to behavioral adaptations and often has direct effects on populations (Swenson et al. 1997, Miller et al. 2003, Swenson 2003, Steyaert et al. 2013).

To understand the frequency and patterns of cannibalism by bears, we performed a systematic review of peer-reviewed scientific literature. Our aims were to document instances of cannibalism in bears and search for patterns, including the prevalence of different types of cannibalism and their frequency among different species and regions.

We also identified the most pressing knowledge gaps and provide guidelines on how to collect data when a potential intraspecific predation event or cannibalism is detected in the field.

Literature review

On 10 March 2021, we performed a systematic literature search to determine the frequency of documentation of cannibalism among bears. We searched Web of Science for the terms “cannibal*”, “infanticide”, and “mortality” matched with the search terms “*Ursus*” and “bear” in both English and Japanese. We then read each entry and removed duplicate reports and mismatched publications, as well as those not from peer-reviewed journals and studies involving captive animals. We augmented our systematic review of the literature using snowball sampling (searching the references of papers we reviewed for additional documentations). In summarizing the results of our review, we considered either studies (entire publications) or events (individual reports of cannibalism within publications).

Results

We documented 39 studies detailing 198 cannibalism events. Cannibalism was most frequently associated with infanticide ($n = 66$, 33.3%), conspecific strife ($n = 30$, 15.2%), and scavenging ($n = 26$, 13.1%; Table 2). Events of filicide ($n = 8$, 4.0%) were less frequently associated with cannibalism and we did not record any publications or events that reported siblicide (Table 2). There were also 68 events of cannibalism, comprising 34.3% of all events, where it was not possible to determine the type (labeled “Undetermined*” in Table 2 and Fig. 1b), 64 of which came from scat studies where it was impossible to determine the origin of the bear remains found in the scat.

Reports included cannibalism in 4 of the 8 bear species, including polar bear ($n_{\text{studies}} = 15$, $n_{\text{events}} = 107$, 54.0%),

Table 2. A literature review of 5 types of cannibalism by bears. The review includes bear species, location, number and type of cannibalism, sex of cannibals, and the study.

Species	Location	Cannibalism events	Type of cannibalism	Sex of cannibal	Study
American black bear	AB, Canada	2	Conspecific strife	Male	Tietje et al. 1986
American black bear	BC, Canada	3	Conspecific strife	Male	Davis and Harestad 1996
American black bear	FL, USA	1	Conspecific strife	Female with cubs	Garrison et al. 2007
American black bear	FL, USA	2	Conspecific strife	Male	Garrison et al. 2007
Asiatic black bear	Japan	1	Conspecific strife	Female	Allen et al. 2021
Asiatic black bear	Russia Far East	1	Conspecific strife	Male	Kolchin 2019
Brown bear	AK, USA	1	Conspecific strife	Male	Dean et al. 1986
Brown bear	AK, USA	1	Conspecific strife	Female	Hessing and Aummiler 1994
Brown bear	Cantabrian Mountains, Spain	1	Conspecific strife	Male	Ballesteros et al. 2021
Brown bear	Greece	1	Conspecific strife	Male	Karamanlidis et al. 2015
Brown bear	Kodiak, AK, USA	1	Conspecific strife	Female	Troyer and Hensel 1962
Brown bear	Scandinavia	2, 1	Conspecific strife	Male, female	Swenson et al. 2001
Brown bear	Trentino, Italy	1	Conspecific strife	Male	Davoli et al. 2018
Polar bear	AK, USA	2	Conspecific strife	Male	Amstrup et al. 2006
Polar bear	Beaufort Sea	1	Conspecific strife	Male	Stirling et al. 2008
Polar bear	MB, Canada	1	Conspecific strife	Male	Jonkel 1970
Polar bear	NT, Canada	1, 1	Conspecific strife	Male, unknown	Taylor et al. 1985
Polar bear	Novaya Zemlya, Russia	2	Conspecific strife	Male	Ivanov et al. 2020
Polar bear	Southampton Island, NU, Canada	1	Conspecific strife	Male	Lunn and Stenhouse 1985
Polar bear	Svalbard, Norway	2	Conspecific strife	Male	Stirling and Ross 2011
American black bear	MA, USA	2	Filicide	Female	Elowe and Dodge 1989
Polar bear	Svalbard, Norway	3	Filicide	Female	Taylor et al. 1985
Polar bear	Wrangel Island, Russia	1	Filicide	Female	Belikov and Kuprijanov 1977
Polar bear	Wrangel Island, Russia	2	Filicide	Female	Uspenski and Kistchinski 1972
American black bear	AZ, USA	3	Infanticide	Male	LeCount 1987
American black bear	BC, Canada	3	Infanticide	Male	Davis and Harestad 1996
American black bear	PA, USA	1	Infanticide	Unknown	Alt and Gruttadauria 1984
Brown bear	AK, USA	1	Infanticide	Male	Dean et al. 1986
Brown bear	AK, USA	2, 1, 1	Infanticide	Female, male, unknown	Hessing and Aummiler 1994
Brown bear	AK, USA	2	Infanticide	Male	Olson 1993
Brown bear	Cantabrian Mountains, Spain	6	Infanticide	Male	Ballesteros et al. 2021
Brown bear	Kodiak, AK, USA	2, 1	Infanticide	Male, unknown	Troyer and Hensel 1962
Brown bear	Sweden	2	Infanticide	Male	Bellemain et al. 2005
Brown bear	Trentino, Italy	1	Infanticide	Male	Davoli et al. 2018
Brown bear	WY, USA	1	Infanticide	Male	Mattson et al. 1992
Polar bear	AK, USA	1	Infanticide	Male	Amstrup et al. 2006
Polar bear	Churchill, MB, Canada	1	Infanticide	Male	Dyck and Daley 2002
Polar bear	Franz Josef Land, Russia	2	Infanticide	Male	Nansen 1897
Polar bear	Franz Josef Land, Russia	1	Infanticide	Male	Parovshchikov 1964
Polar bear	Franz Josef Land, Russia	1	Infanticide	Unknown	Ivanov et al. 2020
Polar bear	MB, Canada	1	Infanticide	Male	Jonkel 1970
Polar bear	Novaya Zemlya, Russia	2	Infanticide	Male	Ivanov et al. 2020
Polar bear	Svalbard, Norway	2	Infanticide	Male	Derocher and Wiig 1999
Polar bear	Svalbard, Norway	1	Infanticide	Male	Stirling and Ross 2011
Polar bear	Svalbard, Norway	1	Infanticide	Male	Stone and Derocher 2007
Polar bear	Svalbard, Norway	26	Infanticide	Male	Taylor et al. 1985
American black bear	AB, Canada	1	Scavenging	Male	Tietje et al. 1986
American black bear	UT, USA	3	Scavenging	Unknown	Miller et al. 2017

Table 2. Continued

Species	Location	Cannibalism events	Type of cannibalism	Sex of cannibal	Study
Brown bear	AK, USA	2, 1	Scavenging	Female, unknown	Hessing and Aummiller 1994
Polar bear	Churchill, MB, Canada	1	Scavenging	Male	Dyck and Daley 2002
Polar bear	Franz Josef Land, Russia	1	Scavenging	Male	Nansen 1897
Polar bear	NT, Canada	7	Scavenging	Unknown	Taylor et al. 1985
Polar bear	Novaya Zemlya, Russia	8, 1	Scavenging	Unknown, Male	Ivanov et al. 2020
Polar bear	Vize Island, Russia	1	Scavenging	Male	Ivanov et al. 2020
American black bear	MT, USA	1	Undetermined*	Unknown	Jonkel and Cowan 1971
American black bear	WA, USA	1	Undetermined*	Unknown	Lindzey and Meslow 1977
American black bear	FL, USA	1	Undetermined*	Unknown	Garrison et al. 2007
American black bear	ON, Canada	18	Undetermined*	Unknown	Obbard and Howe 2008
Asiatic black bear	Iwate Prefecture, Japan	1	Undetermined*	Unknown	Sakamoto and Aoi 2006
Asiatic black bear	Toyama Prefecture, Japan	2	Undetermined*	Male	Arimoto et al. 2011
Brown bear	WY, USA	12	Undetermined*	Unknown	Mattson et al. 1992
Polar bear	Hudson Bay, Canada	32	Undetermined*	Unknown	Gormezano and Rockwell 2013

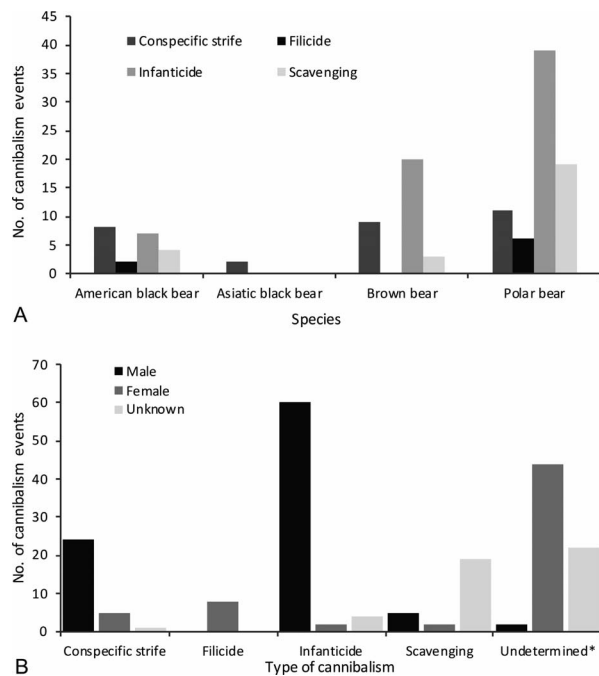


Fig. 1. Summary of cannibalism among bears, including (a) the type of cannibalism among 4 species: American black bear (*Ursus americanus*), Asiatic black bear (*U. thibeticus*), brown bear (*U. arctos*), or polar bear (*U. maritimus*); and (b) the type of cannibalism by sex of the bear. Undetermined* indicates incidents where it was not possible to determine type of cannibalism.

brown bear (*Ursus arctos*; $n_{\text{studies}} = 10$, $n_{\text{events}} = 44$, 22.2%), American black bear (*U. americanus*; $n_{\text{studies}} = 10$, $n_{\text{events}} = 42$, 21.2%), and Asiatic black bear (*U. thibeticus*; $n_{\text{studies}} = 4$, $n_{\text{events}} = 5$, 2.5%). Most events by polar bears and brown bears were infanticide ($n_{\text{polar}} = 39$, $n_{\text{brown}} = 20$; Fig. 1a). Most events by American black bears were conspecific strife ($n = 8$) or infanticide ($n_{\text{american}} = 7$). All cannibalism events with a known cause for Asiatic black bears were conspecific strife ($n = 2$). There were also a large number of undetermined events for each species recorded ($n_{\text{polar}} = 32$, $n_{\text{brown}} = 12$, $n_{\text{american}} = 21$, $n_{\text{asiatic}} = 3$).

Males more frequently showed cannibalism associated with infanticide ($n_{\text{male}} = 60$, $n_{\text{female}} = 4$) and conspecific strife ($n_{\text{male}} = 24$, $n_{\text{female}} = 5$) than did females, but scavenging was more equal among sexes ($n_{\text{male}} = 5$, $n_{\text{female}} = 2$; Fig. 1b). All events associated with infanticide by polar bears ($n = 38$) and American black bears ($n = 6$) were by males. The exception to this pattern was brown bears, which had 2 reported infanticide events by females, compared with 16 events for males. Brown bears were also the exception for cannibalism associated with conspecific strife, with 3 events by females and 6 events by males. In comparison, all 10 conspecific strife events by polar bears and 7 of 8 events by American black bears were by males.

The first study of cannibalism in bears was published in 1897 (3 events; Nansen 1897), but then there was a gap in publications until the 1960s when 2 studies (5 events)

of cannibalism were published. Most decades since had between 5 and 7 studies published (1970s = 5, 1980s = 7, 1990s = 5, 2000s = 9, 2010s = 7), with varying number of events reported (1970s = 7, 1980s = 50, 1990s = 31, 2000s = 35, 2010s = 44). Publications of cannibalism by bears among continents varied greatly, with 23 studies (123 events) in North America, 12 studies (69 events) in Europe, and 5 studies (6 events) in Asia.

Discussion

Our review of cannibalism in bears showed that cannibalism takes multiple forms, each with its own potential evolutionary drivers. Although cannibalism among predators is generally believed to increase fitness (by increasing nutrition while simultaneously reducing competition for resources; Gómez et al. 2021), in bears it often appears to be an opportunistic consumption of an available bear carcass (via scavenging) or is not directly connected with the primary cause of death (although cannibalism often follows the intraspecific killing via infanticide, filicide, or conspecific strife). This appears to be most clearly exhibited by sexually selected infanticide, where male bears and other carnivores kill unrelated dependent young to increase mating opportunities (Swenson et al. 1997, Miller et al. 2003, Bellemain et al. 2006), and the consumption of cubs as food is not the primary reason for the infanticide. We found no documented cases of siblicide (where one sibling kills another) in bears, although it is relatively common in some other animals (particularly raptors; Allen et al. 2020). Our review showed that cannibalism is relatively common among bears, but much less frequent than other types of predation or foraging behavior. Our review leaves many questions unanswered and highlights the need for further research with emphasis on hypothesis-driven research to understand the reasons for the different types of cannibalism in bears.

Likely differences in available resources or behaviors among species cause different motivations for cannibalism among bears, but it is also primarily a male behavior. Most documented cannibalism events were by polar bears, perhaps because polar bears are easier to observe over the long time periods necessary to document predation events. But polar bears are also the most carnivorous and predatory of bears (Derocher et al. 2000, 2002; Ordiz et al. 2020), and may be more likely to view young conspecifics as a food source. The high frequency of infanticide by polar bears is often explained by evolutionary reasons, such as sexually selected infanticide, as in other bear species (e.g., Swenson et al. 1997, Miller et al.

2003, Bellemain et al. 2006). However, studies have also highlighted that male polar bears use young as a food source, while also reducing competition for limited resources (Derocher and Wiig 1999). This is important because cannibalism may increase if there is increased food deprivation due to future climate change (Gormezano and Rockwell 2013, Petherick et al. 2021). There is reason to believe that brown bears also sometimes view conspecifics as a food source—cannibalism among female brown bears was documented to be associated with infanticide and conspecific strife, and brown bears regularly kill dependent yearling cubs (Swenson et al. 2001). In contrast, for other species such as American black bears and Asiatic black bears that are less carnivorous, infanticide was entirely, and conspecific strife was primarily, a male behavior (e.g., Naganuma et al. 2021).

Although sexually selected infanticide is likely the primary cause for most infanticide events, there are exceptions. The most notable exception is when females kill dependent young that are not theirs. For example, Hessing and Aummiller (1994) observed a female brown bear with cubs that killed and ate 1 of 2 cubs belonging to a different bear and killed 2 cubs during a previous year. This occurred at a salmon (*Oncorhynchus* spp.) spawning ground, where food availability was high and therefore killing cubs as a food source was unlikely and not typically observed at such locations (L. Aummiller, Vital Ground Foundation, pers. comm.). An attempted infanticide can also lead to a male bear killing an adult female (e.g., Tamatani et al. 2021), which does not fully support sexually selected infanticide, although such events are often initiated by the male trying to increase his mating opportunities. For example, Dean et al. (1986) documented a male that initially tried to kill a cub, but when the mother intervened, the male killed and ate her. Variation in infanticide occurs throughout bear species, with some events primarily occurring before mating seasons in some areas and after mating seasons in others (Shimozuru et al. 2019). Reporting whether infanticide includes the consumption of cubs could help reveal motivations for the events that seem to be exceptions, but often such information is missing in the literature.

Cannibalism associated with scavenging, and to some degree conspecific strife, seemed to be more directly linked to viewing conspecifics as a food source compared with other forms of cannibalism, but neither is without risk. Scavenging on bear carcasses that died from causes other than intraspecific killing increases the risk of parasitic infection or disease (Moleón et al. 2017). For some species, there could be selection pressure against eating a dead conspecific, except when the benefits of the

Table 3. Instances of cannibalism by bears found from a review of social media and the internet. This includes bear species, location, number and type of cannibalism, sex of cannibals, and the hyperlink for the event.

Species	Location	Cannibalism events	Type of cannibalism	Sex of cannibal	Hyperlink address
Brown bear	AK, USA	1	Conspecific strife	Male	https://youtu.be/XJDFG7cTIVs
Brown bear	Banff, AB, Canada	1	Conspecific strife	Male	https://www.cbc.ca/news/canada/calgary/grizzly-bear-eats-black-bear-in-banff-1.1414994
Brown bear	AK, USA	1	Infanticide	Male	https://youtu.be/t3DxCqU0oV0
Brown bear	Banff, AB, Canada	1	Infanticide	Male	https://www.cbc.ca/news/canada/calgary/banff-bear-grizzly-split-lip-eat-ate-cubs-alberta-parks-canada-1.5557895
Polar bear	Unknown	1	Infanticide	Male	https://www.youtube.com/watch?v=Rfo233Q6aOg
Polar bear	MB, Canada	1	Scavenging	Female with cubs	https://youtu.be/xlkOP4OgSrl
American bear	BC, Canada	1	Undetermined	Male	https://www.cbc.ca/news/canada/british-columbia/bear-eats-bear-central-bc-1.4833151
Brown bear	Banff, AB, Canada	1	Undetermined	Male	https://calgaryherald.com/news/local-news/grizzly-bear-known-as-split-lip-eats-another-marked-grizzly-bear
Brown bear	Katmai National Park, AK, USA	1	Undetermined	Unknown	https://www.nps.gov/katm/blogs/death-of-bear-130.htm
Polar bear	Baffin Island, NU, Canada	1	Undetermined	Male	https://www.youtube.com/watch?v=MWbQyY6kfxc
Polar bear	MB, Canada	8	Undetermined	Male	https://www.cbc.ca/news/canada/british-columbia/bear-eats-bear-central-bc-1.4833151
Polar bear	Unknown	1	Undetermined	Male	https://www.youtube.com/watch?v=UfRM0kRGqKc

food resource outweigh the risks of contracting a parasite or disease. However, bears are often food-limited, even when there are abundant resources, and are frequent scavengers (Krofel et al. 2012, Allen et al. 2015, Inagaki et al. 2020), which may make bears less wary of eating conspecifics compared with the other, more predatory carnivores. Most incidents of conspecific strife, which come with the risk of injury or death, were performed by male bears, but there are exceptions, including one documented event of conspecific strife by a female American black bear. This female had cubs of her own, and an abandoned cub attempted to associate with them, but the family group killed and consumed the foreign cub (Garrison et al. 2007).

Although a direct link to increased fitness can be drawn for some cases of cannibalism, in cases of filicide (where a mother kills and eats her young), it appears to reduce fitness by directly reducing the number of progeny. Filicide was rarely documented among bears, with 6 of the 8 events recorded for polar bears. Most of these events were when a mother killed a cub because it was starving or it appeared unlikely to survive (Uspenski and Kistchinski 1972, Belikov and Kuprijanov 1977). There are also occasional cases where a cub does not emerge from a den, which may be the result of filicide or at least scavenging, and these should be explored in more depth when found in the future. Hessing and Aummiller (1994) documented a conspecific female that killed another female's depen-

dent cub but then abandoned it, and the mother returned and ate the cub. Although we counted this as scavenging in our review, it again points to mothers trying to regain energy invested in their cubs that are unlikely to, or do not, survive.

One drawback of our study is that it was limited to peer-reviewed literature, but instances of cannibalism can be reported via other means, such as in gray literature (i.e., theses and reports) or on social media. Our primary reason for not including gray literature is that there is no way to systematically search and review gray literature. Instances in gray literature are also often reported in peer-reviewed literature, causing double-counting of the same events. Events in social media have similar issues but also lack the rigor of events documented in peer-reviewed literature. For instance, we performed an extensive review of the internet and social media (Table 3), but found very few instances from social media, and the reports often lacked important information such as date, time, and location. The cannibalism events reported in gray literature (e.g., Black and Auger 2004, Steyaert 2012) and social media (e.g., Table 3) are no less important than those in peer-reviewed literature, but we encourage authors in the future to publish these events in peer-reviewed literature so they can more easily be evaluated and used by the scientific community.

We did come across some lack of clarity that would be helpful to address in future research. There were many

reports of infanticide, and although some authors assumed that cannibalism always accompanies infanticide (e.g., Davoli et al. 2018), most studies neglected to report whether or not the cubs were consumed after being killed. For the sake of our literature review of cannibalism, we only considered the cases where a conspecific was reported to be consumed, but this means that our literature review may have underestimated cannibalism events by bears, especially cases of sexually selected infanticide, which is the most common form of cannibalism. Although this generally is limited to infanticide, other studies seemed to confuse predation (killing a conspecific) with cannibalism (consuming a conspecific) or considered the killing and consuming of a congeneric (different bear species) to be cannibalism (e.g., Mattson et al. 1992). These unclear definitions limit the ability of researchers to understand cannibalism, and we recommend in the future using definitions similar to those we have provided in Table 1.

There were also several cases of cannibalism where the type and cause could not be determined. Many of these were based on methods that do not allow determination of the cause (e.g., bones and fur found through scat analyses), so we suggest in the future that researchers documenting cannibalism in the field record as many details as possible. This includes noting age and sex of the cannibal; age, sex, and reproductive status of the consumed bear; exact location of the event and potential relocation of the carcass; inspection of wounds; and consumption of the carcass. Similar to guidelines for documentation of damages caused by predators on livestock (e.g., Černe et al. 2019), we recommend detailed photo-documentation of the carcass, animal tracks, and other signs around the carcass from various angles and distances together with a scale. Special attention should be given to wounds on the carcass that occurred premortem, which can reveal the cause of death but which often require flaying the body parts with bite wounds. Crucial information for the interpretation of the cannibalistic event is also relatedness between the consumer and the consumed bear, which enable scientists to distinguish between filicide, siblicide, and sexually selected infanticide. Unless both victim and consumer are previously known bears with established pedigrees, we recommend collecting genetic samples of the victim, as well as the consumer. The latter is usually more difficult to obtain because of limited amount of DNA left at the site. One option is to search for a scat or hair around the carcass, or to take a saliva swab from the carcass (e.g., from the surrounding of the killing wound or at parts that were consumed; Černe et al. 2019). However, in most cases of cannibalism,

saliva swabs will result in mixed samples also containing the more numerous DNA from the consumed bear. Such mixed samples often produce multiple alleles at ≥ 1 loci or some of the consumer alleles may be completely obscured, which significantly increases the complexity of the genetic analysis (Roon et al. 2005). But when a pure sample from the victim (which usually can be easily obtained from the tissues available) is analyzed in parallel, statistical approaches developed for human forensics can be applied to separate the consumer's and victim's genotypes and determine their relatedness (Hu et al. 2014). Following these recommendations will allow scientists to accurately document cannibalism and increase our understanding of cannibalism among bears and other carnivores.

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Literature cited

- ALLEN, M.L., L.M. ELBROCH, C.C. WILMERS, AND H.U. WITTMER. 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. *American Naturalist* 185:822–833.
- , A. INAGAKI, AND M.W. WARD. 2020. Cannibalism in raptors: A review. *Journal of Raptor Research* 54:424–430.
- , H.U. WITTMER, A. INAGAKI, K. YAMAZAKI, AND S. KOIKE. 2021. Food caching by bears: A literature review and new observations for Asiatic and American black bears. *Ursus* 32:e10.
- ALT, G.L., AND J.M. GRUTTADAURIA. 1984. Reuse of black bear dens in northeastern Pennsylvania. *Journal of Wildlife Management* 48:236–239.
- AMSTRUP, S.C., I. STIRLING, T.S. SMITH, C. PERHAM, AND G.W. THIEMANN. 2006. Recent observations of intraspecific predation and cannibalism among polar bears in the southern Beaufort Sea. *Polar Biology* 29:997–1002.
- ARIMOTO, I., Y. GOTO, C. NAGAI, AND K. FURUBAYASHI. 2011. Autumn food habits and home-range elevations of Japanese black bears in relation to hard mast production in the beech family in Toyama Prefecture. *Mammal Study* 36:199–208.
- BALLESTEROS, F., G. PALOMERO, J.C. BLANCO, AND J.V. LÓPEZ-BAO. 2021. Sexually selected infanticide or predation? Killing and consumption of a female brown bear in a male infanticide attempt. *European Journal of Wildlife Research* 67:1–4.

- BECHARD, M.J. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. *Wilson Bulletin* 95:233–242.
- BELIKOV, S.E., AND A.G. KUPRIANOV. 1977. Behavior of the polar bear on Wrangel Island. *The Polar Bear and its Conservation in the Soviet Arctic: Collection of Scientific Papers*. Moscow: Central Laboratory for Nature Conservation 40:55.
- BELLEMAIN, E., J.E. SWENSON, AND P. TABERLET. 2006. Mating strategies in relation to sexually selected infanticide in a non-social carnivore: The brown bear. *Ethology* 112: 238–246.
- BLACK, H.L., AND J. AUGER. 2004. Black bears of Utah's East Tavaputs Plateau: Final report for Utah Division of Wildlife Resources. Utah Division of Wildlife Resources, Salt Lake City, Utah, USA.
- BOJARSKA, K., AND N. SELVA. 2012. Spatial patterns in brown bear *Ursus arctos* diet: The role of geographical and environmental factors. *Mammal Review* 42:120–143.
- ČERNE, R., M. KROFEL, M. JONOZOVIČ, A. SILA, H. POTOČNIK, M. MARENČE, P. MOLINARI, J. KUSAK, T. BERCE, AND M. BARTOL. 2019. A fieldguide for investigating damages caused by carnivores: Brown bear, grey wolf, golden jackal, red fox, Eurasian lynx. Slovenia Forest Service - LIFE DINALP BEAR project, Ljubljana, Slovenia. https://dinalpbear.eu/wp-content/uploads/GIDC_ENG_v34_web.pdf. Accessed 4 Mar 2022.
- DAVIS, H., AND A.S. HARESTAD. 1996. Cannibalism by black bears in the Nimpkish Valley, British Columbia. *Northwest Science* 70:88–92.
- DAVOLI, F., M. COZZO, F. ANGELI, C. GROFF, AND E. RANDI. 2018. Infanticide in brown bear: A case-study in the Italian Alps—Genetic identification of perpetrator and implications in small populations. *Nature Conservation* 25:55–75.
- DEAN, F.C., L.M. DARLING, AND A.G. LIERHAUS. 1986. Observations of intraspecific killing by brown bears, *Ursus arctos*. *Canadian Field-Naturalist* 100:208–211.
- DEROCHER, A.E., AND Ø. WIIG. 1999. Infanticide and cannibalism of juvenile polar bears (*Ursus maritimus*) in Svalbard. *Arctic* 52:307–310.
- , ———, AND M. ANDERSEN. 2002. Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biology* 25:448–452.
- , ———, AND G. BANGJORD. 2000. Predation of Svalbard reindeer by polar bears. *Polar Biology* 23:675–678.
- DYCK, M.G., AND K.J. DALEY. 2002. Cannibalism of a yearling polar bear (*Ursus maritimus*) at Churchill, Canada. *Arctic* 55:190–192.
- ELOWE, K.D., AND W.E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53:962–968.
- GARRISON, E.P., J.W. MCCOWN, AND M.K. OLI. 2007. Reproductive ecology and cub survival of Florida black bear. *Journal of Wildlife Management* 71:720–727.
- GÓMEZ, J.M., M. VERDÚ, AND A. GONZÁLEZ-MEGÍAS. 2021. Killing conspecific adults in mammals. *Proceedings of the Royal Society B* 288:20211080.
- GORMEZANO, L.J., AND R.F. ROCKWELL. 2013. What to eat now? Shifts in polar bear diet during the ice-free season in western Hudson Bay. *Ecology and Evolution* 3: 3509–3523.
- HESSING, P., AND L. AUMILLER. 1994. Observations of conspecific predation by brown bears, *Ursus arctos*, in Alaska. *Canadian Field-Naturalist* 108:332–336.
- HRDY, S.B., 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1:13–40.
- HU, N., B. CONG, S. LI, C. MA, L. FU, AND X. ZHANG. 2014. Current developments in forensic interpretation of mixed DNA samples. *Biomedical Reports* 2:309–316.
- INAGAKI, A., M.L. ALLEN, T. MARUYAMA, K. YAMAZAKI, K. TOCHIGI, T. NAGANUMA, AND S. KOIKE. 2020. Vertebrate scavenger guild composition and utilization of carrion in an East Asian temperate forest. *Ecology and Evolution* 10:1223–1232.
- IVANOV, E.A., I.A. MIZIN, A.G. KIRILOV, N.G. PLATONOV, I.N. MORDVINTSEV, S.V. NAIDENKO, AND V.V. ROZHNOV. 2020. Observations of intraspecific killing, cannibalism, and aggressive behavior among polar bears (*Ursus maritimus*) in the eastern Barents Sea and the Kara Sea. *Polar Biology* 43:2121–2127.
- JONKEL, C. 1970. The behavior of captured North American bears (with comments on bear management and research). *Bioscience* 20:1145–1147.
- JONKEL, C.J., AND I.M. COWAN. 1971. The black bear in the spruce–fir forest. *Wildlife Monographs* 27:3–57.
- KARAMANLIDIS, A.A., J.J. BEECHAM, C. CHATZIOANNOU, M. DE GABRIEL HERNANDO, K. GRIVAS, L. KRAMBOKOUKIS, AND G. PAPAPOSTAS. 2015. Intraspecific predation on a subadult brown bear in Greece. *Ursus* 26:7–10.
- KOLCHIN, S.A. 2019. The first record of cannibalism in the Asiatic black bear (*Ursus thibetanus*) in the Russian Far East. *Zoologicheskyy Zhurnal* 98:222–226.
- KROFEL, M., I. KOS, AND K. JERINA. 2012. The noble cats and the big bad scavengers: Effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology* 66:1297–1304.
- LECOUNT, A.L. 1987. Causes of black bear cub mortality. *Bears: Their Biology and Management* 7:75–82.
- LINDZEY, F.G., AND E.C. MESLOW. 1977. Population characteristics of black bears on an island in Washington. *Journal of Wildlife Management* 41:408–412.
- LUNN, N.J., AND G.B. STENHOUSE. 1985. An observation of possible cannibalism by polar bears (*Ursus maritimus*). *Canadian Journal of Zoology* 63:1516–1517.
- MATTSON, D.J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation* 81:161–177.
- , R.R. KNIGHT, AND B.M. BLANCHARD. 1992. Cannibalism and predation on black bears by grizzly bears in the Yellowstone ecosystem, 1975–1990. *Journal of Mammalogy* 73:422–425.

- MILLER, J.A., T.S. SMITH, J. AUGER, H.L. BLACK, AND L. ALLPHIN. 2017. The late-denning activities of the American black bear in Utah. *Ursus* 27:78–89.
- 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.
- MOLEÓN, M., C. MARTÍNEZ-CARRASCO, O.C. MUELLERKLEIN, W.M. GETZ, C. MUÑOZ-LOZANO, AND J.A. SÁNCHEZ-ZAPATA. 2017. Carnivore carcasses are avoided by carnivores. *Journal of Animal Ecology* 86:1179–1191.
- NAGANUMA, T., M. TANAKA, S. TEDUKA, S. STEYAERT, K. TOCHIGI, A. INAGAKI, H. MYOJO, K. YAMAZAKI, AND S. KOIKE. 2021. Animal-borne video systems provide insight into the reproductive behavior of the Asian black bear. *Ecology and Evolution* 11:9181–9190.
- NANSEN, F. 1897. *Farthest North*. Volume 2. MacMillan and Company Ltd., London, UK.
- NARITA, R., A. SUGIMOTO, AND A. TAKAYANAGI. 2006. Animal components in the diet of Japanese black bears *Ursus thibetanus japonicus* in the Kyoto area, Japan. *Wildlife Biology* 12:375–384.
- ORBARD, M.E., AND E.J. HOWE. 2008. Demography of black bears in hunted and unhunted areas of the boreal forest of Ontario. *Journal of Wildlife Management* 72:869–880.
- OLSON, T.L. 1993. Infanticide in brown bears, *Ursus arctos*, at Brooks River, Alaska. *Canadian Field-Naturalist* 107:92–94.
- ORDIZ, A., M. KROFEL, C. MILLERET, I. SERYODKIN, A. TALLIAN, O.G. STØEN, T.R. SIVERTSEN, J. KINDBERG, P. WABAKKEN, H. SAND, AND J.E. SWENSON. 2020. Interspecific interactions between brown bears, ungulates, and other large carnivores. Pages 36–44 in M. Melletti and V. Penteriani, editors. *Bears of the world: Ecology, conservation and management*. Cambridge University Press, Cambridge, Massachusetts, USA.
- PAROVSHCHIKOV, V. 1964. A study of the population of the polar bear of Frans Joseph Land. *Acta Sociologia Zoologica Bohemoslov* 28:167–177.
- PETHERICK, A.S., J.D. REUTHER, S.J. SHIRAR, S.L. ANDERSON, AND L.R. DESANTIS. 2021. Dietary ecology of Alaskan polar bears (*Ursus maritimus*) through time and in response to Arctic climate change. *Global Change Biology* 27:3109–3119.
- ROON, D.A., M.E. THOMAS, K.C. KENDALL, AND L.P. WAITS. 2005. Evaluating mixed samples as a source of error in non-invasive genetic studies using microsatellites. *Molecular Ecology* 14:195–201.
- SAKAMOTO, Y., AND T. AOI. 2006. Food habits of the Asiatic black bear *Ursus thibetanus japonicus* in the northern Ohu Mountains, Japan. *Bulletin of the Iwate University Forests* 37:17–27. [In Japanese with English abstract.]
- SHIMOZURU, M., Y. SHIRANE, H. TSURUGA, M. YAMANAKA, M. NAKANISHI, T. ISHINAZAKA, S. KASAI, T. NOSE, Y. MASUDA, Y. FUJIMOTO, AND T. MANO. 2019. Incidence of multiple paternity and inbreeding in high-density brown bear populations on the Shiretoko Peninsula, Hokkaido, Japan. *Journal of Heredity* 110:321–331.
- STEYAERT, S. 2012. The mating system of the brown bear in relation to the sexually selected infanticide theory. Dissertation, Norwegian University of Life Sciences, Ås, Norway.
- STEYAERT, S.M., C. REUSCH, S. BRUNBERG, J.E. SWENSON, K. HACKLÄNDER, AND A. ZEDROSSER. 2013. Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. *Biology Letters* 9:20130624.
- STIRLING, I., E. RICHARDSON, G.W. THIEMANN, AND A.E. DEROCHE. 2008. Unusual predation attempts of polar bears on ringed seals in the southern Beaufort Sea: Possible significance of changing spring ice conditions. *Arctic* 61:14–22.
- , AND J.E. ROSS. 2011. Observations of cannibalism by polar bears (*Ursus maritimus*) on summer and autumn sea ice at Svalbard, Norway. *Arctic* 64:478–482.
- STONE, I.R., AND A.E. DEROCHE. 2007. An incident of polar bear infanticide and cannibalism on Phippssoya, Svalbard. *Polar Research* 43:171–173.
- SWENSON, J.E. 2003. Implications of sexually selected infanticide for hunting of large carnivores. Pages 171–189 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife management*. Island Press, Covelo, California, USA.
- , B. DAHLE, AND F. SANDEGREN. 2001. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12:81–91.
- , F. SANDEGREN, A. SÖDERBERG, A. BJÄRVALL, R. FRANZEN, AND P. WABAKKEN. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450–451.
- TAMATANI, H., A. HIORNS, AND T. YAMAMOTO. 2021. An apparent case of infanticide in the Asiatic black bear in Japan. *Ursus* 32:e16.
- TAYLOR, M., T. LARSEN, AND R. SCHWEINSBURG. 1985. Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). *Arctic* 38:303–309.
- TIETJE, W.D., B.O. PELCHAT, AND R.L. RUFF. 1986. Cannibalism of denned black bears. *Journal of Mammalogy* 67:762–766.
- TROYER, W.A., AND R.J. HENSEL. 1962. Cannibalism in the brown bear. *Animal Behavior* 10:3–4.
- USPENSKI, S.M., AND A.A. KISTCHINSKI. 1972. New data on the winter ecology of the polar bear (*Ursus maritimus* Phipps) on Wrangel Island. *Bears: Their Biology and Management* 2:181–197.

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