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Possible sexually selected infanticide by polar bears in western Hudson Bay

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Abstract: Infanticide occurs in a diversity of taxa and may provide benefits to the perpetrator through nutritional gain, reduced competition, or increased fitness from mating opportunities through sexually selected infanticide (SSI). Infanticide, however, is rarely observed. We documented a probable infanticide event by a 23-year-old adult male polar bear (*Ursus maritimus*) on a 3-month-old cub in western Hudson Bay, Canada, during the spring of 2023. We subsequently documented a 21-year-old solitary female who was lactating and in breeding condition with swollen labia, suggesting polar bears return to estrous quickly in the absence of cubs. Using the literature, we examined the relationships among polar bear cub-of-the-year, adult male survival, and the ratio of male/female mortality. We suggest SSI as the plausible explanation for the infanticide event observed and discuss how indirect effects from climate change may affect the prevalence of infanticide as a mechanism regulating polar bear populations.

Key words: climate change, Hudson Bay, intraspecific competition, polar bears, sex ratio, sexually selected infanticide, sexual selection, *Ursus maritimus*

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Infanticide is a form of intraspecific competition that occurs across a diversity of taxa (Ebensperger 1998, Lukas and Huchard 2014). Hypotheses to explain it include nutritional gains through cannibalism (predation hypothesis), social pathology, reducing intra-litter competition (parental manipulation hypothesis), obtaining access to limited resources (resource competition hypothesis), or to increase reproductive fitness of the perpetrator (sexually selected infanticide hypothesis [SSI]; [Hrdy 1974, 1979; Hrdy and Hausfater 1984]). Sexually selected infanticide is more common for species with high sexual size dimorphism, extended parental care, and a long lactation to gestation ratio (van Schaik 2000, Harano and Kutsukake 2018). For infanticide to be considered SSI, the perpetrator who kills the offspring should shorten the interbirth interval of the mother and on average, increase their own mating opportunities (Hrdy 1979). A key aspect of SSI is that perpetrators are not the parent of the offspring killed, or this behavior would be maladaptive (Hrdy and Hausfater 1984). Observing instances of infanticide is rare and confirming the requirements for SSI is even more challenging, particularly in species that occur at low density and live in remote locations. Nevertheless, SSI is widespread and documented in social and nonsocial animals, including primates (Hrdy 1979, Ebensperger 1998), ungulates (Watts et al. 2020), rodents (Haines et al. 2018), felids (Pusey and Packer 1994), and ursids (McLellan 2005, Garrison et al. 2007, Hiroo et al. 2021). Sexually selected infanticide is thought to be a significant factor regulating brown bear (*Ursus arctos*) populations as a response to hunting and altered sex ratios (Swenson et al. 1997, McLellan 2005, Bellemain et al. 2006, Leclerc et al. 2017), although this may vary across populations (Miller et al. 2003).

Polar bears (*U. maritimus*) are closely related to brown bears and infanticide has been widely reported (Taylor et al. 1985, Derocher and Wiig 1999, Dyck and Daley 2002, Stone and Derocher 2007, Stirling and Ross 2011, Ivanov et al. 2020). Despite the occurrence of infanticide in polar bears, the context of these events is rarely known and there is limited evidence for SSI (Parovshchikov 1964, Taylor et al. 1985, Ivanov et al. 2020). Polar bears may be the most cannibalistic ursid, and infanticide events outside of the breeding season are thought to be food-motivated (Allen et al. 2022). Infanticide in polar bears can occur during the breeding season and SSI is a tractable hypothesis to explain these events because of the species' life history, which includes high sexual dimorphism, a male-biased operational sex ratio, variation in male reproductive success, and a long lactation/gestation ratio (Ramsay and Stirling 1986, 1988; Derocher et al. 2005; Richardson et al. 2020; Allen et al. 2022). Further, a recent study found 91% of female brown bears that lost their litters during the breeding season gave birth the following year, suggesting infanticide is a common male reproductive strategy even though it is rarely observed (Steyaert et al. 2014). These authors hypothesized that this phenomenon may frequently occur in species with similar life histories.

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Removal of dominant male brown bears through harvest may increase SSI according to the immigrant male hypothesis as it relates to an influx of infanticidal males (Swenson et al. 1997), which can lead to avoidance of high-quality habitats by females and result in negative effects on reproduction (Wielgus et al. 2001). Research in Scandinavia documented infanticide in resident and nonresident males (Bellemain et al. 2006). The mate recognition hypothesis proposed by McLellan (2005) suggests any male can be infanticidal providing they can recognize a female they previously mated with to avoid killing cubs they sired. These two hypotheses were developed to understand SSI in bears and have different predictions: the former predicts that the hunting of dominant males increases SSI and lowers cub survival whereas the latter predicts a negative relationship between adult male survival and cub survival (McLellan 2023).

In this note we describe an observation of infanticide consistent with SSI and/or the predation hypothesis in a polar bear subpopulation in western Hudson Bay, Canada, and outline an observation of cub loss to illustrate the challenges of understanding if, and when, SSI occurs. We also examine the relationship between cub survival and adult male survival and cub survival and the ratio of male/female mortality for polar bears across the Arctic to investigate the possible role of infanticide in population dynamics.

Study area and population

Our observations were made on the sea ice in Hudson Bay, a large inland sea off the northeastern coast of Manitoba, Canada. Hudson Bay is a seasonal sea ice area where the ice begins to form in mid- to late-November through to December and remains ice-covered until spring when the thaw results in ice-free conditions by July–August (Gagnon and Gough 2005). Western Hudson Bay polar bears (WH) fast during the ice-free period for 3–5 months before returning to the sea ice at freeze-up, except for pregnant females that overwinter on land and fast until March when they return to the sea ice with cubs (Stirling et al. 1977). Mating occurs on the sea ice in March–June with a mating system defined as female defense polygyny, serial monogamy, or polyandry (Ramsay and Stirling 1986, Derocher et al. 2010, Stirling et al. 2016, Richardson et al. 2020). The WH subpopulation has declined from 1,200 in the mid-1990s to 618 in 2021 with lower reproductive rates compared with neighboring subpopulations (Lunn et al. 1997, Stapleton et al. 2014, Atkinson et al. 2022, Northrup et al. 2022). We made observations while conducting polar bear research and monitoring. We captured bears using standard handling procedures following Stirling et al. (1989) or biopsied them using methods similar to those described by Pagano et al. (2014).

Observation 1

On 7 March 2023, while searching at an altitude of 150 m from a helicopter for tracks or bears along the edge of landfast sea ice in Hudson Bay near Cape Churchill, Manitoba, we followed solitary tracks eastward from the landfast ice toward the floe edge, which then turned back west toward shore. We followed the tracks briefly before spotting a single bear. While maneuvering to biopsy the bear we saw a second bear running north on the landfast ice. We biopsied the first bear and pursued the second bear. The second bear was a large adult male in good condition that was carrying a dead, 3–4-month-old cub-of-the-year in its mouth (Fig. 1A), which he subsequently dropped, and then he moved east toward the pack ice. We pursued and biopsied the male before returning to land at the cub. The dead cub was a male, weighed 12.2 kg, and a skin sample was collected for genetic analysis (Fig. 1B). The cub was not consumed, appeared to have been killed with a bite to the neck, and had fresh blood from bite marks on its neck. The temperature was −20°C and the cub was not frozen, which indicate that the cub likely died not long before our observations.

We had both skin samples genotyped at 24 microsatellite loci at the Molecular Biology Service Unit (University of Alberta, Edmonton, Alberta, Canada), following Malenfant et al. (2016). Sample genotypes were compared to the genotypes of previously typed individuals from WH (Malenfant et al. 2016, Environment and Climate Change Canada, unpublished data). Matching genotype analysis was performed using GenAIEx 6.5 (Peakall and Smouse 2012) allowing for up to 4 mismatching alleles. Matches were visually assessed and rejected as matching if they differed at >4 alleles at a maximum of 2 loci. The adult male matched one database genotype: a male first captured as a 1-year-old in 2001 that was therefore now 23 years old. The dead cub was not the offspring of this male (4 loci had no matching alleles). The biopsy sample of the first single bear encountered contained only hair and did not yield DNA. We used the genetics of the cub to find all bears sharing ≥1 allele at each locus. Only one bear shared an allele at each locus, a female first captured as a 3-year-old in 2009 and that was 17 years old when observed.

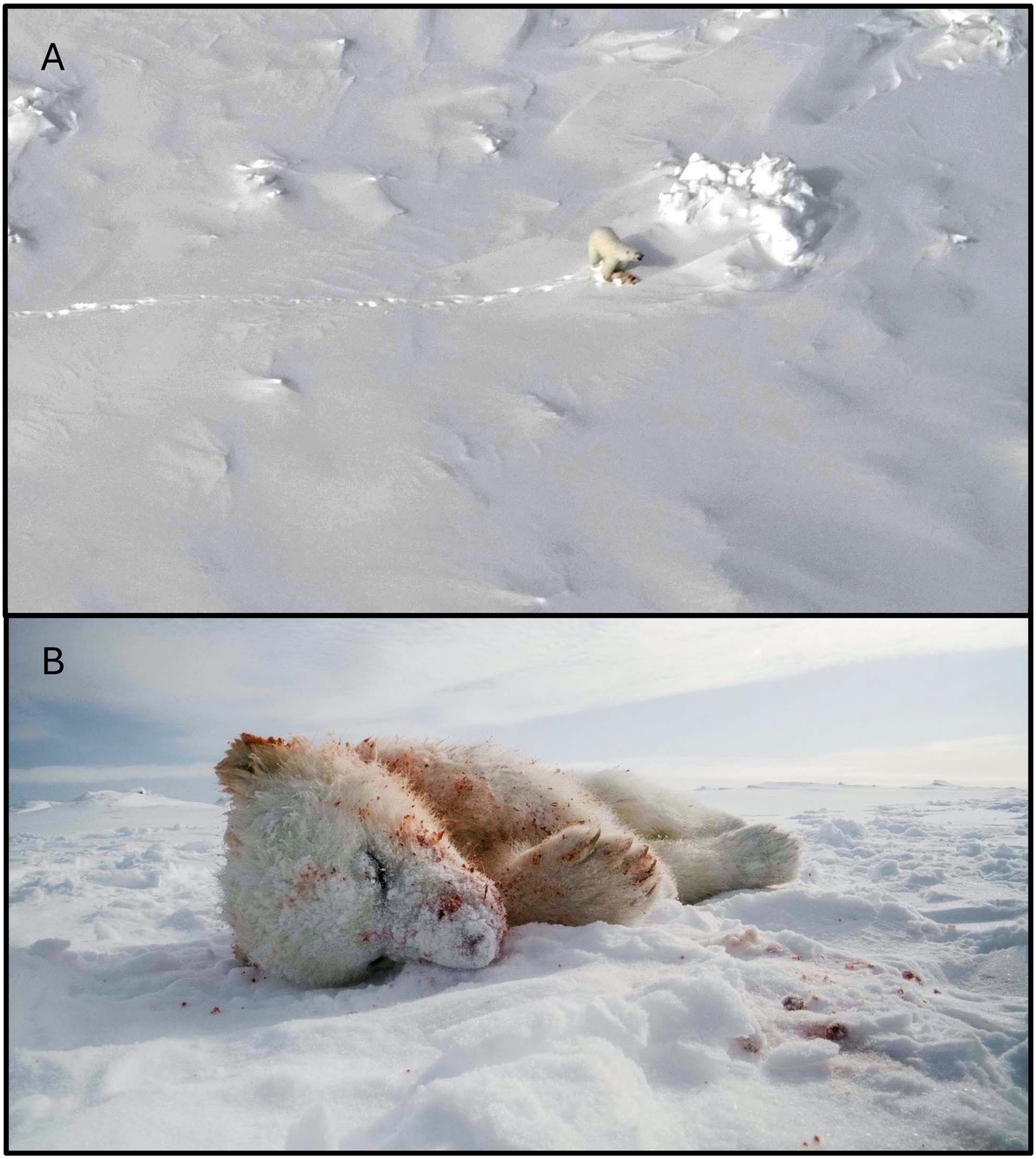

Fig. 1. Adult male polar bear (*Ursus maritimus*; 23 yr of age) stands over a male cub recently killed in Western Hudson Bay in the spring of 2023 (A). Adult male was running with the 3–4-month-old cub-of-the-year in his mouth before dropping it when circled by the helicopter (as we attempted to determine the identity of the prey item being carried). Male cub-of-the-year killed by the adult male (B). Photo credit P. Bikis.

Observation 2

On 19 April 2023, we followed tracks of a single bear and subsequently immobilized it on the landfast ice east-southeast of Cape Churchill. The bear was a solitary adult female that was lactating (Fig. 2A), in good body condition, and had recently been nursing despite the absence of offspring. She was in breeding condition as determined by her swollen labia (Fig. 2B). The female was identified from existing tags as a 21-year-old that was first captured as a cub in 2002. She had been biopsy-sampled the previous autumn (2022) during field research when she was accompanied by twin 9-month-old cubs. Although these cubs were not with their mother when she was caught, their fate was unknown.

Cub survival in relation to adult male survival

We used the published literature from 11 polar bear subpopulations across the circumpolar Arctic to explore the relationship between cub-of-the-year survival and adult male survival, which is hypothesized to have a negative relationship under the mate recognition hypothesis for SSI in bears (McLellan 2005, 2023). Similarly, we explored the relationship between cub-of-the-year survival and the ratio of male/female mortality, which is hypothesized to have a positive relationship under the mate recognition hypothesis because SSI is predicted to be a more advantageous reproductive strategy due to there being fewer mating opportunities when adult sex ratios are male-biased (McLellan 2005, 2023). We used published studies that estimated vital rates and used total survival to incorporate the impacts of hunting on adult male survival. We used point estimates when models were time-invariant, or we averaged survival estimates when annual survival was estimated. We used mean cub survival if sex-specific estimates were provided. We used a survival rate of 0.95 for adult males in the Barents Sea because there is no harvest and natural survival was estimated as 0.95 (Larsen 1986). We found a negative relationship between cub survival and adult male survival that approached significance (linear regression, $F_{1,9} = 3.625$, $P = 0.089$; Fig. 3). There was a nonsignificant

Fig. 2. Solitary adult female polar bear (*Ursus maritimus*) captured on the sea ice in Hudson Bay in spring 2023 that is both lactating (left) and in breeding condition with swollen labia (right). Female was seen the previous autumn with 2 cubs-of-the-year.

relationship (linear regression, $F_{1,9} = 2.485$, $P = 0.149$; Fig. 4) between cub-of-the-year survival and the ratio of male-to-female mortality but the slope was positive.

Discussion

Understanding the role of infanticide in population dynamics is important but difficult to document. For polar bears, habitat remoteness, low density, multimonth mating season, and small footprint of infanticide make it challenging to document these events. A growing body of literature suggests that many infanticidal events in carnivores are motivated by sexual selection (Swenson et al. 1997, Balme and Hunter 2013, Steyaert et al. 2014) and we propose this may also be the case for polar bears. A negative relationship may exist between cub-of-the-year survival and adult male polar bear survival across the circumpolar Arctic as predicted by the SSI mate recognition hypothesis. Cub survival also appeared higher in subpopulations that were likely female-biased and supports the SSI mate recognition hypothesis that adult sex ratios may influence population dynamics where SSI becomes more advantageous when adult sex ratios are male-biased (McLellan 2005).

For Observation 1, although we did not observe the male killing the cub, this was the most likely scenario. Our observation met one criterion for SSI because the adult male was unrelated to the cub. A second criterion is the adult female would be available to breed during the current mating season, which is broadly supported by Observation 2 of a solitary female that was lactating and in breeding condition with swollen labia, suggesting that females can enter estrous state quickly. In Scandinavia, female brown bears that lose their cubs during the mating season return to mating behavior within days (Steyaert et al. 2014). Within ursids and other species there is little support for social maladaptation, resource competition, or parental manipulation hypotheses to explain infanticide (Swenson et al. 1997,

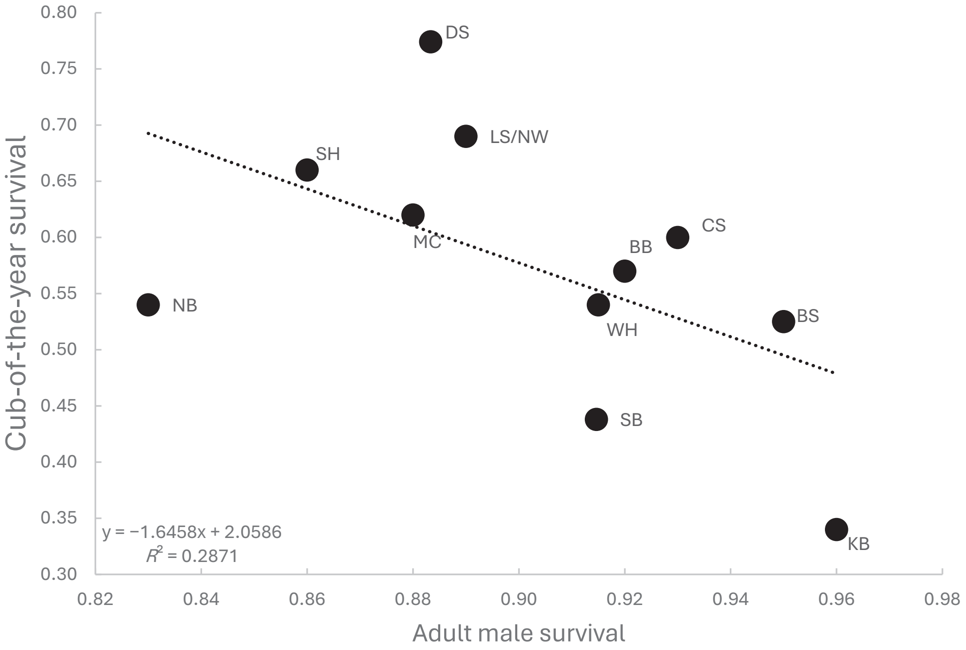

Fig. 3. Relationship between cub-of-the-year survival and adult male survival (includes harvest) across 11 polar bear (*Ursus maritimus*) subpopulations: BB (Baffin Bay; Taylor et al. 2005), BS (Barents Sea; Larsen 1986, Cubaynes et al. 2021), CS (Chukchi Sea; Regehr et al. 2018), DS (Davis Strait; Peacock et al. 2013), KB (Kane Basin; Taylor et al. 2008a), LS/NW (Lancaster Sound/Norwegian Bay; Taylor et al. 2008b), MC (M'Clintock Channel; Taylor et al. 2006), NB (Northern Beaufort Sea; Stirling et al. 2011), SB (Southern Beaufort Sea; Bromaghin et al. 2015), SH (Southern Hudson Bay; Obbard et al. 2007), and WH (Western Hudson Bay; Lunn et al. 2016). Note that BB, DS, SH, and WH are seasonal ice areas where estimates are derived from autumn research where cubs-of-the-year were approximately 7–10 months old. All other subpopulations were assessed during the spring when cubs-of-the-year were approximately 4–6 months old.

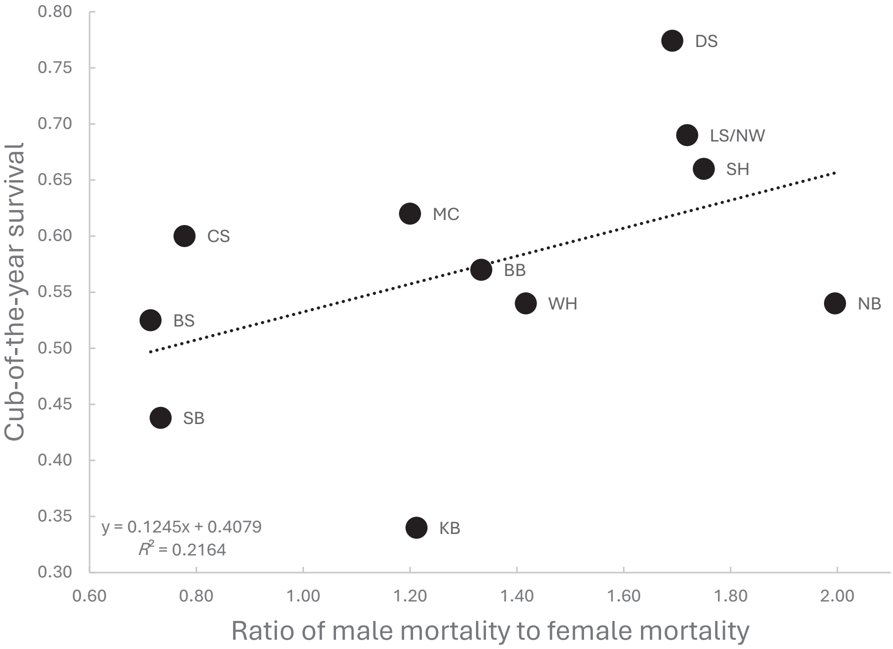

Fig. 4. Relationship between cub-of-the-year survival and the ratio of male mortality to female mortality across 11 polar bear (*Ursus maritimus*) subpopulations: BB (Baffin Bay; Taylor et al. 2005), BS (Barents Sea; Larsen 1986, Cubaynes et al. 2021), CS (Chukchi Sea; Regehr et al. 2018), DS (Davis Strait; Peacock et al. 2013), KB (Kane Basin; Taylor et al. 2008a), LS/NW (Lancaster Sound/Norwegian Bay; Taylor et al. 2008b), MC (M'Clintock Channel; Taylor et al. 2006), NB (Northern Beaufort Sea; Stirling et al. 2011), SB (Southern Beaufort Sea; Bromaghin et al. 2015), SH (Southern Hudson Bay; Obbard et al. 2007), and WH (Western Hudson Bay; Lunn et al. 2016). Note that BB, DS, SH, and WH are seasonal ice areas where estimates are derived from autumn research where cubs-of-the-year were approximately 7–10 months old. All other subpopulations were assessed during the spring when cubs-of-the-year were approximately 4–6 months old.

Ebensperger 1998, van Schaik 2000, Balme and Hunter 2013). Thus, the two most likely hypotheses to explain our first observation are the predation hypothesis and SSI (Hrdy and Hausfater 1984). The differentiation between the two requires information on behaviors both before and after the infanticidal event, which are unavailable, but we speculate that the latter may be the motivating factor based on published research and characteristics related to life history.

The male was old but appeared healthy, which contrasts other observations of polar bear infanticide or cannibalism where the perpetrator was in poor condition and thought to be food-motivated from malnutrition (Lunn and Stenhouse 1985, Stone and Derocher 2007, Stirling and Ross 2011, Ivanov et al. 2020). Cubs in spring have minimal fat content (Wiig and Derocher 2001) and thus would be of little nutritional gain to an adult male, especially compared with blubber-rich seals, which are their primary prey (Stirling and McEwan 1975). Food-motivation is thus unlikely to be a motivating factor for the behavior. The cub mass was above average for spring cubs (Ramsay and Stirling 1988) and thus unlikely to be a contributing factor to its death because heavier cubs have higher survival (Derocher and Stirling 1996). We documented a likely case of infanticide, but we were unable to determine whether cannibalism would have occurred. Derocher and Wiig (1999) documented an adult male killing 3 unattended cubs at a maternity den in Svalbard and only one of the cubs was partially consumed, further rejecting nutritional gain as a motivating factor. Similarly, Ivanov et al. (2020) discounted nutritional gain for an adult male polar bear that killed and cannibalized a 3–4-month-old cub in spring because a local garbage dump provided a constant food source, and they suggested SSI as a possible explanation. We suggest that SSI was a probable motivating factor in our Observation 1 but we cannot rule out nutritional gain (i.e., predation hypothesis).

It is unknown whether the male's age in our observation contributed to the infanticide. Male polar bears >20 years of age have lower survival compared with prime age males (ages 5–19; Regehr et al. 2007, Lunn et al. 2016, McGeachy et al. 2024) and have higher reproductive success at 11–17 years old; however, bears as old as 26 years have successfully fathered cubs (Richardson et al. 2020). The mating system of polar bears has a skewed operational sex ratio, biased toward males because of extended maternal care, and thus there is intense competition for unencumbered females (Ramsay and Stirling 1986, Biddlecombe et al. 2019). Thus, as adult males age, SSI may become a mating strategy if they are no longer able to compete for available females with adult males in their prime. The ages of infanticidal male polar bears are rarely known. In Scandinavian brown bears, 2 known infanticidal males were 9 and 11 years old and putative infanticidal males ranged from 6 to 27 years old (Bellemain et al. 2006). In Alaska, 8 events of known-age adult male brown bears were observed attacking family groups with ages ranging from 5 to 15 years old with a mean of 9.4 years old (Miller et al. 2003). McLellan (2005) found that SSI became a more advantageous mating strategy for older males using simulations. Only Lunn and Stenhouse (1985) and our study have reported the age of infanticidal or cannibalistic male polar bears, and both reported an age of 23 years. Lunn and Stenhouse (1985) reported that the adult male was in poor condition and consumed a 17-year-old adult female, with a possible 2-year-old offspring nearby, and suggested that she may have died defending her cub.

Observation 2 of an adult female without cubs lactating and in a breeding state (swollen labia) was consistent with research that ursids are induced ovulators and can enter estrous state quickly amidst lactation anestrous (Erickson et al. 1964, Steyaert et al. 2014). The cubs, which would have been yearlings in spring 2023, could have been killed by an infanticidal male, died of natural or other causes (e.g., starvation), or recently have been weaned. We believe it was unlikely that the cubs died from starvation because the female was in good condition and lactating. However, the cubs could have died of other causes or been weaned. This observation highlights the episodic nature of data collected during polar bear research and highlights the challenges of understanding cub mortality.

Evidence of SSI in polar bears is rare but Taylor et al. (1985) reported dependent yearlings killed by an adult male in spring. The mother was radiocollared and was observed with 3 different adult males that had fresh cuts over the next 10 days. Such cuts are consistent with fighting from intrasexual competition for females in estrous (Ramsay and Stirling 1986, Derocher et al. 2010). Most polar bear infanticide observations have occurred outside of the mating season, but polar bears inhabit a remote environment during the mating season where few observers are present; and terrestrial, boat-based research and eco-tourism are largely restricted to the postmating season. The small size of spring cubs likely makes SSI events brief and thus difficult to detect. Thus, we suggest SSI may occur more often than reported. We acknowledge that the alternative, that SSI is rarely observed because it rarely occurs, is also possible.

Climate change has reduced sea ice extent and duration throughout the Arctic; however, negative impacts on polar bear populations have not been documented for all subpopulations probably because the number of ice-free days has not yet reached fasting limits in some areas (Stern and Laidre 2016, Molnár et al. 2020). Once fasting limits are reached, indirect effects from climate change may create a negative feedback loop reducing recruitment as a result of females using lower quality habitat to avoid adult males, and increased cub mortality from SSI ultimately resulting in reduced or negative growth rates (Fig. 5). Changes in habitat use by female polar bears were modelled as a response to climate-changed-induced sea ice loss and a shorter spring feeding period; this resulted in predictions that females would undertake riskier foraging behaviors (Reimer et al. 2019). Increases in cannibalism linked to nutritional stress was suggested if hunting opportunities diminish from melting sea ice (Derocher et al. 2004, Stirling and Derocher 2012). Further, climate change also negatively affects adult female survival when sea ice is reduced (Regehr et al. 2010, Lunn et al. 2016). We suggest that a reduction in female survival as the climate continues to warm could result in an increasingly male-biased operational sex ratio and increase SSI.

The WH population was female-biased (Derocher and Stirling 1995), but the most recent aerial survey suggests it is now male-biased (Atkinson et al. 2022). A male-biased adult sex ratio in polar bears could increase the already male-biased operational sex ratio that occurs naturally and thus SSI may become more prevalent as an alternative reproductive strategy for males and could be a contributing factor leading to low reproductive rates in WH. The neighboring Southern Hudson Bay (SH) subpopulation has different demographic characteristics despite its proximity to WH, including a female-biased adult sex ratio and higher cub survival that we postulate may be related to lower adult male survival in SH (Fig. 3; Obbard et al 2007,

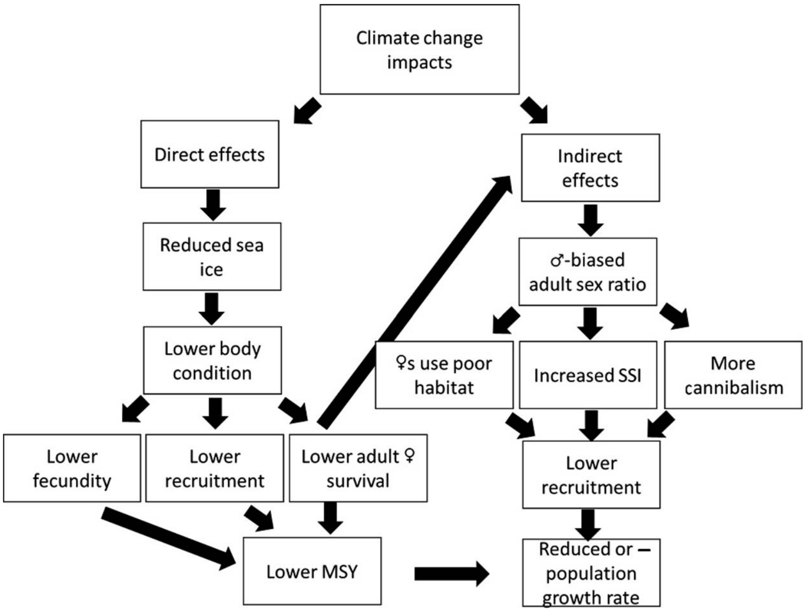

Fig. 5. Flow chart showing how direct and indirect effects of climate change could alter polar bear (*Ursus maritimus*) population dynamics and influence the MSY (maximum sustainable yield) and population growth rate from increased SSI (sexually selected infanticide).

Northrup et al 2022). McLellan (2005) found that SSI became more advantageous as a reproductive strategy for male brown bears as the adult sex ratio became skewed toward males, suggesting phenotypic plasticity in this mating strategy. Similarly, we found a negative relationship approaching significance between cub survival and adult male survival and a nonsignificant but positive relationship between cub survival and the ratio of male/female mortality (Figs. 3, 4). The lowest rate of cub survival occurred in Kane Basin and was associated with the highest adult male survival rate (Fig. 3). In the Barents Sea subpopulation, no hunting has occurred since the 1970s (Prestrud and Stirling 1994) and Larsen (1985) thought low cub survival was related to an increasing number of adult males (Fig. 3). Derocher and Wiig (1999) suggested that density-dependent regulation may be more prevalent as carrying capacity was approached. This subpopulation has experienced rapid sea ice loss due to climate change (Stern and Laidre 2016) and infanticide and cannibalism was frequently reported there (Derocher and Wiig 1999, Stone and Derocher 2007, Stirling and Ross 2011, Ivanov et al. 2020, Allen et al. 2022). The role of SSI and the predation hypothesis cannot be determined from these data alone, but we suggest vital rates, population density, habitat use, and climate change may interact with SSI.

Indirect effects of climate change may result in a male-biased adult sex ratio and increase the variance associated with male reproductive success; and selection for alternative mating strategies could influence population dynamics (Møller 2003, McLellan 2005, Frank et al. 2017). The infanticidal male in Observation 1 was old and may not have been able to compete with prime-aged males for mates. As climate change continues to affect sea ice, the vital rates of polar bear populations will respond. We recommend that monitoring programs include adult sex ratio quantification and consider possible implications of changes over time. Sexually selected infanticide in brown bears may be an important population regulatory mechanism (Bunnell and Tait 1981, Swenson et al. 1997, McLellan 2005, Bellemain et al. 2006, Steyaert et al. 2014, Leclerc et al. 2017) and we suggest that SSI in polar bears may play a similar role.

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