Quantitative Genetics of Polar Bear (*Ursus maritimus*) Behaviours

by

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Abstract

Conflict plays a central role in sexual selection by shaping the behaviours and traits that contribute to reproductive success. It drives competition between individuals, influences mate choice and mating strategies, and ultimately shapes the evolution of sexual dimorphism, courtship displays, and other aspects of reproductive behaviour in many species. Informing conservation management strategies aiming at reducing human-wildlife conflicts involves understanding the interplay of genetic, social, and environmental effects on behavioural phenotypic variation. The objectives of this thesis were to investigate the heritable and non-heritable dynamics shaping complex human-polar bear (*Ursus maritimus*) conflict risk behaviour observed in Churchill, Manitoba. The study aims to understand the influence of climate change and human settlements on population-level behaviour, and understand the individual-level influences of innate, social, and remaining environmental cues driving polar bear conflict risk behaviour expressed by individuals within the Western Hudson Bay subpopulation. These concepts build on the foundations of quantitative genetics and animal behaviour, using data from an extensively monitored wild polar bear subpopulation near Churchill, Manitoba. The findings suggest that conflict risk behaviour is very closely tied to individuals' ability to survive and reproduce, and that polar bears have a high affinity for environmental learning and for avoiding serious conflicts. Dynamics in conflict risk behaviour over time underscore the influence of environmental stressors, contrasting with minimal cohort effects. Conservation management strategies focused on reducing human-wildlife conflicts should aim to improve the environmental conditions for wildlife by preserving habitat quality and connectivity.

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Chapter 1: Introduction

Individuals are driven by biological needs related to nutrition, reproduction, and maintaining homeostasis, which allow them to survive, reproduce, and grow. When individuals are stressed, they express the relative symptoms of their environment where they must either acclimatize, move, or die. How individuals automatically respond to perceived disruptions in an attempt for survival and well-being, and to return to stable internal conditions creates a divergence of possible expressions and impulses to fight or flight (Cannon 1915). The possibility for alternate expressions may only be as limited as an individual's current state of nervous system, developmental stage, experiences during development, and their populations' demographic history. A population's demographic history influences the evolution of stress response mechanisms, as higher population density may lead to heightened vigilance, increased cortisol levels, or more aggressive behaviours to manage the stress of more social interactions and competition. Furthermore, declines in population size can decrease genetic diversity, and epigenetic mechanisms can influence stress responses of future generations.

Genetic diversity is necessary for populations to adapt to changing environments and other selective pressures (Hoffmann 1997). This diversity primarily arises from the additive genetic effects within complex and quantitative traits, often influenced by many loci, mostly of small effect (Fisher 1930). Natural selection acts on individuals' traits (i.e., life-history, physiological, behavioural, and morphological), thereby shaping populations' demographic history (Darwin 1859). Given that selection is the differential of individuals' survival and reproduction within a population, traits most closely tied to an individual's fitness experience the strongest selection (Roff and Mousseau 1987). As a result, traits and beneficial alleles that

increase fitness become more common and less variable in the population, ultimately driving shifts in the genetic composition across generations.

While selection shapes long-term changes in the genetic predispositions of behaviours, an animal's ability to learn from environmental experiences facilitates rapid behavioural changes, which may be perpetuated through cultural transmission (El Mouden et al. 2014). The interplay between an individual's genetics and its environment contributes to the observable variation in a trait. Complex methods, including cross-fostering, can further disentangle the effects of maternal care and genetic inheritance, helping to reveal the nature of how traits develop and vary. Environmental influences (nuture) can include aspects such as exposure to toxins, availability of resources, cultural influences, and learning experiences, which can interact with genetic predispositions to influence the development of traits. Genetic diversity within individuals develops from random mutations and the inheritance of genes from their parents (i.e., genetic transmission), which are also affected by the parents' environmental conditions. Environmental conditions can directly shape individuals' traits, and these environmental effects are subject to social influences through cultural transmission across and between generations. Cultural transmission encompasses socially acquired responses to environmental cues, influenced by interactions and the direct effects of genetic and environmental factors passed down from previous generations (Boyd and Richerson 1988; Cavalli-Sforza and Feldman 1981).

Animal behaviours are motivated by biological needs related to nutrition, reproduction, and maintaining homeostasis. Consequently, an individual's physiology influences their behaviour, and in turn, their behaviour influences their physiology. These behaviours are the expressions of the responses to the stimuli an individual encounters, which are detected by the nervous system and executed through muscular actions. Critical developmental periods can

imprint long-lasting behavioural responses, exemplifying the interplay between learned and innate components (Nakamori et al. 2013). Innate behaviours are strongly influenced by genetic predispositions, are usually more developmentally fixed and genetically inherited (Tinbergen 1951). These behaviours are often essential for basic survival functions and many are stress responses.

Many complex behaviours are learned through recognition and communication, whether through solitary or social interactions, and therefore rely on individuals' morphology. Some behaviours develop gradually, while others are learned quickly, but the capacity for learning seems constrained by genetic predispositions (Cauchard et al. 2013; Morand-Ferron and Quinn 2015). Types of learned behaviours include imprinted behaviours, spatial learning, associative learning (classical and operant conditioning), and cognition. Spatial learning relies on an individual's memory of their environmental spatial structure. The nervous system processes information about the spatial relationships between individuals and their surroundings, forming a cognitive map that aids in selecting habitat for food, mates, and denning (Gaulin and Fitzgerald 1989). Associative learning allows individuals to link experiences, either through associating arbitrary stimuli with specific responses (classical conditioning) or by learning to associate their behaviour with positive or negative consequences through trial and error, influencing whether the behaviour is repeated or avoided (operant conditioning; Black et al. 1972). Cognition represents a more intricate form of learning, involving awareness, reasoning, recollection, and judgement (Rendell et al. 2011).

Learning occurs on an individual basis, with animals engaging in processes like recognition, communication, and problem-solving independently. Social learning introduces a collaborative aspect, where animals solve problems by observing, communicating, and imitating

behaviours with others (Heyes 1994). Social learning contributes to the development of culture - a system for transferring information through social interactions or teaching (Boyd and Richerson 1988). This cultural transfer of information can modify behavioural characteristics across generations, ultimately influencing the fitness of individuals within a population.

Evolution and Ecology of Study Species

Polar bears (*Ursus maritimus*) exhibit a circumpolar distribution and a southern range limited by the annual distribution of sea ice (Amstrup 2003; DeMaster and Stirling 1981). They are highly adapted to sea ice as it allows them to travel, hunt, mate, and in some areas den (Amstrup 2003; Florko et al. 2020). The ongoing consequences of climate change, including declines in sea ice duration, thickness, and extent (Stroeve and Notz 2018), pose a threat to the survival of the Western Hudson Bay subpopulation (Regehr et al. 2007). In Hudson Bay, an ice-free period typically occurs between July and November, during which polar bears fast ashore, relying on their fat reserves (Atkinson et al. 1996; Stirling et al. 1999). Warmer spring air temperatures and earlier sea ice break-up have extended the fasting period and shortened the springtime hyperphagic period, aligning with ringed seal (*Pusa hispida*) parturition (Cherry et al. 2013; Pilfold et al. 2012). Consequently, observed declines in polar bear body condition, reproduction, and population size have been linked to earlier sea ice break-up (Regehr et al. 2007; Stirling et al. 1999).

As large carnivores, female polar bears provide high levels of maternal care, produce few offspring, have delayed maturation, low population growth rates, specialized niche requirements, and intraspecific competition for resources (Derocher et al. 2010; Ramsay and Stirling 1986; Slater et al. 2010). These characteristics align with a slow life history strategy where female

polar bears prioritize the survival and well-being of individual offspring (Lack 1954). Young polar bears require extended maternal care to learn essential survival skills such as hunting and navigating ice floes as the Arctic environment is extremely harsh and challenging resulting in large home ranges (McCall et al. 2015). Furthermore, polar bear cubs need to accumulate significant fat reserves through nursing (Ramsay and Stirling 1986).

Polar bears in the Western Hudson Bay subpopulation exhibit a predominantly solitary nature on the ice, maintaining low densities except during the summer and autumn fasting period ashore (Derocher and Stirling 1990). The social structure of polar bears does not appear to be organized along clear maternal or paternal lines, as their behaviours are highly centered around individual survival, mating, and maternal care (Stirling et al. 2004). Pregnant females enter maternity dens beginning in August and September, emerging in early spring, followed by the mating season on the ice spanning late March to early June (Lunn et al. 2004). Within maternity dens, females give birth to one to three cubs between November and December (Derocher et al. 1992). Cubs in the Western Hudson Bay subpopulation typically are weaned at 2.5 years old (Ramsay and Stirling 1986), before which mothers are the sole providers of parental care (Derocher and Stirling 1996). Females typically have litters every three years (Lone et al. 2013; Ramsay and Stirling 1986). In the Western Hudson Bay subpopulation, litter size and cub survival are mass-dependent (Derocher et al. 1992; Derocher and Stirling 1996). During the period ashore, bears gather in higher densities, yet maintain spatial segregation by reproductive-age classes (Derocher and Stirling 1990; Ferguson et al. 1997; Latour 1981b; Taylor et al. 1985; Towns et al. 2010). This phase is characterized by reduced aggression for some groups, and playful interactions are not uncommon (Latour 1981a).

Foraging behaviours have evolved to optimize feeding efficiency, involving activities such as searching, recognizing, and capturing food. Theoretical frameworks, like the optimal foraging model, propose a trade-off that emphasizes the balancing of the costs and benefits of avoiding predation and obtaining food (Charnov 1976). This suggests that, especially in high population density environments, there can be advantages to expending energy over longer distances to access food. During the sea ice melt, polar bears in the Western Hudson Bay subpopulation exhibit seasonal migrations and strong site fidelity to specific coastal areas, such as Wapusk National Park and the Churchill Wildlife Management Area in Manitoba, Canada (Cherry et al. 2013; Stirling et al. 1999). The timing of migratory behaviour is linked to local concentrations of sea ice, such as sea ice break-up and its duration (Cherry et al. 2016). Homing ability is crucial for locating resources and optimizing space-use (Cherry et al. 2016; Derocher and Stirling 1990).

Male bears engage in intense intraspecific competition for access to females, often resulting in canine breakage, scarring, and other injuries (Derocher et al. 2010; Ramsay and Stirling 1986). Females with cubs often avoid male conspecifics due to associated risks of cannibalism and aggression (Taylor et al. 1985). While polar bears use various forms of communication like vocalizations and body language, they also use chemical signals through pedal scents to locate mates and avoid conspecifics (Owen et al. 2015). Male-biased dispersal may help alleviate intrasexual competition and contribute to inbreeding avoidance (Moore & Ali 1984; Pusey and Wolf 1996).

Heritability

The additive genetic variance underlying traits is shaped by a population's demographic history, resulting in population-specific heritability estimates (Wilson et al. 2010). Estimating the additive genetic variance relies on the observed phenotypic similarity among related individuals who experience similar environmental conditions, introducing variance from spatial autocorrelation within the heritable component (Stopher et al. 2012). As a result, it is difficult to separate genetic, environmental, and social effects on phenotypic variation to the same level of accuracy as cross fostering studies (Falconer and Mackay 1996; Kolliker et al. 2000). Here the heritable factors encompass both the contributions of genetic and cultural transmission to behavioural variation (Stopher et al. 2012). The remaining influence of non-inherited factors shaping behaviours encompasses the phenotypic plasticity of behaviours, reflecting individuals' learning ability from environmental cues.

The phenotypic variation observed in quantitative traits is shaped by a combination of genetic and environmental effects. Genetic effects include additive, non-additive, and maternal genetic variation (Falconer and Mackay 1996; Kruuk and Hadfield 2007). Additive genetic effects result from the contribution of many genes from both parents. Maternal genetic effects specifically originate from the genes transmitted by the mother, affecting an offspring's phenotype through epigenetic changes, imprinted genes, and mitochondrial DNA transmission (Watson et al. 2022; Wilson et al. 2005). Environmental effects encompass maternal environments (i.e., pre-, and post-natal care, including protection, social learning, and feeding), common environments (i.e., shared interactions within a group), permanent environments (i.e., long-term exposure to specific factors like habitat unique to individuals), and temporal effects (i.e., changes in seasons, weather, and food availability; Wilson et al. 2010).

Strong directional selection reduces the additive genetic variance in a trait, leading to low heritability estimates (Hoffmann 1997; Mousseau and Roff 1987). Thus, fitness-related traits, like life-history traits, typically exhibit low heritability, while behavioural traits exhibit moderate heritability, and morphological traits tend to have higher heritability (Dochtermann et al. 2019; Fisher 1930; Kruuk et al. 2000; Mousseau and Roff 1987). These patterns align with the expectation that beneficial alleles, which enhance population fitness, will increase in frequency, become less variable, and ultimately become fixed (Fisher 1930).

Thesis Outline

The objective of this thesis is to investigate the heritable and non-heritable dynamics shaping complex human-polar bear conflict risk behaviour observed in Churchill, Manitoba. I estimated yearly binary conflict risk behaviour (*not captured/captured*) and the relatedness of individuals within a 4634-individual pedigree. Conflict risk behaviour encompasses all capture related incidences, whether an individual was entering Churchill, live-trapped using baited culvert traps, as well as more serious encounters with humans. The pedigree spans births from 1966 to 2019 for the Western Hudson Bay polar bear subpopulation. I applied animal models, a type of mixed-effects model that fits population pedigrees and phenotypic traits (Wilson et al. 2010). From these models, I estimated the repeatability, heritability, and remaining environmental variance components underpinning conflict risk behaviour expressed by dependent and independent age classes. These methods were applied to generate overall estimates spanning four decades and for each of these decades. The study aims to understand the influence of climate change and settlements on population-level behaviour, and understand the individual-level influences of innate, social, and remaining environmental cues driving polar bear conflict risk behaviours

expressed by individuals within the Western Hudson Bay subpopulation. These concepts build on the foundations of quantitative genetics and animal behaviour, using data from an extensively monitored wild polar bear subpopulation near Churchill, Manitoba.

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Chapter 2: Heritability of polar bear (*Ursus maritimus*) conflict risk behaviour in the Western Hudson Bay subpopulation

Abstract

As human activities expand into once-remote areas such as the Arctic, interactions between humans and wildlife are becoming more common. Climate change-driven alterations to ecosystems are profoundly affecting habitat and resource availability for ice-dependent top predators like polar bears (*Ursus maritimus*). In the Western Hudson Bay subpopulation of polar bears, warmer spring air temperatures and earlier sea ice break-up have extended the fasting period. Lower body condition, a measure of relative fatness, and the presence of attractants in human settlements, has contributed to an increase in human-wildlife conflict. In this study I estimated yearly binary conflict risk behaviour (not captured/captured) and the relatedness of individuals within a 4634-individual pedigree sampled over six generations. I fit animal models to estimate the repeatability, heritability, and remaining environmental variance components underpinning conflict risk behaviour expressed by dependent (cubs-of-the-year, yearlings, and 2-year-olds; $\leq$ 2 years old) and independent (subadults and adults; $\geq$ 3 years old) age classes in Churchill, Manitoba. The findings suggest that conflict risk behaviour is very closely tied to individuals' ability to survive and reproduce (dependent: h^2=0.01; SE=5.4x10^{-5}; independent: h^2=0.07; SE=4.6x10^{-4}), and that polar bears have a high affinity for environmental learning and for avoiding serious conflicts. Dynamics in conflict risk behaviour over time underscore the influence of environmental stressors, contrasting with minimal cohort effects. Effective conservation strategies should prioritize habitat preservation and proactive management to mitigate human-wildlife conflicts.

Introduction

Human-wildlife interactions are becoming more frequent in once-remote areas like the Arctic due to the expansion of human activities and the changing dynamics of ecosystems driven by climate change (Heemskerk et al. 2020; Wilder et al. 2017). As human populations grow and industries seek new frontiers, we observe more opportunities and challenges regarding shipping, resource extraction, tourism, and settlements facilitated by the Arctic's increasing accessibility (Dawson et al. 2018; Kerr 2002; Smith and Stephenson 2013). Declines in genetic diversity resulting from human-wildlife interactions on contemporary timescales are expected to reduce populations' capacity to adapt to additional environmental change. However, genetic and environmental maternal effects can generate rapid phenotypic change in a population under selection through phenotypic plasticity and are essential for behavioural change at ecological timescales (Räsänen and Kruuk 2007).

Polar bears depend heavily on sea ice as it allows them to travel, hunt, mate, and in some areas den (Amstrup 2003; Florko et al. 2020). Thus, climate change and associated declines in sea ice duration, thickness, and extent (Stroeve and Notz 2018) threaten the persistence of polar bears (Regehr et al. 2007). An ice-free period typically takes place in Hudson Bay between July and November where polar bears fast ashore and depend on their fat reserves for survival (Atkinson et al. 1996; Stirling et al. 1999). Warmer spring air temperatures and earlier sea ice break-up have extended the fasting period and shortened the springtime hyperphagic period coinciding with ringed seal (*Pusa hispida*) parturition (Cherry et al. 2013; Pilfold et al. 2012; Stirling et al. 1999; Stirling and Archibald 1977). Consequently, declines in polar bear body condition, reproduction, and population size have been observed and linked to earlier sea ice break-up (Regehr et al. 2007; Stirling et al. 1999).

Between 1970 and 2018, prolonged ice-free conditions in the Hudson Bay have been linked to an increase in conflict risk behaviour by polar bears in Churchill, Manitoba (Heemskerk et al. 2020; Towns et al. 2009). The number of bears displaying conflict risk behaviour increased until 2001, and then stopped increasing likely due to changes in management protocols and population declines (Heemskerk et al. 2020). Polar bears most observed near settlements are subadult males, subadult females, and females with young, likely driven by nutritional stress and less access to higher quality food sources (Towns et al. 2009; Heemskerk et al. 2020).

To reduce human-polar bear conflicts, including minimizing the killing and disturbance of polar bears, protecting human safety and property, and preventing food conditioning in polar bears, the Polar Bear Alert Program and the Polar Bear Holding Facility were established in Churchill, Manitoba in 1970 (Kearney 1989; Struzik 2014). Most polar bear attacks in towns across their circumpolar distribution involve human-derived attractants and bears with below-average body condition (Wilder et al. 2017). Furthermore, polar bears near towns are more likely to associate humans and settlements with food due to past tourism practices, waste disposal sites, and community bone piles (Lunn and Stirling 1985). They are also more inclined to engage in risky interactions when nutritionally stressed (Towns et al. 2009; Wilder et al. 2017).

In this study, I unravel the relative contribution of heritable behaviours due to both genetic (developmental predispositions to behaviours) and cultural (socially learned behaviours) transgenerational effects, compared to the remaining non-heritable environmental effects shaping human-polar bear interactions in Churchill, Manitoba (remaining phenotypic plasticity). The study aims to understand the influence of climate change and settlements on population-level behaviour, and understand the individual-level influences of innate, social, and asocial

environmental cues driving polar bear conflict risk behaviours within the western Hudson Bay subpopulation. Using animal models with pedigree, I estimated the repeatability, heritability, and remaining environmental variance components underpinning conflict risk behaviour expressed by dependent and independent age classes.

Methods

Data Compilation and Spatiotemporal Scope

Overview

This study relies on the principles of quantitative genetics. I aim to understand the genetic, social, and environmental influences on relatively recent human-polar bear interactions in Churchill, Manitoba. I estimated yearly binary conflict risk behaviour (*not captured/captured*) and the relatedness of individuals within a 4634-individual pedigree. Conflict risk behaviour encompasses all capture related incidences, whether an individual was entering Churchill, live-trapped using baited culvert traps, as well as more serious encounters with humans. The pedigree spans births from 1966 to 2019 for the Western Hudson Bay polar bear subpopulation. I applied animal models, a type of mixed-effects model that fits population pedigrees and phenotypic traits (Wilson et al. 2010). From these models, I estimated the repeatability, heritability, and remaining environmental variance components underpinning conflict risk behaviour expressed by dependent and independent age classes. I estimated the repeatability $(h^2 + c^2)$ of conflict risk behaviour using the sum of the proportion of additive genetic (h^2) derived from pedigree data, and permanent environmental effects (c^2) derived from the repeated measures of individuals's observations over time. These methods were applied to generate overall estimates spanning four decades and for each of these decades. Ultimately, I aim to offer guidance enhancing our

understanding of conflict risk behaviour to foster the safety and well-being of wildlife and humans.

Capture Data

To quantify conflict risk behaviour, I used capture data provided by Manitoba conservation staff within the high-priority management area of the Polar Bear Alert Program around Churchill, Manitoba (Kearney 1989). The Polar Bear Alert Program collected capture data between 1966 and 2019, and the Manitoba Government provided this dataset. Manitoba conservation staff immobilized or live-trapped polar bears using baited culvert traps, and these bears were held at the Polar Bear Holding Facility (Stirling et al. 1989). While in the facility, polar bears receive water, snow, antibiotics for infections, and are only fed if they are a lone cub-of-the-year to avoid food conditioning which very infrequently (Pilfold et al. 2016). The bears are also weighed, measured, assessed for body condition, given a unique identification number, and classified by sex and age class (Pilfold et al. 2016; Stirling et al. 2008). For individuals (i.e., cubs-of-the-year, yearlings, or 2-year-olds) recorded in the capture dataset that had not yet been sampled in the population, their age was visually determined. Older individuals and those sampled during population sampling had their age determined based on cementum annulus deposition from an extracted vestigial premolar tooth (Calvert and Ramsay 1998). Adult females with offspring are relocated as soon as possible, while other individuals are held for at least 30 days or until sea ice freeze-up for their first capture and until freeze-up if captured again in the same year (Pilfold et al. 2016).

Conflict Risk Behaviour Data

From the capture dataset, I generated a binary dataset for conflict risk behaviour (*not captured/captured*). I excluded records for natural death observations from the conflict risk

behaviour dataset. For each individual with a capture history, I created an observation indicating whether they were captured or not captured for each year, starting from each individual's birth year up until the year of their last recorded capture observation. Therefore, all individuals are considered problem bears and here I am assessing the variation in the behaviour. The animal models require that all individuals included in the capture data be included as offspring in the pedigree data. To maximize the available capture data and to meet this requirement, I incorporated 338 individuals with capture data into the pedigree with unknown parentage. The first capture was recorded in 1966, and the dataset was artificially truncated to only include observations on or before 2010 to avoid biasing the dataset with younger individuals with incomplete capture histories. Therefore, only individuals born between 1966 and 2010 were included in the dataset. Although the original capture data extends to 2019, individuals born closer to 2019 would have few available capture data.

Pedigree Data

Environment and Climate Change Canada provided pedigree data for the Western Hudson Bay polar bear subpopulation that was constructed using field and genetic data from individuals sampled in northeastern Manitoba near Churchill, Canada. Field sampling data offered dam-offspring associations, while parentage analyses using multi-locus microsatellites to genotype individuals offered additional linkage information (Malenfant et al. 2016). Between mid-July and late December beginning in 1966, Environment and Climate Change Canada handled and sampled polar bears of various ages and sexes. From 1980 to 2019 (excluding 1985 and 1986), additional sampling of only adult females and their cubs-of-the-year occurred in February and March. The pedigree contains 4634 polar bears (443 sires, 923 dams, and 1130 founders i.e., individuals of unknown parentage) from over six generations that were sampled between 1966

and 2019. An earlier version of this polar bear pedigree for 4449 individuals sampled between 1966 and 2011 is visualized in Malenfant et al. (2016). The pedigree reflects a well connected relatedness network despite being incomplete. Capture and handling protocols received annual approval from Environment and Climate Change Canada's Prairie and Northern Region Animal Care Committee. The Province of Manitoba and Parks Canada also issued annual wildlife research permits for the research.

Repeatability and Heritability

I studied polar bear conflict risk behaviour (*not captured/captured*) as a trait for dependent age classes (cubs-of-the-year, yearlings, and 2-year-olds; ≤ 2 years old) and independent age classes (subadults and adults; ≥ 3 years old). This differentiation was necessary as polar bears are reliant on their mother for survival until they reach 3 years of age. To estimate the repeatability and heritability of polar bear conflict risk behaviour, I used univariate animal models, a type of generalized linear mixed model that uses population pedigree and phenotypic data (Wilson et al. 2010). I used the pedigree data to create an inverse genetic relatedness matrix and fit it as the random effect '*animal*' to estimate additive genetic variance (V_A). I partitioned the phenotypic variance (V_P) of conflict risk behaviour into additive genetic variance (V_A) and residual variance (V_R), which is interpreted as environmental effects and can be further partitioned by including other effects in the model. Here, the narrow-sense heritability (h^2) is the proportion of variance in a trait explained by the random effect '*animal*' (i.e., additive genetic variance) relative to the total phenotypic variance.

$$h^2 = \frac{V_A}{V_P} = \frac{V_A}{V_A + V_R} = \frac{V_A}{V_A + V_{PE} + V_M + V_{YObs} + V_{YBirth} + V_R} \quad (1)$$

I included random effects to estimate variance components: V_A=additive genetic '*animal*', V_{PE}=permanent environmental '*ID*', V_M=maternal '*dam*' (i.e., identity of individual's mother), V_{YObs}=annual '*year of observation*', V_{YBirth}=cohort '*year of birth*', and V_R=residual environmental effects '*error*' (Table 1). I included year of observation and year of birth as categorical factors. I did not include sex and age as fixed effects for the following reasons: (1) avoid issues of multicollinearity with maternal effects and cohort effects, (2) increase the interpretability of conflict risk behaviour heritability, and (3) because the models assume that there are no average genetic differences between social groups within the population. Thus, the models assume that the probability of being captured is the same for all individuals. Future studies should address this assumption by including more detailed capture probabilities as some individuals may become food conditioned to trapping practices. Furthermore, subadult males, subadult females, and females with young are more likely to be involved in conflicts (Towns et al. 2009; Heemskerk et al. 2020). Age, in relation to bears being dependent or independent from their mother's care, was addressed through separate models. The inclusion of '*dam*' as a random effect accounted for nonindependence in sibling observations for both dependent and independent age class models. It also accounted for nonindependence in mother-offspring observations for dependent age classes.

Nonindependence in individuals with repeated measures of conflict risk behaviour was controlled for by fitting '*ID*' as a random effect, which is also interpreted as permanent environmental effects. Permanent environmental effects are unique to individuals and include environmental effects from long-term exposure to specific factors, such as habitat. Repeatability $(h^2 + c^2)$ is estimated as the sum of the proportion of additive genetic (h^2) and permanent environmental effects (c^2). Repeatability of a trait signifies the proportion of phenotypic variance

attributed to individual differences, indicating how consistent and predictable the trait is within individuals over time (Falconer and Mackay 1996; Nakagawa and Schielzeth 2010). Natural selection acts on heritable traits that affect an individual's fitness, or its ability to survive and reproduce in a given environment. For effective selection, a consistent relationship between a behavioural trait and an individual's fitness is necessary. Repeatability sets the upper limit for heritability and can be influenced by samle size. In this study, the opportunity for repeated observations is inherently limited due to the relatively short period that cubs remain with their mothers. This constraint on sample size can affect the precision of repeatability estimates (Jablonszky and Garamszegi 2024). Smaller sample sizes can lead to greater within-individual variance and potentially bias heritability estimates, underscoring the need for careful consideration of study design and sample collection in behavioural research.

I ran animal models in the R (V. 4.1.3; R Core Team 2023) package *MCMCglmm* (V. 2.35; Hadfield 2010). These models were presented across and for each of the four decades (1970, 1980, 1990, 2000) for both dependent and independent age classes (Table 1). The analysis of variance components over time was restricted to these four decades after the capture data was truncated. The *MCMCglmm* package allows incomplete pedigrees and uses Bayesian inference with Markov chain Monte Carlo methods. To account for the binomial distribution of conflict risk behaviour (*not captured/captured*), I used the *threshold* family in *MCMCglmm* (de Villemereuil 2018; Hadfield and O'Hara 2015). An inverse-Gamma distribution was used for estimating the random effect variances, except for the residual variance (V_R), which was held fixed at a value of 1 (de Villemereuil 2012, 2018). All models were run for 2,000,000 iterations, with a burn-in of 20,000 iterations, saving samples every 100 iterations, and the effective sample sizes surpassed 8,000 iterations. Chains were visually inspected and passed the Heidelberg

stationary test to ensure convergence. Therefore, the analysis proceeded only after confirming that the samples were stable and representative of the desired distribution, which is critical for the reliability of the results.

Summary Statistics

The capture dataset used for the overall independent age classes animal model contained 361 individuals, all of which had known maternal lineages, resulting in a total of 2246 observations of conflict risk behaviour (*not captured/captured*; Table 2). Of these individuals, 113, or approximately 31%, exhibited repeat conflict risk behaviour as they had capture histories with more than one capture observation. The mean number of capture observations per individual in this model was 1.5 captures over their capture histories, with a range of 0 to 8 captures. The mean number of not captured observations per individual was 4.7 non-captures over their capture histories, with a range of 0 to 26 not captured observations. Approximately 24% of the observations pertained to captured observations. The capture dataset included 145 females and 216 males, representing approximately 40% and 60% of the sample, respectively. The mean day of capture observations was the 294th day of the year (October 21st). Year of birth spanned from 1967 to 2007, while the year of observation spanned from 1970 to 2010. Age at capture ranged from 3 to 29 years old for independent age classes (subadults and adults; $\geq$ 3 years old).

The capture dataset used for the overall dependent age classes animal model contained 787 individuals and a total of 1999 observations of conflict risk behaviour (*not captured/captured*; Table 2). Of these individuals, 81, or approximately 10%, exhibited repeat conflict risk behaviour as they had capture histories with more than one capture observation. The mean number of capture observations per individual in this model was 0.79 over their capture histories, with a range of 0 to 3 captures. The mean number of not captured observations was 1.7

non-captures over their capture histories, with a range of 0 to 3 not captured observations. Approximately 31% of the observations pertained to captured observations. The capture dataset included 362 females and 425 males, representing approximately 46% and 54% of the sample, respectively. The mean day of capture observations was the 295th day of the year (October 22nd). Year of birth and year of observation spanned from 1967 to 2010. Age at capture ranged from 0 to 2 years old for dependent age classes (cubs-of-the-year, yearlings, and 2-year-olds; $\leq$ 2 years old).

Results

Repeatability and Heritability

Independent Age Classes

Conflict risk behaviour expressed by independent bears across four decades (1970, 1980, 1990, 2000) was moderately repeatable, with individual differences accounting for 23% of the observed phenotypic variation. Repeatability is an indication of how consistent and predictable a trait is within individuals over time. Therefore, individual reponses over time were somewhat consistent. Repeated behaviour encompasses the variance due to the heritable transmission of genetic and social influences as well as the unique environmental conditions an individual encounters throughout its life. Here, the social influences refer more towards maternal effects as well as some sibling effects.

Heritable differences in independent bears expressing conflict risk behaviour contributed to 7% of the observed phenotypic variation, leaving the remaining 93% attributed to non-heritable differences. Thus, the behaviour is highly influenced by environmental cues and displays high levels of phenotypic plasticity. In contrast, the influence of heritable genetic and social effects on conflict risk behaviour appears relatively minimal, as reflected in Table 3 and

Fig 1. For independent age classes, mean estimates of the variance proportions in conflict risk behaviour were as follows: heritability (h^2=0.07; SE=4.6x10^{-4}), permanent environmental for individuals (c^2=0.16; SE=5.5x10^{-4}), maternal (m^2=0.05; SE=3.1x10^{-4}), annual (y_{Obs}^2=0.15; SE=3.6x10^{-4}), cohort (y_{Birth}^2=0.03; SE=1.6x10^{-4}), and residual variance for the remaining common environmental effects (ε^2=0.54; SE=3.4x10^{-4}; Table 2; Table 3; Fig 1).

Dependent Age Classes

Dependent individuals reliant on their mother's care exhibit a more direct influence of maternal behaviour and complete surrender to phenotypic plasticity, with 99% of behavioural differences attributed to non-heritable differences. This is in contrast to minimal individual effects during this developmental stage. This aligns with expectations, as maternal effects are anticipated to exert a more immediate influence during this period. This is evident in the extremely low repeatability estimate, where individual differences account for only 2% of the observed phenotypic variation. For dependent age classes, the mean estimates of the proportions of variance in conflict risk behaviour were as follows: heritability (h^2=0.01; SE=5.4x10^{-5}), permanent environmental for individuals (c^2=0.01; SE=3.7x10^{-5}), maternal (m^2=0.15; SE=2.2x10^{-4}), annual (y_{Obs}^2=0.18; SE=3.3x10^{-4}), cohort (y_{Birth}^2=0.01; SE=7.6x10^{-5}), and residual variance for the remaining common environmental effects (ε^2=0.65; SE=3.4x10^{-4}; Table 2; Table 3; Fig 1).

Variance Components Over Time

Independent Age Classes

Dynamics in the expression of conflict risk behaviour by dependent (Table 4; Table 5; Fig 2) and independent (Table 6; Table 7; Fig 3) individuals were shaped by varying influences of genetic, environmental, and social factors over time. Independent individuals exhibited moderate levels

of genetic, social, and individual-level effects. Maternal effects peaked in the 1980s, while annual effects were prominent in the 1970s and diminished over time. Cohort effects remained consistently low. Although genetic and individual effects were more pronounced in independent age classes compared to dependent age classes over time, the relative environmental and genetic effects generally displayed consistency with some fluctuations.

Dependent Age Classes

The influence of individual effects for dependent individuals decreased over time, approaching negligible levels. Maternal effects remained moderate, with their highest contribution to the variance of conflict risk behaviour observed in the 1980s. Annual effects were minimal in the 1970s but generally gained influence in the subsequent decades, particularly in the 1980s and 1990s. Cohort effects exhibited an upward trend, becoming substantial in the 1990s and 2000s. Overall, non-heritable environmental effects increased, while heritable genetic and social effects decreased over time for conflict risk behaviour expressed by dependent age classes.

Discussion

The low heritability of conflict risk behaviour suggests that avoiding serious conflicts confers greater individual reproductive success than other behavioural alternatives in this population. This suggests that conflict risk behaviour has been shaped by strong selective pressures reducing genetic variation, driven by the benefits of intraspecific competition and the risks associated with conflicts, including death from previous hunting pressures. Female reproductive success is limited by resource availability, while male reproductive success is primarily limited by access to potential mates (Trivers 1972). Individuals prioritize their own lifetime reproductive success

over the survival and well-being of the species or group (Davies 2012). Thus, maximizing their population's birth rate from a selfish perspective, as individual selection is more powerful than group selection.

The moderate repeatability of conflict risk behaviour suggests that bears exposed to more environmental conditioning related to human settlements over their lifetimes would likely have more learning opportunities associated with those behaviours. For instance, the return of weaned cubs to the Churchill dump indicates that these bears have likely learned its location from their mothers (Lunn and Stirling 1985). Cultural transmission of the use of human food sources has also been observed in black bears (*Ursus americanus*; Mazur and Seher 2008). However, the low heritability estimate suggests minimal cultural transmission in this population. Furthermore, this cultural transmission is likely primarily due to maternal transmission because the social structure of polar bears does not appear to be organized along clear maternal or paternal lines, as their behaviours are highly centered around individual survival, mating, and maternal care (Stirling et al. 2004). Bears may also learn the behaviour from other bears or through positive reinforcement of investigative behaviours.

Higher incidences involving subadult males, subadult females, and females with young (Towns et al. 2009; Heemskerk et al. 2020) are likely influenced by shared environmental stimuli and biological needs associated with individuals' reproductive-age class. Among these groups, males typically exhibit more aggressive behaviour, while subadult bears may display less caution compared to older and more experienced bears (Ramsay and Stirling 1986). This may be attributed to subadults facing more nutritional stress than older bears as the development of body size, hunting skills, and experience requires time (Stirling and Latour 1978). Furthermore, higher testosterone levels in males is linked to more aggressive behaviours. Handling in Churchill was

previously linked to a higher recapture probability and lower survival, likely driven by previous food rewards, being in poor nutritional condition, or because these bears were subject to being killed by humans near settlements (Lunn and Stirling 1985; Regehr et al. 2007).

The low heritability of conflict risk behaviour suggests that this behavioural trait is more closely tied to individuals' fitness compared to other behavioural traits which tend to have moderate heritability estimates (Fisher 1930; Kruuk et al. 2000; Mousseau and Roff 1987). This implies that conflict risk behaviour has experienced strong selection likely due to the costs and benefits associated with intense intraspecific competition between large adult males for access to females (Derocher et al. 2010; Ramsay and Stirling 1986). Females with cubs also experience high costs associated with conflict risk behaviour as they risk cannibalism and aggression by male conspecifics (Taylor et al. 1985). Due to the complexity of conflict risk behaviour, there has likely been destabilizing selection on traits contributing to conflict risk which may preserve variation; however, it appears that selection has mostly resulted in a reduction in genetic variability over time. While the additive genetic variance that underlies a population's fitness provides a direct estimation of its adaptive potential (Young et al. 2023), estimates of additive genetic variance for behavioural traits are correlated with a population's ability to survive and reproduce.

The average capture date for independent bears was October 21st, which corresponds with the expectation that nutritionally stressed bears nearing the end of the fasting period pose a greater risk to humans than bears during good sea-ice conditions (Stenhouse et al. 1988; Wilder et al. 2017). Thus, engaging in conflict with humans may occur when individuals are highly motivated by food seeking behaviour. Annual effects emerged as a substantial source of variation in conflict risk behaviour for all age classes compared to cohort effects, which aligns with

expectations that climate change is a major stressor. Sea ice dynamics underwent significant changes in the 1990s, with earlier break-up and later freeze-up of ice observed in many Arctic regions (Stirling et al. 1999). These changes directly influenced polar bear habitat and foraging opportunities, particularly for cohorts born during this period. This was evident in the high variance observed in annual and cohort effects (Figure 2). Polar bear cubs born in years with reduced sea ice coverage may have experienced altered maternal care strategies and nutritional stress, potentially influencing their development and behaviour.

Furthermore, generational effects felt by settlements or other stressors may be relatively minor or captured within the heritable component. This is expected due to the lack of strong matrilineal structure in the population and due to the severity of climate change on individuals meeting their energetic needs. High maternal effects observed for dependent age classes aligns with expectations that maternal behaviour is highly responsible for individuals' behaviours during this developmental period.

Individuals' biological needs drive behavioural expressions that are heavily influenced by their relative environmental conditions, developmental stage, and demographic history. Ultimately creating complex and repeatable behavioural patterns through space and time. The finding that polar bears have a high affinity for environmental learning and for avoiding conflicts aligns with theories of natural selection and life history strategies. Individuals' behaviours related to conflict can be influenced by inheritance, social learning, and asocial learning. Such learning is correlated with polar bears' large brain size, well-developed memory, behavioural plasticity, curiosity, and opportunism (Ramsay and Stirling 1986). While many aspects of polar bear behaviour are driven by innate, evolutionary adaptations, interactions with humans can also lead to learned behaviors that contribute to conflict. For instance, polar bears have evolved

strong predatory instincts adapted to hunting seals on sea ice. This includes skills for stalking prey, and when these innate hunting instincts come into contact with human environments, polar bears may exhibit aggressive behaviours as they seek food. Furthermore, polar bears are naturally curious animals and will investigate novel environments. This curiosity can lead them to explore human settlements, where they might come into conflict with people. They also have a strong innate drive to maintain homeostasis and in the absence of natural prey, they may venture into human settlements in search of food.

Restricted movement within their home ranges compared to other subpopulations, stemming from season-specific area fidelity, may limit their ability to acclimitize to new social dynamics despite displaying high behavioural plasticity (Cherry et al. 2016; Malenfant et al. 2016; Mauritzen et al. 2001; Paetkau et al. 1995). Perhaps their status as top predators gives them great flexibility and safety to primarily use asocial environmental learning (trial and error) to nagivate challenges rapidly. But yet their highly specialized nature may present a major constraint in their evolution in light of the challenges that climate change and settlements bring to this population.

Conservation management strategies focused on reducing human-wildlife conflicts should aim to improve the environmental conditions for wildlife by addressing the risks of climate change, preserving habitat quality, and connectivity. Potential strategies to reduce human-wildlife conflict include aversive conditioning, temporary housing, relocation, and lethal management (Gillin et al. 1994; Heemskerk et al. 2020; Regehr et al. 2007; Towns et al. 2009). Although their effectiveness is limited and proactive management strategies should be prioritized to prevent food-conditioning (Hopkins and Kalinowski 2013; Mazur 2010; Treves and Karanth 2003). The use of real-time satellite telemetry data to alert communities of approaching bears

and drones as a deterrent may provide helpful tools in mitigating human-bear conflicts (Jagielski et al. 2022; Laidre et al. 2022). Focusing on meeting the biological needs of individuals, species, and populations is expected to promote well-being and diminish the expression of survival-oriented behaviours.

Table 1. Univariate animal models to estimate repeatability and heritability of polar bear conflict risk behaviour (*not captured/captured*) for dependent (cubs-of-the-year, yearlings, and 2-year-olds; ≤ 2 years old) and independent age classes (subadults and adults; ≥ 3 years old). Random effects were included in the intercept (μ - population mean) only models to estimate variance components including additive genetic '*animal*', permanent environmental '*ID*', maternal '*dam*' (i.e., identity of individual's mother), annual '*year of observation*', and cohort effects '*year of birth*'. Year of observation and year of birth were included as categorical factors.

Age classes	**Response**	**Fixed effects**	**Random effects**
Dependent	Conflict risk behaviour (0,1)	μ	animal, ID, dam, year of observation, year of birth
Independent	Conflict risk behaviour (0,1)	μ	animal, ID, dam, year of observation, year of birth

Table 2. Phenotypic means, variances, and estimated random-effect sizes for polar bear conflict risk behaviour (*not captured/captured*) animal models for dependent (cubs-of-the-year, yearlings, and 2-year-olds; ≤ 2 years old) and independent age classes (subadults and adults; ≥ 3 years old). N_{ind} indicates the number of individuals and N_{obs} indicates the total number of observations for conflict behaviour. V_{Obs} is the variance in observations and V_P is the total phenotypic variance and is the sum of the variance components.Variance components; V_A=additive genetic '*animal*', V_{PE}=permanent environmental '*ID*', V_M=maternal '*dam*' (i.e., identity of individual's mother), V_{YObs}=annual '*year of observation*', V_{YBirth}=cohort effects '*year of birth*', and V_R=residual.Values in parentheses represent standard deviations (SD) or standard errors (SE).

Age classes	$\mathbf{N_{Ind}}$	$\boldsymbol{N_{Obs}}$	**Mean (SD)**	$\boldsymbol{V_{Obs}}$	$\boldsymbol{V_P}$ **(SE)**	$\boldsymbol{V_A}$	$\boldsymbol{V_{PE}}$	$\boldsymbol{V_M}$	$\boldsymbol{V_{YObs}}$	$\boldsymbol{V_{YBirth}}$	$\boldsymbol{V_R}$
Dependent	787	1999	0.31 (0.46)	0.22	1.55 ($7.5x10^{-4}$)	0.01	0.01	0.23	0.29	0.01	1
Independent	361	2246	0.24 (0.43)	0.18	1.86 ($1.8x10^{-3}$)	0.13	0.31	0.09	0.28	0.05	1

Table 3. Random-effect sizes for polar bear conflict risk behaviour (*not captured/captured*) animal models for dependent (cubs-of-the-year, yearlings, and 2-year-olds; ≤ 2 years old) and independent age classes (subadults and adults; ≥ 3 years old), estimated as proportions of phenotypic variation (V_P) explained by each source of variation (i.e., V_A; V_{PE}; V_M; V_{YObs}; V_{YBirth}; V_R). h^2=heritability, c^2=permanent environmental, m^2=maternal, $y_{Obs}{}^2$=year of observation, $y_{Birth}{}^2$=cohort, ε^2=residual variance, and ($h^2 + c^2$)=repeatability. Values in parentheses represent standard errors.

Age classes	h^2	c^2	m^2	$y_{Obs}{}^2$	$y_{Birth}{}^2$	ε^2	$(h^2 + c^2)$
Dependent	0.01 ($5.4\text{x}10^{-5}$)	0.01 ($3.7\text{x}10^{-5}$)	0.15 ($2.2\text{x}10^{-4}$)	0.18 ($3.3\text{x}10^{-4}$)	0.01 ($7.6\text{x}10^{-5}$)	0.65 ($3.4\text{x}10^{-4}$)	0.02 ($6.6\text{x}10^{-5}$)
Independent	0.07 ($4.6\text{x}10^{-4}$)	0.16 ($5.5\text{x}10^{-4}$)	0.05 ($3.1\text{x}10^{-4}$)	0.15 ($3.6\text{x}10^{-4}$)	0.03 ($1.6\text{x}10^{-4}$)	0.54 ($3.4\text{x}10^{-4}$)	0.23 ($7.7\text{x}10^{-4}$)

Table 4. Phenotypic means, variances, and estimated random-effect sizes for polar bear conflict risk behaviour (*not captured/captured*) animal models for dependent age classes (cubs-of-the-year, yearlings, and 2-year-olds; ≤ 2 years old) by decade. N_{ind} indicates the number of individuals and N_{obs} indicates the total number of observations for conflict risk behaviour. V_{Obs} is the variance in observations and V_P is the total phenotypic variance and is the sum of the variance components.Variance components; V_A=additive genetic '*animal*', V_{PE}=permanent environmental '*ID*', V_M=maternal '*dam*' (i.e., identity of individual's mother), V_{YObs}=annual '*year of observation*', V_{YBirth}=cohort effects '*year of birth*', and V_R=residual.Values in parentheses represent standard deviations (SD) or standard errors (SE).

Decade	$\mathbf{N_{Ind}}$	$\boldsymbol{N_{Obs}}$	**Mean (SD)**	$\boldsymbol{V_{Obs}}$	$\boldsymbol{V_P}$ **(SE)**	$\boldsymbol{V_A}$	$\boldsymbol{V_{PE}}$	$\boldsymbol{V_M}$	$\boldsymbol{V_{YObs}}$	$\boldsymbol{V_{YBirth}}$	$\boldsymbol{V_R}$
1970-1979	32	67	0.22 (0.42)	0.18	2.77 (0.01)	0.46	0.45	0.37	0.18	0.31	1
1980-1989	176	427	0.24 (0.43)	0.18	2.76 (0.01)	0.06	0.04	0.47	0.93	0.26	1
1990-1999	358	833	0.31 (0.46)	0.22	10.09 (0.04)	0.06	0.04	0.68	4.19	4.12	1
2000-2009	283	621	0.38 (0.49)	0.24	3.38 (0.02)	0.07	0.04	0.34	0.68	1.25	1

Table 5. Random-effect sizes for polar bear conflict risk behaviour (*not captured/captured*) animal models for dependent age classes (cubs-of-the-year, yearlings, and 2-year-olds; ≤ 2 years old) by decade, estimated as proportions of phenotypic variation (V_P) explained by each source of variation (i.e., V_A; V_{PE}; V_M; V_{YObs}; V_{YBirth}; V_R). h^2=heritability, c^2=permanent environmental, m^2=maternal, $y_{Obs}{}^2$=year of observation, $y_{Birth}{}^2$=cohort, ε^2=residual variance, and ($h^2 + c^2$)=repeatability. Values in parentheses represent standard errors.

Decade	h^2	c^2	m^2	$y_{Obs}{}^2$	$y_{Birth}{}^2$	ε^2	$(h^2 + c^2)$
1970-1979	0.15 (2.4×10^{-3})	0.14 (2.3×10^{-3})	0.12 (2.2×10^{-3})	0.06 (1.3×10^{-3})	0.10 (1.9×10^{-3})	0.42 (2.6×10^{-3})	0.29 (3.4×10^{-3})
1980-1989	0.02 (5.0×10^{-4})	0.02 (3.6×10^{-4})	0.17 (1.2×10^{-3})	0.31 (1.9×10^{-3})	0.08 (1.3×10^{-3})	0.40 (1.7×10^{-3})	0.04 (6.2×10^{-4})
1990-1999	0.01 (1.3×10^{-4})	0.00 (8.7×10^{-5})	0.07 (3.9×10^{-4})	0.41 (1.6×10^{-3})	0.40 (1.6×10^{-3})	0.11 (5.3×10^{-4})	0.01 (1.6×10^{-4})
2000-2009	0.02 (4.2×10^{-4})	0.01 (2.6×10^{-4})	0.11 (8.2×10^{-4})	0.19 (1.5×10^{-3})	0.34 (2.2×10^{-3})	0.33 (1.6×10^{-3})	0.03 (4.9×10^{-4})

Table 6. Phenotypic means, variances, and estimated random-effect sizes for polar bear conflict risk behaviour (*not captured/captured*) animal models for independent age classes (subadults and adults; ≥ 3 years old) by decade. N_{ind} indicates the number of individuals and N_{obs} indicates the total number of observations for conflict risk behaviour. V_{Obs} is the variance in observations and V_P is the total phenotypic variance and is the sum of the variance components.Variance components; V_A=additive genetic '*animal*', V_{PE}=permanent environmental '*ID*', V_M=maternal '*dam*' (i.e., identity of individual's mother), V_{YObs}=annual '*year of observation*', V_{YBirth}=cohort effects '*year of birth*', and V_R=residual.Values in parentheses represent standard deviations (SD) or standard errors (SE).

Decade	**N_{Ind}**	**N_{Obs}**	**Mean (SD)**	**V_{Obs}**	**V_P (SE)**	**V_A**	**V_{PE}**	**V_M**	**V_{YObs}**	**V_{YBirth}**	**V_R**
1970-1979	20	68	0.29 (0.46)	0.21	3.19 (0.02)	0.25	0.24	0.28	1.20	0.22	1
1980-1989	85	409	0.12 (0.33)	0.11	3.34 (0.02)	0.66	0.48	0.52	0.51	0.17	1
1990-1999	211	885	0.26 (0.44)	0.19	1.86 (0.01)	0.16	0.28	0.10	0.20	0.12	1
2000-2009	199	815	0.29 (0.45)	0.21	1.75 (0.01)	0.24	0.24	0.08	0.12	0.07	1

Table 7. Random-effect sizes for polar bear conflict risk behaviour (*not captured/captured*) animal models for independent age classes (subadults and adults; ≥ 3 years old) by decade, estimated as proportions of phenotypic variation (V_P) explained by each source of variation (i.e., V_A; V_{PE}; V_M; V_{YObs}; V_{YBirth}; V_R). h^2=heritability, c^2=permanent environmental, m^2=maternal, y_{Obs}^2=year of observation, y_{Birth}^2=cohort, ε^2=residual variance, and ($h^2 + c^2$)=repeatability. Values in parentheses represent standard errors.

Decade	h^2	c^2	m^2	y_{Obs}^2	y_{Birth}^2	ε^2	$(h^2 + c^2)$
1970-1979	0.07 ($1.4x10^{-3}$)	0.07 ($1.4x10^{-3}$)	0.09 ($1.5x10^{-3}$)	0.34 ($2.7x10^{-3}$)	0.06 ($1.4x10^{-3}$)	0.36 ($2.1x10^{-3}$)	0.14 ($2.0x10^{-3}$)
1980-1989	0.20 ($2.5x10^{-3}$)	0.14 ($2.1x10^{-3}$)	0.05 ($3.1x10^{-4}$)	0.15 ($3.6x10^{-4}$)	0.03 ($1.6x10^{-4}$)	0.54 ($3.4x10^{-4}$)	0.34 ($3.3x10^{-3}$)
1990-1999	0.08 ($1.3x10^{-3}$)	0.15 ($1.5x10^{-3}$)	0.06 ($8.9x10^{-3}$)	0.10 ($1.1x10^{-3}$)	0.06 ($7.2x10^{-3}$)	0.55 ($1.2x10^{-3}$)	0.23 ($3.3x10^{-3}$)
2000-2009	0.13 ($1.6x10^{-3}$)	0.14 ($1.6x10^{-3}$)	0.04 ($8.0x10^{-4}$)	0.07 ($6.8x10^{-3}$)	0.04 ($5.4x10^{-4}$)	0.58 ($1.0x10^{-3}$)	0.27 ($2.3 x10^{-3}$)

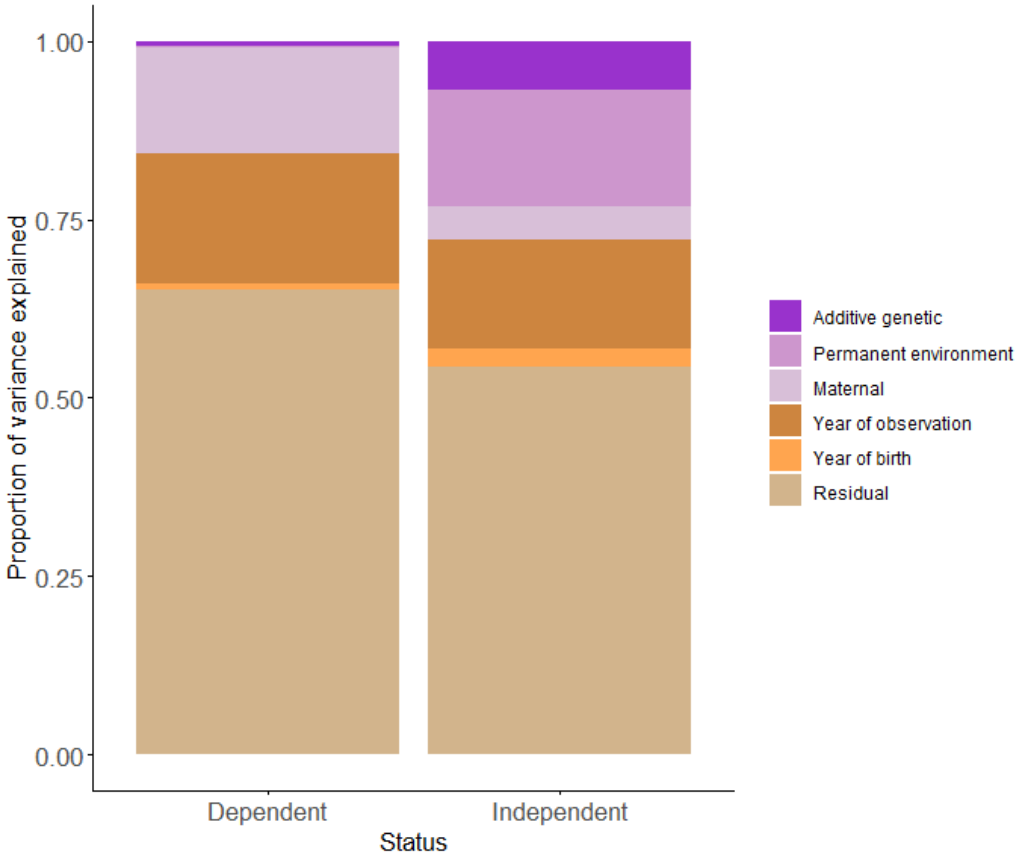

Figure 1. Proportion of variance explained by random effects for polar bear conflict risk behaviour (*not captured/captured*) for dependent and independent age classes in the Western Hudson Bay subpopulation observed in Churchill, Manitoba between 1970 and 2010.

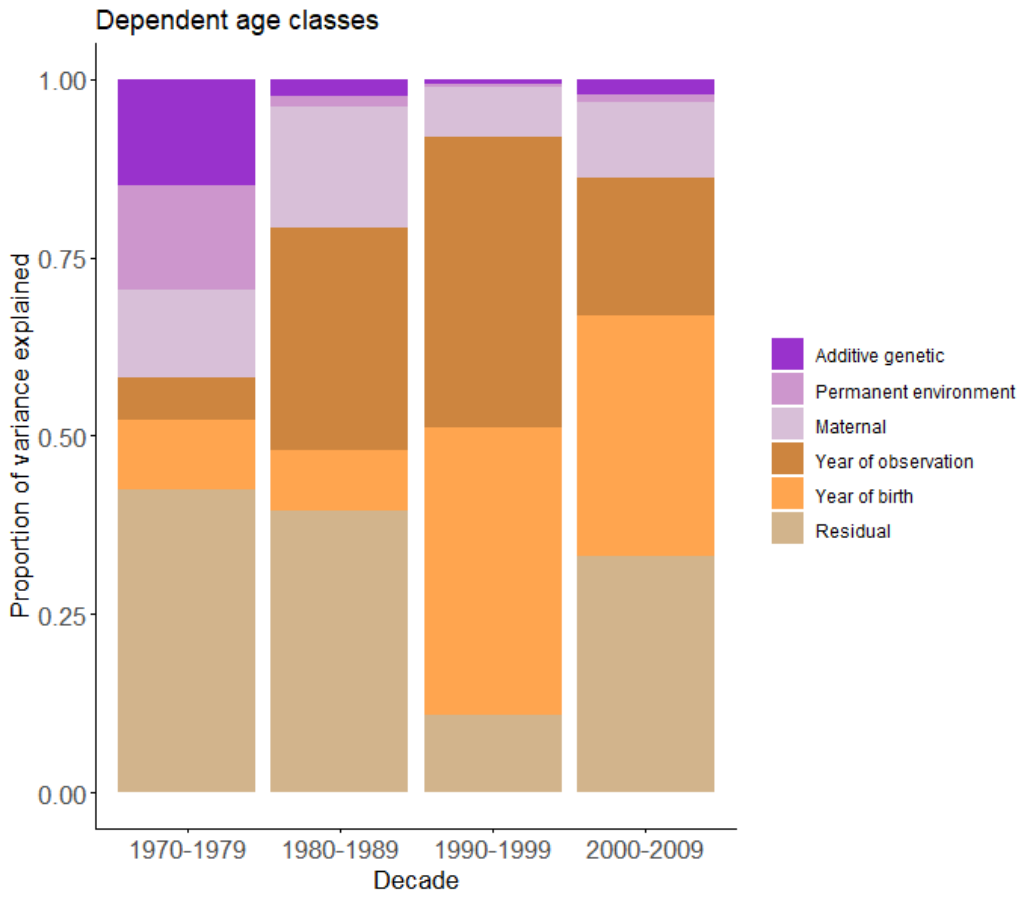

Figure 2. Proportion of variance explained by random effects for polar bear conflict risk behaviour (*not captured/captured*) for dependent age classes in the Western Hudson Bay subpopulation observed in Churchill, Manitoba by decade between 1970 and 2010.

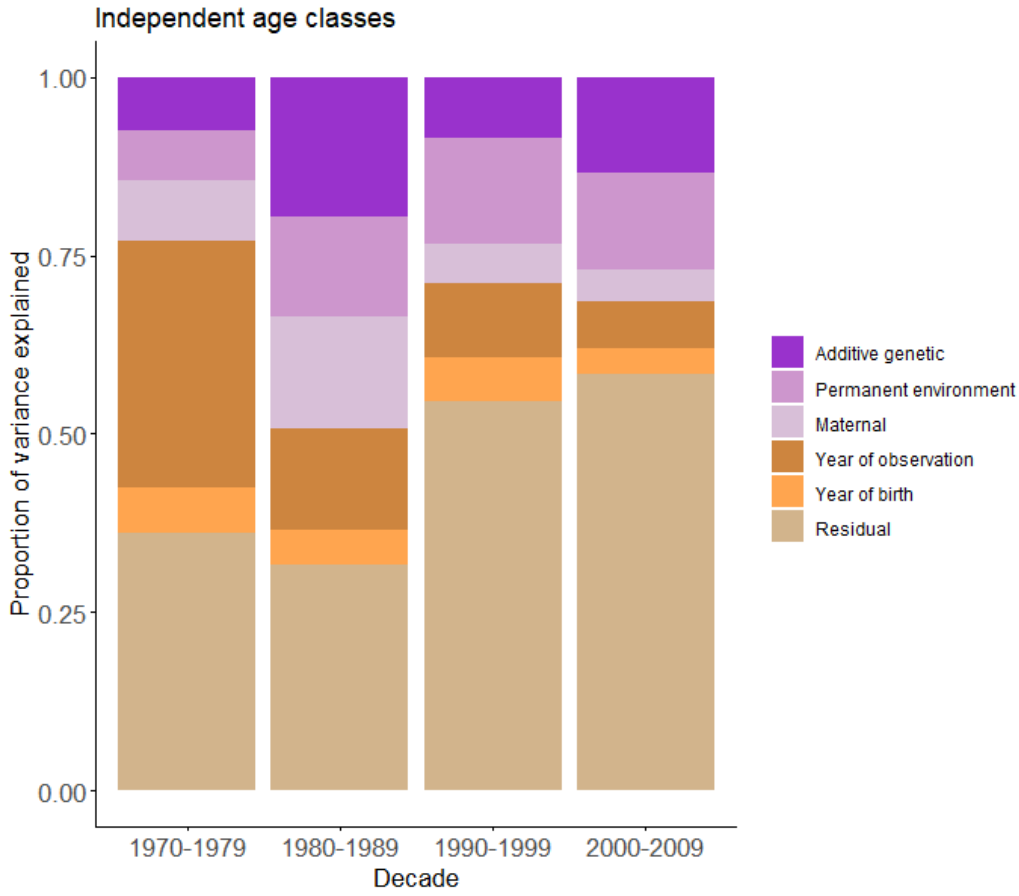

Figure 3. Proportion of variance explained by random effects for polar bear conflict risk behaviour (*not captured/captured*) for independent age classes in the Western Hudson Bay subpopulation observed in Churchill, Manitoba by decade between 1970 and 2010.

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Chapter 3: Quantitative Genetics of Polar bear (*Ursus maritimus*) Behaviours: Synthesis

The low heritability of conflict risk behaviour underscores its close association with individuals' ability to survive and reproduce, and its high susceptibility to environmental cues in the Western Hudson Bay polar bear subpopulation. This suggests that conflict risk behaviour has been shaped by strong selective pressures, driven by the benefits of intraspecific competition and the risks associated with conflicts. Female reproductive success is limited by resource availability, while male reproductive success is primarily limited by access to potential mates (Trivers 1972). The moderate repeatability of conflict risk behaviour suggests a notable influence of environmental conditioning, with bears exposed to human settlements having more learning opportunities associated with conflict risk behaviours. The findings also underscore the influence of environmental factors, such as climate change, on conflict risk behaviour variability, with annual effects emerging as a substantial source of variation compared to cohort effects.

Polar bears in the Western Hudson Bay subpopulation generally exhibit behaviours aimed at avoiding conflicts, especially those that could lead to serious physical confrontations. Their solitary nature reduces the frequency of interactions that might lead to aggressive encounters (Derocher and Stirling 1990). When potential conflicts arise, bears often engage in non-physical displays of dominance, such as vocalizations and body size posturing, to deter rivals without engaging in fights (Biddlecombe et al. 2019; Ramsay and Stirling 1986; Stringham 2011; Taylor et al. 1985). However, mother polar bears are highly protective of their cubs and will aggressively defend them if necessary, although they still prefer to avoid unnecessary risks (Stirling 1974). During the ice-free season, when polar bears are more likely to encounter each other onshore, they continue to prioritize avoidance of direct conflict (Ferguson et al. 1997; Jagielski et al. 2022; Latour 1981b; Taylor et al. 1985). Once sea ice becomes available again,

polar bears generally do not continue to use human food sources (Lunn and Stirling 1985). Brown and black bears also tend to return to their natural feeding habits once access to human food sources are removed, resulting in fewer human-bear conflicts (Baruch-Mordo et al. 2014; Lewis et al. 2015). Comparing repeated conflict risk behaviour involving the presence of attractants in human settlements to addictive behaviours suggests that both are driven by external stimuli that can lead to repetitive actions despite potential negative consequences. This tendency to avoid conflict is a crucial adaptive behaviour, minimizing the risk of injury that could jeopardize their ability to survive and reproduce in a demanding environment.

Estimating the heritability of conflict risk behaviour provided a framework for considering the heritability of polar bear home range behaviour. It raises questions about the driving forces behind polar bears' movement patterns within their home ranges and population regions. I attempted to analyze pedigree and GPS radio-telemetry data describing the home range size expressed by 128 adult female polar bears in the Western Hudson Bay subpopulation during the ice-on (December-June) and the ice-off period (July-November). Given that movement behaviour is directly linked to an individual's pursuit of optimal survival and well-being, it is plausible to consider it as a highly selected trait with substantial phenotypic plasticity (Stopher et al., 2012). Consequently, spatial-learning skills are hypothesized to evolve proportionally to navigational demands. Females' energy expenditures are notably high, particularly for reproductive behaviours, marked by prolonged periods of heightened stress during pre-natal and post-natal care, and the avoidance of males in general (Stirling et al. 1993). Males also face substantial costs associated with reproductive behaviours as male bears engage in intense intraspecific competition for access to females which drives male-biased dispersal (Moore and Ali 1984; Pusey and Wolf 1996). Sex differences in spatial ability are predicted to evolve only in

species where range expansion differentially enhances the reproductive success of males and females (Bateman 1949; Trivers 1972).

In a sense polar bears inherit not only genetic predispositions but also the physical environment and social dynamics from preceding generations, which shape their individual biological needs. Accurately estimating the contributions of genetic, environmental, and social transgenerational effects at the population-level for a wild polar bear subpopulation remains elusive due to constraints in data availability, the inability to statistically regulate for these effects, and spatial autocorrelation. When focusing on finer spatiotemporal scales, like home range overlap or centroid drift of mothers and daughters, these investigations lose biological relevance. Despite this, the movement behaviour of mothers and daughters is anticipated to closely mirror each other, reflecting the strong bond they share for survival and well-being. This is evident in Svalbard, where daughters showed high philopatry to the area where they were born, resulting in matrilineal structure within the main denning areas (Zeyl et al. 2010). Beyond this caregiving context, the movement of females is expected to predominantly mirror their biological needs related to obtaining food, mates, and denning. Young female black bears (*Ursus americanus*) and brown bears (*Ursus arctos*) often remain within or near their maternal home ranges, subsequently incorportating portions of these areas into their own home ranges (Glenn and Miller 1980; Jonkel and Cowan 1971).

Theories describing natural selection and life history strategies organize the patterns observed across life-history, physiological, behavioural, and morphological traits shaping individuals, species, and populations related to their age- and stage- specific patterns created through space and time spanning their birth and weaning (dependent offspring), to maturation and death (independent offspring). Life histories delineate how resources and energy are

distributed across various life stages and generations, ultimately influencing the overall fitness of organisms within their specific evolutionary and ecological contexts. In the context of conflict risk behaviour, life history strategies play a crucial role in determining the allocation of energy resources towards competitive interactions. Organisms must navigate trade-offs between investing energy in conflict risk behaviours, such as aggression or mate defense, and allocating resources towards essential life-history functions, including survival, reproduction, and growth (Koskela et al. 1997; Verbeek et al. 1996). Intraspecific conflict can confer individual benefits such as gaining mates, dominance rights, and desirable territory, therefore resulting in sexual selection favouring aggressive behaviours (Darwin 1871). Individual selection should primarily explain why conflicts are usually a 'limited war' strategy involving ritualized tactics not causing serious injury compared to a 'total war' strategy resulting in death (Smith and Price 1973).

Environmental variability and human-caused disturbances can exacerbate these trade-offs by altering resource availability and energy landscapes (Biddlecombe et al. 2021; Durner et al. 2017). Habitat degradation, resource depletion, and human-induced stressors can increase competition among individuals, leading to heightened conflict and elevated energy expenditures (Sih et al. 2011). Understanding the interplay between life history strategies, conflict risk behaviour, and energy dynamics is necessary for predicting the resilience of wildlife populations to environmental change. In social species, including humans, the evolution of conflict risk behaviour incorporates psychological and cognitive dimensions. Emotions like aggression and fear, as well as empathy and cooperation, play crucial roles in how conflicts are managed within groups. Aggression and fear can trigger defensive or offensive actions, essential for immediate survival, while empathy and cooperation facilitate long-term group cohesion and mutual support (Aureli and De Waal 2000; De Waal 2006). Kin selection and altruism also emerged as major

factors, reducing conflicts among relatives and promoting group cohesion (Trivers 1971; West et al. 2007). By prioritizing the welfare of relatives, individuals indirectly ensure the propagation of their shared genes.

Group dynamics and intergroup conflict are rooted in the evolutionary distinction between in-groups and out-groups (Brewer 2007; Kurzban and Leary 2001). Favoritism toward in-group members and hostility towards out-groups likely evolved as mechanisms to enhance group survival and cohesion (Choi and Bowles 2007). This distinction fosters trust and cooperation within groups while simultaneously preparing them to compete with or defend against outsiders (Balliet and Van Lange 2013). These behaviours can be observed in various social structures, from animal packs to human societies, where solidarity within the group is balanced by competition and vigilance towards external threats (Bowles 2006; Silk et al. 2003). In human history, this dynamic has also led to the development of complex social strategies such as alliances, treaties, and diplomacy to manage and mitigate intergroup conflicts, thereby promoting broader social stability and cooperation across groups (Bowles 2011; Richerson 2005). Focusing on meeting the biological needs of individuals, species, and populations is expected to promote well-being and diminish the expression of destructive survival-oriented behaviours.

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