

**University of Alberta**

The Mating System and Life History of the Polar Bear

by

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## **Abstract**

Mating systems evolve in response to factors that influence the distribution and availability of mates. In turn mating systems can influence species life histories as a result of sexual selection. Most of what is known about sexual selection in large mammals comes from long-term studies of gregarious species and little information exists on the mating systems and opportunity for sexual selection in solitary carnivores. In this thesis I combine long-term mark-recapture and genetic data to describe the mating system and the opportunity for sexual selection in the western Hudson Bay polar bear (*Ursus maritimus*) population. Using genetically based parentage assignments I provide the first estimates of lifetime reproductive success in male and female polar bears. These data along with information on individual phenotypes are then used to explicitly test the hypothesis that male biased size dimorphism in polar bears is the result of sexual selection on male traits. I conclude my thesis by examining long-term trends in sea ice availability in western Hudson Bay and examine the potential influence of sea ice conditions during early development on polar bear growth. The overall objective of this thesis is to provide much needed insight into the mating system and life history of polar bears, to aid further investigations into the evolutionary ecology of the species.

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# Chapter 1

## 1 Introduction

### 1.1 Life History and Climate Variation

An organism's life history can be defined as its lifetime pattern of growth, reproduction and mortality (Begon et al. 1990). Life history strategies evolve in response to selective pressures that optimize the fitness of individuals (Stearns 1992, Roff 2002). Both natural and sexual selection are expected to act on phenotypic traits if differences in phenotypes result in difference in individual fitness (Falconer and Mackay 1996). Phenotypes in turn can influence the demography of populations (Pelletier et al. 2007). Although genetic variance forms the basis for evolution of phenotypic traits, selective agents that result in differential fitness among phenotypes are what lead to evolutionary change and optimization of life histories.

Environmental variation is arguably one of the most important selective agents influencing the evolution and persistence of life history traits (Stearns 1992). Among long-lived vertebrates environmental variation is known to influence growth (Post et al. 1997), survival (Gaillard et al. 1997), reproductive success (Albon et al. 1983), and consequently the demography of populations.

Large scale patterns of climatic variability such as the El Nino Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) are known to affect the life history and population dynamics of both marine and terrestrial species (Stenseth and Mysterud 2002). In the southern hemisphere, the population dynamics of several Antarctic seabird species have been linked to ENSO-mediated shifts in the availability of sea ice (Croxall et al. 2002, Barbraud and Weimerskirch 2003, Jenouvrier et al. 2005a, Jenouvrier et al. 2005b) as well as to changes in sea surface temperature (Pinaud and Weimerskirch 2002, Jenouvrier et al. 2003) both of which are believed to affect the availability of key forage species. Similarly, the NAO has been linked to oceanographic processes which influence the availability of primary prey species affecting calving rates in the endangered North Atlantic right whale (*Eubalaena glacialis*) (Greene and Pershing 1994), hatching success in Northern Fulmars (*Fulmarus glacialis*) (Thompson and



Ollason 2001), and adult survival in common guillemot (*Uria aalge*) and Brünnich's guillemot (*U. lomvia*) (Sandvik et al. 2005). Although environmental variation as a result of cyclical climate phenomena such as ENSO and NAO are known to influence the life history traits and population dynamics of a variety of vertebrate taxa, understanding how persistent change in the earth's climate affects the life history traits and population dynamics has long been an area of ecological research. More recently, understanding how rapid unidirectional environmental change, resulting from anthropogenic global warming has become a dominant issue in ecological research.

Over the last 100 years, the earth's climate has warmed by approximately 0.74°C and the Intergovernmental Panel on Climate Change predicts an additional increase in global temperatures, as a consequence of anthropogenic influences, of between 1.4°C and 5.8°C during the 21<sup>st</sup> century as a result of elevated atmospheric CO<sub>2</sub> levels (IPCC 2007). There is a mounting body of evidence that these rapid changes in the Earth's climate are having significant impacts on the physiology, phenology, distribution, and abundance of species (Hughes 2000, McCarty 2001, Stenseth and Mysterud 2002, Root et al. 2003). One of the fastest warming areas of the planet is the Arctic (IPCC 2007) where significant changes in sea ice extent are expected to impact a wide variety of marine mammals including the polar bear (*Ursus maritimus*) (Laidre et al. 2008). Polar bear life history is intimately linked to the sea ice environment, with sea ice providing the platform from which bears hunt, travel, mate, and in some areas den (DeMaster and Stirling 1981). Over the last 20 years, in association with climate warming, there have been significant declines in both the spatial and temporal extent of sea ice cover in the Arctic (Parkinson and Cavalieri 1989, Parkinson et al. 1999, Comiso 2002, Comiso and Parkinson 2004, Stroeve et al. 2007). It has been suggested that these spatial and temporal changes in the sea ice environment will result in reduced availability and abundance of the polar bears primary prey, seals (Stirling and Derocher 1993, Derocher et al. 2004). In turn, reductions in prey availability have the potential to influence the life history of individuals (growth, reproduction, and survival) (Boggs 1992) and thereby the population dynamics of polar bears.

## **1.2 Polar Bear Life History**

In general, polar bears life history is characterized by slow growth, delayed maturation, small litters and extended maternal care all of which result in low population growth rates (DeMaster and Stirling 1981, Ramsay and Stirling 1988, Derocher and Stirling 1994, Stirling 2011). Growth patterns in polar bears have been studied extensively (e.g. Kingsley 1979, Derocher and Stirling 1998, Bechshøft et al. 2008), however data on factors that influence changes in growth rates are largely lacking (but see Rode et al. 2010, Robbins et al. 2012). Polar bears are sexually dimorphic, with males weighing about 2.1 times as much as females (Kingsley 1979, Derocher et al. 2005). Size dimorphism in polar bears is believed to be the result of sexual selection arising from contest competition for mates (Ramsay and Stirling 1986), however this hypothesis has never been quantitatively tested in relation to variance in male mating or reproductive success. Mating takes place on the sea ice from March through May (Lønø 1970, Rosing-Asvid et al. 2002) and ovulation is presumed to be induced as in other bear species (Boone et al. 2004). As with several other bear species, polar bears exhibit delayed implantation (Wimsatt 1963) and females typically give birth to one to three cubs in late-December/early January (Derocher et al. 1992, Derocher 1999). Polar bears differ from other ursids in that overwinter dormancy is limited to parturient females that require maternity dens for reproduction (Watts and Hansen 1987). Polar bear cubs are altricial when born (Ramsay and Dunbrack 1986, Van de Velde et al. 2003) and remain in the maternity den with their mothers until approximately mid-March before returning the sea ice (Messier et al. 1994, Ferguson et al. 2000). Cubs can remain associated with their mothers for up to 3.5 years (Ramsay and Stirling 1988, Derocher et al. 1992) but may be weaned as early as 1.5 years of age in western Hudson Bay (Derocher and Stirling 1996) but 2.5 years is the normal age of weaning in most populations (Ramsay and Stirling 1986).

Information on age- and sex-specific survival and reproduction are critical to understanding fitness trade-offs and the evolution of life history traits such as growth patterns, reproductive investment and life span (Stearns 1992, Roff 2002). Although advancements have been made in assessing age- and sex-specific survival in polar bears (Regehr et al. 2007, Hunter et al. 2010, Stirling et al. 2011, Peacock et al. 2013), as well as age-specific reproduction in females (Ramsay and Stirling 1988, Derocher and Stirling 1994) to date published data on male reproductive success and age at sexual maturity are limited (Rosing-Asvid et al. 2002, Cronin et al. 2009, Zeyl et al. 2009), primarily due to the difficulty in following known individuals for long

periods of time. In addition, although reproductive success of female polar bears has been examined in detail (Ramsay and Stirling 1988, Derocher and Stirling 1994), little information exists on female mating behaviour and mate choice (Wiig et al. 1992) and whether extra-pair mating is common in polar bears (see Zeyl et al. 2009). Thus, despite being intensively studied in a number of areas of the Arctic, knowledge of the polar bear mating system and male reproductive success are lacking. Understanding how male reproductive success varies in relation to age and individual phenotypic quality is an important first step in assessing the evolutionary pressures that have resulted in sex-specific differences in polar bear life history. Furthermore, because environmental variation can play an important role in the life histories of individual species, examining how changes in the sea ice environment have influenced the evolution of life history traits in polar bears (e.g., growth) will be important in understanding the demographic responses of polar bear populations to reduced sea ice availability in a warming world.

The effects of reduced access to seals, the primary prey of polar bears, as a result of changing sea ice dynamics are already evident at the southern limit of the polar bears' range. In western Hudson Bay, polar bears are forced ashore during an extensive ice-free period each summer that can last for up to 5 months in which bears must subsist on stored fat reserves (Ramsay and Stirling 1988). Increasing spring air temperatures and earlier sea ice break-up have extended this period resulting in significant declines in the body mass of adult female polar bears (Stirling et al. 1999, Stirling and Parkinson 2006). Declines in individual phenotypic quality (i.e., body mass) can influence population dynamics through recruitment, because lighter female polar bears produce smaller litters and lighter cubs (Derocher and Stirling 1994) that are less likely to survive (Derocher and Stirling 1996). Sea ice-mediated changes in individual phenotypic quality have the potential to influence a number of individual life history traits (e.g., growth rates, age at first reproduction, litter size, and longevity) all of which influence polar bear demographics. Currently, the interrelationships between sea ice variability, phenotypic quality, life history traits, and the population dynamics of polar bears are just beginning to be understood.

### **1.3 Study Population**

In western Hudson Bay polar bears come ashore during an extensive ice-free period that lasts on average from mid-July to early November (Stirling et al. 1977, Stirling et al. 1999). Bears in this region arrive onshore shortly after sea ice break-up (Stirling et al. 1977, Lunn et al. 2004, Cherry et al. 2013) and remain relatively inactive while on land (Knudsen 1978, Latour 1981, Lunn and Stirling 1985), subsisting on fat deposited during the primary feeding period in spring and early summer prior to breakup (Nelson et al. 1983, Derocher and Stirling 1990, Ramsay et al. 1991). In November, all polar bears except pregnant females return to the sea ice as it begins to reform (Derocher et al. 1993). Pregnant females remain on land fasting for up to 8 months while using only their stored fat reserves to meet their own basic energetic demands as well as the increased energetic demands of gestation and lactation (Watts and Hansen 1987, Polischuk et al. 2001). Denning female polar bears in western Hudson Bay already endure one of the longest periods of food deprivation known for any mammal and thus any significant further reduction in the availability of sea ice is likely to have profound effects on reproduction. Changes in sea ice conditions over the past two decades have led to significant declines in physical condition of bears in the western Hudson Bay population (Stirling et al. 1999, Stirling and Parkinson 2006). Regehr et al. (2007) found a 22% decline in the size of the western Hudson Bay polar bear population; however the proximate and/or ultimate cause of this decline remains unclear.

In this dissertation I make use of 32 years of capture-recapture data from the western Hudson Bay polar bear population (Figure 1.1). Each year from late-August to early-October bears are sampled non-selectively, immobilized with Telazol®, and a series of standard phenotypic measurements are taken (Stirling et al. 1989). In addition to the collection of phenotypic data, long-term collection of tissue and blood samples have also allowed for genetic profiling of over 2400 individuals in this population. All animal handling procedures were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee and the animal Care Committee of the Canadian Wildlife Service (Prairie and Northern Region). Currently, this is the only polar bear population in the world for which detailed long-term demographic data on individual bears is available to assess lifetime reproductive success of both males and females. These data, along with previously collected information on growth, survival and longevity provide new insight into selective pressures that have shaped polar bear life history. Furthermore, understanding how variability in the sea ice environment affects polar bear life

history traits and those of the pagophilic seals they depends upon, will be crucial for predicting the long-term impacts of climate warming on this species.

#### **1.4 Dissertation Outline**

To optimize fitness, organisms need to both survive and reproduce. Although much is known about survival in polar bears, information on male reproduction in polar bears and solitary carnivores in general is lacking due the difficulty in studying wide ranging and solitary species. In therians, the divergence in sex roles stemming from anisogamy and parental care has resulted in a divergence in reproductive strategies between the sexes (Clutton-Brock 1991). In turn, sexual differences in reproductive strategies favour differential expression of traits and life histories between the sexes. As a result, detailed information on male reproductive success is required to understand sex-specific variation in growth, age at maturity, size at maturity, age specific mortality as well as longevity.

In Chapter 2, I investigate the genetic mating system of the polar bear by using 25 microsatellite markers to assign parentage among 2229 offspring born from 1975-2005 in the western Hudson Bay polar bear population. These data also allow me to provide the first estimates of lifetime reproductive success and the opportunity for sexual selection in polar bears. My results are discussed in light of what is currently known about carnivore mating systems, the opportunity for sexual selection and the life history of large mammals.

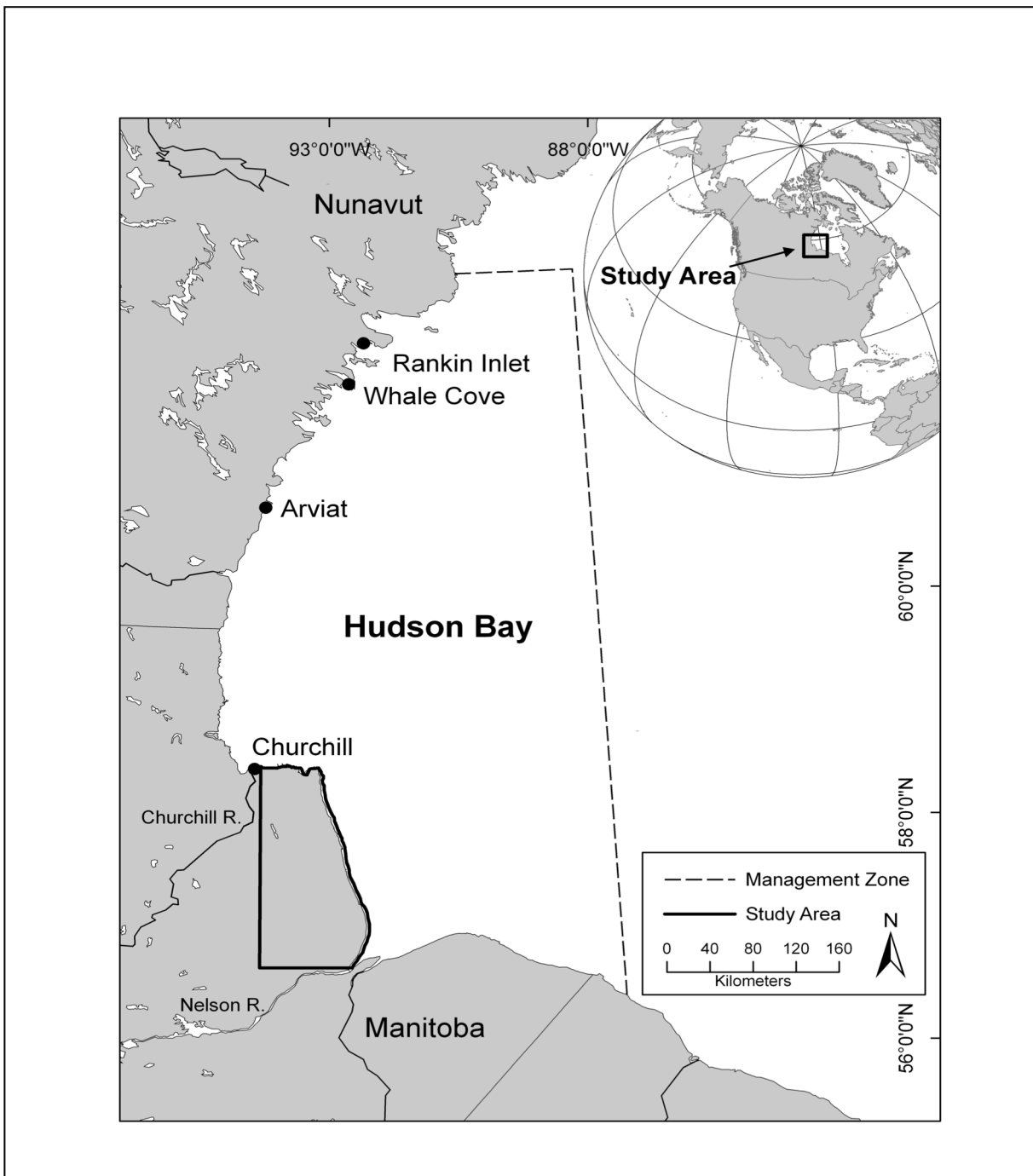
In mammals, male mating strategies are primarily influenced by the ability of individual males to monopolize breeding females (Emlen and Oring 1977). As a result male reproductive success in polygynous, size dimorphic species is predicted to be related to male body size (Andersson 1994). It is generally accepted that sexual selection in males and fecundity selection in females are the major evolutionary agents of selection promoting size dimorphism in a variety of species (Blanckenhorn 2005). Although sexual dimorphism in carnivores is common (Ralls 1977) quantitative evidence for sexual dimorphism as result of differential reproductive success in relation to phenotypic variation amongst individuals is lacking.

In Chapter 3, I use formal selection analyses (Lande and Arnold 1983) to describe lifetime selection on body size and skull width in male and female polar bears in relation to estimates of lifetime mating and reproductive success from Chapter 2. These data allow me to quantitatively test the hypothesis that sexual size dimorphism in polar bears has evolved as result of differential selection on male and female traits in relation to lifetime estimates of reproductive success. I further examine the potential importance of body size to polar bear life history by examining the potential for viability selection on body size.

Because life history traits are often negatively correlated (e.g., survival and reproduction), the optimality of any life history pattern is a function of a series of trade-offs that can influence individual fitness (Stearns 1992, Roff 2002). One of the most important factors influencing life history trade-offs is how organisms allocate finite energy stores to growth, reproduction and survival (Stearns 1992). Individual variation in nutrition during early development can affect how individuals invest in life history traits (Grafen 1988). Long-term studies of birds and mammals have shown that conditions experienced in early development can have a significant influence on individual fitness (Lindstrom 1999), potentially resulting in cohort effects that can influence the demography of populations (Albon et al. 1987, Clutton-Brock et al. 1988, Post et al. 1997).

Environmental variation can play an important role in access to resources, so in Chapter 4, I examine long-term trends in sea ice extent in western Hudson Bay to test the hypothesis that previously observed declines in the size of bears in western Hudson Bay are related to interannual variation in sea ice conditions during early development. I discuss my results in the context of polar bear life history, demography and the future viability of the western Hudson Bay polar bear population.

In the concluding Chapter 5, I summarize my primary results, discuss them in the larger framework of what is known about large mammal life histories and provide suggestions for future research that will expand our knowledge of polar bear life history and how it is likely to respond to climate mediated reductions in the availability of sea ice habitat.



**Figure 1.1:** Study area and western Hudson Bay polar bear management zone located near Churchill, Manitoba.

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## Chapter 2

### 2 Genetic mating system and opportunity for sexual selection in a solitary carnivore: the polar bear (*Ursus maritimus*)

#### 2.1 Introduction

Mating systems evolve in response to ecological, behavioural and physiological factors that influence the distribution and availability of members of the opposite sex (Emlen and Oring 1977). Amongst mammals, variation in the distribution of resources influences the distribution of individuals and in turn affects the development of mammalian mating systems (Clutton-Brock and Harvey 1978). In most mammals, female reproductive success is constrained primarily by access to resources; whereas male reproductive success is constrained primarily by access to potential mates (Trivers 1972). When resources are clumped and the distribution of females is predictable, males can gain access to females by defending resources (resource defence polygyny); alternatively when females are gregarious, males can gain access to females by controlling female aggregations (female or harem defence polygyny) (Emlen and Oring 1977). Although the spatial distribution of resources and individuals plays an important role in the evolution of mammalian mating systems, there are few studies on the mating systems of solitary species (Clutton-Brock 1989, McEachern et al. 2009). Studies of solitary species may be of particular importance because mate density may influence mate competition and mate choice (Kokko and Rankin 2006) and therefore the opportunity for sexual selection (Darwin 1871).

Within mating systems, the opportunity for sexual selection arises from variance in mating success amongst individuals (Arnold and Wade 1984a). In species with little male investment in offspring the opportunity for sexual selection is strongly affected by factors that influence the ability of males to monopolize mates (Emlen and Oring 1977). Sexual selection theory predicts a relaxation of sexual selection in solitary species as a result of the inability of males to monopolize multiple breeding females (Emlen and Oring 1977). Although mate density has been shown to play an important role in the opportunity for sexual selection (Clutton-Brock et al. 1997, Coltman et al. 1999b), it may interact in complex ways with other factors such as oestrus synchrony and operational sex ratios (OSR – ratio of males to females that are available to mate

at any given time) to influence variance in mating success amongst individuals (Emlen and Oring 1977, Ims 1988).

In solitary species with synchronized oestrous the ability of males to monopolize breeding females is expected to be limited (Emlen and Oring 1977) potentially resulting in decreased variance in male mating success (Ims 1988). Alternatively, if oestrus is asynchronous and the OSR becomes biased toward males, dominant males may be able to sequentially monopolize breeding females leading to increased variance in male mating success (Say et al. 2001). Adult sex ratios (ASR) and sex-based differences in potential reproductive rate (i.e. the relative time spent in reproductive and non-reproductive states) can also bias OSR (Clutton-Brock and Vincent 1991, Clutton-Brock and Parker 1992, Kvarnemo and Ahnesjo 1996) influencing the degree of mate competition. In long-lived species with extended maternal care, OSR is expected to be biased toward males (Ramsay and Stirling 1986, Kvarnemo and Ahnesjo 1996). As a result intense competition among males to gain access to breeding females create the potential for high variance in male mating success (Emlen and Oring 1977) and an increased opportunity for sexual selection (Wade and Arnold 1980, Arnold and Wade 1984b). Although density, oestrus synchrony and OSR play an important role in mating systems and sexual selection (Emlen and Oring 1977), estimates of variance in lifetime mating/reproductive success in male mammals are strongly biased toward gregarious species in which females exhibit oestrus synchrony and annual reproduction (e.g. northern elephant seals, *Mirounga angustirostris*: Le Boeuf and Reiter 1988, soay sheep, *Ovis aries*: Coltman et al. 1999b; roe deer, *Capreolus capreolus*: Vanpe et al. 2008). Understanding how density, OSR and oestrus synchrony interact to influence mammalian mating systems will help improve our understanding of the opportunity for sexual selection.

The polar bear, (*Ursus maritimus*), is a highly size dimorphic solitary carnivore species, with a circumpolar distribution, the southern limit of which is determined by the annual distribution of sea ice (DeMaster and Stirling 1981). They occur at low densities throughout their range (1.0 – 11.0 bears/1000 km<sup>2</sup>) (Taylor and Lee 1995, Evans et al. 2003, Aars et al. 2009) and females can occupy home ranges that vary from 185 km<sup>2</sup> to 540,000 km<sup>2</sup> (Ferguson et al. 1999, Mauritzen et al. 2001). Mating takes place on the sea ice from March through May (Lønø 1970, Rosing-Asvid et al. 2002) and ovulation is presumed to be induced as in other bear species (Boone et al. 2004).

Analysis of female reproductive tracts from northwest and eastern Greenland indicate that ovulation occurs in both April and May (Rosing-Asvid et al. 2002) suggesting that oestrus is asynchronous. Female polar bears normally enter oestrus every 3 years after weaning their young at 2.5 years of age (Ramsay and Stirling 1986). This extended length of maternal care results in a skewed OSR among adults that may exceed 2-3 males per breeding female, increasing the potential for male-male competition (Ramsay and Stirling 1986, Kvarnemo and Ahnesjo 1996). Rates of facial scarring and canine breakage, as well as observations of fresh wounds on male polar bears during the spring breeding season suggest that intense competition for access to oestrus females occurs (Ramsay and Stirling 1986, Derocher et al. 2010). However, no information has been published examining lifetime variance in mating or reproductive success in male or female polar bears. Thus, polar bears provide a unique opportunity to examine how low population density, male biased OSR and asynchronous oestrous interact to influence the mating system and opportunity for sexual selection in a solitary carnivore species.

Most of what is known about the polar bear mating system has been inferred from behavioural observations (Hagen 1976, Ramsay and Stirling 1986, Wiig et al. 1992, Derocher et al. 2010, Stirling 2011) and evidence of male-male contest competition (e.g. fresh cuts/wounds) during the breeding season (Ramsay and Stirling 1986, Derocher et al. 2010). Lack of data on individual mating success and reliance on behavioural observations has led to variation in the classification of the polar bear mating system which has been described as polyandrous (Ramsay and Stirling 1986, Wiig et al. 1992), polygynous (Berta and Sumich 1999, Derocher et al. 2010) and promiscuous (Zeyl et al. 2009). Although behavioural observations provide insights into mating systems, the application of molecular techniques has shown that discrepancies can exist between behavioural and genetic estimates of individual mating success (Amos et al. 1993, Coltman et al. 1999a, Dunn et al. 2012). Observations of mating behaviour in solitary species are rare and thus molecular assignments of parentage may be the only means by which mating systems can be investigated. In addition to providing insights into mating behaviour and important life history traits (e.g. age of first reproduction/reproductive senescence), quantification of genetic mating systems allows for the assessment of the opportunity for sexual selection via standardized measures of mating and reproductive success (i.e. Bateman's principles) (Bateman 1948, Crow 1958, Wade 1979, Wade and Arnold 1980). Genetic parentage analysis of polar bears in the



Beaufort and Chukchi seas (Cronin et al. 2006) as well as in the Barents Sea (Zeyl et al. 2009) have provided insights into the polar bear mating system, but both studies lacked the long-term data necessary to examine variance in lifetime mating/reproductive success of both sexes.

Herein I combine 41 years of capture-recapture data along with high-resolution microsatellite data from polar bears to describe the genetic mating system and the opportunity for sexual selection in the western Hudson Bay population. In accordance with selection theory, I test the prediction that (i) the opportunity for sexual selection will be greater in males than in females, and (ii) that the standardized variance in male breeding success will be lower in polar bears compared with more gregarious large mammals due to the limited ability of males to monopolize mates.

## **2.2 Methods**

### **2.2.1 Study Population and Sample Collection**

The western Hudson Bay polar bear population occupies the ice-covered waters of Hudson Bay at low densities but are forced ashore during an ice-free period (Stirling et al. 1999) in which all individuals in the population remain on land for several months and are available for sampling. Free-ranging polar bears in the study population were located and immobilized from a helicopter. From 1984 on, bears were immobilized with Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa) using standard chemical immobilization techniques (Stirling et al. 1989). Before 1984, other immobilizing drugs were used (see summary in Messier 2000). Each animal was assigned a unique identification number that was applied as both a permanent tattoo on both sides of the upper lip and as a white plastic tag placed in each ear. The age of each bear was determined through mother offspring relationships (i.e. known age cubs-of-the-year or yearlings) or by counting growth-layer groups in the cementum of an extracted vestigial premolar (Calvert and Ramsay 1998). Samples for genetic analysis were taken from skin collected when ear tags were applied, from fat biopsies, and/or as blood samples collected from the femoral vein. Skin, fat and blood samples were then transferred from the field to a -70°C for storage. Immobilization and handling protocol for free-ranging polar bears in western Hudson Bay has been reviewed and

approved by the Animal Care Committee of the Canadian Wildlife Service, Prairie and Northern Region.

### **2.2.2 DNA Extraction and Microsatellite Genotyping**

Total genomic DNA was extracted from skin tissue or from white blood cells recovered from ACK treated blood using DNeasy Blood and Tissue Kits (QIAGEN). I genotyped 2441 individuals captured between 1980 and 2006, including duplicate samples from 69 individuals to estimate genotyping error rate. Individuals were genotyped at 26 loci (Table 1) including CXX20, 110 and 173 (Ostrander et al. 1993), G1A, G10B, G1D, G10L (Paetkau and Strobeck 1994) G10C, G10M, G10P, G10X (Paetkau et al. 1995), UarMU05, UarMU10, UarMU23, UarMU26, UarMU50, UarMU51, UarMU59 (Taberlet *et al.* 1997), G10H, G10J, G10U (Paetkau et al. 1998), MSUT-1, MSUT-2, MSUT-4, MSUT-6 and MSUT8 (Kitahara et al. 2000). Loci were amplified in fifteen reactions (PCR A-O; Table 1) in a final volume of 15  $\mu$ L containing 10 mM Tris-Cl, 50 mM KCL, 0.1% Triton X-100, 0.16 mg/mL BSA, 160  $\mu$ M dNTPs and optimized concentrations of primers, MgCl<sub>2</sub> and Taq DNA polymerase. Reactions were pooled into three (Load 1-3; Table 1) loading mixtures, resolved on an Applied Biosystems 377 DNA Sequencer (Load 1; Dye Set C), 3100-Avant DNA Analyzer (Load 2; DS-30) or 3730 DNA Analyzer (Load 3; DS-33) and sized relative to Genescan size standards. Genotyping was performed using Genotyper and Genemapper software (Applied Biosystems).

### **2.2.3 Genetic Diversity and Tests of Disequilibrium**

Number of observed alleles ( $N_A$ ) and observed heterozygosities ( $H_O$ ) and expected heterozygosities ( $H_E$ ) were calculated using the Excel microsatellite toolkit (Park 2001) and departures from Hardy-Weinberg (HWE) and linkage disequilibrium (LD) were assessed using exact tests (Guo and Thompson 1992) and a Markov Chain using GENEPOP 3.4 (Raymond and Rousset 1995). Null allele frequencies were estimated for each locus in CERVUS 3.0 (Marshall et al. 1998, Kalinowski et al. 2007). Genotyping error rate was estimated from differences in duplicate genotypes.

#### 2.2.4 Parentage Analysis

Parentage analysis was conducted using the likelihood approach in CERVUS 3.0 (Marshall et al. 1998, Kalinowski et al. 2007) to identify the most likely mother and father for all sampled individuals born from 1975-2005 ( $n = 2229$ ). I ran CERVUS simulations for 10,000 cycles, using a genotype error rate of 0.0036, and allowed individuals to be missing data for up to 2 of the 25 loci (MSUT-4 was dropped due to null alleles). Because I obtained genetic material for most tagged individuals in the population I first assumed that the proportion of tagged individuals provided a good estimate of the proportion of sampled candidates for each sex (~80% of adult males and adult females are marked). However, my initial simulations and parentage analysis resulted in low paternity assignment rates (~40%) which I suggest to be the result of an open mating system in Hudson Bay involving males from adjacent populations. As a result the proportion of sampled candidate males and females was set conservatively at 0.33 and 0.77 respectively and held constant across years due to the unknown nature of the mating system. Parentage analysis was conducted independently for each year of the study to account for a changing pool of candidate parents. Because I was interested in the age of first and last reproduction I considered all known male and female bears that were  $\geq 1$  year of age (the earliest age at which individuals are weaned in the study population) at the time of conception as potential candidate parents. I did not restrict the maximum age of these candidates because we do not have known fates for most individuals and I was interested in potential patterns of reproductive senescence. Using this approach I assigned mother and father offspring relationships at a strict (99%) and relaxed (95%) level of statistical confidence allowing for one mismatching locus. I assigned mothers to cubs at less than 95% confidence if a known sibling was assigned a mother at a high level of confidence or if the mother from the field at sampling was chosen as the best candidate without statistical confidence. Similarly, for paternity analysis, cubs were assigned fathers at less than 95% confidence if a known sibling was assigned a father at a high level of confidence and the same father was the top candidate for the cub in question.

Maternal assignments were made without any *a priori* knowledge of known mother offspring relationships at capture. This allowed us to test the accuracy of my parentage analysis by comparing maternal assignments to known mother offspring relationships from field data. Cubs

were considered to be adopted/fostered if they mismatched their field mother at 5 or more loci. Mother offspring relationships were determined for each cohort before paternity analysis. Multiple paternities were assigned in multi-cub litters if two cubs with same mother were assigned different fathers at a high level of statistical confidence ( $\geq 95\%$ ) or if one cub was assigned a father at a high level of statistical confidence ( $\geq 95\%$ ) and the same father was not assigned as the sire of the remaining cub(s) in the litter.

I investigate age-related variation in reproduction by estimating relative age-specific reproductive success using age frequency data from my capture sample. Because bears are sampled non-selectively in the study population I assumed that the age structure of my capture sample ( $n = 2670$  males and  $n = 3111$  females from 1980-2010) represents the population age-structure over the long-term. Age frequency data were smoothed using a log-polynomial model (Caughley 1977) and the predicted proportion of individuals in each age class was calculated for the breeding range of males (2-25 years) and females (3-28 years). I then calculated the expected frequency of maternities and paternities for each age class assuming all age classes have equal reproductive rates by multiplying the total number of maternities and paternities assigned to breeders by the proportion of individuals in each age class. The observed value divided by the expected value represents relative age-specific reproduction. To test for a difference in the age distribution of maternities and paternities I compared their respective cumulative frequency distributions via a two-sample Kolmogorov-Smirnov test. Age assortative mating has been suggested to play an important role in the opportunity for sexual selection (Farrell et al. 2011), therefore, I tested for a correlation, between the ages of all known mated pairs ( $n = 493$ ).

I estimated the opportunity for selection ( $I$ ) for each sex by estimating lifetime reproductive success (LRS - total number of offspring produced) and lifetime mating success (LMS - total number of known mates acquired) for males and females born before 1986 and 1985 respectively. I restricted my analysis to this group of individuals because only 5% of paternities and maternities were assigned to males and females  $> 20$  and  $> 21$  years old respectively; therefore individuals reaching this age were considered to be no longer reproductively active at the end of my study. Estimates of LRS and LMS were based on males and females known to survive until 2 and 3 years old respectively, including those known not to breed, as non-breeders

represent an important component of fitness variance (Shuster 2009). I assessed the contribution of non-breeders to the total variance in LRS and LMS following Brown (1988). To test whether male LMS was randomly distributed I compared the observed frequency of assigned paternities with the number expected under a Poisson distribution with the same mean. My estimates of LRS and LMS were biased downward because I was unable to sample all cubs born each year, and some males may migrate out of the population to breed. I also did not restrict the parentage analysis to dependent young as I was interested in developing a pedigree for my study population and therefore my estimates of LRS include a survival component. The standardized variance in LRS ( $I$ , the opportunity for selection) and LMS ( $I_m$ , the opportunity for sexual selection) (Wade 1979, Wade and Arnold 1980) for each sex were calculated following Jones (2009). I also calculated the ratio of the opportunity for selection in the two sexes ( $I_m/I_f$ ) to examine differences in selection intensity between the sexes. Finally, I performed a least squares regression of relative mating success on relative reproductive success to determine the Bateman gradient ( $\beta_{ss}$ ) for males (Bateman 1948, Arnold and Duvall 1994). All analyses were implemented in R (version 2.13.1; R Core Development Team). Results are presented as means  $\pm$  1 SD where appropriate.

## 2.3 Results

### 2.3.1 Genetic Profiling

Complete 26 locus genotypes were obtained for 2420 individuals while 18 and 3 individuals were missing data for one or two loci, respectively. The mean number of observed alleles ( $N_A$ ) was 7.65 (range 3-10) and mean  $H_O$  and  $H_E$  were 0.671 (range 0.116-0.843) and 0.673 (range 0.115-0.841), respectively (Table 1). Two loci deviated from HWE (G1A and MSUT4) at a 5% level of significance but only MSUT4 was significantly out of HWE following a strict Bonferroni correction for multiple tests (Rice 1989). MSUT4 displayed an excess of homozygotes that may be due to a low frequency of null alleles (2.8%) at this locus. Forty-one pair-wise tests of LD were significant following correction for multiple tests likely due to the presence of close relatives in the dataset.

### 2.3.2 Parentage Analysis

Using the assignment criteria, a total of 1665 (74.70%) cubs were assigned a mother, of these 1631 were at 95% confidence and 1553 (93.27%) were at 99% confidence, 34 (2.05%) cubs were assigned mothers at < 95% confidence (Table 1). A total of 526 individual females (524 of known age) were assigned at least 1 cub from 1197 litters including 765 singleton, 406 twin and 26 triplet litters (mean litter size =  $1.38 \pm 0.53$  cubs). The number of litters assigned among successful females ranged from 1-8 ( $2.29 \pm 1.36$ ) and the number of cubs assigned per female ranged from 1-15 ( $3.16 \pm 2.06$ ). Six cases of cub fostering involving 6 different litters were detected. The true mother for 4 of the cubs was assigned with 99% confidence with zero or 1 mismatching loci. The remaining 2 cubs could not be assigned a mother with a high degree of confidence but both mismatched their field mothers at 5 or more loci. Mother-offspring relationships observed in the field were compared to those assigned by CERVUS (excluding obvious cases of cub adoption) which revealed an overall error rate in assignments of ~3.7% (n = 62 assignments). Of these assignments 34 were cases in which the field mother had the highest likelihood (LOD) but with a lack of statistical confidence (i.e. < 95%), 18 were cases in which the field mother did not have the highest LOD and 10 cases that were too young have bred (1 and 2 year old females). This low overall error rate reinforced my confidence in the parentage assignments.

A total of 873 (39.17%) cubs were assigned a father, of these 810 were at 95% confidence and 661 (76.68%) at 99% confidence, 63 (7.31%) cubs were assigned fathers at < 95% confidence (Table 1). Five paternities were assigned to yearling males and were removed from all further analysis. A total of 292 individual males (288 of known age) sired at least one cub (range: 1-13 cubs,  $2.96 \pm 2.33$ ) with the number of mates ranging from 1-9 ( $2.17 \pm 1.63$ ). Males sired a mean of  $1.37 \pm 0.53$  cubs per mating. The maximum number of litters and cubs sired by a single male in one year were 4 and 6, respectively. From a total of 212 polytocous litters I detected 14 cases of multiple paternity (6.60% of litters). No cases of incestuous mating and no repeat breedings between adult females and adult males were detected (i.e. females never mated with an individual male across multiple years). There was a significant difference between the age frequency distributions of maternal and paternal assignments (K-S two sample test  $D = 0.13$   $p < 0.001$ ) (Figure 2.2). The mean age of reproductive females ( $12.4 \pm 5.2$  years; range: 3-31; n =

1193) was similar to the mean age of reproductive males ( $13.0 \pm 4.5$  years; range: 2-25;  $n = 628$ ), however the distribution of paternity was leptokurtic, favouring males between 11-15 years old (Figure 2.2). There was no evidence for age assortative mating among 493 mating pairs in which the age of both individuals was known (Pearson  $\rho = 0.004$ ,  $p = 0.93$ ) (Figure 2.3).

### 2.3.3 Opportunity for Sexual Selection

LRS of male ( $n = 216$ ) and female ( $n = 234$ ) polar bears varied from 0-13 offspring ( $2.37 \pm 2.73$ ) and 0-15 offspring ( $3.51 \pm 2.68$ ) respectively. LMS varied from 0-9 ( $1.68 \pm 1.89$ ) known mates for males and 0-8 ( $2.48 \pm 1.76$ ) known mates for females. The distribution of male LMS was positively skewed and deviated significantly from a Poisson distribution with the same mean ( $\chi^2 = 44.31$ ,  $df = 5$ ,  $p < 0.001$ ) (Figure 2.4). Among successful males, reproductive tenure ranged from 1 to 19 years ( $4.9 \pm 4.4$  years) with successful males siring an average of  $1.41 \pm 0.55$  offspring per mating. In years in which males were successful, annual mating success ranged from 1-4 females ( $1.13 \pm 0.38$  females) and reproductive success ranged from 1-6 offspring ( $1.60 \pm 0.84$  offspring). For males that sired  $\geq 1$  litter, the mean interval between litters was  $3.2 \pm 2.7$  years (range: 1-15). Using information on lifetime reproductive and mating success I estimated the opportunity for selection ( $I_{males} = 1.34$  and  $I_{females} = 0.58$ ) and sexual selection ( $I_m = 1.26$  and  $I_f = 0.50$ ). There were 71 males and 32 females that were not assigned any offspring. These individuals accounted for 36% and 39% of the variance in LRS and LMS in males and 27% and 31% of the variance in LRS and LMS in females, respectively. The variance ratio between the sexes in relative fitness,  $I_{males}/I_{females}$ , was 2.31. Finally, Bateman's gradient was positive and significantly different from zero for male bears ( $r^2 = 0.93$ ,  $DF = 1,215$ ,  $p < 0.001$ ; Figure 2.5).

## 2.4 Discussion

This study represents the largest analysis of parentage in a solitary carnivore population to date and provides insight into how population density, OSR and oestrous asynchrony interact to determine the mating system and opportunity for sexual selection in a long-lived species. These results, in association with previous behavioural observations, indicate that the mating system of polar bears in Hudson Bay is most accurately characterized as serial female-defence polygyny,

where receptive females are sequentially located, defended and bred by dominant males. Strong age-related variation in male mating success is presumed to result from a competitive mating system (Ramsay and Stirling 1986) in which most of the mating is done by prime-aged males that gain access to breeding females through direct contest competition and/or endurance rivalry. A biased OSR coupled with asynchronous oestrus and an extended mating season help maintain a significant degree of mate competition between males, despite the low density of breeding females.

One of the unexpected outcomes of this study was that more than half of the cubs born in western Hudson Bay were sired by male bears that do not show fidelity to my study area during the ice-free period (Table 1). An inability to assign paternities despite having ~80% of the males in my study area genotyped suggests that a high degree of gene flow occurs between the polar bear subpopulations in western Hudson Bay, southern Hudson Bay and Foxe Basin. These findings support previously reported low pair-wise  $F_{ST}$  values between western Hudson Bay and Foxe Basin bears (Paetkau et al. 1999) and indicate the need for further investigation of the factors that influence interbreeding between polar bear subpopulations.

Although advancements have been made in assessing age- and sex-specific survival in polar bears (Regehr et al. 2007), as well as age-specific reproduction in females (Ramsay and Stirling 1988, Derocher and Stirling 1994) this is the first study to demonstrate age-related variation in male reproductive success in polar bears. Behavioural observations and previous parentage analysis indicate that male polar bears as young as 3 and 4 years old may associate and mate with adult females (Cronin et al. 2009, Zeyl et al. 2009, Derocher et al. 2010). Results from this study support these observations and suggest that males as young as 2 years old successfully sire cubs in western Hudson Bay, although this is uncommon (Figure 2.2). In support, histological examination of testes from polar bears harvested in Greenland suggest that males as young as two years old produce spermatozoa (Rosing-Asvid et al. 2002) and therefore may be physiologically capable of producing spermatozoa. Increased rates of canine breakage, scarring and wounding in male polar bears beyond 8 years old (Ramsay and Stirling 1986, Derocher et al. 2010) coincide with observed increases in male mating success in my study (Figure 2.2). Together these data suggest that male bears may enter into contest competition before reaching



their asymptotic body size at ~ 10 years old in western Hudson Bay (Derocher and Stirling 1998).

The mean age of mating males (12.4 years) was similar to the mean age of mating males in the southern Beaufort Sea (12.9 years) (Cronin et al. 2009) and is consistent with reported observations of the age of male bears paired with breeding females in the Barents Sea (mean = 13.6 years) (Derocher et al. 2010) and Canadian Arctic (median = 10.5 years) (Ramsay and Stirling 1986). However, the results from this study showed a leptokurtic distribution in male reproductive success, with 75% of the paternities being assigned to males 10-20 years old, with a marked peak in male reproduction between 11-15 years old accounting for 46% of all paternities (Figure 2.2). The results are consistent with the life history of male polar bears (i.e. prolonged periods of growth) and are similar to observations in black bears (*U. americanus*) and brown bears (*U. arctos*) where intermediate aged males had increased reproductive success (Zedrosser et al. 2007, Costello et al. 2009). The low mating success of young males and a decline in male mating success beyond 22 years of age (Figure 2.2) corresponds with observations of a lack of scarring in young males and a reduction in the presence of unhealed wounds during the mating season in male polar bears  $\geq 20$  years old (Ramsay and Stirling 1986, Derocher et al. 2010). These data suggest that older males likely employ different mating tactics (i.e. not contest competition) to gain access to breeding females. Costello et al. (2009) suggested that at lower densities young male black bears may find unattended females more often. A similar mechanism may apply to both young and old males in my study population. In the Canadian Arctic up to 68% of females without cubs (i.e. females available to breed) were unattended by adult males (Ramsay and Stirling 1986). Although it was unknown if the females observed had already been bred, these data provide support for the hypothesis that the dispersed nature of breeding females may provide mating opportunities for young and old bears. However, the results from this study contrast with estimates of age-related male mating success in polar bears in the Barents Sea (Zeyl et al. 2009), where male bears between 10-14 years old were found to be slightly underrepresented among successful fathers. In contrast to Zeyl et al. (2009), there was no evidence of incestuous mating between male polar bears and their offspring. The potential for paternal incest in polar bears is likely limited due to the brief reproductive tenure of most males

(4.9 years), the delayed maturation of females (4-5 years) and the extended length of maternal care (ca. 2.5 years) all of which lower the likelihood of a male breeding with his offspring.

Patterns of age-specific variation in female reproduction reported here were similar to earlier studies in the same population (Ramsay and Stirling 1988, Derocher and Stirling 1994) and support the existence of reproductive senescence in female polar bears. Despite increasing documentation of age-specific variation in female reproduction, little information still exists on female mate choice in polar bears (Wiig et al. 1992). Female mate choice, however, may partially explain my observed patterns in age-related male reproductive success. In species with no paternal care, evolutionary theory predicts that females should be selective and avoid mating with young males by choosing to mate with intermediate age males as their age may reflect genetic quality via viability selection (Trivers 1972). Age-assortative mating has been suggested to play an important role in the strength of sexual selection in fallow deer (*Dama dama*), where increased mating success by younger and subordinate males may lead to a weakening of directional selection on male traits (Farrell et al. 2011). The role of male age in female mate choice was investigated by comparing the ages of known mated pairs. This analysis however did not reveal any patterns of age-assortative mating (Figures 2.2 & 2.3). Nevertheless, distinguishing between female mate choice and the results of male-male competition in species where they occur together remains difficult.

Although female mate choice is difficult to detect, my age-related reproductive data suggest that male-male competition likely plays an important role in the polar bear mating system, which is supported by my observations of a significant skew in male lifetime mating success (Figure 2.4). However, the estimates of LMS were low, which may partially be explained by the brief reproductive tenure of adult males and the low mean annual mating success of individuals. In polar bears, male annual mating success is likely limited by the reduced availability and unpredictable occurrence of oestrous females (Ramsay & Stirling 1986). In addition, behavioural observations of extended pair bonding/mate guarding in polar bears (Ramsay and Stirling 1986, Wiig et al. 1992, Derocher et al. 2010) suggest that male mating tactics may further limit the ability of adult males to mate with large numbers of females during the mating season. Pairing behaviour summarized by Molnár et al. (2008) indicates that mating pairs stay together on

average for 17.5 days (range: 1-4 weeks). If males are able to keep the time spent searching for females between matings to a minimum, a maximum annual mating success of ~ 4-6 females per year might be expected, the lower end of which was observed in this study. However, search time is likely an important factor influencing male mating success, considering that solitary female polar bears can occupy home ranges in excess of 150,000 km<sup>2</sup> in Hudson Bay (Parks et al. 2006). Mate guarding and courting behaviour, similar to that observed in polar bears (Stirling 2011) have been observed in brown bears (Herrero and Hamer 1977, Hamer and Herrero 1990) and likely serves as a mechanism to ensure that other males do not breed with ovulating females. Mate guarding to assure paternity has been demonstrated in other mammals, although extra-pair or extra-group paternity is significantly lower in species where males continuously associate with breeding females than in species where males only intermittently associate with breeding females (Clutton-Brock and Isvaran 2006). However, in species with induced ovulation males must assess the trade-off between extended pair bonding/mate guarding to ensure ovulation and fertilization has occurred against the opportunity for additional mates (Lariviere and Ferguson 2003). Mate guarding behaviour is predicted to increase with male biased OSR's (Weir et al. 2011). However, male polar bears may modify mate guarding behaviour in relation to the density of conspecifics and potential paternity risk which may explain the ability of some males to breed with up to 4 different females in one year. Such behavioural modifications have been observed in other species (Komdeur 2001). In general, mate guarding in solitary species may be less costly than in social species because fewer potential mating opportunities are likely to be sacrificed in favour of paternity assurance.

Multiple paternity has been documented in many vertebrates (Birkhead and Moller 1998) including black bears (Schenk and Kovacs 1995, Kovach and Powell 2003) and brown bears (Bellemain et al. 2006). The percentage of multiple paternities detected in this study (6.6% of multiparous litters) was similar to the only other reported value for polar bears (6.9%) in the Barents Sea (Zeyl et al. 2009) and, in general, were much lower than reported values for brown bears (15-28% litters) (Bellemain et al. 2006) and black bears (28% and 29% of litters) (Kovach and Powell 2003, Costello et al. 2009). Kovach and Powell (2003) noted a lack of prolonged association between male and female black bears during the mating season, which may, promote promiscuity. In addition, higher population densities among terrestrial bear species may increase

the opportunity for multiple paternity as a result of increased encounter rates between ovulating females and breeding males. Evidence from another induced ovulator, the domestic cat (*Felis catus*), also suggests that density can play an important role in paternity success with higher population densities leading to increased rates of multiple paternity among litters (Say et al. 1999). While low levels of multiple paternity do not preclude the existence of a promiscuous mating system in polar bears, other multiparous promiscuous mammals have much higher levels of multiple paternity (e.g. 74 % of twins in soay sheep, *Ovis aries*, have two sires, Pemberton et al. 1999; 55% of litters in round tailed ground squirrels, *Xerospermophilus tereticaudus*, Munroe and Koprowski 2011).

Although describing mating behaviour is important in the classification of mating systems, it is demographic factors such as the OSR and density that influence individual behaviours to shape the evolution of mating systems and the opportunity for sexual selection (Emlen and Oring 1977, Clutton-Brock and Parker 1992, Jones et al. 2004). In polar bears, the primary factor influencing OSR is the interbirth interval of females that can range from 1 to 4 years although 3 years is most common (Ramsay and Stirling 1986). Factors that affect the interbirth interval therefore may influence the opportunity for sexual selection. For example, dramatic reductions in spring sea ice can reduce cub survival (Regehr et al. 2007), which would increase the number of breeding females the following spring, effectively reducing the OSR and decreasing mate competition. In addition to interannual variation, seasonal changes in OSR may also influence the intensity of sexual selection (Forsgren et al. 2004). One primary factor influencing OSR during the mating season is the degree of oestrous synchrony. For example, in Soay sheep, the behavioural advantage of larger males diminishes as the number of receptive females rises during the breeding season leading to increased mating opportunities for smaller males (Preston et al. 2003). Alternatively, if oestrous is highly asynchronous, dominant males may be able to sequentially monopolize females. In the domestic cat, variance in male reproductive success can be up to four times greater in years when females breed asynchronously compared with years in which females breed synchronously (Say et al. 2001), which supports theoretical analyses that the temporal availability of mates can have pronounced effects on the opportunity for sexual selection in males (Ims 1988). Although detailed patterns of oestrous phenology in relation to behavioural interactions are lacking for polar bears, evidence from black bears indicates that

temporal pattern of oestrus follows a bell shaped distribution (Bridges et al. 2011). If patterns of oestrous are similar in polar bears, I would expect OSR to be strongly skewed toward males (i.e. > 3 males per breeding female) at the beginning and end of the mating season when relatively few females are available for breeding. Thus, both annual and seasonal fluctuations in OSR are likely play an important role in mate competition and the opportunity for sexual selection in polar bears.

Although OSR plays an important role in the polar bear mating system the primary demographic factor that likely has the greatest influence on variance in male mating success is population density. Decreases in density not only influence the distribution of mates but also conspecifics and there is now an increasing amount data indicating that mating systems may function differently in high or low density populations (Kokko and Rankin 2006). Density dependent processes can play an important role in determining the opportunity for sexual selection (Clutton-Brock et al. 1997). In both black bears (Costello et al. 2009) and brown bears (Zedrosser et al. 2007), decreased densities of mature males increased the reproductive success of younger males (< 7 years old), potentially weakening directional selection on male traits (see Farrell et al. 2011). Although decreases in population density have the potential to influence mate competition and mate choice (Kokko and Rankin 2006) much of the information available on variance in male mating and reproductive success among size dimorphic mammals comes gregarious species (e.g. red deer, Clutton-Brock et al. 1988, northern elephant seals, Le Boeuf and Reiter 1988, Soay sheep, Coltman et al. 1999b) where social and ecological conditions promote the monopolization of mates (i.e. high environmental potential for polygyny, Emlen and Oring 1977).

The ability of male bears to monopolize paternity varies amongst terrestrial species with reported values ranging from 13-36% of known offspring being sired by a single male (Craighead et al. 1995, Kovach and Powell 2003). The inability of male polar bears to monopolize paternity in this study (the 2 most successful males sired only 3.0% of all assigned offspring) is unsurprising given that the estimated density of polar bears on the sea ice in Hudson Bay (3.5 bears/1000km<sup>2</sup>) (Taylor and Lee 1995) is an order of magnitude lower than the densities of brown and black bears reported by Craighead et al. (1995) and Kovach and Powell (2003). Similarly, terrestrial

breeding pinnipeds tend to exhibit much higher degrees of mate monopolization in comparison to ice-breeding species where females are more dispersed and have brief synchronous mating seasons (Stirling 1983, Lindenfors et al. 2002). The inability of male bears to monopolize mates in my study was reflected by a low standardized variance in male LMS ( $I_m = 1.26$ ), which was lower than values for other size dimorphic species (e.g. northern elephant seals,  $I_m = 21.77$ , Le Boeuf and Teiter 1988; bighorn sheep, *Ovis canadensis*,  $I_m = 2.45-8.32$ , Coltman et al. 2002) and more similar to species with low levels of size dimorphism (e.g. harbour seals, *Phoca vitulina*,  $I_m = 0.96-1.24$ , Coltman et al. 1998; roe deer,  $I_m = 0.75$ , Vanpe et al. 2008). However, my results conform with predictions based on mating system theory and previous theoretical analysis, that variance in male mating success should be low when females are highly dispersed (Emlen and Oring 1977, Ims 1988).

Amongst mammals, it is generally accepted that high variance in male reproductive success in association with size based advantages in male-male competition has formed the foundation for the evolution of male-biased size dimorphism (Andersson 1994). Although studies have documented a positive relationship between the opportunity for sexual selection and male-biased size dimorphism in ungulates (Vanpe et al. 2008), standardized variance in male mating success only needs to exceed zero for the opportunity for sexual selection to exist (Arnold 1994, Jones 2009). Moreover, it is the difference in fitness variance between the sexes that determines the degree to which the sexes will diverge in character (Shuster 2009). In accordance with selection theory the variance in male LMS and LRS exceeded that of females in my study and although my estimates of  $I_{males}/I_{females}$  were lower than those of other taxa with similar degrees of sexual size dimorphism (e.g.  $I_m/I_f = 3.53$ , red deer, Clutton-Brock et al. 1988;  $I_m/I_f = 4.16$ , northern elephant seals, Le Boeuf and Reiter 1988) they were greater than values reported for less size dimorphic species (e.g.  $I_m/I_f = 1.42$ , roe deer, Vanpe et al. 2008). Despite my low standardized estimates of male LMS my sexual selection gradient (i.e. Bateman gradient) indicated that male reproductive success was strongly dependent on mate acquisition (Figure 2.5), suggesting that much of the variation in male reproductive success is attributable to sexual selection (i.e. variance in male mating success). Furthermore, the age-related skew in male reproductive success that I documented suggests that random processes that influence mate encounter rates are unlikely to play a significant role in the polar bear mating system in Hudson Bay. Finally, it is

important to note that the metrics I have presented only provide measures for the opportunity for sexual selection and that more detailed analysis of phenotypic correlates of fitness (i.e. standardized selection gradients) (Lande and Arnold 1983) are required to demonstrate that sexual selection is acting on specific male traits in polar bears.

While this data set provides insight into the opportunity for sexual selection among solitary carnivores it does suffer from shortcomings associated with an inability to continuously monitor all individuals in the study population. In general, it is assumed that the results of this analysis have underestimated mean LRS/LMS as it was not possible to sample all cubs from each cohort, in addition to new evidence (this study) that suggests male bears likely sire offspring with females from adjacent subpopulations. However, it is unknown to what extent I have underestimated or overestimated the variance in LRS/LMS or to what extent my estimates of the opportunity for sexual selection may be biased. Low biased estimates of mean LMS should result in an increase in my estimate of the opportunity for sexual selection and therefore my results may be conservative.

In summary, these results indicate that the opportunity for sexual selection in male polar bears is likely mediated by demographic (OSR) and physiological factors (oestrous asynchrony) that increase the degree of mate competition in a species that occurs at low density. Furthermore, despite a significant degree of male biased size dimorphism (Derocher et al. 2005) my analysis revealed relatively low variance in male mating success in accordance with mating system theory. Further studies examining mating system variation in species that occur at low densities are needed to understand how demographic and physiological factors interact to influence to evolution of mammalian mating systems and the opportunity for sexual selection in species where variance in male mating success is predicted to be low.

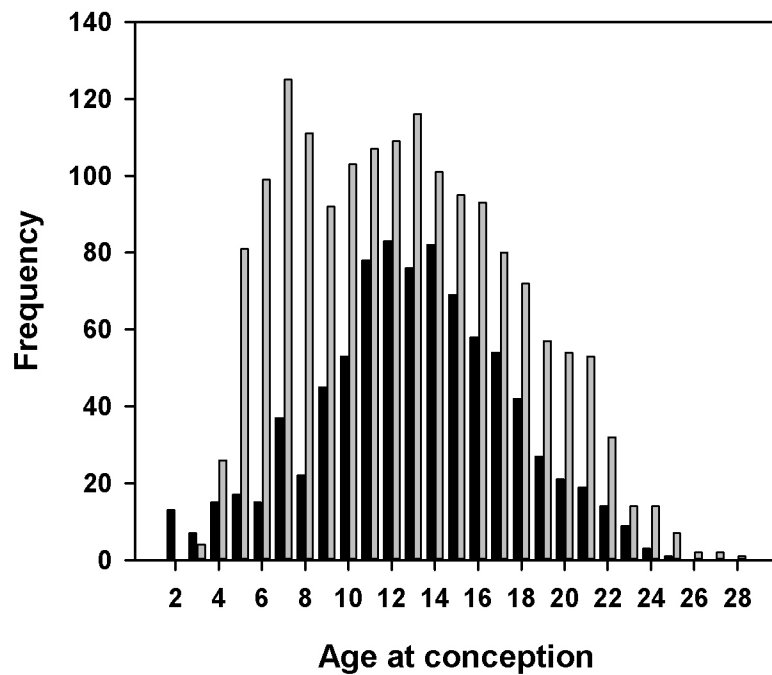
**Table 2.1:** Microsatellite loci used in paternity analysis of polar bears in western Hudson Bay. (NA, number of alleles; Ho, observed heterozygosity; He, expected heterozygosity; P(HWE), Hardy-Weinburg equilibrium.)

| Locus   | 5' Primer                    | 3' Primer                   | Primer (nM) | Taq (U) | MgCl <sub>2</sub> (mM) | Load/PCR | N <sub>A</sub> | Ho    | He    | P(HWE)  |
|---------|------------------------------|-----------------------------|-------------|---------|------------------------|----------|----------------|-------|-------|---------|
| CXX110  | HEX-AATCTAAGCCAATATTCTCC     | GCATCCAAGTAAATCAAGA         | 480         | 0.55    | 2.08                   | 1/A      | 10             | 0.589 | 0.593 | 0.4168  |
| CXX173  | PET-ATCCAGGTCTGGAATACCCC     | TCCTTTGAATTAGCACTTGGC       | 213         | 0.81    | 2.08                   | 3/I      | 6              | 0.693 | 0.691 | 0.0941  |
| CXX20   | FAM-CCCATTACTGGAGTCTTCCT     | TGAATAGTCTCTGCGGTCA         | 240         | 0.45    | 2.33                   | 2/E      | 9              | 0.785 | 0.794 | 0.3098  |
| G10B    | FAM-GCCTTTAATGTTCTGTTGAATTTG | GACAAATCACAGAAACCTCCATCC    | 240         | 0.4     | 1.9                    | 1/C      | 7              | 0.589 | 0.599 | 0.0911  |
| G10C    | AAAGCAGAAGGCCTTGATTCTCTG     | FAM-GGGGACATAAACACCGAGACAGC | 160         | 0.4     | 1.9                    | 1/C      | 8              | 0.683 | 0.689 | 0.3151  |
| G10H    | CAACAAGAAGACCACTGTAA         | FAM-AGAGACCACCAAGTAGGATA    | 224         | 0.3     | 1.9                    | 1/D      | 10             | 0.769 | 0.767 | 0.291   |
| G10J    | NED-GATCAGATATTTTCAGCTTT     | AACCCCTCACACTCCACTTC        | 320         | 0.4     | 2.25                   | 2/F      | 4              | 0.642 | 0.626 | 0.6571  |
| G10L    | TET-GTACTGATTTAATTCACATTTCCC | GAAGATACAGAAACCTACCCATGC    | 225         | 0.4     | 1.9                    | 1/B      | 6              | 0.426 | 0.424 | 0.3579  |
| G10M    | TTCCCTCATCGTAGGTTGTA         | NED-AATAATTTAAGTGCATCCAGG   | 320         | 0.4     | 2.25                   | 2/F      | 9              | 0.789 | 0.796 | 0.7055  |
| G10P    | ATCATAGTTTACATAGGAGGAAGAAA   | HEX-TCATGTGGGAAATACTCTGAA   | 450         | 0.75    | 2.67                   | 2/G      | 9              | 0.745 | 0.751 | 0.8757  |
| G10U    | NED-TGCAGTGTCAAGTTGTTAGGAA   | TATTTCCAATGCCCTAAGTGAT      | 320         | 0.45    | 2.33                   | 2/H      | 7              | 0.569 | 0.569 | 0.8879  |
| G10X    | CCACCTTCTTCCAATTCTC          | HEX-TCAGTTATCTGTGAAATCAAAA  | 320         | 0.55    | 2.08                   | 1/A      | 9              | 0.742 | 0.731 | 0.8424  |
| G1A     | TET-ACCCTGCATACTCTCCTCTGATG  | GCACTGTCCTTGCGTAGAAGTGAC    | 225         | 0.4     | 1.9                    | 1/B      | 8              | 0.537 | 0.541 | *0.0047 |
| G1D     | ACAGATCTGTGGGTTTATAGGTTACA   | FAM-CTACTCTTCTACTCTTTAAGAG  | 320         | 0.4     | 1.9                    | 1/C      | 5              | 0.619 | 0.63  | 0.2282  |
| MSUT1   | VIC-CCTTGGGATTCGGGATTGT      | AGTCCTCACCCCTCCCTTTT        | 213         | 0.27    | 1.67                   | 3/J      | 8              | 0.746 | 0.736 | 0.3897  |
| MSUT2   | FAM-AGTGAATCCTAAACAGGTTA     | TAATATGAATATGGTGTGCT        | 350         | 0.54    | 2.08                   | 3/K      | 9              | 0.764 | 0.778 | 0.1043  |
| MSUT4   | PET-GTGCCAAGTGTAGATGA        | TGAGTAATATTCTTTTCTCT        | 213         | 0.81    | 2.08                   | 3/L      | 10             | 0.666 | 0.704 | *<0.000 |
| MSUT6   | NED-CATATGGTGACTAAGATAAC     | AAGAGATGATTTCTGTCTC         | 355         | 0.54    | 2.08                   | 3/M      | 3              | 0.517 | 0.524 | 0.7845  |
| MSUT8   | NED-GATCCTGGGACTTCTCAG       | TCCAGAGAAAGAGGACTG          | 100         | 0.54    | 2.08                   | 3/M      | 6              | 0.761 | 0.77  | 0.6983  |
| UarMU05 | AATCTTTTCACTTATGCCCA         | FAM-GAAACTTGTTATGGGAACCA    | 350         | 0.54    | 2.08                   | 3/K      | 10             | 0.779 | 0.768 | 0.8666  |
| UarMU10 | TTCAGATTCATCAGTTTGAC         | VIC-CAGCATAGTTACACAAATCTCC  | 213         | 0.27    | 1.67                   | 3/N      | 7              | 0.649 | 0.649 | 0.4056  |
| UarMU23 | FAM-GCCTGTGTGCTATTTTATCC     | AATGGGTTTCTTGTTAATTAC       | 213         | 0.135   | 1.67                   | 3/O      | 3              | 0.116 | 0.115 | 0.0526  |
| UarMU26 | HEX-GCCTCAAATGACAAGATTTT     | TCAATTAATAATAGGAAGCAGC      | 450         | 0.75    | 2.67                   | 2/G      | 9              | 0.84  | 0.841 | 0.9797  |
| UarMU50 | TET-GGAGGCGTTCTTTTCAGTTGGT   | TGGAACAAAACCTAACACAAATG     | 224         | 0.3     | 1.9                    | 1/D      | 9              | 0.787 | 0.781 | 0.2794  |
| UarMU51 | NED-GCCAGAATCCTAAGAGACCT     | AAGAGAAGGGACAGGAGGTA        | 320         | 0.45    | 2.33                   | 2/H      | 8              | 0.8   | 0.802 | 0.2165  |
| UarMU59 | TET-GCTGCTTTGGGACATTGTAA     | CAATCAGGCATGGGGAAGAA        | 320         | 0.4     | 1.9                    | 1/B      | 10             | 0.843 | 0.83  | 0.1541  |
| AVERAGE |                              |                             |             |         |                        |          |                | 7.65  | 0.671 | 0.673   |

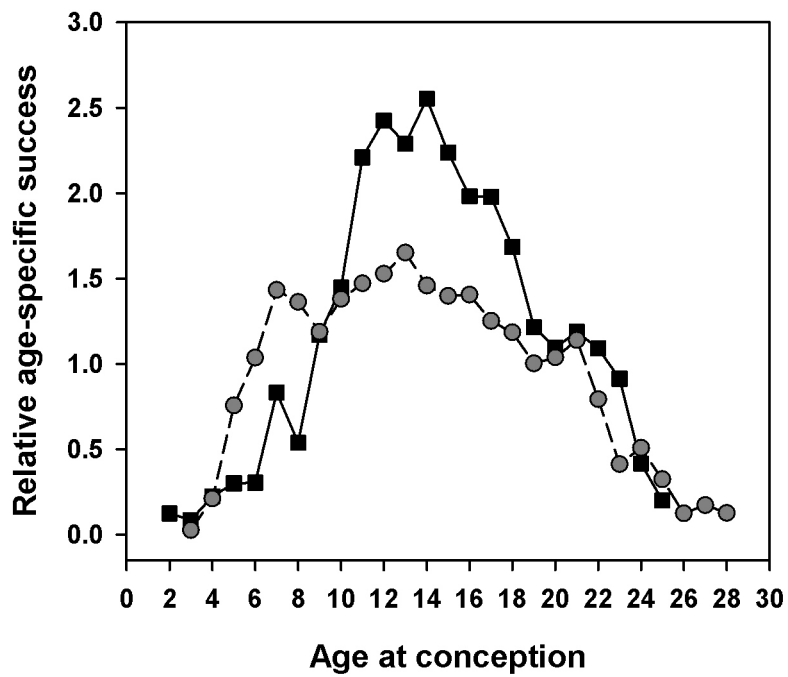


**Table 2.2:** Sample size and assignments results for each polar bear cohort from 1975-2005 in western Hudson Bay.

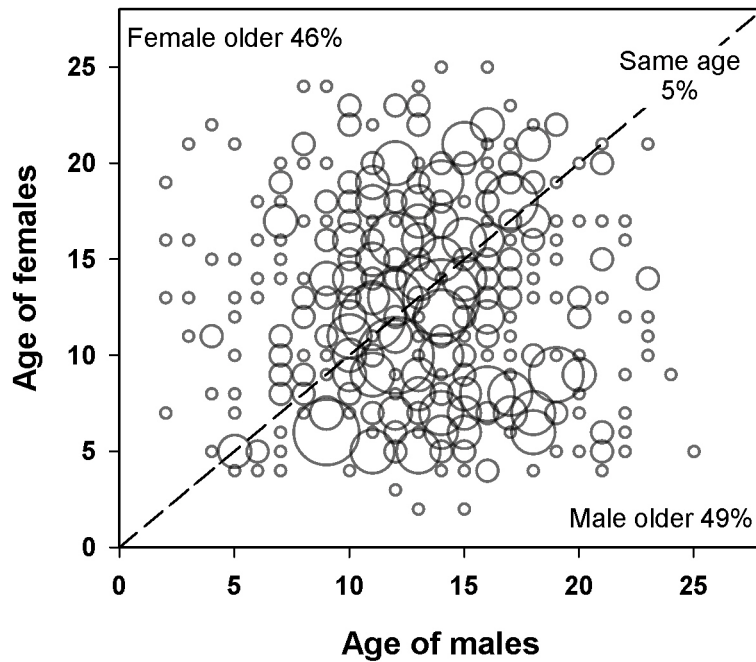
| Cohort | No. of cubs | No. candidate mothers | No. candidate fathers | No. maternal assignments (proportion) | No. paternal assignments (proportion) | Both parents assigned (proportion) |
|--------|-------------|-----------------------|-----------------------|---------------------------------------|---------------------------------------|------------------------------------|
| 1975   | 25          | 131                   | 63                    | 9 (.36)                               | 2 (.08)                               | 1 (.04)                            |
| 1976   | 42          | 143                   | 69                    | 12 (.29)                              | 1 (.02)                               | 0 (.00)                            |
| 1977   | 22          | 156                   | 81                    | 8 (.36)                               | 2 (.09)                               | 1 (.05)                            |
| 1978   | 34          | 177                   | 102                   | 10 (.29)                              | 8 (.24)                               | 1 (.03)                            |
| 1979   | 41          | 188                   | 113                   | 17 (.41)                              | 8 (.20)                               | 4 (.10)                            |
| 1980   | 43          | 207                   | 128                   | 14 (.33)                              | 7 (.16)                               | 3 (.07)                            |
| 1981   | 66          | 227                   | 149                   | 33 (.50)                              | 15 (.23)                              | 7 (.11)                            |
| 1982   | 68          | 248                   | 171                   | 34 (.50)                              | 17 (.25)                              | 8 (.12)                            |
| 1983   | 43          | 288                   | 197                   | 25 (.58)                              | 8 (.19)                               | 5 (.12)                            |
| 1984   | 47          | 323                   | 230                   | 25 (0.53)                             | 17 (.36)                              | 11 (.23)                           |
| 1985   | 44          | 357                   | 239                   | 28 (.64)                              | 10 (.23)                              | 3 (.07)                            |
| 1986   | 49          | 377                   | 266                   | 30 (.61)                              | 17 (.35)                              | 14 (.29)                           |
| 1987   | 107         | 402                   | 285                   | 80 (.75)                              | 43 (.40)                              | 34 (.32)                           |
| 1988   | 74          | 424                   | 312                   | 56 (.76)                              | 34 (.46)                              | 28 (.38)                           |
| 1989   | 97          | 477                   | 366                   | 87 (.90)                              | 36 (.37)                              | 33 (.34)                           |
| 1990   | 77          | 513                   | 404                   | 66 (.86)                              | 19 (0.25)                             | 16 (.21)                           |
| 1991   | 61          | 557                   | 457                   | 32 (.52)                              | 17 (0.28)                             | 12 (.20)                           |
| 1992   | 55          | 597                   | 493                   | 39 (.71)                              | 19 (0.35)                             | 14 (.25)                           |
| 1993   | 125         | 626                   | 525                   | 110 (.88)                             | 56 (.45)                              | 51 (.41)                           |
| 1994   | 160         | 662                   | 544                   | 141 (.88)                             | 75 (.47)                              | 68 (.43)                           |
| 1995   | 106         | 728                   | 603                   | 87 (.83)                              | 55 (.53)                              | 44 (.43)                           |
| 1996   | 103         | 798                   | 693                   | 82 (.80)                              | 52 (.50)                              | 45 (.44)                           |
| 1997   | 116         | 853                   | 744                   | 109 (.94)                             | 51 (.44)                              | 48 (.41)                           |
| 1998   | 84          | 903                   | 797                   | 67 (.80)                              | 31 (.37)                              | 30 (.36)                           |
| 1999   | 110         | 964                   | 852                   | 93 (.85)                              | 66 (0.61)                             | 55 (.51)                           |
| 2000   | 63          | 1008                  | 892                   | 57 (.90)                              | 29 (.46)                              | 27 (.43)                           |
| 2001   | 129         | 1065                  | 945                   | 111 (.87)                             | 63 (.49)                              | 55 (.43)                           |
| 2002   | 87          | 1093                  | 979                   | 64 (.74)                              | 39 (.45)                              | 29 (.33)                           |
| 2003   | 70          | 1165                  | 1036                  | 66 (.94)                              | 41 (.59)                              | 41 (.59)                           |
| 2004   | 42          | 1200                  | 1088                  | 37 (.88)                              | 18 (.43)                              | 17 (.40)                           |
| 2005   | 41          | 1239                  | 1119                  | 37 (.90)                              | 17 (.41)                              | 14 (.34)                           |
| Total  | 2229        | -                     | -                     | 1665                                  | 873                                   | 719                                |



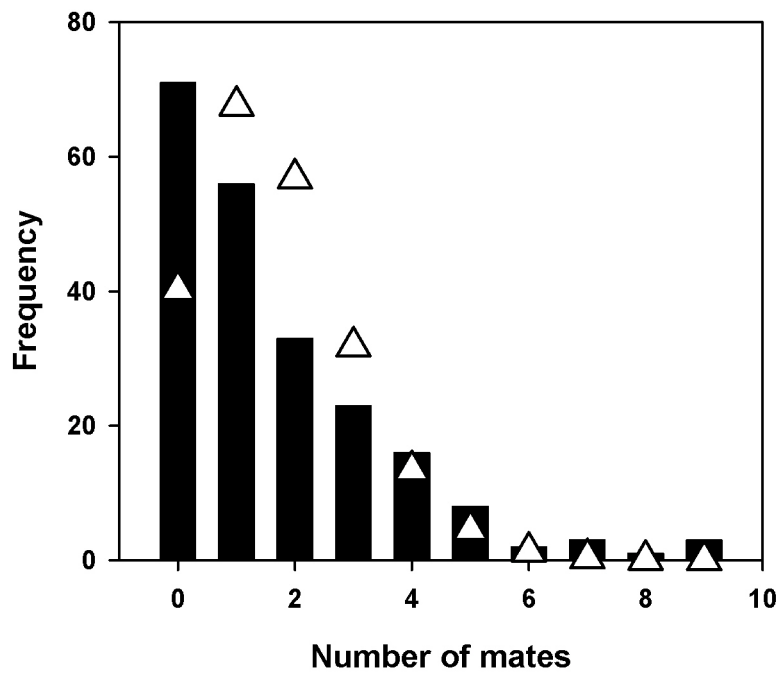
**Figure 2.1:** Number of maternities and paternities assigned to male (black bars) and female (grey bars) polar bears from the western Hudson Bay population in relation to age from 1975-2005.



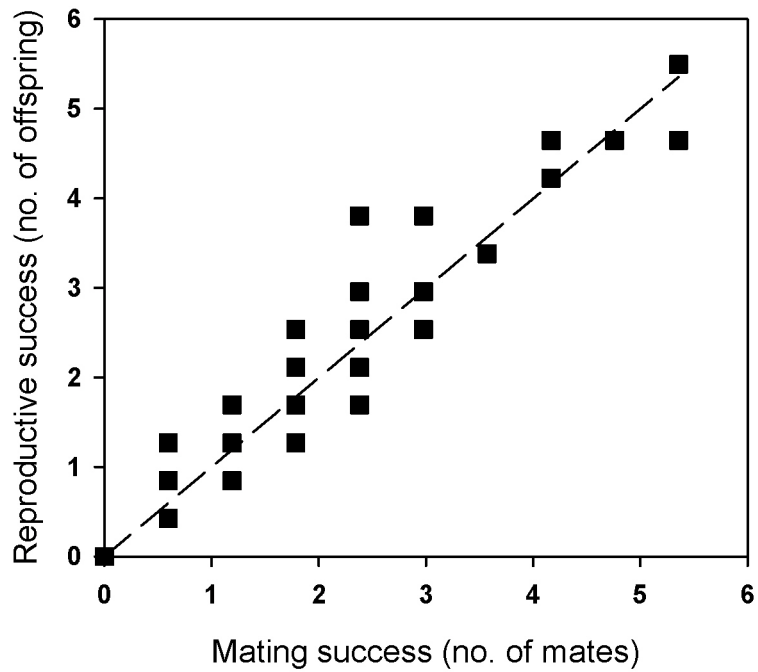
**Figure 2.2:** Relative age-specific maternities (grey circles; dashed line) and paternities (black square; solid line) for all known aged polar bears from western Hudson Bay, 1975-2005.



**Figure 2.3:** Age composition of all known age mating pairs (n = 493) in the year of mating for polar bears from western Hudson Bay, 1975-2005. Bubble size indicates the frequency of mating pairs for each known age combination (range: 1-7 pairs). Dotted line indicates mating pairs where the male and female are the same age.



**Figure 2.4:** Lifetime male mating success including unsuccessful male polar bears ( $n = 216$ ) from western Hudson Bay, 1975-2005. Triangles indicate expected number assuming mating is random amongst individual male bears.



**Figure 2.5:** Bateman gradient describing the relationship between lifetime mating and reproductive success in male polar bears ( $n=216$ ) from western Hudson Bay, 1975-2005. Data are scaled to show relative mating and relative reproductive success ( $r^2 = 0.93$ ,  $df = 1,215$ ,  $p < 0.001$ ).

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## Chapter 3

### 3 Measures of selection in a large size dimorphic carnivore: evidence for sexual selection in polar bears

#### 3.1 Introduction

Among mammals, sex-specific reproductive strategies and life histories are influenced by anisogamy and parental care, with female reproductive success being limited by access to resources and male reproductive success being limited by access to mates, creating the potential for sexual selection (Trivers 1972). In polygynous species where male-male competition determines access to oestrus females, intrasexual selection is expected to favour male traits that improve an individual's competitive ability (Trivers 1972, Andersson 1994). Competitive exclusion of conspecifics creates the potential for high variance in male reproductive success (Emlen and Oring 1977) and an increase in the opportunity for sexual selection (Arnold and Wade 1984). Because mating systems can shape both the intensity and direction of sexual selection (Emlen and Oring 1977, Shuster 2009) as well as the distribution of phenotypes (Blanckenhorn 2005), knowledge of mating system dynamics is a necessary component in assessing the role of sexual selection in wild populations.

Among mammals one of the most conspicuous traits associated with taxa experiencing sexual selection is male biased sexual size dimorphism (SSD) (Isaac 2005). Levels of SSD are frequently linked to the level of mating system polygyny in mammals (Alexanders et al. 1979, Loison et al. 1999, Lindenfors et al. 2002) and classic examples of highly dimorphic polygynous pinnipeds (Le Boeuf and Reiter 1988), ungulates (Clutton-Brock et al. 1988) and primates (Clutton-Brock et al. 1977) with high variance in male mating success are frequently cited as providing support for this trend. However, observed patterns, for the most part have been restricted to socially polygynous species where the opportunity for sexual selection is expected to be high as a result of the environmental potential for polygyny (Emlen and Oring 1977). Similarly, empirical

studies that test for selection on phenotypic traits in large mammals have focussed on socially polygynous and promiscuously mating species (Coltman et al. 1999, Kruuk et al. 2002, Robinson et al. 2006, Poissant et al. 2008). Studies of selection of phenotypic traits in solitary mammals, where male fitness variance and the opportunity for sexual selection are predicted to be low as a result of a reduced environmental potential for polygyny (Emlen and Oring 1977), are limited.

Among large mammals body size is often positively associated with male reproductive success promoting SSD (Clutton-Brock et al. 1982, Fisher and Lara 1999, McElligott et al. 2001, Wilson et al. 2002, Zedrosser et al. 2007). However, sexual size dimorphism is not restricted to male mammals with female biased size dimorphism is observed in several mammalian orders (Ralls 1976). Although fecundity selection is typically proposed as the mechanism by which female biased size dimorphism evolves (Blanckenhorn 2005), among large carnivores, large size may have several benefits, including the increased potential to prevent infanticide (Kruuk 1972, Ralls 1976), increased investment in offspring (Bernardo 1996, Derocher and Stirling 1998b, Crocker et al. 2001) and increased hunting success (Radloff and Du Toit 2004, Swanson et al. 2011). Because varying selective pressures can act on either sex or on both sexes at different magnitudes, one of the common criticisms of studies of SSD is the tendency for investigators to focus on a single selective pressure in one sex (Ydenberg and Forbes 1991). The limitations of such studies are evident in the context of quantitative genetic models that cite the need for the sexes to experience differential selection for SSD to evolve (Lande 1980, Lande and Arnold 1985). Studies that investigate potential selective pressures on both sexes should therefore provide greater insight into the evolutionary processes that result in SSD.

In most species, SSD results from sex specific differences in growth rate and/or growth duration (Badyaev 2002). Although sexual selection is often proposed as the ultimate cause of growth rate variation between the sexes, differences in the ontogeny of growth in males and females provide a proximate cause for SSD (Blanckenhorn 2005, Walker and McCormick 2009). In polar bears (*Ursus maritimus*), SSD results from difference in



both growth rate and growth duration between the sexes (Derocher and Stirling 1998a) resulting in males being roughly twice the mass of females (Kingsley 1979, Derocher et al. 2005). Polar bears also exhibit SSD in several skeletal measures including body length, head length and zygomatic breadth as well as differences in foreleg guard hair length (Derocher et al. 2005). In addition, different skeletal measures exhibit variation in the magnitude of dimorphism between the sexes (Derocher et al. 2005), suggesting that selection may be affecting different components of body size. SSD in polar bears is frequently attributed to sexual selection acting on males that confer an advantage in the polar bear mating system that is best characterized as serial female defence polygyny (Chapter 2). The degree of mate competition among males is suggested to be strongly influenced by the operational sex ratio which may exceed 3 males per breeding female (Ramsay and Stirling 1986, Wiig et al. 1992). Increased rates of facial scarring and canine breakage as well as observations of fresh wounds on male polar bears during the spring breeding season all suggest that intense competition for access to oestrus females occurs and that the physical outcome of these interactions determine access to breeding females (Ramsay and Stirling 1986, Derocher et al. 2010). Despite a strong degree of SSD, variance in male mating success among polar bears is more closely associated with species that exhibit limited degrees of SSD and mate monopolization (Chapter 1) and thus questions the generality of the supposition that SSD is related to high variance in male mating success in large mammals.

Although differential mating success among male polar bears (Chapter 2) provides an indication for the potential for sexual selection to act on male traits (Price 1984), sexual selection can only occur if mating success is correlated with phenotypic variation among individuals (Coltman et al. 2002). Here I present the results of an analysis using parent-offspring assignments (see Chapter 2) to characterize lifetime fitness and lifetime selection on two size dimorphic skeletal traits (body length and zygomatic breadth) in both male and female polar bears from the western Hudson Bay polar bear population. My primary goal was to quantify the form, direction and intensity of selection on these traits to test the frequently proposed hypothesis that SSD in polar bears is the result of sexual selection on male body size. I also investigated the potential role of viability

selection in the evolution of polar bear body size is investigated by examining the covariance between longevity and trait values in both sexes.

## **3.2 Methods**

### **3.2.1 Study area and population**

The western Hudson Bay polar bear population occupies the ice-covered waters of Hudson Bay in the winter. During the ice-free summer, bears spend most of their time onshore in northeastern Manitoba. Techniques used to capture, mark, sample, age and genotype bears are reviewed in (Chapter 1). Briefly, free-ranging polar bears in the study population were located from a helicopter and immobilized with Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa) (Stirling et al. 1989). At the time of first capture, each animal was assigned a unique identification number that was applied as both a permanent tattoo on the inside of the upper lip and as a plastic tag placed in each ear. Individuals are either of known age or are aged by counting the growth-layer groups in the cementum of an extracted vestigial premolar (Calvert and Ramsay 1998). Samples for genetic analysis were taken from skin collected when ear tags were applied, from fat biopsies, and/or as blood samples collected from the femoral vein. The immobilization and handling protocol for polar bears in western Hudson Bay was reviewed and approved annually through the Animal Care Committee of the Canadian Wildlife Service, Prairie and Northern Region.

### **3.2.2 Parentage Analysis**

Parentage analysis was conducted using the likelihood approach in CERVUS 3.0 (Marshall et al. 1998, Kalinowski et al. 2007) with 25 microsatellite loci to identify the most likely mother and father for all sampled individuals born in 1975-2005 ( $n = 2229$ ). Parental offspring relationships were restricted to males and females born before 1986 and 1985, respectively. I restricted my analysis to these individuals because only 5% of paternities and maternities were assigned to males and females  $> 20$  and  $> 21$  years old,

respectively; therefore individuals reaching this age were considered to be no longer reproductively active at the end of my study. Fitness components were derived for males and females known to survive until a minimum of 2 and 3 years of age respectively.

### **3.2.3 Fitness Components**

The following fitness components were examined in relation to phenotypic traits: (i) lifetime reproductive success (LRS): total number of known cubs born to a female or sired by a male that survived to two years old; (ii) lifetime breeding success (LBS): total number of cubs born to a female or sired by a male; (iii) longevity (in years): last known age at which an individual was known to be alive (either from a physical capture or from a parentage assignment); (iv) lifetime mating success (LMS): total number of known mates for each individual across its lifetime. Relative fitness for each individual and each fitness component were calculated by dividing individual values by the mean value for all individuals (Lande and Arnold 1983). Relative fitness was calculated separately for each sex.

### **3.2.4 Phenotypic traits**

Fitness measures were related to the following two phenotypic traits (i) body length: straight-line distance from the tip of the nose to the caudal end of the last tail vertebra measured to the nearest centimetre when the bear was sternally recumbent and (ii) zygomatic breadth: maximum head width between the zygomatic arches measured with callipers to the nearest millimeter. To examine differences in growth duration between the sexes von Bertalanffy growth models (Derocher and Stirling 1998a) were fit to mean age-specific trait values to determine the age at which individual reached 97% of their asymptotic body size. I chose 97% as it corresponds to size at which most females reach sexual maturity in western Hudson Bay (Derocher and Stirling 1998a). The analysis of selection acting through LRS, LBS and LMS used phenotypic measures recorded at the last handling for each individual. Because polar bears continue to grow into middle age

there is the possibility that the detection of significant associations between traits and fitness could simply result from individual reaching older age. To avoid this age-adjusted measures were calculated for each trait by dividing individuals into separate age groups 1-22 years and  $\geq 23$  years for females and 1-21 years and  $\geq 22$  years for males. Age-specific trait mean and standard deviations for the age at which an individual was last measured were then used to standardized trait values to a mean of zero and variance of one for selection analyses. The same age adjusted traits were used to test for viability selection through longevity, but trait values were taken as the first available measure for each individual upon reaching the mean age at which individuals reached 97% of their asymptotic body size, to avoid potential issues with selective disappearance of individuals. For individuals that did not reach their asymptotic body size, I used the closest age-standardized measure.

### **3.2.5 Selection Analysis**

For LRS, LBS, longevity and LMS standardized directional ( $S_i$ ) and nonlinear ( $c_i$ ) selection differentials were calculated using linear and second order polynomial regressions, using ordinary least squares regression (Arnold and Wade 1984). Selection differentials reveal net (total) selection acting on traits without regard to potential selection acting on correlated traits (Preziosi and Fairbairn 2000). I then calculated standardized selection gradients for the same fitness components and traits, which through a multivariate version of selection differentials, estimates selection action on a trait while corrected for selection on correlated traits (Lande and Arnold 1983). Standardized linear (i.e. directional) selection gradients were obtained for each sex and each fitness component using multiple regressions that included both phenotypic traits. Linear selection gradients ( $\beta_i$ ) were estimated as the partial coefficients from a multiple regression that included both traits. Quadratic ( $\gamma_{ii}$  i.e. stabilizing or disruptive) and correlational ( $\gamma_{ij}$  i.e. indirect) selection gradients were estimated in separate models in which all linear, quadratic and pairwise cross-products of traits were included. Quadratic selection gradient coefficients and standard errors were doubled following Stinchcombe et al. (2008). Because extreme correlation between phenotypic traits can interfere with

statistical detection of selection (Lande and Arnold 1983, Wheeler et al. 2012).

Correlation between traits and fitness measures were investigated using Spearman rank correlations. To further assess the potential for collinearity among traits, I examined the variance inflation factors (VIF) to ensure that they did not exceed 10 (O'Brien 2007).

Following parameter estimation, the same models were fit to estimate the significance of each of the selection coefficients using generalized linear models (GLM) with unstandardized fitness measures and standardized trait values, to control for age-related variation in size. A negative binomial error structure and logarithmic link function were specified for all models due to overdispersion in the data. The significance of each term was assessed as the change in deviance, distributed as a  $\chi^2$  on dropping each term from the model. Because Bonferroni adjustment is inappropriate for correlated variables (Rice 1989) the probability values associated with each model term are reported.

Finally, to visualize potential non-linear, non-quadratic relationships between sex-specific traits and fitness, I used univariate cubic spline estimates (Schluter 1988) of fitness as a function of standardized phenotypic traits. Plots were created using generalized additive models (GAM) with a negative binomial error structure and log link function. Generalized cross-validation was used to determine a separate smoothing factor ( $\lambda$ ) for each curve. All analyses were implemented in R (version 2.6.0; R Core Development Team, Boston, MA, USA).

### **3.3 Results**

Parentage analysis allowed me to examine selection on lifetime fitness measures in 216 male and 234 female polar bears. Both body length and zygomatic breadth showed substantial variation with age in both males and females (Figure 3.1). Males reached 97% of their asymptotic body length and zygomatic breadth at 8.4 and 15.8 years of age, respectively. Females grew faster than males reached 97% of their asymptotic body length and zygomatic breadth at 5.7 and 8.2 years of age, respectively. There were significant positive correlations between LMS, LBS, LRS and longevity for both sexes

ranging from  $\rho = 0.37$  to  $0.97$  (Table 3.1). Standardized trait values were also significantly correlated for males ( $\rho = 0.45$ ) and females ( $\rho = 0.31$ ) (Table 3.1). Examination of VIF revealed no significant multicollinearity.

Estimates of linear selection differentials were positive and significant, suggesting that male LRS, LBS and LMS increase with both body length and zygomatic breadth (Table 3.2, Figure 3.2). The non-linear selection differentials for male body length in relation to LRS and LMS approached significance ( $p < 0.10$ ), but did not show any relationship between fitness and zygomatic breadth. Linear selection gradients were not significant for male body length for any of the fitness measures, but approached significance for LRS and LMS. Linear selection gradients were positive and significant for zygomatic breadth in relation to the LRS, LBS and LMS (Table 3.2, Figure 3.3). Quadratic selection gradients were significant for male body length in relation to LRS and LMS and approached significance for LBS. Cubic splines revealed that male fitness was curvilinear in relation to body length with a steep increase in fitness in individuals that were 2 standard deviations above the mean (Figure 3.2). Fitness in relation to zygomatic breadth was more linear and increased across the distribution of trait values (Figure 3.3). In females, the only significant selection coefficient was a negative quadratic selection gradient for body length in relation to LRS, which indicates potential for stabilizing selection on female body length. Although not significant, all 4 quadratic selection differentials for female body length were negative, suggesting potential selection against large body size in females. Although also not significant, selection differentials for zygomatic breadth in relation to LRS, LBS and LMS for females were all negative and support the observed declines in fitness in relation to increasing trait values in (Figure 3.3). There was no significant relationship between either trait and longevity for males or females (Table 3.2). None of the interaction terms in the selection analysis were significant and are therefore not presented.

### **3.4 Discussion**

Although several studies have shown an association between phenotypic traits and

lifetime fitness in ungulates (Kruuk et al. 2002, Coltman et al. 2005, Robinson et al. 2006, Poissant et al. 2008) evidence of phenotypic selection in large carnivores remains limited (but see Swanson et al. 2011). Consistent with the serial female defence polygyny mating system in polar bears (Chapter 1), these results provide direct quantitative evidence that lifetime fitness in male polar bears is influenced by body size. Body size also influences male reproductive success in other ursids (Kovach and Powell 2003b, Zedrosser et al. 2007) and may influence the outcome of contest competition (Nie et al. 2012), but quantification of selection on male traits in relation to male mating success in a large carnivore has not been documented until my study. Positive linear and quadratic selection on male traits in relation to LMS and potential stabilizing selection on female body size in relation to LRS provide support for the hypothesis that SSD in polar bears has evolved as a result of differential selection between the sexes. Although reported for other large mammals (Robinson et al. 2006) I found no evidence for viability selection in either sex in relation to body size. However, the detection of viability selection may be difficult, particularly in males, if large dominant individuals sacrifice longevity for increased reproductive success or if viability selection occurs before sexual maturity.

Polar bear life history is characterized by slow growth, delayed maturation, and low reproductive rates. Although life history theory suggests that natural selection should favour rapid development to sexual maturity as a result of cumulative mortality costs in most species (Blanckenhorn 2000, Blanckenhorn et al. 2007), for species that inhabit highly seasonal environments, trade-offs between growth and survival may constrain the age and size at which individuals reach reproductive maturity. Similar to previous investigations (e.g. Derocher and Stirling 1998a, Rode et al. 2010), males in this study invested more in growth than females, reaching their asymptotic body size at a later age. The results of this study however, provide the first quantitative support for the importance of the extended growth period in adult male polar bears in relation to the expression of age-dependent traits that are correlated with lifetime fitness. Furthermore, these results also suggest that body size in adult females may be constrained in relation to LRS, highlighting the potential costs of increased growth relative to reproductive lifespan. Because asymptotic body size and age at maturity are strongly correlated in

marine mammals (Laws 1956) it is likely that female polar bears need to reach a size at which they can meet the increased energetic demands of gestation and lactation during denning period (Watts and Hansen 1987, Ramsay and Stirling 1988, Polischuk et al. 2001).

Estimates of selection on phenotypic traits in relation to lifetime fitness are rare in wild populations (Kingsolver et al. 2001) and results presented here provide insight into the intensity of sexual selection on male traits. Reproductive success in male polar bears follows theoretical predictions (Emlen and Oring 1977) with a reduced opportunity for sexual selection relative to other female defence based mating systems (Chapter 1). The strength of selection on male traits observed here, however, are similar to those in species that exhibit higher variance in male mating success. For example, in Soay sheep (*Ovis aries*) using LBS the standardized selection gradient for horn size in males was 0.393 (0.17 SE) (Robinson et al. 2006) and in red deer (*Cervus elaphus*) using LRS the standardized selection gradient on antler size was 0.44 (0.18 SE) (Kruuk et al. 2002). Although, directional selection gradients for male body length approached significance, quadratic selection gradients for both LMS 0.50 (0.14) and LRS 0.63 (0.17) were both significant (Table 3.2) and are ‘very strong’ using the criteria of Kingsolver et al. (2001). Although positive quadratic selection coefficients are predicted to result in disruptive selection (Lande and Arnold 1983), visualization of fitness surfaces for male body length (Figure 3.2) show that the data presented here conform to what has been referred to as “threshold selection” (Ritz and Kohler 2010) where the form of selection changes significantly beyond a threshold value (i.e. there is no positive selection for smaller males as would be predicted by a disruptive selection). Results suggest that male bears that are greater than one standard deviation above the population mean body length are likely to experience significant increases in lifetime mating, breeding, and reproductive success (Figure 3.2). Although, larger males would be presumed to fare better in intrasexual conflicts, it also may also be that these males may be challenged less frequently and/or that they may win contests quickly (see Stirling 2011) and therefore might be able to invest more in courtship and mate searching behaviours. Body length is a strong predictor of body mass in polar bears (Thiemann et al. 2011) and therefore observed trends in



selection for body length may be a function of the relationship between these two traits. In phenotypic selection analyses, investigators must assess whether the phenotypic traits being investigated are the actual targets of selection or are simply correlated with some another trait that is being targeted. Multiple regression provides a means of controlling for traits in selection analyses and can assist in determining whether certain traits are the target of selection. My results revealed that there was a significant linear selection gradient for zygomatic breadth in relation to LRS, LBS and LMS after correcting for body length. Zygomatic breadth is more dimorphic than body length in polar bears (Derocher et al. 2005) and a significant selection gradient after controlling for body size suggests that zygomatic breadth may be the target of selection in male bears.

Skull size dimorphism is a common trait in ursids (Virgl et al. 2003, Derocher et al. 2005, Bechshøft et al. 2008, McDonough and Christ 2012) and is even evident in extinct cave bear (*U. spelaeus* Rosenmuller) where occipital and zygomatic breadth were the two most size dimorphic skull traits (Grandal-d'Anglade and Lopez-Gonzalez 2005). Among carnivores, skull dimorphism has been suggested to be functionally related to jaw- and neck-musculature (Wiig 1986) and therefore male bears with larger skulls may have stronger necks and jaws. Neck and jaw strength may be important in male-male conflicts, as polar bears have long necks which would make both a males head and neck the closest targets of aggression for challenging males. The importance of skull size in male reproductive success was documented in brown bears (*U. arctos*) where the circumference of a males skull (at the zygomatic arches) was a predictor of annual reproductive success (Zedrosser et al. 2007) and therefore would presumably have a strong influence on lifetime reproductive success.

A frequently proposed alternative hypothesis for the evolution of SSD in cranial traits is intersexual niche partitioning (Shine 1989), which has been suggested as a potential selective pressure promoting both male and female biased SSD among terrestrial carnivores (Brown and Lasiewsk.Rc 1972, Swanson et al. 2011). However, clarifying the role of diet as a selective pressure in the evolution of size dimorphism is problematic, as many carnivore species exhibit polygynous mating systems which make it difficult to

separate sexual selection from other selective pressures (Ralls 1977). In polar bears, Derocher et al. (2005) suggested that intersexual niche partitioning, in which male polar bears feed to a greater extent on large prey species such as adult bearded seals (*Erignathus barbatus*) (~400kg), could be a factor influencing the degree of SSD in polar bears. Evidence from fatty acid diet analysis has confirmed that male polar bears in western Hudson Bay consume higher proportions of bearded seals than females, although ringed seals (*Pusa hispida*) dominated the diet for both sexes (Thiemann et al. 2008). Preferential access to prey has also been suggested to influence the degree of SSD in brown bears (McDonough and Christ 2012), however similar trends in size dimorphism in more omnivorous populations of brown bears and black bears (*U. americanus*) (Kingsley et al. 1988, Virgl et al. 2003) suggest that SSD in ursids has evolved irrespective of diet specialization, providing little support for the intersexual niche partitioning hypothesis. Similar contrasts in other taxonomic groups, where for example, sexual selection has resulted in body and head size dimorphism in herbivorous lizards that do not partition food resources (Carothers 1984). Thus, sex-based differences in resource utilization are likely the result, but not the cause, of SSD in some species (Shine et al. 2002).

Intra-sexual competition among male mammals need not be restricted to male-male contest competition and fitness variance can result from other forms of competition including scramble competition, endurance rivalry, and sperm competition. In solitary species such as polar bears, in which females are widely and unpredictably distributed, males are expected to roam widely in search of oestrus females, defending individuals for part or all of their reproductive cycle (Clutton-Brock 1989). In some species, mate searching behaviour can be an important determinant of encounter rates with breeding females (Brown and Weatherhead 1999, Gludas and Rodriguez-Robles 2011) which in turn can influence male reproductive success (Lane et al. 2009). Male black bears search widely for females during the breeding season (Kovach and Powell 2003a, Costello et al. 2009) and field observations indicate that male polar bears employ search strategies that involve straight line tracks to potentially increase the detection of oestrus females (Stirling 2011), however see Laidre et al. (2013). Increased search effort in association

with an extended breeding season in polar bears may lead to high energetic costs in adult males potentially promoting the importance of endurance rivalry. Similar to several other dimorphic species including elephant seals (Deutsch et al. 1990), fallow deer (McElligott et al. 2001) and red deer (Mitchell et al. 1976) male polar bears spend little time feeding during the breeding season (Ramsay et al. 1991, Cherry et al. 2009). As a result fasting endurance may play an important role in mating success in polygynous species (Trillmich and Trillmich 1984, McElligott et al. 2001). Fasting endurance increases with body size in mammals, because as body size increases, the amount of stored fat becomes a larger proportion of body mass and larger individuals metabolize somatic stores at a lower weight specific rate (Lindstedt and Boyce 1985). Thus, larger male bears with greater energetic reserves may be able to invest more in mate searching and mate guarding behaviours. Finally, although sperm competition in mammals can be important in male reproductive success (Ginsberg and Huck 1989, Gomendio et al. 1998, Preston et al. 2003), recent evidence suggests that ovulation mode in mammal (spontaneous vs. induced) may play an important role in sperm competition (Iossa et al. 2008). In general, sperm competition is predicted to be reduced in induced ovulators, as the first male to copulate with a female is expected to have a competitive advantage (Gomendio et al. 1998). This prediction is supported by phylogenetic analysis of testis size (Iossa et al. 2008) and sperm quantity (Soulsbury and Iossa 2010) (two proxies of sperm competition) both of which were reduced in induced ovulating species in comparison to spontaneous ovulators. Together this information along with the low observed rates of multiple paternity (Chapter 1) suggests that sperm competition likely plays a limited role in intra-sexual selection in male polar bears.

Because SSD is a measure of difference in size between the sexes, it is important to consider the role that size plays in the fitness of both sexes. For example, increased SSD can result from smaller female body size if selection favors an early age at first reproduction (Clutton-Brock and Harvey 1978). However, the consistency in reproductive maturity in relation to the final adult body size in most marine mammals (Laws 1956), along with the lack of directional selection on female body size I observed would suggest that selection for smaller female body size does not contribute to SSD in

polar bears. Indeed, the only significant positive relationship for female size was a negative quadratic selection gradient for body length in relation to LRS (Table 3.2, Figure 3.2), indicating potential stabilizing selection on this trait. Stabilizing selection for adult female body length suggests a fitness optimum for overall structural size in adult female polar bears, which likely results from energetic trade-offs between growth, somatic maintenance, and reproduction. Recent energetics modeling has shown that straight line body length can provide reliable measures of structural mass in polar bears (Molnár et al. 2009), however length is not directly related to storage mass which may partially explain why female trait values did not covary with most fitness measures. Research on reproductive success in female polar bears in western Hudson Bay found that body mass was positively correlated with litter size and litter mass at den emergence (Derocher and Stirling 1998b) and that cubs of heavier females were more likely to survive (Derocher and Stirling 1996). Selection on body mass in relation to lifetime fitness measures (e.g. LRS and longevity) was demonstrated in other large mammals (e.g. bighorn sheep, Poissant et al. 2008) and should be examined along with body condition and fecundity selection (e.g. litter size and cub mass) in future investigations of lifetime reproductive success in female polar bears.

Although viability selection for body size occurs in both sexes in other larger mammals (e.g. Soay sheep; Robinson et al. 2006), I did not find any evidence for increased viability as a result of body size. My results may be partially explained by the fact that viability selection may be stronger in juvenile bears where survival is lower (Regehr et al. 2007) and growth rates are higher (Derocher and Stirling 1998a, Rode et al. 2010). For example, survival of cubs of the year from spring to autumn, in triplet litters, increases with cub body size in western Hudson Bay (Derocher and Stirling 1996), indicating the potential for the operation of viability selection through early survival (e.g. Rioux-Paquette et al. 2011). Evolution of larger body size may be inhibited by the physiological constraints and viability costs of fast growth (Blanckenhorn 2000), and in male mammals fitness trade-offs between growth and survival are often evident at early life stages where increased body size results in higher juvenile mortality and reduced longevity (Clutton-Brock et al. 1985). In general, sexual selection is predicted to result in increased mortality

and weakened selection for longevity in males, compared to females (Bonduriansky et al. 2008). As a result of fitness trade-offs, males may compromise longevity for increased reproductive success (Partridge and Harvey 1985). Adult male bears that experienced the greatest lifetime reproductive success in this study appeared to have reduced longevity in comparison to males with intermediate reproductive success (Figure 2.4), highlighting the potential survival costs of increased reproductive success. These observations contrast with research that suggests that high quality individuals enjoy both high mating success and high survival (e.g. Pelletier et al. 2006). Although males invest more heavily in reproduction at intermediate ages (Chapter 1), reaching an age at which individuals become competitive (i.e. ~ 10 years old) is an important component of LRS (Figure 3.4). At the other end of the age-distribution, increased longevity > 20 years of age does not appear to result in any increase in reproductive success (Figure 3.4) as few paternities were assigned to males beyond 20 years old (Chapter 1). Alternatively, for females, longevity may be one of the most important factors influence LRS as a result of increased time investment in reproduction. Female bears exhibited a much stronger relationship between LRS and longevity than males (Figure 3.4). The extended length of maternal care in polar bears limits the reproductive rate of females and those successfully weaning their cubs usually produce a litter every 3 years. Using the age of first reproduction of 5 years, a female living to 20 years of age might have 5 litters. Living an additional three years could increase females LRS by 20%. Similar sex-related relationships between fitness and longevity have been reported in red deer where fitness was closely related to longevity in both males and females, but to a lesser extent for males (Kruuk et al. 2000).

Knowledge of species life histories is important for population management, particularly for harvested species. Results presented here thus provide important information for the management of polar bears in Canada, where male bears are harvested at twice the level of females and phenotype-based selective harvesting (i.e. trophy hunting) occurs (Taylor et al. 2008). Trophy hunting in some species (e.g. bighorn sheep) can negatively influence the expression of heritable traits such as horn size and body size (Coltman et al. 2003). In harvested species, mean rates of phenotypic change can significantly exceed rates of change resulting from natural selective pressures, and are likely dependent on the

strength and consistency of selection (Darimont et al. 2009). Although morphometric data on harvested polar bears are limited, data on bacula length from harvested bears (Dyck et al. 2004) indicate that a wide range of male phenotypes are harvested across a variety of age classes in the Canadian Arctic. These data suggest that phenotypic selection may not be as high in polar bear as in other species where minimum harvest requirements are based on phenotypic traits (e.g.  $\frac{3}{4}$  curl bighorn rams; Coltman et al. 2003). Furthermore, the low density of polar bears, the limited variance in male mating success and the potential high degree of gene flow between subpopulations should all limit the degree to which hunting influences selection on male body size.

My results support previous studies that found a positive relationship between mating success and male body size in large mammals (Clutton-Brock et al. 1988, Fisher and Lara 1999, McElligott et al. 2001) and, in addition, demonstrate a lack of directional selection on female trait values. However, it is important to note that other behavioral and morphological traits not examined in this study may be the target(s) of selection and that further investigations are required to examine the potentially important role of other traits such as body mass and body condition in determining reproductive success in both sexes. In addition, while I have provided quantitative support for positive directional selection on male traits in relation to lifetime fitness, for SSD to evolve, the traits in question need to be (i) heritable, (ii) the genetic correlation between the sexes needs to be  $< 1$ , and (iii) there has to be differential lifetime selection between the sexes (Lande 1980, Badyaev 2002). Although I have only addressed the final criterion, ongoing research on the study population has shown that both traits investigated here are heritable and that the genetic correlation between the sexes is  $< 1$  (R. Malenfant unpublished Ph.D. data), supporting my general conclusions regarding the evolution of SSD in polar bears as a result of sexual selection.

The results obtained here provide insight into the evolution of sex-specific life history strategies in response to selective pressures in both sexes of a long-lived carnivore. This study has also provided direct quantitative evidence for the evolution of SSD as a result of sexual selection acting on male traits. From a theoretical point of view, my results

provide insight into the potential strength of sexual selection in species that occur at low densities where variance in male mating success is low (Chapter 2). These results challenge the frequently reported and generally accepted relationship between the degree of polygyny and male biased size dimorphism in mammals (e.g. Vanpe et al. 2008) and illustrate the need for future investigations to assess the importance of variance in male mating success in relation to the operation of sexual selection in wild large mammals.

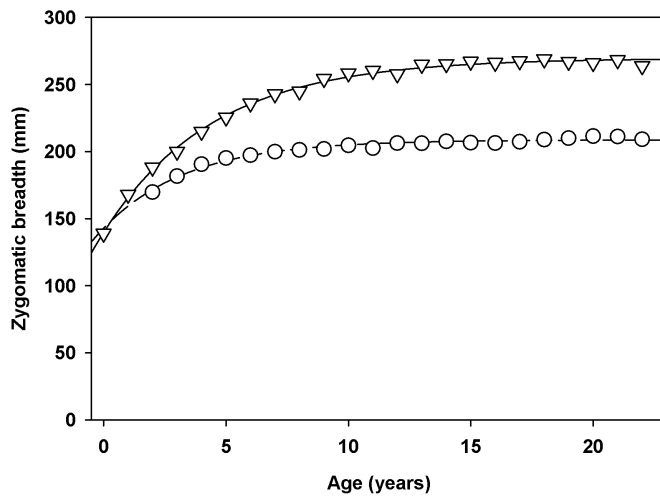
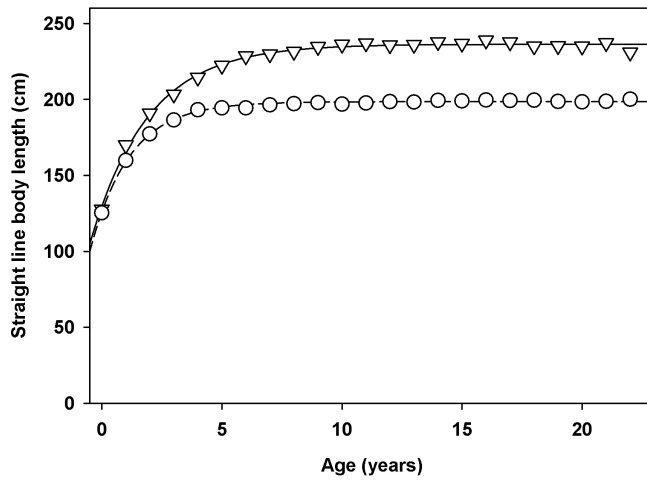
**Table 3.1:** Correlation matrices for traits and fitness measures for male (below diagonal) and female (above diagonal) polar bears in western Hudson Bay. Significance of Spearman rank correlations denoted by (\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ , and ns (not significant). LMS (total number of known mates), LBS (total number of offspring surviving to weaning), and LRS (total number of offspring produced), LONG (longevity in years), Length (straight line body length), Zygo (zygomatic breadth).

|        | LMS     | LBS     | LRS     | LONG     | Length   | Zygo     |
|--------|---------|---------|---------|----------|----------|----------|
| LMS    |         | 0.94*** | 0.76*** | 0.71***  | -0.01 ns | -0.07 ns |
| LBS    | 0.97*** |         | 0.72*** | 0.67***  | -0.02 ns | -0.09 ns |
| LRS    | 0.85*** | 0.83*** |         | 0.59***  | 0.06 ns  | -0.08 ns |
| LONG   | 0.42*** | 0.42*** | 0.37*** |          | -0.01 ns | 0.02 ns  |
| Length | 0.17**  | 0.15*   | 0.11 ns | 0.08 ns  |          | 0.31***  |
| Zygo   | 0.14*   | 0.19**  | 0.17**  | -0.02 ns | 0.45***  |          |

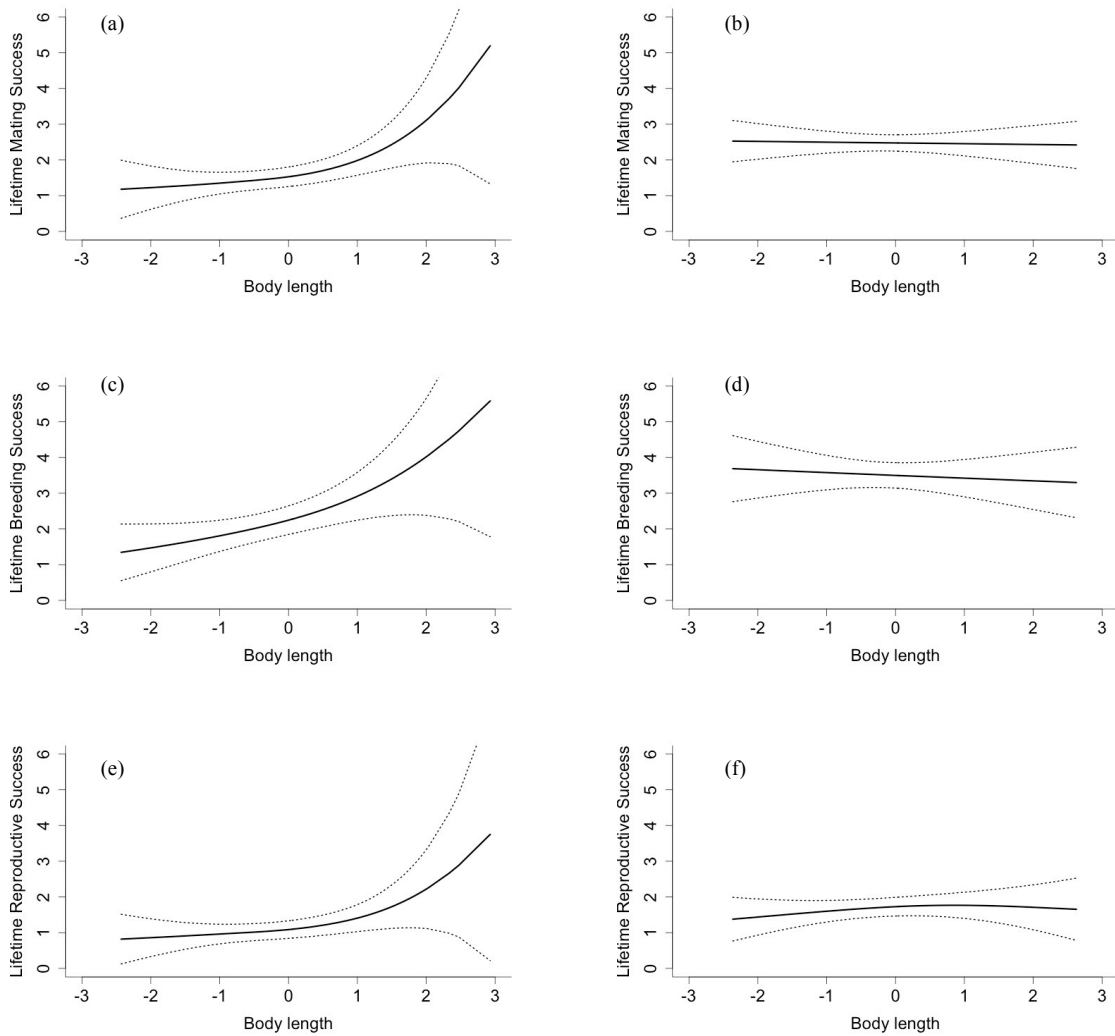


**Table 3.2:** Sex-specific selection differentials (directional  $S_i$ , and nonlinear  $c$ ) and gradients (linear and quadratic) for body length (length) and zygomatic breadth (zygo) in male and female polar bears. Fitness was defined as LRS (total number of offspring produced), LBS (total number of offspring surviving to weaning), Longevity (in years) and LMS (total number of known mates). ( $^+$   $p < 0.10$ ,  $*$   $p < 0.05$ ,  $**$   $p < 0.01$ ,  $***$   $p < 0.001$ ).

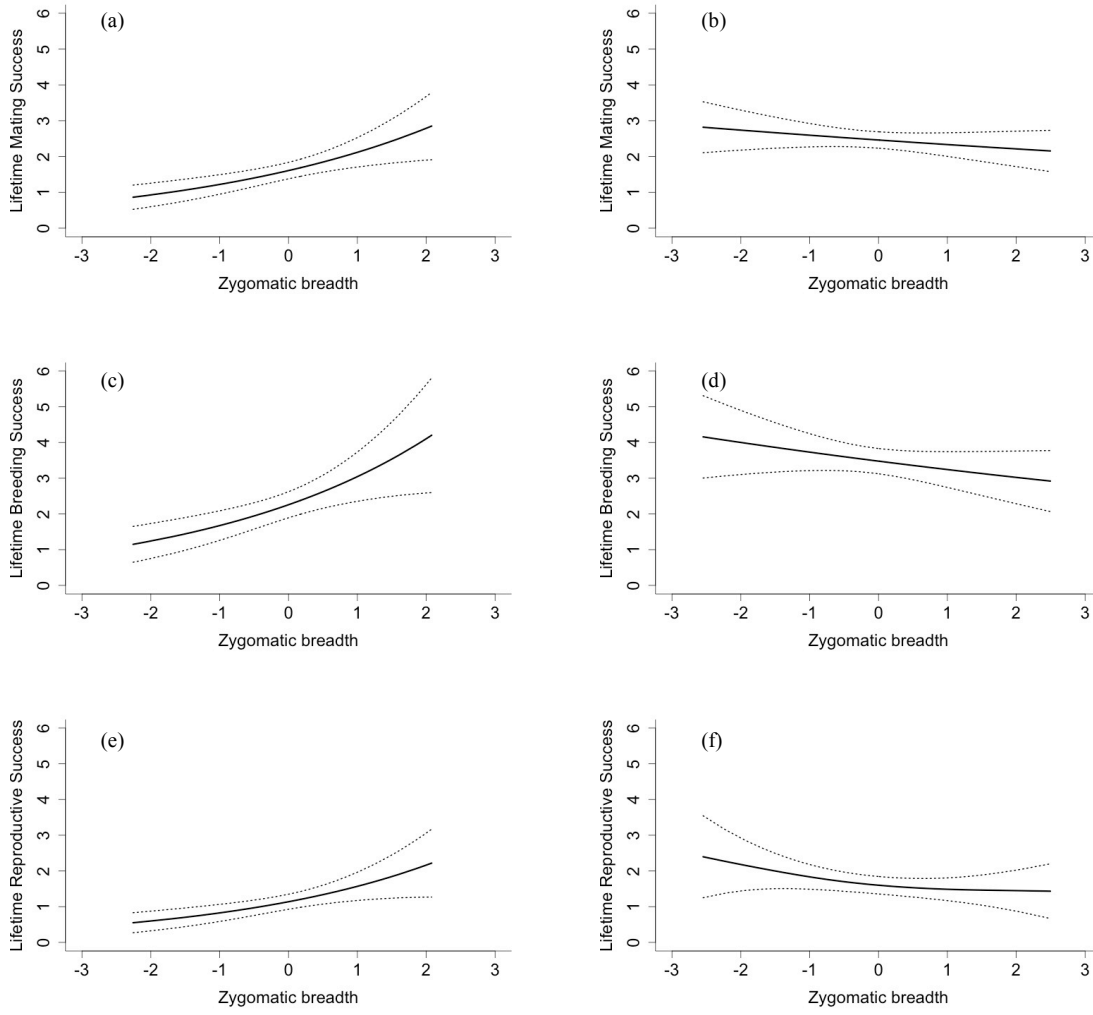
| trait                    | fitness metric | $S_i$   | SE   | $c_{ii}$          | SE   | $\beta_i$          | SE   | $\gamma_{ii}$     | SE   |
|--------------------------|----------------|---------|------|-------------------|------|--------------------|------|-------------------|------|
| male length<br>(n=214)   | LRS            | 0.29**  | 0.09 | 0.47 <sup>+</sup> | 0.14 | 0.19 <sup>+</sup>  | 0.10 | 0.63*             | 0.17 |
|                          | LBS            | 0.29**  | 0.08 | 0.35              | 0.12 | 0.20               | 0.09 | 0.45 <sup>+</sup> | 0.15 |
|                          | Longevity      | 0.02    | 0.02 | 0.00              | 0.02 | 0.03               | 0.03 | 0.03              | 0.04 |
|                          | LMS            | 0.28**  | 0.08 | 0.40 <sup>+</sup> | 0.12 | 0.19 <sup>+</sup>  | 0.08 | 0.50*             | 0.14 |
| male zygo<br>(n=212)     | LRS            | 0.32**  | 0.10 | 0.18              | 0.17 | 0.23*              | 0.11 | 0.26              | 0.20 |
|                          | LBS            | 0.30*** | 0.08 | 0.19              | 0.14 | 0.21*              | 0.09 | 0.23              | 0.17 |
|                          | Longevity      | 0.00    | 0.02 | 0.01              | 0.04 | -0.02              | 0.03 | 0.08              | 0.05 |
|                          | LMS            | 0.28*** | 0.08 | 0.19              | 0.14 | 0.19*              | 0.09 | 0.23              | 0.16 |
| female length<br>(n=234) | LRS            | 0.04    | 0.06 | -0.15             | 0.10 | 0.09               | 0.07 | -0.24*            | 0.12 |
|                          | LBS            | -0.02   | 0.05 | -0.01             | 0.08 | 0.00               | 0.05 | -0.01             | 0.08 |
|                          | Longevity      | -0.01   | 0.06 | -0.02             | 0.10 | -0.02              | 0.07 | -0.04             | 0.12 |
|                          | LMS            | -0.01   | 0.04 | -0.08             | 0.07 | 0.01               | 0.05 | -0.08             | 0.08 |
| female zygo<br>(n=232)   | LRS            | -0.11   | 0.07 | 0.17              | 0.11 | -0.14 <sup>+</sup> | 0.07 | 0.12              | 0.13 |
|                          | LBS            | -0.07   | 0.05 | 0.08              | 0.08 | -0.07              | 0.05 | 0.10              | 0.10 |
|                          | Longevity      | 0.02    | 0.07 | -0.06             | 0.10 | 0.03               | 0.07 | -0.11             | 0.12 |
|                          | LMS            | -0.05   | 0.05 | 0.05              | 0.08 | -0.06              | 0.05 | 0.08              | 0.09 |



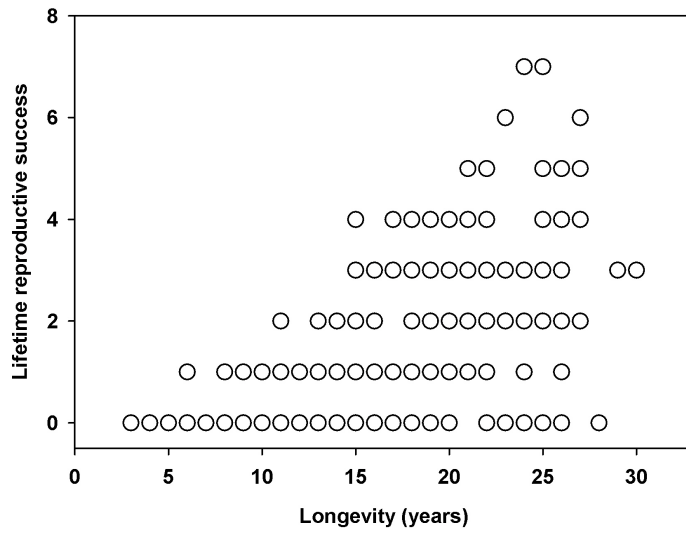
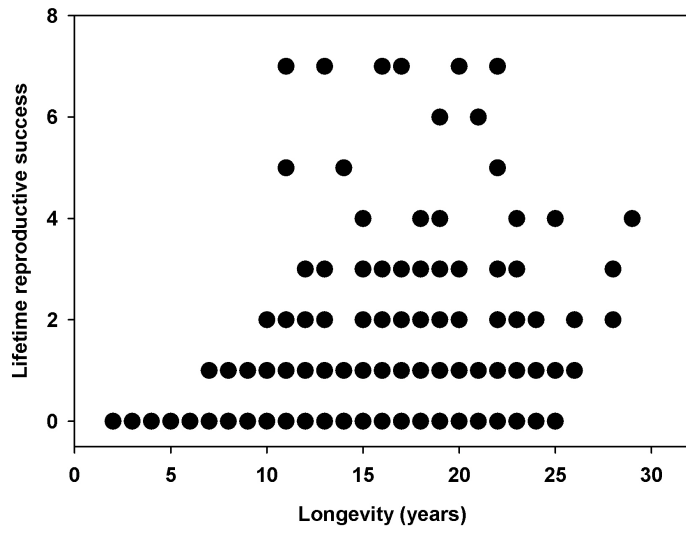
**Figure 3.1:** Change with age in mean body length and mean zygomatic breadth in male (downward triangles) and female (circles) polar bears for individuals included in selection analyses (ages 0-21 and 22+ shown). von Bertalanffy growth curves are fitted for males (solid lines) and females (dashed lines) for each trait. Note: no zygomatic measurements were taken for 0 or 1 year old females for the cohorts for which lifetime reproductive success was available.



**Figure 3.2:** Cubic spline visualization of selection (using LRS, LBS and LMS) on standardized straight line body length for male (a, c, e) and female (b, d, f) polar bears in western Hudson Bay. Trait values were corrected for age effects. Standard errors (dotted lines) were obtained by bootstrapping.



**Figure 3.3:** Cubic spline visualization of selection (using LRS, LBS and LMS) on standardized straight-line body length for male (a, c, e) and female (b, d, f) polar bears in western Hudson Bay. Trait values were corrected for age effects. Standard errors (dotted lines) were obtained by bootstrapping.



**Figure 3.4:** Correlation between lifetime reproductive success and longevity in (a) male (n=216) and (b) female (n=234) polar bears in western Hudson Bay.

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## Chapter 4

### 4 Effects of trends in sea ice extent on body size of polar bears in western Hudson Bay

#### 4.1 Introduction

Environmental variability can have a significant influence on fitness components and population dynamics (Forchhammer et al. 2001, Croxall et al. 2002, Forcada et al. 2005). Consequently, understanding how climate change will affect populations is a major focus in ecology (Jenouvrier et al. 2003, Grosbois et al. 2008, Hunter et al. 2010).

Environmentally mediated shifts in the availability of essential prey has been suggested to be one of the primary mechanisms by which global warming may affect large predatory species (Durant et al. 2003, Derocher et al. 2004, Le Boeuf and Crocker 2005, Both et al. 2006, Durant et al. 2007). Changes in the availability of key prey species will likely influence how individuals allocate resources to competing energy demands of growth, reproduction and body maintenance (Boggs 1992, Stearns 1992) potentially influencing the demography of predator populations. Although cyclical climate patterns such as the North Atlantic Oscillation (NAO) and El Nino Southern Oscillation (ENSO) are known to influence life history traits and population dynamics in a wide variety of vertebrate taxa, studies documenting the direct and long-term effects of global warming on the life history traits and population dynamics of individual species are limited (Durant et al. 2007).

Environmental conditions experienced during early development, *in utero* as well as post-partum, influence the growth, reproduction, and survival of several large mammal species and have the potential to create long-term fitness consequences (Albon et al. 1987, Clutton-Brock 1988, Post et al. 1997, Lindstrom 1999, Forchhammer et al. 2001). For example, red deer (*Cervus elaphus*) calves born following warm wet winters are smaller than those born following cold dry winters (Albon et al. 1983; Post et al. 1997). These poorer quality cohorts in turn produce lower birth weight calves that are less likely to

survive (Albon et al. 1987, Clutton-Brock et al. 1988) resulting in cohort effects that can influence population dynamics (Toigo et al. 2006). Although several studies have identified cohort effects in a number of large herbivores (Skogland 1990, Post et al. 1997, Forchhammer et al. 2001, Pettorelli et al. 2002, Solberg et al. 2004), studies of cohort effects in large carnivores are rare (Hastings et al. 1999, Pistorius et al. 1999, Garrott et al. 2012).

Cohort effects result from differences in individual growth and survival that can be attributed to density-dependent (e.g. direct competition for resources) and/or density-independent factors (e.g. environmental variation). Density-independent factors, such as environmental variation can have a significant influence on the phenotypic quality (e.g. body size) of juveniles in several ungulate species (Côté and Festa-Bianchet 2001, Forchhammer et al. 2001, Weladji and Holand 2003). These environmentally induced cohort effects may be of particular importance to individual fitness as juvenile phenotypic quality (e.g. body mass) is often positively associated with early survival (Baker and Fowler 1992, Derocher and Stirling 1996, Festa-Bianchet et al. 1997, Proffitt et al. 2008) and has been shown to be a good predictor of phenotypic quality in adults (Clutton-Brock et al. 1992, Schultz and Johnson 1995, Atkinson et al. 1996, Birgersson and Ekvall 1997). Amongst polygynous mammals, adult phenotypic quality has a strong influence on individual fitness, with larger and heavier individuals typically experiencing greater reproductive success (Clutton-Brock et al. 1982, Berube et al. 1999, Gaillard et al. 2000, Côté and Festa-Bianchet 2001, Forchhammer et al. 2001, Nussey et al. 2006). As a result, conditions experienced during early development can have an important influence on life history traits and population dynamics (Lindstrom 1999).

To date, most studies investigating cohort effects in large mammals have focused on ungulates and large scale climatic patterns such as the NAO (e.g. Post et al. 1997, Forchhammer et al. 2001, Aanes et al. 2005), which exhibit substantial interannual variation resulting in shifts in phenotypic quality among cohorts. Polar bears (*Ursus maritimus*) however provide an opportunity to examine how long term decreases in habitat availability associated with climate warming can affect access to prey resources in



a large long-lived carnivore. Polar bears are a sea ice obligate species because they require the presence of sea ice to provide a platform from which to hunt their primary prey, ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980). At the southern limit of their range, in western Hudson Bay, bears are forced ashore during an ice free period between spring breakup and autumn freeze-up that lasts for several months (Stirling et al. 1999). Reduced access to prey resources have been suggested to influence polar bear growth (Stirling and Derocher 2012), however this hypothesis has not been explicitly tested despite previously observed declines in body size in the western Hudson Bay population (Atkinson et al. 1996). In this chapter I investigate trends in sea ice conditions and polar bear body length in western Hudson Bay over 5 decades and test the hypothesis that changes in the availability of sea ice during development result in phenotypic variation in body size among polar bear cohorts.

## **4.2 Methods**

### **4.2.1 Study Area and Population**

The western Hudson Bay polar bear population occupies the ice-covered waters of Hudson Bay for most of the year and moves onshore in northeastern Manitoba when the sea ice melts. Techniques to capture, mark, sample and age bears are reviewed in (Chapter 1). Briefly, free-ranging polar bears in the study population were located from a helicopter and immobilized with Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa) (Stirling et al. 1989). At the time of first capture, each animal was assigned a unique identification number that was applied as both a permanent tattoo on the inside of the upper lip and as a plastic tag placed in each ear. Individuals were either of known age or were aged by counting the growth-layer groups in the cementum of an extracted vestigial premolar (Calvert and Ramsay 1998). Body length was measured as the straight-line distance from the tip of the nose to the caudal end of the last tail vertebra measured to the nearest centimeter when the bear was sternally recumbent. The immobilization and

handling protocol for free-ranging polar bears in western Hudson Bay was approved annually by the Animal Care Committee of the Canadian Wildlife Service, Prairie and Northern Region.

#### **4.2.2 Sea Ice Analysis**

I examined trends in sea ice concentration in the western Hudson Bay population management zone (Figure 1.1) from 1979-2012 using passive microwave satellite data (resolution 25 x 25 km) from the National Snow and Ice data Center in Colorado (NASA Team algorithm) which provides daily sea ice concentrations to the nearest percentage (Cavalieri et al. 2012). Sea ice imagery was sampled daily using 381 sampling points each falling within a different 25 x 25 km pixel within the western Hudson Bay management zone (Figure 1.1). The mean ice concentration of all pixels was used as the mean sea ice concentration for every day of the year. From these data I derived three sea ice metrics (i) break-up date: defined as the ordinal date at which spring sea ice reached 50%, 30% or 10% sea ice concentration and stayed below that concentration for at least three consecutive days, (ii) freeze-up date: the ordinal date at which autumn sea ice reaches either 50%, 30%, or 10% sea ice concentration and stayed unchanged or increased for at least three consecutive days and (iii) fasting-period: defined as a the number of days between 50% break-up and 50% freeze-up, 30% break-up and 30% freeze-up, 10% break-up and 10% freeze-up, and 50% break-up and 10% freeze-up. The latter metric was chosen as these ice concentrations relate to when bears migrate onshore and offshore in the summer and autumn respectively (Stirling et al. 1999, Cherry et al. 2013). In general, the time between break-up and freeze-up represents a period during which bears subsist primarily on stored fat reserves (Ramsay and Stirling 1988) and therefore may have a significant influence on individual growth and survival.

To increase the length of the time series for break-up dates to include data from 1971-1978, for which there are no satellite data, I used the break-up dates derived by Stirling et al. (1999) that use Canadian Ice Service data. When I compared the estimated dates of 50% sea ice break-up for the period in which I had overlapping data (i.e. 1979-2011), my

estimates of break-up were highly correlated (Pearson  $r = 0.95$ ,  $p < 0.001$ ) with Stirling et al. (1999). When compared the mean date of 50% break-up was 9.4 days later using the data and methodology from Stirling et al. (1999) compared to the dates derived using the passive microwave data. This mean difference in break-up date was used as a correction factor and was subtracted from the raw data values obtained by Stirling et al. (1999) to extend the data series for 50% break-up back to 1971. I could not perform similar comparative analyses for freeze-up or the fasting-period as data were unavailable. To examine long-term trends in sea ice conditions I used linear models to examine the relationship between each sea ice metric using year as continuous covariate across the sea ice imagery time series (1971-2012). All models were tested for autocorrelation using the Durbin-Watson test and an autocorrelation function was used to examine autocorrelation in model residuals from lag 1 – lag 15 years for each regression. Residual plots and tests revealed no autocorrelation in the sea ice time series meeting the assumption of independence.

#### **4.2.3 Analysis of Cohort Body Size**

To test for inter-cohort variability and trends in straight line body length I used measurement from adult females  $\geq 5$  years old and adult males  $\geq 8$  years old following (Atkinson et al. 1996). Because some bears are measured multiple times as adults the mean body length was taken for each individual and individual adult body lengths were weighted based on the number of observations from each individual. Sex-specific inter-cohort variability was assessed using an ANOVA in which birth year was a categorical variable. Long-term trends in body length were assessed using individual body size regressed against year of birth in a weighted regression. To examine whether juvenile body length was related to adult body length I followed the methodology of Atkinson et al. (1996) and compared the relative size of male and female bears at 2 years of age with their relative size as adults (defined as  $\geq 5$  years of age for females and  $\geq 8$  years of age for males) using partial correlation analysis controlling for birth year. I also extended the analysis to include partial correlations between male relative body length at 4 years of age and relative body length as an adult.

To examine if variation in sea ice conditions during development influenced adult body length in male and female polar bears I tested for possible effects of the dates of sea ice break-up and freeze-up, and the consequent duration of the ice-free period on mean cohort body lengths. Cohort-specific mean body length for each sex was determined separately and were weighted by the inverse of their variance following Burnham (1987). I examined the potential cumulative effects of conditions experienced throughout development by including the effects of sea ice conditions (break-up, freeze-up and ice-free period) from  $t_0 - t_5$  for females and from  $t_0 - t_7$  for males for each of the three sea ice covariates. I assumed that despite interannual variation, the cumulative effects of changing sea ice conditions across multiple years were additive and covariates represented the cumulative conditions experience during development by an individual. For example, a model examining the influence of break-up during the first 3 years of development is identified as break-up  $t_2$  and represents the sum of the ordinal break-up dates from  $t_0$ ,  $t_1$  and  $t_2$ , where  $t_0$  is the birth year. Non-linear effects of sea ice condition on growth were investigated by including first order polynomials. Using this approach I examined 96 candidate models for females and 112 candidate models for males. To select the most appropriate model based on predicted relationships between variation in mean cohort body length and sea ice conditions, I used Akaike's Information Criterion (AIC) (Burnham and Anderson 1998). The model with the lowest AIC was considered as the model that explained most of the variation in adult body length for both sexes and models with  $\Delta AIC < 2$  are presented for consideration in model inference (Burnham and Anderson 1998). All analyses were implemented in R (version 2.6.0; R Core Development Team, Boston, MA, USA).

### 4.3 Results

Trends in sea ice break-up were consistent across all three ice concentrations examined and were highly correlated (Table 4.1). Trends in the progressively earlier dates of 50% sea ice break-up were evident in the passive microwave satellite data set (1979-2012) as

well as the extended data series (1971-2012) including values derived from Stirling et al. (Stirling et al. 1999) with the date of break-up 5.5 days and 5.4 days earlier per decade, respectively (Figure 4.1). The date of 50% sea ice break-up ranged from June 2 to July 11 with a mean break-up on June 22 (SE = 1.84 days) from 1979-2012. There was also a trend towards a delay in the date of freeze-up for all three sea ice concentrations examined (Table 4.1). The date of 10% freeze-up averaged 4.7 days later per decade (Figure 4.2). The date by which 10% sea ice freeze-up occurred ranged from November 4 to December 4 with a mean of November 18 (SE = 1.33 days) from 1979-2012. Correspondingly, the ice-free period also showed significant long-term increasing trends (Table 4.1). The ice-free period (between 50% sea ice in spring and 10% sea ice in autumn) ranged from 127 to 178 days with a mean of 148 days (SE = 2.65 days) (Figure 4.3).

Adult body length declined in both males (Figure 3.4,  $n = 524$ ,  $R^2 = 0.04$ ,  $p < 0.001$ ) and females (Figure 4.4,  $n = 836$ ,  $R^2 = 0.06$ ,  $p < 0.001$ ) with increasing birth year. There was no significant difference in slopes between the sexes ( $t = 0.02$ ,  $df = 1356$ ,  $p = 0.94$ ). From 1960-2006 mean cohort body length ranged from  $191.7 \pm 2.2$  cm to  $206.3 \pm 3.8$  cm for females and from  $224.2 \pm 4.0$  cm to  $241.0 \pm 8.1$  cm for males and there was significant inter-cohort variability in body size for both males ( $F_{4,499} = 1.75$  ;  $p < 0.003$ ) and females ( $F_{46,289} = 2.66$  ;  $p < 0.001$ ). A total of 73 females were handled both as two year olds and as adults. The mean body length of two-year-old and adult females was  $176.9 \pm 0.6$  cm and  $194.9 \pm 0.9$  cm, respectively. A total of 56 males were handled as both two year olds and adults and a total of 58 males were handled as both four year olds and adults. The mean body length of males measured at two-year-old and as adults was  $188.5 \pm 0.9$  cm and  $234.8 \pm 0.9$  cm respectively. The mean body length of males measured at 4 years old and as adults was  $213.6 \pm 1.1$  cm and  $233.5 \pm 1.0$  cm respectively. On average females increased in body length by 10.6 % between two-years-old and adulthood while, on average, males increased by 25 % between two-years-old and adulthood. Four year-old males showed reduced growth rates and only grew an average of 9.3 % before reaching adult body size. Relative female body length as a two year old was significantly related to relative adult body length (Figure 4.5,  $r_{\text{partial}} = 0.52$ ,  $p < 0.001$ ). Relative body length of

males at 2 and 4 years of age were also significantly related to relative adult body length (Figure 4.6,  $r_{\text{partial}} = 0.36$ ,  $p = 0.004$  and  $r_{\text{partial}} = 0.60$ ,  $p < 0.001$  respectively).

Observed inter-cohort variability of male and female body length was closely related to prevailing sea ice conditions during development (Table 4.2). The selected best model describing adult female body length based on AIC included the cumulative effects of 50% sea ice break-up during the first 5 years of development and accounted for 54% of the variation in mean female cohort body size (model M4, Table 4.2). The second most supported model ( $\Delta\text{AIC} = 0.84$ ) included the cumulative effects of sea ice break-up in the first 4 years of development. The third most supported model ( $\Delta\text{AIC} = 1.99$ ) included a quadratic effect of the date of 50% sea ice break-up in the first 5 years of development (model M46, Table 4.2). The selected best model describing adult male body size included a quadratic effect of the date of 30% sea ice break-up in the year of birth (model 65, Table 4.2) and explained 45% of the variation in mean male cohort body length. The second most supported model ( $\Delta\text{AIC} = 1.34$ ) included a quadratic relationship between date of 10% sea ice break-up and adult male body length (model M73, Table 4.2).

#### **4.4 Discussion**

Polar bear life history is intimately linked to the sea ice environment with both theoretical and empirical studies highlighting the impacts of reduced sea ice availability on polar bear reproduction, survival, growth and body condition (Regehr et al. 2007a, Molnár et al. 2010, Regehr et al. 2010, Rode et al. 2010, Molnar et al. 2011). Although several studies have examined long-term trends in sea ice conditions in Hudson Bay (Gagnon and Gough 2005, Hochheim et al. 2011, Joly et al. 2011), I examined sea ice trends (i.e. break-up and freeze-up) in western Hudson Bay management zone (Figure 1.1) that have been linked to declines in both polar bear body condition and survival in the western Hudson Bay polar bear population (Stirling et al. 1999, Regehr et al. 2007b). These results are consistent with previous findings that sea ice in western Hudson Bay is breaking up at significantly earlier date across a range of sea ice concentrations and now,

further indicates a similarly significant trend toward a later date of sea ice freeze-up. Together, long-term trends in break-up and freeze-up have contributed to a significant increasing duration of the ice-free period experienced by polar bears in western Hudson Bay. Consequently, these results suggest that over the long-term, polar bears in western Hudson Bay have experienced reduced access to their primary prey during the critically important hyperphagic spring feeding period (Stirling et al. 1999) but, because of the increasingly long ice-free period, are having to survive for longer periods on land with reduced fat stores. These trends result in poorer survival in dependent young, juvenile bears and senescent adult bears (Regehr et al. 2007a) and are predicted to have a negative influence on future cub litter size and adult male survival in western Hudson Bay (Molnár et al. 2010, Molnár et al. 2011) and, consequently, have important implications for the long-term viability of the western Hudson Bay polar bear population.

Research in western Hudson Bay documented declines in the body length of juvenile (Derocher and Stirling 1998) and adult female polar bears (Atkinson et al. 1996). However, no significant trend in adult male body length was evident (Atkinson *et al.* 1996). In contrast, my analysis of the longer data set revealed that body length of both adult females and males have declined over the last 5 decades and, further, that the rates of change are rapid (see Gingerich 2009), corresponding to 0.021 and 0.026 standard deviations per year in males and females, respectively, or 0.31 and 0.39 haldanes (haldane = one standard deviation per generation) assuming a generation length of 15 years. Significant correlations between juvenile body length and adult body length in both sexes suggest that conditions during early development are important for polar bear growth. It is noteworthy that body length is a heritable trait in polar bears (R. Malenfant unpublished data) and therefore genetic components of variation likely also play an important role in determining rates and limits to growth. Previously identified declines in adult female body length in the study population were attributed to the greater environmental sensitivity of females resulting from their more abbreviated period of growth compared to adults males (i.e. ~ 5 years instead of ~ 8 years) (Atkinson et al. 1996). However, it is now clear that males, despite their extended period of growth are also sensitive to sea ice conditions during early development (Figure 4.6, Table 4.2) and

may exhibit a limited degree of compensatory growth when faced with poor sea ice conditions in their birth year.

Nutrition is one of the most important factors influencing growth (Laws 1956) and low seal abundance was suggested to influence temporal patterns of polar bear body mass in the Beaufort Sea (Kingsley 1979). Geographical variation in the growth of polar bears has also been attributed to variation in the availability of prey resources (Derocher and Stirling 1998) and long-term declines in polar bear body length and skull size are believed to have resulted from nutritional limitation in the southern Beaufort Sea polar bear population (Rode et al. 2010). Polar bears in Hudson Bay prey primarily on ringed and bearded seals (Thiemann et al. 2008). However detailed long-term data on changes in the abundance of these species in Hudson Bay are limited due to the difficulty in obtaining precise estimates of seal densities during aerial surveys (Lunn et al. 1997, Chambellant et al. 2012a). Although seal abundance is difficult to estimate, other lines of evidence suggest that ringed seal and polar bear productivity covary (Stirling and Øritsland 1995) and may also do so in relation to changes in sea ice conditions (Stirling 2002). In general, ringed seal body condition, reproduction and survival are negatively influenced by both very light or heavy sea ice and/or both early and later sea ice break-up (Stirling et al. 1982, Smith 1987, Harwood et al. 2000, Smith and Harwood 2001, Stirling 2002) suggesting a potential optimum date of break-up for survival of ringed seal pups (Chambellant et al. 2012b). The relationship between a potential optimum date of break-up for seal productivity and polar bear foraging may partially be captured in the analysis of sea ice mediated changes in cohort body length. The two most supported models for adult males included a quadratic effect for the date of 30% and 10% sea ice break-up in the birth year, suggesting that there may also be a break-up optimum for polar bear growth. This result was somewhat surprising given the extended duration of growth in male bears, but suggests an important interaction between environmental conditions, seal productivity and maternal investment in male cubs in their first year of life. Maternal investment has been shown to be important in the growth of pinnipeds (e.g. Bryden 1968) and more recent research has shown that maternal condition plays an important role in the growth of brown bears and polar bear cubs (Robbins et al. 2012). Adult females



responded differently to sea ice conditions and were most influenced during development ( $t_0$ - $t_4$ ), but there was model support for a quadratic effect of the date of 50% sea ice break-up in the first 5 years of life. These results conform with general predictions of fitness variance in sexually dimorphic species in which growth patterns differ between the sexes and the effects of ecological factors on individual phenotypic quality and fitness may differ between males and females (Lindstrom 1999). The apparent increased sensitivity of male polar bears to environmental conditions early in development is similar to that of red deer, where greater sensitivity of males to environmental variation during early development has important fitness consequences (e.g. Clutton-Brock et al. 1982, Rose et al. 1998).

Although environmental conditions can play an important role in early development density dependent effects can also be important (Kruuk et al. 1999) and have been shown to result in changes in body size in several large ungulate species (Fowler 1987, Skogland 1990, LeBlanc et al. 2001). Among large carnivores, density-dependent size has been reported in brown bears (*U. arctos*) (Zedrosser et al. 2006) and northern fur seals (*Callorhinus ursinus*) (Fowler 1990). Density-dependent factors have also been suggested to possibly influence polar bear growth through potential competition for prey resources (Derocher and Stirling 1998, Rode et al. 2010). Although there was an overall decline in the size of the polar bear population in western Hudson Bay (Regehr et al. 2007a), potentially reducing density dependent effects, from the data presented here there appears to be no additional nutritional benefits to bears, given continual declines in body condition and body size in the western Hudson Bay polar bear population. Alternative, reductions in the availability of sea ice habitat during the spring feeding period might be expected to result in a seasonal increase in the overall density of bears and potential increased competition for resources. Shifts in the distribution and density of individuals may have important implications for energetic intake in growing juvenile bears, which tend to be more susceptible to kleptoparasitism from larger adult bears (Stirling 1974). Although the carrying capacity of polar bear populations appears to be limited by the overall abundance of ringed seals (Stirling and Øritsland 1995), in Hudson Bay, bears from the western Hudson Bay, southern Hudson Bay and Foxe Basin populations overlap

significantly in their habitat use during winter and early spring (Peacock et al. 2010), making it difficult to investigate the possibility of density dependent responses in any one population.

Contrary to the results of my selection analysis in (Chapter 3) which demonstrated positive directional selection on male body length, in western Hudson Bay adult males polar bears have actually decreased in size. Why might this be? Pemberton (2010) argued that counter gradient variation in which ecological forces result in phenotypic gradients that contrast with expected evolutionary gradients may be a driving factor in studies where observed phenotypic change is in the opposing direction of selection. For example, decreases in the body weight of Soay sheep (*Ovis aries*) occurred on St. Kilda Island despite selection for higher body weight. Alternatively changes in body size may result from environmental conditions that select against faster growing individuals (e.g. selective disappearance). In western Hudson Bay cubs-of-the-year and yearlings experience similar survival rates in relation to spring sea ice conditions (Regehr et al. 2007a), however, cubs-of-the-year have higher mass specific milk intake and greater skeletal growth rates than yearlings (Arnould and Ramsay 1994) and therefore may be more sensitive to changes in maternal condition, particularly if females stop lactating as a result of poor body condition in years of early sea ice break-up (Derocher et al. 1993, Stirling et al. 1999).

Finally, these results suggest that environmental conditions experienced in early development may have lasting impacts on male's lifetime reproductive success as a result of reduced body length in poor quality cohorts. For example, standardized mean cohort body length for the smallest (2003) and largest (1965) cohorts indicate that the average male born in 2003 would be -1.33 S.D. below the long-term average body length whereas males born in 1965 would be 0.85 S.D. above the long term average. Given observed variation in male mating success in relation to adult male body length (Chapter 3) these differences could have a significant influence on male lifetime reproductive success. The negative influence of earlier sea ice break-up on adult male body length also suggests that degrading sea ice conditions may operate to constrain sexual selection on male bears born

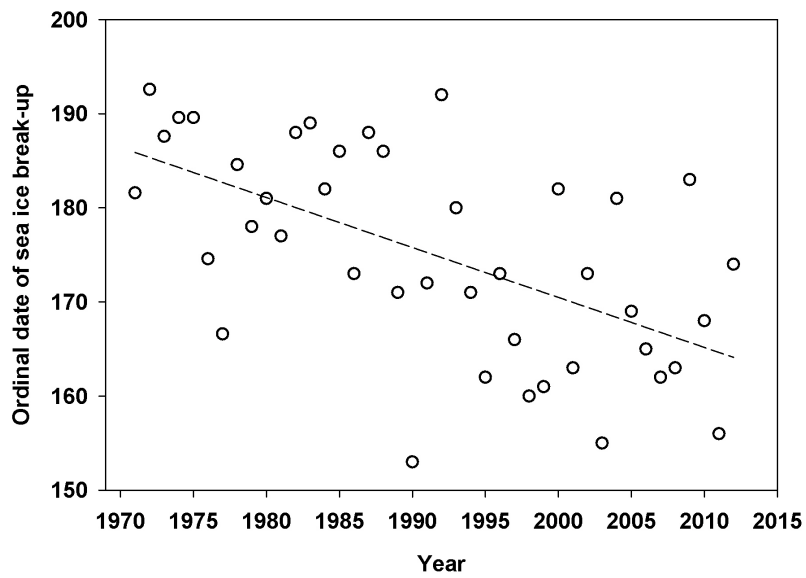
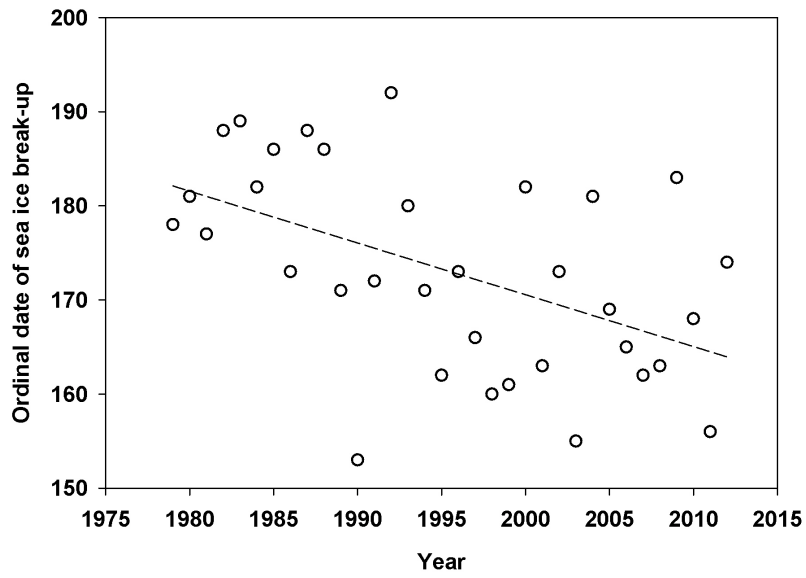
in western Hudson Bay. As the phenotypic quality of resident males declines in western Hudson Bay, one potential outcome may be that males from adjacent populations will experience greater reproductive success as their access to prey resources during development may not be as constrained. For example, sea ice persists for up to one month longer in Foxe Basin than in western Hudson Bay during the spring break-up period (Sahanatien and Derocher 2012). This differential access to prey resources is likely to influence male growth and adult body length and therefore male mating success. Males from the Foxe Basin polar bear population are larger than males from western Hudson Bay (Derocher and Stirling 1998) and environmentally mediated access to prey resources may further influence these differences. Because body length is a heritable trait, increased mating success of larger males from adjacent populations could result in larger and potentially faster growing cubs that fare poorly in years of early sea ice break-up. Environmentally mediated interactions between natural and sexual selection may therefore result in unforeseen eco-evolutionary dynamics in the western Hudson Bay population. The costs of sexually selected traits are well recognized in mammals (Promislow 1992) and it is generally accepted that among sexually dimorphic species, lower survival in juvenile males occurs as a result of the increased costs of growth and development (Clutton-Brock et al. 1985). The influence of selective pressures on evolved life history traits represents a new challenge for understanding the fitness consequences and subsequent demographic responses of polar bear populations to long-term climate change.

**Table 4.1:** Trends in the date of sea ice break-up, freeze-up and the duration of the fasting period from 1979-2012 in western Hudson Bay. Coefficients and standard errors (SE) are presented from linear models describing the trend in ordinal date of each sea ice metric across the time series.

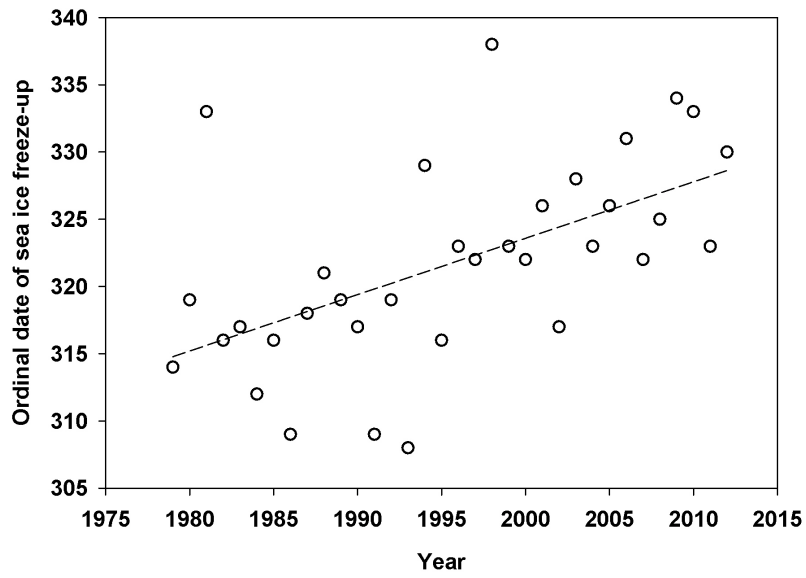
| Ice metric     | % sea ice | Coefficient | SE   | <i>t</i> | R <sup>2</sup> | P       |
|----------------|-----------|-------------|------|----------|----------------|---------|
| Break-up date  | 50%       | -0.55       | 0.16 | -3.359   | 0.24           | 0.002   |
|                | 30%       | -0.49       | 0.17 | -2.968   | 0.19           | 0.005   |
|                | 10%       | -0.49       | 0.18 | -2.683   | 0.16           | 0.011   |
| Freeze-up date | 50%       | 0.40        | 0.14 | 2.935    | 0.19           | 0.006   |
|                | 30%       | 0.49        | 0.13 | 3.877    | 0.30           | < 0.001 |
|                | 10%       | 0.47        | 0.10 | 4.314    | 0.35           | < 0.001 |
| Fasting period | 50%-50%   | 0.95        | 0.24 | 4.037    | 0.32           | < 0.001 |
|                | 30%-30%   | 0.98        | 0.23 | 4.309    | 0.35           | < 0.001 |
|                | 10%-10%   | 0.96        | 0.23 | 4.237    | 0.34           | < 0.001 |
|                | 50%-10%   | 0.97        | 0.20 | 4.828    | 0.40           | < 0.001 |

**Table 4.2:** Model selection of the analysis of variation in mean cohort body length for adult female and adult male polar bears in western Hudson Bay in relation to sea ice condition during development.  $\Delta$  AIC: difference between a given model and the model with the lowest AIC. Only models with  $AIC < 2$  are presented.

| Model         | Covariates  | NP | AIC     | $\Delta$ AIC |
|---------------|---|----|---------|--------------|
| <b>Female</b> |   |    |         |              |
| M4            | 50% break-up $t_0$ - $t_4$  | 2  | 101.187 | 0            |
| M3            | 50% break-up $t_0$ - $t_3$  | 2  | 102.025 | 0.838        |
| M46           | 50% freeze-up $t_0$ - $t_4$ + (50% freeze-up $t_0$ - $t_4$ ) <sup>2</sup> | 3  | 103.180 | 1.992        |
| <b>Male</b>   |   |    |         |              |
| M65           | 30% break-up $t_0$ + (30% break-up $t_0$ ) <sup>2</sup>                   | 3  | 135.249 | 0            |
| M73           | 10% break-up $t_0$ + (10% break-up $t_0$ ) <sup>2</sup>                   | 3  | 136.586 | 1.337        |



**Figure 4.1:** Ordinal date of sea ice break-up (50% sea ice/50% water) in western Hudson Bay from 1979-2012 (a) and from 1971-2012 (b) using corrected data from Stirling et al. (1999) from 1971-1978 (see methods).

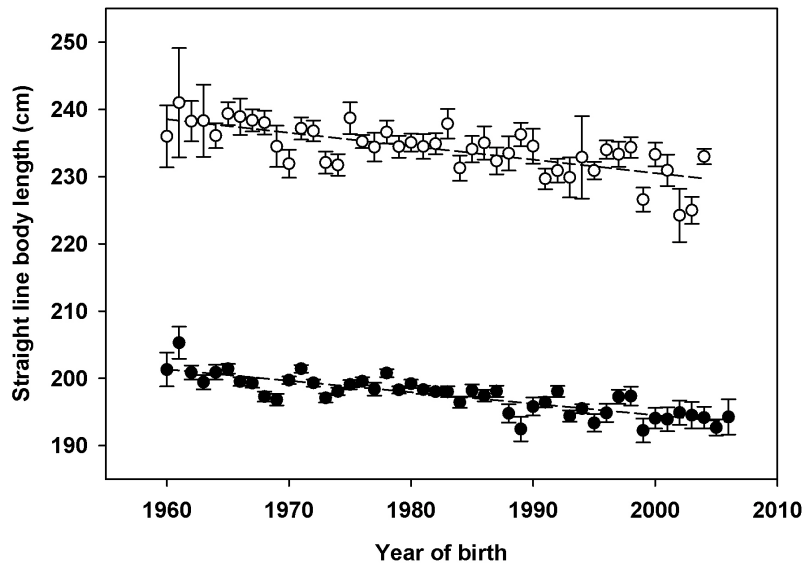


**Figure 4.2:** Ordinal date of sea ice freeze-up (10% sea ice/90% water) in western Hudson Bay from 1979-2012.

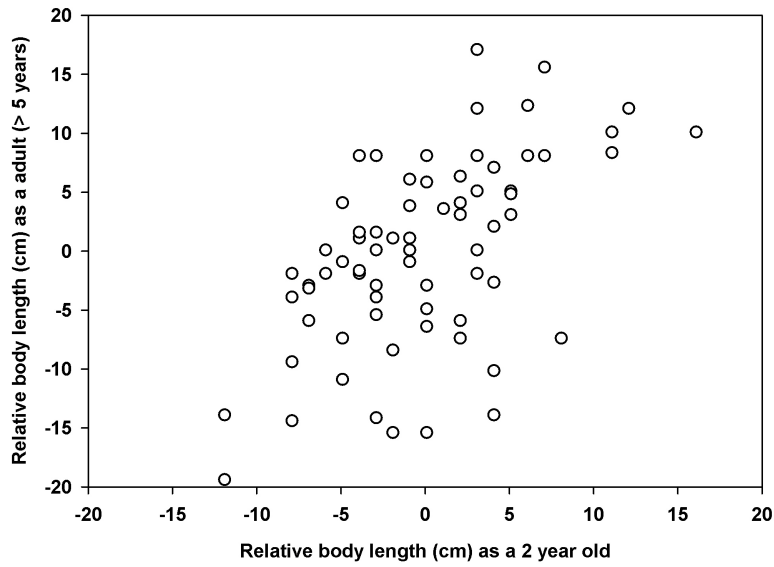


**Figure 4.3:** Ice-free period defined as the number of days between 50% break-up and 10% freeze-up (see methods) from 1979-2012 in western Hudson Bay.

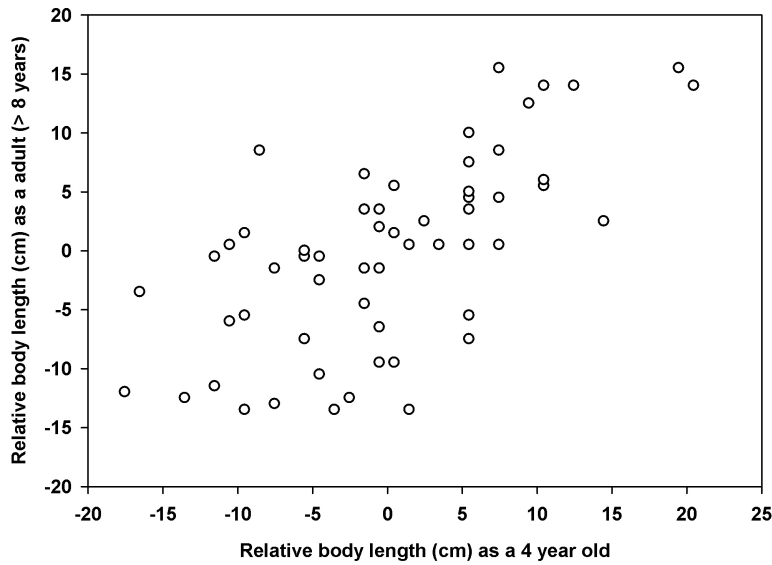
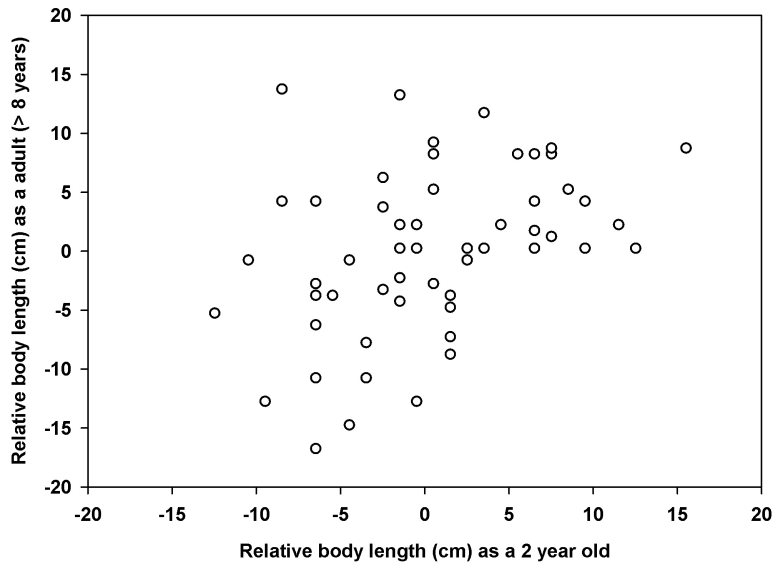




**Figure 4.4:** Trends in mean (SE) cohort body length for adult male (open circles; 1960-2004) and adult female polar bears (closed circles; 1960-2008) in western Hudson Bay.



**Figure 4.5:** Relationship between relative female polar bear body length as 2 year olds and adults for western Hudson Bay, 1960-2008.



**Figure 4.6:** Relationship between relative male polar bear body length as 2 year olds (a) and 4 year olds (b) in relation to relative adult body length in western Hudson Bay, 1960-2004.

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## Chapter 5

### 5 Synthesis, Future Directions and Concluding Remarks

To date, most of what is known about mating systems and the opportunity for sexual selection in large mammals comes from long-term studies of ungulates and pinnipeds (Clutton-Brock et al. 1988, Amos et al. 1993, Coltman et al. 1999, Hoelzel et al. 1999, Vanpe et al. 2008, Porschmann et al. 2010). While these and other studies have provided valuable insight into the evolution of life history traits and the role that natural and sexual selection play in wild populations, it is evident that our understanding of processes such as sexual selection, require knowledge from a wide variety of species. This bias in the literature is not surprising given the difficulty of studying solitary, large carnivores such as polar bears, that have life spans that can be twice that of more intensely study ungulate species (e.g. Loison et al. 1999) making estimates of lifetime selection difficult to obtain. In addition, because behavioural observations are limited, molecular techniques, many of which have only recently been developed to the point that they can be applied in a cost-effective manner to quantitative studies, provide the only reliable means by which some aspects of mating systems can be investigated. These difficulties have limited our scope and understanding of several aspects of large carnivores, including mating systems, sexual selection, evolution of size dimorphism, heritability of traits and lifetime fitness.

#### 5.1 Mating System, Sexual Selection and Population Genetics

One of the primary findings of this dissertation is that variance in male mating success need not be high in order for sexual size dimorphism to evolve. Studies investigating variance in male mating success in large mammals have been biased toward gregarious species (e.g. pinnipeds and ungulates), where the ability to monopolize a large number of mates allows for greater variance in male reproductive success (Emlen and Oring 1977). For example, in southern (*Mirounga leonina*) and northern elephant (*Mirounga angustirostris*) seals alpha males can sire between 50-70% of the calves on a breeding beach (Hoelzel et al. 1999). Similar patterns have been noted in ungulate species such as

the fallow deer (*Dama dama*), where dominant males can monopolize up to 60% of the paternities in a single cohort (Say et al. 2003). In addition, many of these studies focus on species with limited amounts of parental care (i.e. offspring are weaned in the first year of life) in comparison to polar bears (*Ursus maritimus*), most of which keep their young for 2.5 years. Parental care, and in particular maternal investment, is an important factor influencing mating systems, reproductive strategies, operational sex ratios and the opportunity for sexual selection in wild populations (Clutton-Brock 1988). In Chapter 2, I demonstrated that the opportunity for sexual selection for polar bears was similar to that of more monomorphic species (i.e. low variance). However, in Chapter 3 I provide evidence that the intensity of sexual selection on male body length in polar bears was similar to selection on antler size in red deer (*Cervus elaphus*) (Kruuk et al. 2002), a classical example of a secondary sexual characteristics, which lends support to the hypothesis that male variance need not be high in order for male traits to evolve in polygynous mating species.

Although evidence of direct contest competition (i.e., fresh cuts and wounds) during the spring mating season provides support for the importance of a male's competitive ability, in the context of sexual selection, it is also important to consider the potential role that female mating behaviour and mate choice play in the evolution of traits in male polar bears. Amongst solitary species the evolution of female sexual signalling is likely to play an important role in the evolution of mating systems. For solitary females, effective advertisement of oestrus will not only ensure that a mate can be found, but more likely that a female will attract multiple mates allowing for either mate choice or mate competition to occur. The ability of oestrus female polar bears to attract multiple mates is supported by behavioural observations of mating groups in which up to 6 satellite males have been observed in association with a paired female (Ramsay and Stirling 1986, Wiig et al. 1992, Derocher et al. 2010). In polar bears, oestrous may last up to a month (Wiig et al. 1992) and if ovulation is induced, females may be able to advertise their reproductive status for extended period prior to breeding without risking reproductive failure. Although female mate choice is difficult to elucidate I suggest that female polar bears may passively choose mates through behaviours that promote mate competition or allow

for mate choice. Refusing initial attempts at copulation may increase the likelihood that another male of higher quality may find a mating pair and usurp a female from her initial suitor. Extended pair bonding prior to mating, observed previously in the Canadian high Arctic, may represent a female mating tactic by which females “troll” for available males allowing for the direct comparison of mates as well to potentially inciting male-male conflicts to select the highest quality mates (Stirling 2011).

Previous genetic work on polar bears has focused primarily on population genetic structure (Paetkau et al. 1999), kin-related social structure (Zeyl et al. 2009b), effective population size (Cronin et al. 2009, Zeyl et al. 2009a) and more recently polar bear evolution (Lindqvist et al. 2010, Cronin and MacNeil 2012, Hailer et al. 2012, Miller et al. 2012, Cahill et al. 2013). Although the results from Chapter 2 and 3 provide novel insight into the polar bear mating system and the opportunity for sexual selection in the wild, they also provide insight into the genetics of polar bear populations. My inability to assign paternities to a large number of the offspring in western Hudson Bay suggests that the level of gene flow between polar bear populations is substantial. Although the western Hudson Bay, southern Hudson Bay and Foxe Basin population are treated as separate demographic units from a harvest management perspective, they do meet the standard definition of a biological population (i.e. a single group of interbreeding individuals of the same species). However, it is important to note that although bears from these three subpopulation may not be genetically distinct they do differ substantially in their space use (Taylor et al. 2001, Parks et al. 2006, Peacock et al. 2010, Obbard and Middel 2012) and their demography (Regehr et al. 2007, Peacock et al. 2010) as a result of seasonal variability in the sea ice environment (Stirling et al. 1999, Sahanatien and Derocher 2012). Thus, from a harvest management perspective, despite this new information, it could be argued that the delineation of harvest management units for polar bears should continue to focus on ecological, demographic and movement data.

## **5.2 Senescence and Polar Bear Life History**

Knowledge of age-specific reproductive and survival rates is critical to understanding the demography of age-structured populations (Eberhardt 1985). Amongst long-lived mammals, reproduction and survival are commonly split into three age classes consisting of juveniles, prime-aged adults and senescent adults (Caughley 1966, Gaillard et al. 2000). Reproduction and survival are generally low and variable amongst juveniles, relatively high and stable amongst prime-aged adults and then begin to decline in senescent adults (Gaillard et al. 2000). Evidence of senescent declines in wild populations however are difficult to detect because the survival probability for an given age class is always less than one and therefore only a small proportion of individuals will reach an age at which senescence becomes detectable. To date, the most compelling evidence for senescence among long-lived mammals comes from longitudinal studies of ungulates (Loison et al. 1999, Gaillard et al. 2004), however the main focus of this research has been on age-related changes in survival, and from an evolutionary perspective, survival represents just one component of fitness and therefore more attention needs to be given to age-related changes in reproduction (Monaghan et al. 2008). Studying age-specific reproduction in long-lived species is important in the context of understanding the evolution of life history strategies in large mammals in relation to ageing. Amongst large mammals, ungulates represent one of most well studied taxonomic groups and long-term studies of red deer, roe deer (*Capreolus capreolus*), soay sheep (*Ovis aries*), bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) have provided significant insight into the role that selection plays in wild populations (Coltman et al. 2002, Kruuk et al. 2002, Robinson et al. 2006, Vanpe et al. 2008). However, along the continuum of slow-fast life histories ungulates represent a narrow portion of the continuum with most species exhibiting rapid growth, early maturation, annual reproduction and limited longevity (Wootton 1987). For example, in a review by Loison et al. (1999) the maximum reported longevity for male bighorn sheep and male roe deer were 13 and 14 years of age respectively, ages that correspond to when males in my study population experience their greatest reproductive success (Chapter 2). Thus, along the continuum of slow-fast life histories polar bears provide much needed insight the evolution of life history strategies in longer-lived species.

Both Ramsay and Stirling (1988) and Derocher and Stirling (1994) have described what appear to be senescent declines in the reproductive performance of female polar bears in western Hudson Bay. In the latter study the authors speculated that age-related decreases in reproduction were due to undetermined processes associated with ageing that impaired the accumulation of fat stores necessary for reproduction. Similarly, in a long-term study on bighorn ewes, Bérubé et al. (1999) suggested that if female reproductive success increases with body mass in large mammals then it is reasonable to expect that reproductive senescence could follow a decrease in body mass or condition later in life. Indeed, senescent declines in body condition may play an important role in female reproductive success as ovulation (Leaderwilliams and Rosser 1983), the ability to conceive (Boyd 1984, Samson and Huot 1995), and offspring survival (Atkinson and Ramsay 1995) are all influenced by maternal body condition. Senescent declines in body mass may also be of particular importance to male reproductive success as body size is believed to play an important role in intraspecific competition for females (Chapter 3). However, despite its potential importance, the role of individual quality in the analysis of life histories in wild populations has just begun to be investigated (Nussey et al. 2007, McCleery et al. 2008, Reed et al. 2008). In particular, because senescence is an individual process the accurate measurement of changes in individual phenotypic quality across all ages is considered to be crucial (Nussey et al. 2008a).

In addition to reproductive senescence, recent capture-recapture analyses have indicated that survival senescence likely occurs in both male and female polar bears (Taylor et al. 2005, Regehr et al. 2007). However, to date neither the age of onset nor the functional form of senescent declines in polar bear survival have been investigated rigorously, both of which are believed to be crucial in determining the population dynamic consequences of senescence (Nussey et al. 2008a). For example, important differences may exist between the rates of senescence in male and female bears as a result of differences in life history strategies and associated costs of reproduction. Although senescence is often difficult to demonstrate in wild populations it has been suggested that studies that reveal simultaneous declines in both survival and reproduction provide the greatest evidence for the effect being due to senescence (Bonduriansky and Brassil 2002, Nussey et al. 2008b).

Furthermore, and maybe more importantly, these studies allow for the explicit examination of patterns of covariance in life history traits (e.g. reproduction and survival) across all ages, providing much needed insight into the evolution of life history strategies.

## **5.2 Sea Ice and Polar Bear Life History**

Habitat loss represents one of the greatest threats to species (Groom et al. 2006) and reduced future availability of Arctic sea ice is predicted to have significant impacts on Arctic marine species (Laidre et al. 2008, Ferguson et al. 2010, Post et al. 2013). Changes in sea ice dynamics have now been shown to influence several aspects of polar bear life history including growth (Rode et al. 2010; Chapter 4), reproduction (Hunter et al. 2010) and survival (Regehr et al. 2007). One of the central principles of life history theory is that of energy allocation (Williams 1966) in which individuals are predicted to optimally allocate resources to the competing demands of growth, reproduction and survival (Stearns 1992). The potential importance of reductions in prey availability and thus energy intake in polar bears as a result of reduced sea ice availability in a warming world have been recognized for 20 years (Stirling and Derocher 1993), however understanding if or how polar bears may adapt their life history remains an important question for the conservation of the species.

Adaptation can occur via microevolution, through shifts in the frequency of genotypes, as well through individual phenotypic plasticity (Visser 2008, Hoffmann and Sgro 2011), altering the distribution of phenotypes and fitness of individuals. The effects of climate change on the distribution of phenotypes in wild populations are well documented (Millien et al. 2006), however the extent to which these changes represent genetic versus phenotypic variation is a subject of debate. In general, there has been a lack of observed genetic response to selection in wild populations (e.g. Wilson et al. 2006) and therefore the ability of species to adapt to rapid changes in the earth's climate may be limited by their phenotypic plasticity. In addition, because climate change can result in selection on multiple life history traits simultaneously (e.g. Garant et al. 2008) species level responses to climate change may be complex. In Chapter 4, I postulated that selection against faster



growing cubs during early development might be a mechanism that has resulted in the decline in the size of bears in the western Hudson Bay polar bear population. If that is the case, selection during the first year or two of life may constrain other life history traits such as the age and size at maturity and subsequently an individual's reproductive lifespan. A second potential predicted life history response to reduced sea ice availability is for adult female polar bears to reduce the amount of energy that is allocated to reproduction, by reducing litter size (Molnar et al. 2011). Future projected declines in sea ice availability (de la Guardia et al. 2013) and long-term trends in sea ice extent in western Hudson Bay (Chapter 4) in association with dynamic energy budget models suggest that female polar bears may reduce their litter sizes in response to earlier sea ice break-up (Molnar et al. 2011), however such responses have yet to be observed in the western Hudson Bay polar bear population (N. Lunn, unpublished data).

Finally, there may be some aspects of polar bear life history, such as fasting endurance, that exhibit limited plasticity due to physiological limitations and/or low underlying genetic variation. For example, Molnár et al. (2010) using dynamic energy budget models predicted up to 28% mortality in fasting adult male polar bears in western Hudson Bay if the ice-free period was extended to 180 days. Although my definition of the ice-free/fasting period in western Hudson Bay differed from Molnár et al. (2010) it is clear from data presented in Figure 4.3 that the ice-free period is approaching a duration beyond which the western Hudson polar bear population may no longer be viable. The evolutionary potential of species to respond to climate change will depend on the strength of selection and the underlying genetic variance (i.e. heritability) of the traits under selection (Husby et al. 2011). With detailed information on individual phenotypic traits as well as a detailed pedigree in the western Hudson Bay polar bear population, research can expand on selection analyses presented here, while also estimating the underlying genetic variance of traits (see Wilson et al. 2010). Knowledge of the underlying variability and heritability of life history and morphological traits in polar bears will play an important role in determining the potential evolutionary response of the species to climate change.

### 5.3 Concluding Remarks

Predicting the potential evolutionary response of polar bears to climate change represents a difficult task for the conservation of the species and data from the western Hudson Bay polar bear population will provide the best opportunity to do so. In this dissertation I have contributed to the understanding of the polar bear mating system, age-specific reproduction, selective pressures influencing adult body size and the potential long-term consequences of climate change for the life history of this species. However, my work simply sets the stage for a multitude of other interesting research questions. In Chapter 2 I helped develop a first generation pedigree for the western Hudson Bay polar bear population based on genetically parentage assignments, however, genomics work has continued throughout the writing of this thesis and the current pedigree for the western Hudson Bay population now exceeds 4000 individuals, rivalling the pedigrees of more easily studied island populations of ungulates (e.g. red deer and Soay sheep). In addition, because the long-term research in western Hudson Bay has involved both phenotypic measurements as well as tissue sampling (i.e. blood, fat, hair and claws) I now have the ability to potentially ask and answer questions that simply cannot be addressed elsewhere. For example, I have the data to examine to what extent variation in persistent organic pollutants are influenced by an individuals diet as well as their genetics, something that has never been done before in a wild population. Similarly, advancements in the use of hair as a biomarker to measure cortisol stress levels (Bechshøft et al. 2011), now allows us to examine to what extent inter-annual variability in the sea ice environment influences polar bear health and whether stress is heritable trait. Ultimately, it will take the integration of multiple fields of study including population ecology, foraging ecology, evolutionary ecology, genetics, ecotoxicology, remote sensing, oceanography and climatology to garner a better understanding of what it will take to conserve one of the greatest icons of the natural world.

## 5.4 References

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