Adult polar bear behaviour: Using non-invasive techniques to assess social play

by

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Abstract

Social play is a widespread behaviour among mammalian lineages typically occurring among juveniles in periods of plentiful resources. Adult play is rare, as adult mammals typically use their energy for survival and reproduction. Polar bear social play in the Western Hudson Bay region is a double anomaly because play occurs between adult bears during a fasting period. Polar bears should be conserving as much energy as possible during their fasting period, as they are forced onto land away from their primary food sources. I investigated factors that influence the structure of polar bear social play including body condition, time since sea-ice break-up, role (initiator or terminator of play), and energetic cost. I found no significant effect of body condition on the duration or occurrence of social play, nor the effect of body condition on role. I found that as time since sea-ice breakup increased and minimum daily temperature decreased, occurrences of social play per day increased. Through the use of thermography, I found that polar bears use energy during social play, inferred from the increase in their surface temperature after a bout of social play. However, I was not able to quantify the amount of energy expended and conclude that thermography is a useful tool to non-invasively measure surface temperature during activity but needs to be validated with internal temperature probes and in stricter environmental conditions. During the fasting season, polar bears rely on fat stores built up over the hunting season, and any energy expenditure is considered costly to their fitness. I suggest that polar bear social play is an important life event that must be maintained despite the energetic costs associated with social play.

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Thesis format

This thesis follows the manuscript style, otherwise known as “Sandwich” format as described by the University of Manitoba, Faculty of Graduate Studies. Chapter one is an introductory chapter providing background information on mammalian social play. Chapter two explains the effects of climate change on polar bear body condition and subsequent expected changes in behaviour. In chapter three I explore the use of infrared thermography to assess the energetics of social play. I conclude the thesis with a synthesis discussion.

Chapter 1 Thesis introduction

Play is a widespread behaviour among animal species and can include all motor activity that appears to be purposeless, using modified motor patterns similarly used in other contexts (Bekoff & Byers 1981). Play can be classified as object play, or locomotor play and social play (Bekoff 1984). Object play involved play directly with an object from the environment such as a rock or branch, or a toy (Bekoff & Byers 1981). Locomotor play is any form of play using large muscles (i.e. climbing and running) and can be done without a play partner (Bekoff & Byers 1981). Social play, in general, involves locomotor activity (running, chasing, rearing) exhibited with at least two individuals (Bekoff & Byers 1981, Bekoff 1984) Social play is displayed by many invertebrates, fish, reptiles, and birds and it is a common behaviour exhibited by many species of mammals (Blanchard et al. 1977, Latour 1980, 1981, Pellis & Pellis 1987, Burghardt 2001, 2005, Fagen & Fagen 2004, Graham & Burghardt 2010, Watson & Croft 2010, Burghardt 2015, Pellis & Pellis 2017).

It is relatively simple to identify social play by sight, but it is difficult to create a straightforward definition encompassing every aspect of social play, and many controversies attempting to explain the function of social play exist in the scientific literature (Burghardt 1984, Fraser & Duncan 1998, Burghardt 2005, Pellis et al. 2010). A working definition to distinguish social play from competitive interactions includes five criteria, (1) social play has no obvious or immediate benefit; (2) social play is spontaneous (Trezza et al. 2011) and voluntary; (3) social play is an exaggerated behaviour that occurs usually among juveniles before energy is needed for foraging or competing for mates; (4) social play consists of repeated movements which differ from behaviours associated with foraging or reproduction; and (5) social play occurs in the absence of stressors (Burghardt 2001, 2005, Graham & Burghardt 2010). Social play must occur among two or more individuals and can involve chasing, nipping, wrestling or rough-and-tumble play (Bekoff 1974, Sommer & Mendoza-Granados 1995, Pellis & Pellis 2009). Using the five criteria set by Burghardt (2005) is a basic way to assess whether an exhibited behaviour is considered social play and these criteria are useful in identifying social play despite specific components of social play being very ambiguous in certain species (Pellergrini 2009, Pellis & Pellis 2009, Graham & Burghardt 2010).

Social play is widespread across mammalian taxa, suggesting that a similar set of selection pressures acted upon all mammalian orders diverging in the Cenozoic period (Byers 1984, Burghardt 2014). The selection pressures and overall benefit of social play are largely unknown, and therefore social play is a behaviour that has been considered ‘not fully functional’ and an ‘opportunity behaviour’ with little benefit, that can be suppressed under stressful conditions (Burghardt 1984, Fraser & Duncan 1998, Burghardt 2005). Thus, the adaptive value of play is difficult to identify and is complicated because play could serve multiple functions (Pellis et al. 2010). Hypotheses focused on the function and benefits of social play are often based on juvenile social play, where benefits are delayed and are thought to enhance competitive performance later in life (Fagen 1981). Among groups of conspecifics, the occurrence of social play can vary with location, season, and life stages, or may not occur at all (Baldwin & Baldwin 1974, Berger 1979, Pellis 1981). Therefore, the occurrence of social play is usually not considered essential to the survival of an individual to adulthood, but play may enhance development (Martin & Caro 1985, Spinka et al. 2001). The four most prevalent hypotheses explaining the benefits of social play are the motor-training hypothesis, training-for-the-unexpected hypothesis, fine-tuning-through-repetition-and-training hypothesis and the social cohesion hypothesis (Graham & Burghardt 2010).

The motor-training hypothesis suggests that social play occurs among juveniles to enhance the strength and function of muscles and the nervous system, to better serve movement into adulthood (Brownlee 1954). Social play more commonly occurs during the juvenile life stage, correlating with peak periods of cerebellar synaptic pruning, or brain maturation, suggesting that juvenile social play aids in brain development (Bekoff & Wells 1982, Byers & Walker 1995). The motor-training hypothesis is controversial, as brain development also occurs in mammals who do not play and occurs among animals who have fully developed brains. Therefore, brain development and occurrences of social play might only be correlated, as there is no evidence to suggest that mammals who engage in social play as juveniles have a higher functioning brain and/or are better competitors later in life (Pellis et al. 2010). For example, meerkats (*Suricata suricatta)* who did not gain an advantageous position during play events were no less likely to win competitive interactions as adults (Sharpe 2005a). However, juvenile Belding's ground squirrels (*Urocitellus beldingi)* who often played had better motor ability than those who played less frequently, and also dispersed earlier and had greater breeding success (Nunes et al. 2004). Nonetheless, the benefits of physical exercise through social play are not exclusive to the juvenile life-stage. Adults should also play and continue to build and maintain muscle mass unless they can gain sufficient muscle mass through daily activities.

The training-for-the-unexpected hypothesis and the fine-tuning-through-repetition-and-training hypotheses are similar, however, there are a few key differences. The training-for-the-unexpected hypothesis suggests that social play trains mammals for unexpected situations, including the loss of control of locomotion or position (Spinka et al. 2001). Whereas the fine-tuning-through-repetition-and-training hypothesis indicates that social play allows for an individual to hone their skill set, allowing for a quick and appropriate response to changing situations, helpful in catching prey or competing for mates later in life (Nowicki & Armitage 1979).

During play, individuals may learn from their mistakes without the risks of injury (Klopfer 1970). Social play may train young individuals to counteract a loss of physical control and to chain together conventional movement, such as walking, with unconventional movements, such as falling, to regain control and recover quickly (Spinka et al. 2001). For example, training-for-the-unexpected may be useful in emergency scenarios in arboreal primates such as misjudging the distance of a branch while swinging through trees. If the animal is prepared for unexpected scenarios, they will be more likely to gain control of the situation instead of falling (Graham & Burghardt 2010). Thus, the training-for-the-unexpected hypothesis predicts that social play will expose individuals to new situations and aid in quick recovery from an attack or misjudgement. Exposure to various situations may allow for a greater probability of escape when play transitions into competitive events as the animal ages.

The training-for-the-unexpected hypothesis argues that social play should occur most often in changing and unstable environments to reap the largest benefit and to best prepare to adapt to risks (Graham & Burghardt 2010). In contrast, the occurrence of play diminishes during food shortages or within poor environmental conditions (Baldwin & Baldwin 1976, Sommer & Mendoza-Granados 1995). For example, social play behaviours exhibited by rhesus monkeys (*Macaca mulatta)* declined by 94% (2.51 bouts/hr to 0.15/hr) under conditions of extreme food shortage (Hall 1963). Additionally, free-ranging squirrel monkeys (*Saimiri oerstedi)* experiencing food shortages were never observed playing but were seen foraging for 57 minutes of each waking hour (Baldwin & Baldwin 1972). Squirrel monkeys residing in favorable habitat with sufficient food sources were observed playing up to three hours per day (Baldwin &

Baldwin 1972). This latter study was replicated in a laboratory setting where social play dropped to 1% of the original baseline of play under conditions of food deprivation, suggesting that social play may only occur when all other needs vital to survival are met (Baldwin & Baldwin 1974). Therefore, there may be a threshold to when individuals will allocate energy towards training-for-the-unexpected rather than collecting resources or resting to conserve energy.

The fine-tuning-through-repetition-and-training hypothesis suggests that social play has been selected to modify existing motor patterns to better adapt to a changing scenario (Bekoff & Byers 1981). Continuing to train-for-the-unexpected allows for animals to fine-tune their motor patterns and socio-cognitive ability. The fine-tuning-through-repetition-and-training hypothesis predicts that mammals will continue to play through adolescence, and possibly into adulthood, to fine-tune their skills and movements to be better competitors (i.e. acquire mates and recruit their offspring into the population).

The social cohesion hypothesis suggests that social play functions to form and maintain social bonds, typically among group-living species (Bekoff 1977). Social play presumably increases social cohesion among conspecifics and should decrease aggressive encounters among play partners (Baldwin 1982). Wolves (*Canis lupus*) engage in social play among all age classes, suggesting that social play increases bonds between pack members which aids in social cohesion and cooperation while hunting (Cordoni 2009). In wolves, dominance relationships established previously are typically maintained during social play (Cordoni 2009). This hypothesis also suggests that play occurs among large-brained species with a slower pace-of-life i.e., delayed maturity, long-lived species, who possess complex social skills to identify which individual they had previously encountered (Fagen 1981, Iwaniuk et al. 2001). Large-brained species are presumably able to read social cues to adapt to the rapidly changing movements and scenarios of play and respond appropriately (Graham & Burghardt 2010).

Three characteristics of playful scenarios that separate social play from other behaviours are role reversal, self-handicapping and the absence of severe injury (Burghardt 2005). Role reversal occurs when the more dominant play partner (i.e., larger, older, or higher in social ranking) exhibits a behaviour during play that would not occur during a competitive bout, such as muzzle-licking among canids (Bekoff & Allen 1998). Animals engaging in social play seem to take turns, for example, the animal being chased may turn around and begin to chase their attacker (Burghardt 2005). Typically, dominance hierarchies are already established in the juvenile life-stage, allowing for observations of role-reversal to occur in social play among juveniles (Burghardt 2005).

Self-handicapping occurs when a play partner intentionally puts themselves into a vulnerable position such as exposing the neck (Bekoff 2001). Typically, the more dominant or stronger play partner will exhibit self-handicapping (Aldis 1975, Bekoff & Allen 1998). For example, older male red-necked wallabies (*Macropus rufogriseus banksianus*) self-handicap when playing with younger individuals and allow for the younger wallaby to climb on top of them and gain an advantageous position, allowing the younger individual to ‘win’ the bout of play (Watson & Croft 2010). Among competitive events, the larger, more dominant individual would overcome the submissive individual relatively quickly but, during bouts of social play, the dominant individual will retreat in order keep the play bout going (Burghardt 2005).

Social play among adult mammals is rare (Burghardt 2005). It is typically thought that adult mammals only engage in social play to maintain levels of sensory stimulus when no vital survival behaviour is occurring (Hutt 1979, Bekoff & Byers 1998). For example, social play between adult brown bears occurs during periods of high salmon (*Oncorhynchus* spp.) abundance (Fagen & Fagen 2004). A concentrated resource, such as that of salmon in a stream, results in an aggregation of brown bears to exploit the resource (Stonorov & Stokes 1972). Social play may occur during these aggregations to cope with the increased risk of injury by conspecifics and to familiarize themselves with one another in a non-threatening way (Judge & de Waal 1993, Antonacci et al. 2010). Characteristics of play occur between brown bear interactors, such as role reversal and self-handicapping by the older more dominant individual (Fagen & Fagen 1990). During bouts of play between adult and sub-adult brown bears, the older brown bear acts more submissively to their younger play partner. The older brown bear increases its risk of injury and overall vulnerability by turning away without resistance in response to play advances (Fagen & Fagen 1990).

Despite the rarity of adult social play, the characteristics of social play exhibited by adult brown bears in a salmon stream are typical of most mammals (Burghardt 2005). Mammals engaging in social play avoid serious injury by modifying the same movements used in serious altercations (Pellis & Pellis 2017). During bouts of social play between two domesticated rats (*Rattus norvegicus),* wrestling occurs to gain access to vulnerable areas such as the neck. When a play partner gains the advantageous position over top of the play partner on their back, the neck is not bitten as in serious competitive events but nuzzled without making teeth to neck contact (Pellis 1988). But, during competitive events rats will bite the neck, rump and lower flanks (Blanchard et al. 1977, Pellis & Pellis 1987). Thus, social play is similar to competitive events, excluding the risk of serious injury (Pellis & Pellis 1998b).

The benefits and characteristics of social play are typically used to analyze observations of juvenile social play or animals who are satiated and not energy limited (Hutt 1979, Bekoff &

Byers 1998). However, polar bears are an example of a mammalian species who engage in social play as adults in periods of food deprivation (Latour 1980, 1981; this study). Observations of adult polar bear behaviour in western Hudson Bay are classified as social play because polar bears exhibit key aspects used to identify social play such as role-reversal, self-handicapping, and repeated and exaggerated movements, there is no obvious or immediate benefit, and it occurs spontaneously and voluntarily (Latour 1981).

In chapter two I explore social play among adult polar bears in the Churchill, MB region. My objective was to gain further understanding of the benefits of social play among polar bears during a period of resource limitation. My analyses explored factors that may influence the occurrence and duration of polar bear social play including body condition index, length of time since sea-ice breakup, and body condition discrepancies between the initiator of social play and the terminator of social play. In finding the factors which influence, or do not influence, the characteristics of social play, I can further investigate polar bear social play using the four main hypotheses set to describe the benefits of social play.

Polar bears play occurs during a resource-limited time, when their energetic reserves are low (Stirling & McEwan 1975, Pagano et al. 2018). During the ice-free season, polar bears should be conserving their fat stores by avoiding energetic behaviours (Knudsen 1978, Latour 1981, Lunn & Stirling 1985) such as play. It can be assumed that play is a costly behaviour that uses kinetic energy, but we know little about the energetic costs associated with social play.

Measuring energetics of free-ranging animals is difficult as these types of studies are typically done *in situ* requiring measures of oxygen consumption and metabolic rate throughout activity (Ndahimana & Kim 2017). Non-invasive methods, such as infrared thermography (IRT), are increasingly used to measure the surface temperature of animals without sedation (Zinn et al.

1985, Heath et al. 2001, Dunbar et al. 2009, Johnson et al. 2011, Lu et al. 2018). In chapter three, I explored the use of IRT to identify whether surface temperature measured with IRT was an accurate representation of internal body temperature. Polar bears in human care offer an opportunity to test the use of IRT in a controlled setting before using these techniques on free-ranging polar bears. During routine veterinary procedures, I measured the surface temperature of the eye and compared it to internal temperatures to assess whether IRT measurements was an accurate representation of internal temperature. I then used IRT to measure surface temperature changes after social play to infer energy usage during play.

My study had a strong focus on using non-invasive methods to study the natural behaviour of species in human care and in the wild. If IRT could be validated as a method to estimate body temperature, it could serve as a non-invasive tool to study thermoregulation and energetics of animals in the wild. Non-invasive tools are imperative in studying the behaviour of wild animals, as to not disturb natural behaviours, or to cause unnecessary stress. My analyses further our understanding of social play behaviour and its occurrence in a changing Arctic environment.

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Chapter 2 The influence of body condition and sea-ice breakup on social play among adult male polar bears in Western Hudson Bay

Abstract

Social play by mammals rarely occurs past the juvenile stage, during periods of low resource abundance, or among solitary species. Polar bears provide us with an example of a species who engages in social play in the adult life-stage, in a period of food stress during the ice-free season on western Hudson Bay. The ice-free season of Hudson Bay has steadily increased over the past three decades, at an advancing rate of 5.5 days earlier per decade. Therefore, environmental changes may create a situation where polar bears need to modify social behaviours to maintain body condition. The objective of my study was to test the hypotheses that timing of sea-ice breakup and subsequent declines in body condition will influence the behaviour of polar bears in the western Hudson Bay region, specifically on social play behaviour. I found that body condition did not significantly influence the frequency or duration of social play between dyads of adult male polar bears. I also found that body condition did not affect whether a polar bear initiated or terminated a bout of play. Polar bears who were not observed engaging in social play were not in poorer body condition than polar bears who played. However, I found that as time spent on land increased, the frequency of social play increased. My findings suggest that social play was an important life event that was maintained as body condition declined due to climate change and/or as part of a natural cyclic seasonal change.

Introduction

The benefits gained through social play among mammalian species remains unclear, but many hypotheses have been put forth, including the motor training hypothesis (Brownlee 1954), training-for-the-unexpected hypothesis (Spinka et al. 2001), fine-tuning-through-repetition-and-training hypothesis (Nowicki & Armitage 1979), and the social cohesion hypothesis (Bekoff

1977, Baldwin 1982). These four hypotheses explaining the benefit of social play are based on juvenile social play, and associated benefits are assumed to decrease with age (Caro 1980, Chalmers 1984).

When resources are plentiful, social play occurrences among juvenile animals typically increase (Pellis & Pellis 2009). While satiated, juvenile animals shift to invest in enhancing social cognition play (Pellis & Pellis 2009). Developing the social skills and congnition through play can lead to enhanced survival and competitive performance later in life (Fagen 1981, Fagen & Fagen 2009). Thus, social play is most commonly associated with the enhancement of the juvenile brain when no other behaviour vital to survival is necessary (Burghardt 2005, Pellis & Pellis 2009).

Although rare, social play does occur among adult mammals (Pellis & Iwaniuk 2000, Palagi 2006, Bekoff 1974, Pellis 1993, Sharpe 2005a, b). Older mammals presumably play less because they must allocate more energy toward gathering resources, vigilance behaviour and reproduction (Caro 1980, Bekoff & Byers 1998, Burghardt 2005). However, social play has been documented among satiated adult animals (Fagen & Fagen 2004). Questions remain as to why adult animals continue to play, as the benefits are not immediate or identifiable by the observer (Martin & Caro 1985, Bekoff & Byers 1998, Palagi 2018).

For polar bears in Hudson Bay, Canada, the ice-free season is a period of low resource availability and conserving energy (Stirling & McEwan 1975, Pilford et al. 2016, Pagano et al. 2018). Polar bears possess large, heavy limbs and the act of lifting their limbs to rear up, chase and/or wrestle may use a significant amount of kinetic energy (Gray 1968). Along with large limbs, polar bears possess thermal barriers such as thick layers of blubber and fur that limit the rate of heat loss to the environment during activity (Øritsland 1970). Mean resting metabolic rate of a polar bear in human care was found to be 0.34 mL O_2 g^{-1} h^{-1} which translates to 37.1 MJ day^{-1}, 17% greater than resting metabolic rate of denning polar bears and up to 21% greater than resting metabolic rate of other ursids (Pagano et al. 2018). Field metabolic rate of wild polar bears was found to be 51.6 MJ day^{-1}, 0.6-1.1 times greater than predicted for similar-sized carnivores (Nagy et al. 1999). Similarly, at a running speed of 7.2 km/h for 45 minutes, polar bear metabolic rate is 13 times higher than the basal rate, which suggests locomotion is energetically costly, even at lower speeds (Hurst et al. 1982). Overall, these data suggest that polar bear locomotion, and predictably social play, has an energetic cost and to conserve energy polar bears should enter a period of rest during the ice-free season.

Adult male polar bears within the Western Hudson Bay sub-population have been observed engaging in social play during the ice-free season (Latour 1980, 1981; this study). Polar bears are ice-adapted and select marine prey while hunting on the sea-ice (Best 1976). Polar bears in western Hudson Bay fast during the summer months once the Hudson Bay sea-ice has broken up and they are forced onto land with no access to prey (Ramsay & Stirling 1988). Play is a time and energy-consuming activity (Palagi 2007, Monteiro de Almeida Rocha et al. 2014), therefore polar bears would not be predicted to engage in social play during the ice-free season, as it is a period of nutritional stress (Stirling & McEwan 1975). Social play may be a costly behaviour, as the attributes that help polar bears survive in an Arctic environment may work against them in social play scenarios. Polar bear social play typically consists of sparring, which is similar to actions used in competitive events and predictably uses the energy needed for survival over the fasting season (Latour 1980, Fagen 1981, Bekoff & Byers 1998).

Polar bears need to reduce their activity level during the ice-free fasting season to maintain body condition (Pilford et al. 2016, Pagano et al. 2018). As the fasting period lengthens, polar bears must gain sufficient fat stores to meet the metabolic requirements needed for walking, sparring, thermoregulation, and to have a reserve of energy to sustain themselves (Stirling & McEwan 1975). An increase in the duration of the ice-free fasting season has been linked to a decrease in body condition of female polar bears in western Hudson Bay (Regher et al. 2007, Hunter et al. 2010, Lunn et al. 2016). Body condition, energy density and adipose tissue lipid content in male polar bears have also declined (Sciullo et al. 2016).

Polar bears typically arrive onshore when the sea-ice cover on Hudson Bay reaches 30% in the spring (Cherry et al. 2013). If Hudson Bay sea-ice cover reaches 30% approximately 60 days earlier than normal, increasing the fasting period from 120 days to 180 days, a decline of 28% in the adult male population of Hudson Bay could occur (Molnar et al. 2011). An increase in time spent on land without access to food resources is directly correlated with a decline in reproductive success and recruitment, affecting polar bears at the individual and population level (Stirling et al. 1999). To increase survival during an increasing fasting season, polar bears need to increase prey consumption in the hunting season, or further reduce their activity levels to conserve energy in the ice-free season (Pilford et al. 2016).

Social play is assumed to be a low benefit behaviour that is dropped when the cost of playing outweighs any immediate or delayed benefit (Fraser & Duncan 1998, Spinka et al. 2001). It is unclear why polar bears in western Hudson Bay devote energy to social play during a resource-limited time (Latour 1981). The Western Hudson Bay population of polar bears are among the populations that experience the longest ice-free season (Parkinson 2014) and in the literature, observations of social play among polar bears in other parts of the world are absent. With a reduced caloric intake during the ice-free season (Pilford et al. 2016), polar bears tend to conserve energy through reduced activity (Knudsen 1978, Latour 1981, Lunn & Stirling 1985).

Although male polar bears are not using energy to mate or hunt during the ice-free season, they are devoting a portion of their energy budget towards social play behaviour (Latour 1981). But, if polar bears continue to engage in social play despite an overall decline in body condition, social play may be an important behaviour that contributes to their fitness. If no other behaviour is necessary for survival, polar bears may continue to play during the ice-free season.

I tested the hypothesis that declining body condition affects the characteristics of polar bear social play. This hypothesis predicts that polar bears in healthy body condition will play more often and for a longer duration than those in poor body condition. I also tested the hypothesis that body condition will influence the role that each bear takes in a bout of social play. Among dyads (pairs of bears), the play partner in better body condition should initiate play, whereas the polar bear in poorer body condition is predicted to terminate play.

Polar bears should be conserving as much energy as possible during the ice-free season to survive the fasting season and subsequent winter months, and to be successful in the upcoming hunting and mating season (Stirling & McEwan 1975, Stirling, Lunn & Iacozza 1999, Pagano et al. 2018, Galicia et al. 2019). If the ice-free season is a period of low resource availability (Pagano et al. 2018), polar bears should be conserving as much energy as possible for the greatest chance of survival during the hunting and mating season. Therefore, I predicted that as the ice-free period lengthens, polar bear social play should decrease in frequency. I also predicted that the minimum daily temperature will influence the occurrence of polar bear social play. The occurrences of social play per day may increase as daily minimum temperature decreases, as the metabolic requirements for panting and evaporative cooling are in lower demand (Kingma et al. 2014).

Methods

Biology of the study animal

Free-ranging adult male polar bears lose approximately 1 kg of mass/day while on land in the ice-free season (Atkinson et al. 1996, Derocher & Stirling 1995, Pilford et al. 2016), similar to that of adult male polar bears without access to food in a temporary holding facility (Pilford et al. 2016). The similarities in the mass lost by free-ranging bears and bears in holding suggest that terrestrial food sources are not sufficient to offset the mass lost during the fasting season and do not provide a significant energetic gain. Likewise, energetic demands for searching, consuming and digesting terrestrial food sources increase energy expenditure twofold to eightfold from resting metabolic rate (Erlenbach et al. 2014, Dyck & Morin 2011).

To counteract the consequences of low resource availability, animals have adapted strategies for maintaining body condition and conserving energy (Ruf & Geiser 2015, Portugal et al. 2016). Specifically, members of the *Ursus* genus such as black bears (*Ursus americanus)* enter a dormant state, or torpor, during resource-limited times by reducing body temperature, metabolism, and heart rate (Tøien et al. 2011). However, male polar bears do not enter torpor during the ice-free season but exhibit low metabolic rates and are hypophagic, i.e., a reduction in caloric intake due to environmental changes (Watts & Hansen 1987, Atkinson et al. 1995, Halford 2010, Robbins et al. 2012, Pilfold et al. 2016).

Study site

Wild polar bears were observed in the Churchill Wildlife Management Area approximately 10 km east of the town of Churchill Manitoba (58°45’N, 94°00’W), along the southwestern coast of Hudson Bay. This region consists of flat tundra terrain with elevations less than 50 m (Ritchie 1962). The coastline consists of shallow lakes and ponds, gravel spits and post-glacial beach ridges (Ritchie 1962, Dyck & Baydack 2004), and the vegetation within the Churchill Wildlife Management Area consists primarily of willow (*Salix spp*.), sedges (*Carex spp*.), mosses and lichen (Latour 1980).

The Churchill Wildlife Management Area is a provincially managed area allowing for eco-tourism opportunities for wildlife viewing (Nelitz et al. 2015). Off-road tundra vehicles are permitted to access a trail network to bring tourist groups into the Churchill Wildlife Management Area. Our observations of polar bear social play were made from these vehicles. Data were collected in October and November from 1994 to 1996 and 2001 to 2005.

Data Collection

To identify individual polar bears, images of each side of the face of each polar bear were collected using digital SLR cameras (Nikon D100 6.0-megapixel) equipped with zoom lenses (70-300mm). Facial recognition analysis was performed to confirm that each individual observed was correctly identified, and no two bears were misidentified as the same individual (Anderson et al. 2007, 2010). Body condition was also assessed non-invasively using images of the side profile of the entire body of a bear. Visual assessment of body condition through photographs is widely used (Ferguson et al. 2006, Stirling et al. 2008, Vieira et al. 2015, Spoliansky et al. 2016), however quantitative measurement of pixels is rare. A body condition index was calculated by counting the number of pixels from the top of the back to the bottom of the belly (at the widest point) divided by the number of pixels from the top of the shoulder to bottom of the foot using ImageJ software (Abramoff et al. 2004) (Figure 2.1). The ratio from dividing pixel length is from 0-1, 0.552 being the lowest condition in the dataset and 0.83 being the highest.

Video recordings made with a SONY camcorder (model DCR-TRV900, SONY Corporation, Tokyo, Japan) of social play among polar bears in the wild were collected whenever play was observed. Behavioural components of play included rearing, wrestling, mouthing, facial contact, foreleg pushing, rear and contact, inhibited bites, forward advances, backward retreats, rushing and fleeing (Latour 1981, Bekoff & Byers 1998). The entire play interaction was filmed from the first contact to final retreat and these interactions were then scored using behavioral analysis software, Observer© Video Pro (v. 4.1, Noldus Information Tech., The Netherlands, Eckhardt & Waterman 2004). The polar bear that first contacted a play partner was deemed the initiator of play. Contact could include pushing with a paw, biting or mouthing. The polar bear who ended the bout was deemed the terminator of play. Ending a bout of play consited of walking or running away or laying down to rest. The duration of play was calculated as the duration in seconds between the initiation and termination of play. A new play bout was defined as play beginning after one minute of inactivity (Byosiere et al. 2016).

I obtained sea ice breakup dates from weekly ice graphs from the Canadian Ice Service (CIS, http://icewe b1.cis.ec.gc.ca/IceGraph) for the Hudson Bay from 1995 to 1996 and 2001 through 2005. Polar bears typically come onto land in the spring at 30% ice-cover (Cherry 2011), therefore I considered sea ice breakup as the week that sea ice decreased below 30%. I calculated days since sea ice breakup for each play interaction by subtracting the ordinal date on which the play bout occurred from sea ice breakup date.

I collected minimum daily temperature (ºC) on each date play occurred from Churchill A weather station reports (Government of Canada, https://climate.weather.gc.ca/historical_data/search_historic_data_e.html).

Statistical Analysis

All statistical analyses were conducted in R (R Core Team 2017). The impact of body condition on the frequency of play was modelled using a generalized linear model approach with a Poisson distribution using the LmerTest package in R (Kuznetsova et al. 2017). The average number of times each individual played per season was used as the response variable with body condition as the predictor variable. To assess the hypothesis that body condition influenced the duration of social play, I used a linear mixed-effects model using the lmer function in the lme4 package in R (Bates et al. 2014) with body condition and ordinal date as the predictor variables and the log of duration as the response variable. The model was varied to include ordinal date and role (initiator or terminator of play) to determine which factor most accurately represents the influence of body condition on the duration of play. The best-fitting model was then selected using Akaike's information criterion (AIC) in R base package (R Core Team 2017). Individual identity was included in all analyses as a random effect to account for repeated measures. Normality assumptions for all model were assessed by visualizing residual plots. Play bout durations were log-transformed to normalize these data. I also assessed whether the average body condition of a dyad was correlated with the duration each dyad played using Kendall's rank-based correlation test for non-normal data.

To determine if body condition influences the proportion of times a bear initiates or terminates play, I calculated the proportion of times each bear was the initiator of play and/or the terminator of play among all sampling years. I then ran a generalized linear model with a quasi-binomial distribution and a logit-link function with body condition as the predictor variable and proportion of times a bear initiated play as the response variable. I also ran a separate generalized linear model with a quasi-binomial distribution and a logit-link function with body condition as the predictor variable and proportion of times a bear terminated play as the response variable

To determine whether sea-ice breakup dates and/or ambient temperature influenced the occurrence of social play, I used a generalized linear model with a Poisson distribution using the number of times each bear played per day as the response variable. The number of days since Hudson Bay was at 30% ice cover and minimum daily ambient temperature (ºC) were used as the predictor variables. Individual identity was included as a fixed effect. For the model to converge I set nAGQ = 0. I also used a Kendal rank-based test to determine whether minimum daily ambient temperature and number of occurrences of social play were correlated and whether the minimum daily ambient temperature was correlated with date of sea-ice break-up.

To determine whether body condition indices significantly declined from the beginning of the sampling period (1994-1995) and the end of the sampling period (2004-2005), I used an unpaired Welch's t-test to account for unequal sample sizes.

An independent-sample t-test was run to determine whether there was a significant mean difference in body condition between polar bears who initiated play (n = 393) and polar bears who terminated a bout of play (n = 303).

Results

Body condition of bears observed engaging in social play from 1994 to 1995 and 2001 to 2005 ranged from 0.633 to 0.668 with a mean body condition of 0.648 ± 0.035 across all sampling years (n = 69) (Figure 2.2). I found no difference in body condition of polar bears observed in 1994-1995 (n = 12) and 2004-2005 (n = 34) (95% CI, $T_{26.66} = -1.15$, $p = 0.26$).

I found no influence of body condition on the number of occurrences of play per day ($R^2 = 0.99$, $z_{1.084}$, $p = 0.279$) (Figure 2.3). I found no significant effect of body condition on the duration of play ($R^2 = 0.003$, $T_{59} = 1.59$, $p = 0.12$) (Figure 2.4). The ordinal date had a positive significant influence on the duration of play ($R^2 =0.003$, $T_{59} = 4.11$, $p = <0.001$) (Figure 2.5).

Minimum daily ambient temperature had no effect on the duration of play ($R^2 = 0.002$, $T_{240} = 1.09$, $p = 0.28$).

There was no correlation between the average body condition of a dyad and the duration each dyad played ($n = 54$), with a correlation coefficient of 0.081 ($z = 0.838$, $p = 0.40$). The best competing model to predict the duration of play included the log of duration as a dependent variable and body condition and ordinal date as independent variables with identity as a random effect (Table 2.1). I found that body condition did not influence the proportion of times a bear initiated play ($R^2 = 0.003$, $t_{67} = 0.488$, $p = 0.63$), nor the proportion of times a bear terminated play ($R^2 = 0.001$, $t_{67} = 0.333$, $p = 0.74$).

Date of the sea-ice breakup was related to the number occurrences of play per day. As the number of days since sea-ice breakup increased, the number of bouts of observed play per day also increased ($R^2 = 0.132$, $z_{339} = 3.432$, $p = 0.0006$) (Figure 2.6). I found an effect of minimum daily temperature on the occurrences of play per day ($R^2 = 0.014$, $z_{339} = -2.635$, $p = 0.008$) (Figure 2.7). The minimum daily temperature and the date of sea-ice breakup were not correlated (Kendall's rank-based correlation test, $z = -0.199$, $p = 0.842$).

I also examined if polar bears who engaged in social play ($n = 71$) had higher body condition indices than those who were never observed playing ($n = 10$). I found that the mean body condition of polar bears who were observed engaging in social play over all sampling years (0.649 ± 0.005) did not differ from polar bears who were never observed engaging in social play (0.645 ± 0.017) (Wilcoxon rank-sum test with continuity correction, $W = 281$, $p = 0.650$) (Figure 2.8).

I used a linear model to determine the relationship between the duration of play and the sum of the body condition of both individuals in a play bout ($n = 26$). Only unique occurrences of play were included in the model. There was no effect of the sum of the body conditions and duration of play ($R^2 = -0.03$, $T_{24} = -0.31$, $p = 0.76$).

Discussion

My results indicate that the body condition index does not influence the occurrence and duration of polar bear social play in western Hudson Bay. I found no effect of body condition on the frequency or duration of social play throughout the sampling period, despite a decline in body condition over time (Obbard et al. 2006, Regher et al. 2007, Hunter et al. 2010, Lunn et al. 2016). During the study period, body condition had not declined to the point where the energetic demands of play were too costly to end social play behaviour.

I had predicted that play partners in lower body condition would terminate bout of social play more often, but the body condition of each play partner had no influence on the proportion of times a polar bear was the initiator or terminator of play. Turn-taking or switching between being the initiator and terminator of social play is necessary for social play interactions to remain playful (Cordoni et al. 2016, Palagi et al. 2016). Turn-taking enhances cognitive development during the juvenile life stage and development may continue as play continues into adulthood (Foroud & Pellis 2002, Arakawa 2018). Role reversal in bouts of adult social play shows that adults are continuing to fine-tune complex skills with each role they take on (Palagi 2018). Play partners need to be self-aware and in control of their movements to avoid escalation a playful encounter into a more dangerous interaction.

I found that as time since sea-ice breakup increased, occurrences of social play also increased. I expected occurrences of social play to decline, as mammalian social play tends to decrease under conditions of deprivation (Baldwin & Baldwin 1976, Sommer & Mendoza-Granados 1995). My study showed that polar bear play occurrence increased as the ice-free season increased. I also found that as the minimum daily temperature declines, occurrences of play per day increase. Polar bears play more often per day at the lower end of their thermoneutral zone (ambient temperatures of -30ºC and 5ºC) (Best 1982) throughout the years sampled. At ambient temperatures within the thermoneutral zone, metabolic processes such as evaporative cooling are not urgent while at rest (Kingma et al. 2014) and polar bears presumably have more energy to spend.

Polar bears lose 1kg per day of body mass when they are away from marine food sources (Pilford et al. 2016), suggesting that social play should diminish as the fasting period progresses. In my research, polar bear social play occurred between 94 and 155 days since sea-ice broke up on Hudson Bay. Projections made by Molnar et al. (2011) predict that if the ice-free season increases to 180 days, the adult male population of polar bears in Hudson Bay could decline by 28%. The ice-free season had not reached the suggested critical threshold in the sampling years of this study, which suggests that adult male polar bears had not reached a body condition threshold that might interfere with social play behaviour.

The occurrence of social play late into the ice-free season suggests that either polar bears are not nutritionally stressed during the ice-free season, or that the benefits gained through social play are so important that play needs to occur even though it may use critical energy and fat stores. Analysis of fat composition among polar bears in Baffin Bay, Davis Strait, Foxe Basin, Gulf of Boothia and Lancaster sound found a decline in body condition throughout the fall and winter, with an increase in condition in spring-summer (Galicia et al. 2019). However, the adipose lipid content per gram of adipose tissue of polar bears across all sampled subpopulations increased beyond the occurrence of sea ice break-up (Galicia et al. 2019). Feeding on hauled-out seals or seal pups as sea-ice thaws in spring/summer maximizes energetic gain, which is then stored and used throughout the fasting season (Galicia et al. 2019). An increase in stored energy due to late feeding may aid in the success of polar bears during the upcoming reproductive and hunting season. Continual feeding into the ice-free season may contribute to the healthy body condition of polar bears observed playing in my study. More data are needed to determine exactly what the lower critical body condition is for polar bears to stop engaging in social play. Polar bear body condition has declined since my data were collected (Regher et al. 2007, Hunter et al. 2010, Lunn et al. 2016), but I did not detect a decline in body condition within the span of my sampling years. Data post-2005 would be valuable to determine whether body condition declines are influencing social play behaviour in recent years.

Rode et al. (2018) found that less than 10% of polar bears in the western Hudson Bay sub-population are exposed to humans through recreational activities, including tundra vehicles. Therefore, only a small subset of the population was included in my analyses and observations throughout the years sampled. Large sub-adult and adult males in healthy body condition may have been the only polar bears observed engaging in social play within the sampling area. Polar bears in poorer body condition or younger individuals may avoid other bears and humans and therefore may not be observed (Towns et al. 2009). Indeed, the same set of polar bears engaged in social play frequently over the sampling period (1994 to 1995 and 2001 through 2005). Therefore, the small sample of polar bears observations may have resulted in lower variation in my body condition data. Likewise, linear mixed effect models that included identity as a random effect were the best competing models to predict duration of play, suggesting that the same set of polar bears played consistently.

There was also no difference in body condition between polar bears who engaged in play and those who did not play, possibly due to the small sample size of polar bears who did not play. Polar bears that are in poor condition may avoid the Churchill Wildlife Management Area altogether or move through quickly to investigate opportunities elsewhere, particularly in areas of human settlement (Towns et al. 2009). The number of problem bears captured and brought into the Churchill polar bear handling facility has increased over time, possibly due to nutritional stress and a lengthening of the ice-free season (Towns et al. 2009). Sub-adult male bears have been the most common age and sex-group to interact with humans, predictably due to their higher energetic demands for growth (Lunn & Stirling 1985, Mattson 1990).

Certain traits, including behavioural traits, are usually retained if the trait brings a significant benefit to the individual (Smaldino et al. 2019). Social play is a trait that is typically lost as a mammal reaches adulthood and in conditions of food deprivation (Baldwin & Baldwin 1976, Sommer & Mendoza-Granados 1995). However, polar bear social play continues to occur in the adult life stage and in conditions of low resource availability (Latour 1981; this study). Despite the perceived costs associated with play, polar bears in western Hudson Bay are investing energy into social play which may be a costly investment during the fasting season. Social play among polar bears is a retained behavioural trait, as the benefits of play outweigh the costs, whether immediate or delayed (Smaldino et al. 2019).

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Table 2.1. Comparison of generalized linear models to predict the duration of polar bear social play. Predictive variables included: body condition index, ordinal date and ambient temperature (ºC). Degrees of freedom (df), number of parameters (K), Akaike's information criterion corrected for small sample sizes (AIC_c), delta AIC (ΔAIC), AIC weight (W*i*) and Log-likelihood (L). Each model included identity as a random effect.

Rank	**Model**	**df**	**K**	**AIC_c**	**ΔAIC**	**W*i***	**L**
1	Body condition index, ordinal date	5	4	1430.762	0	7.768e-01	-710.312
2	Body condition index	4	3	1433.549	2.787	1.928e-01	-712.728
3	Body condition index, ordinal date, ambient temperature	6	5	1437.672	6.909	2.454e-02	-712.739
4	Body condition index, ambient temperature	5	4	1440.553	9.791	5.810e-03	-715.207
5	Ambient temperature	4	3	2390.365	959.602	3.276e-209	-1192.439
6	Ordinal date	4	3	2392.935	962.173	9.060	-1192.439
7	intercept	2	2	2584.822	1154.060	1.947e-251	-1290.403

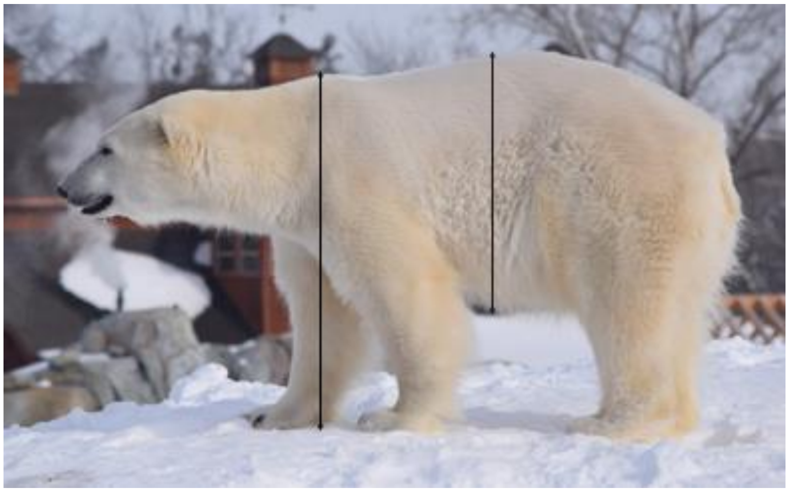

Figure 2.1. Pixels from the highest point of the back from the bottom of the belly are divided by the pixels from the highest point of the haunches to bottom of foot to create an index of polar bear body condition from 0-1.

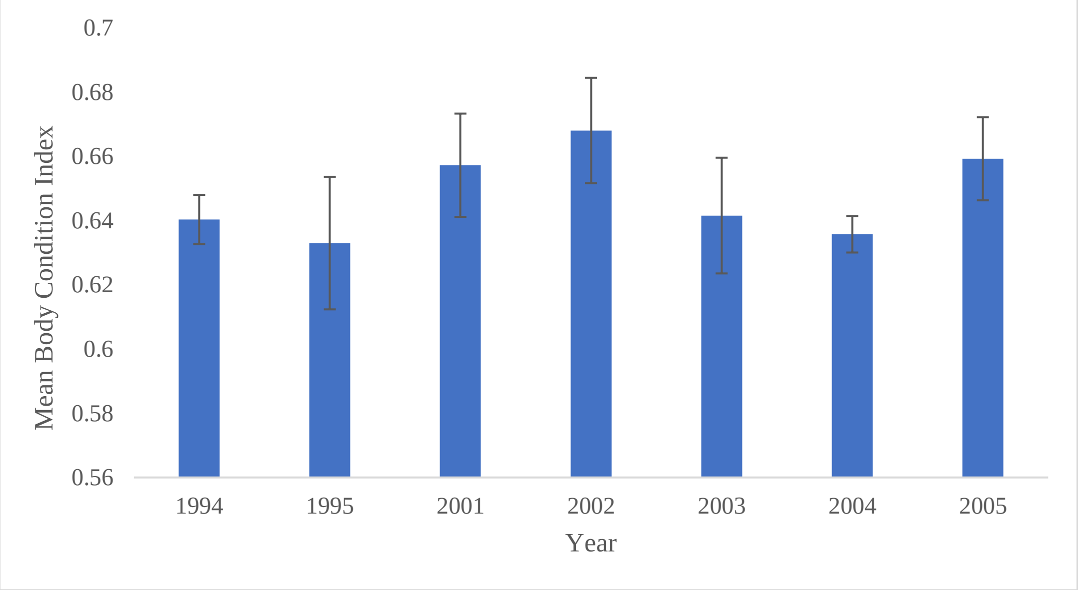

Figure 2.2. Mean body condition of adult male polar bears observed engaging in social play in the Churchill Wildlife Management Area, Western Hudson Bay in 1994 (n = 6), 1995 (n = 3), 2001 (n = 8), 2002 (n = 14), 2003 (n = 7), 2004 (n = 20) and 2005 (n = 11).

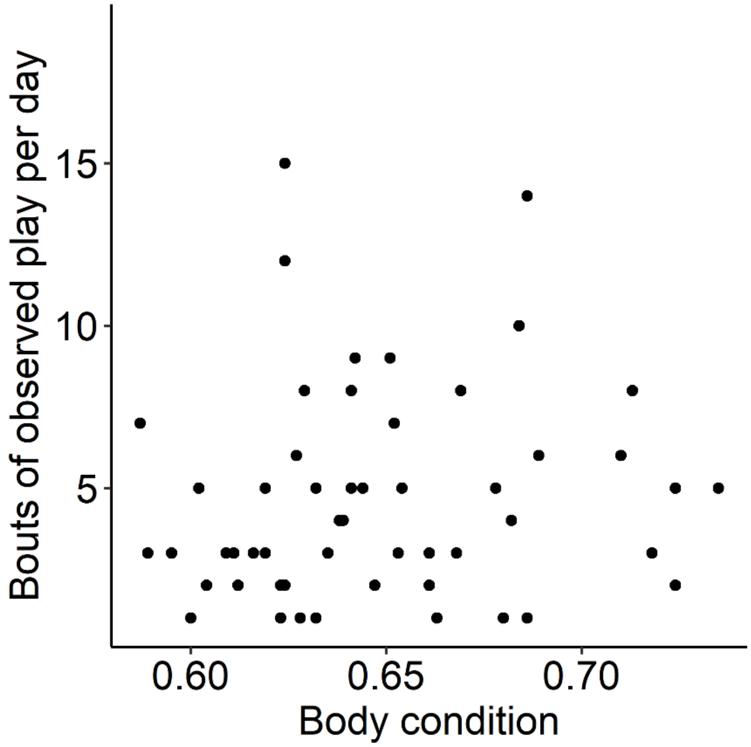

Figure 2.3. The relationship between body condition and the average number of observed bouts of play each polar bear engages in per day including play bouts from 1994 to 1995 and 2001 through 2005 (n = 187, p = 0.28).

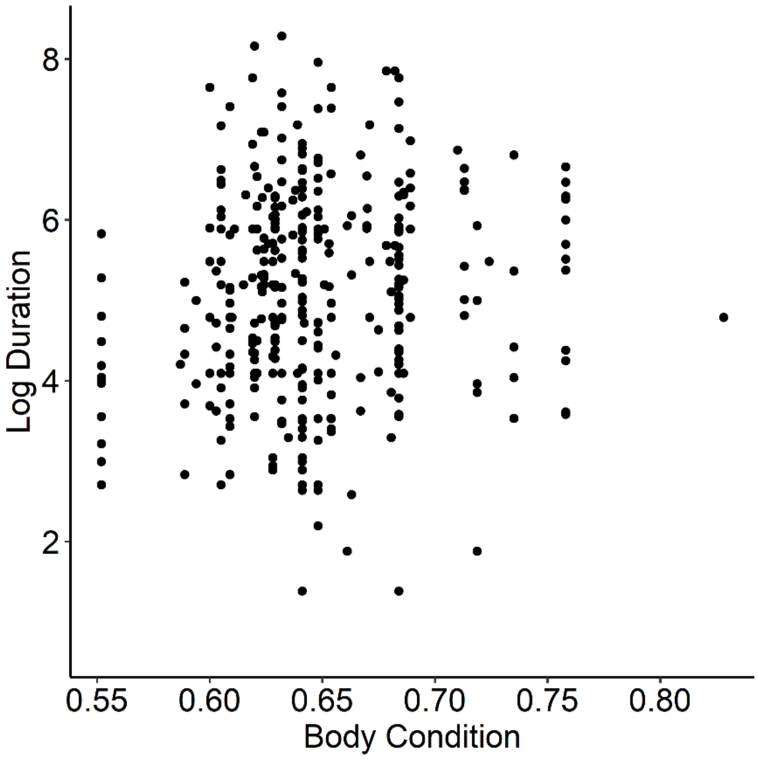

Figure 2.4. The body condition and duration of polar bear play including play bouts from 1994 to 1995 and 2001 through 2005 (n = 696, p = 0.12).

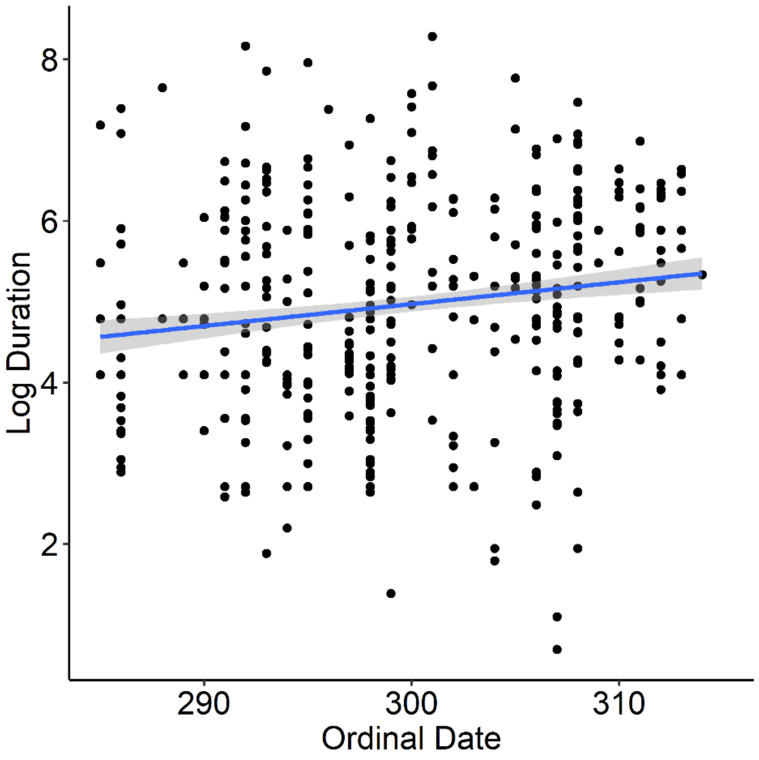

Figure 2.5. The positive relationship between the duration of play (log-transformed) and ordinal date in polar bear play including play bouts from 1994-1995, 2001-2005 (n = 696, p = <0.001).

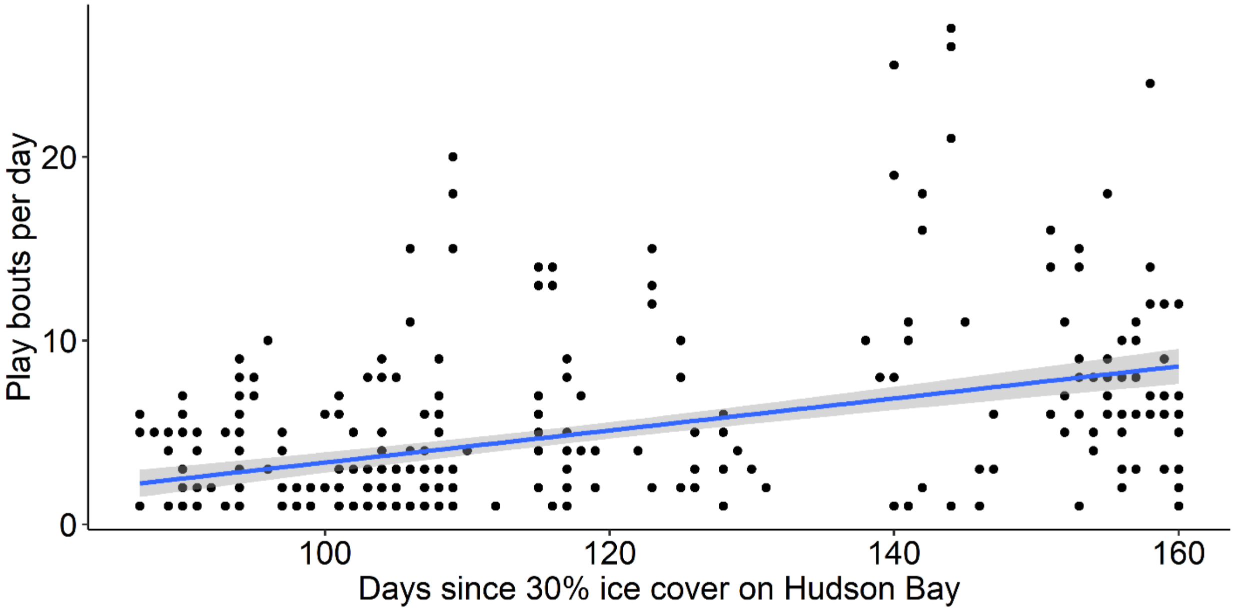

Figure 2.6. The influence of the length of the ice-free season on Hudson Bay on the number of polar bear play bouts per day. A positive relationship between increasing days since 30% ice cover on Hudson Bay and the number of play bouts per day (n = 69, p = 0.001).

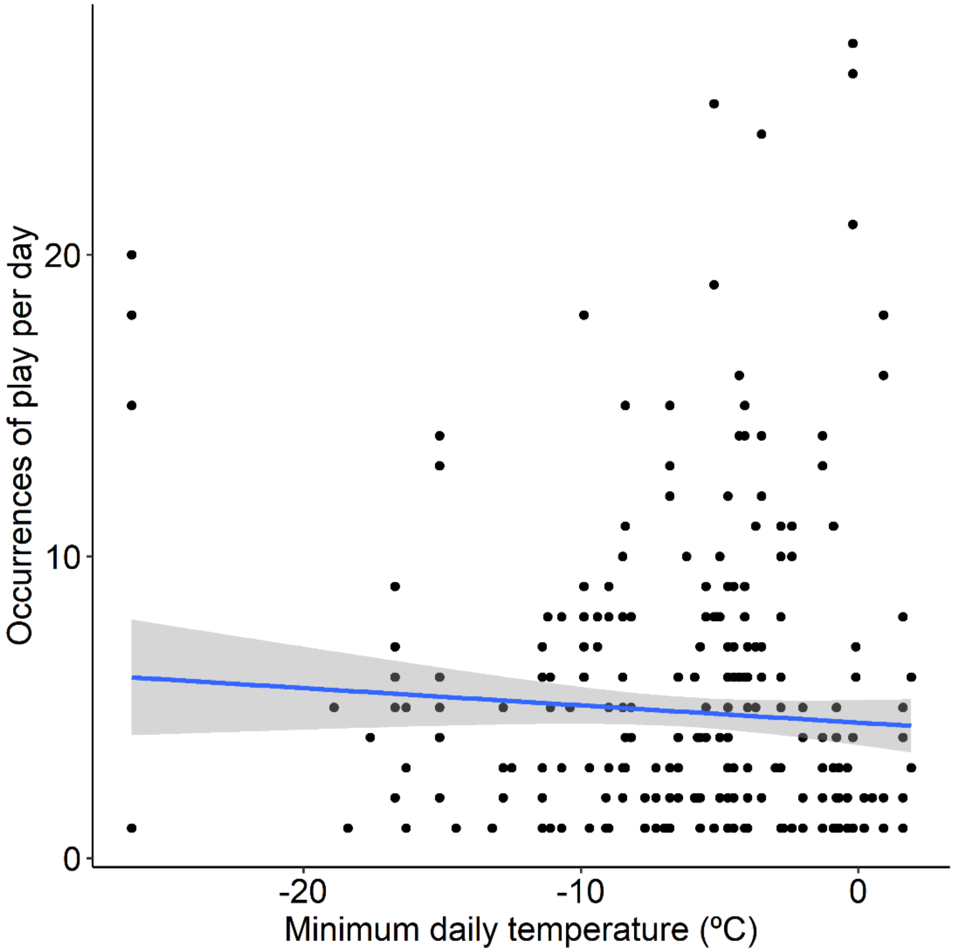

Figure 2.7. Occurrences of polar bear social play increase as minimum daily temperature declines (n = 339, p = 0.008).

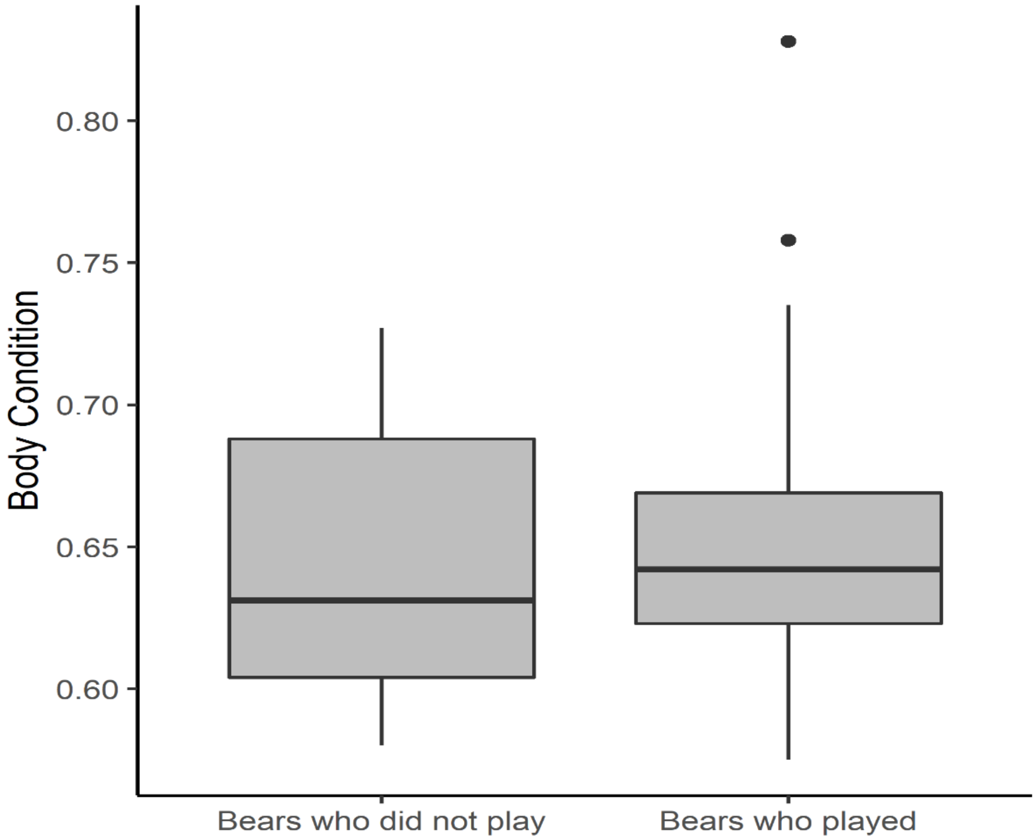

Figure 2.8. No significant difference (W = 281, p = 0.65) in body condition of adult male polar bears never observed engaging in social play (n = 9, x̄ = 0.64 +/- 0.017) and adult male polar bears observed engaging in social play (n = 69, x̄ = 0.649 +/- 0.005) across all sampling years (1994 to 1995 and 2001 through 2005).

Chapter 3 The use of thermography in measuring the surface temperature of polar bear thermal windows

Abstract

Infrared thermography (IRT) is a non-invasive tool that can be used to measure the temperature of various surfaces. Typically, IRT is used for construction or military purposes but is increasingly used as a non-invasive tool used in wildlife studies. I investigated the use of IRT to measure surface temperature changes as a proxy for energetic expenditure. I measured the surface temperature of polar bear (*Ursus maritimus*) eyes, while immobilized, to determine whether the eye is a thermal window which can accurately indicate internal temperature. I found a significant difference (2.68 ºC ± 0.41ºC) between the surface temperature of the eye measured with IRT and the internal rectal temperature. Additionally, I measured surface temperature changes in polar bears after bouts of social play as a proxy for infer energy expenditure. Mean surface temperature of the eye increased by 1.34ºC ± 0.43ºC after social play, indicating that polar bears may expend energy during bouts of social play. During the fasting season, polar bears are relying on fat stores built up over the hunting season, and any energy expenditure beyond what is required to forage and travel is considered costly to their survival. I conclude that IRT is a useful tool to non-invasively investigate the energetics of social play. The energetic cost to a typical adult male polar bear could be significant in years of low resource availability.

Introduction

Social play is a motor activity that uses kinetic energy and is presumed to have some energetic cost (Symons 1978, Bekoff & Byers 1981, Fagen 1981, Smith 1982), but there are few studies that measure the energetic costs of social play. Social play is thought to be both costly and beneficial, as play has been maintained by selection in some species (Caro 1989, Miller & Byers 1991). However, Miller & Byers (1991) argue that the energetic costs of social play are largely unknown. The benefits gained through play are neither apparent or immediate (Burghardt 2001, 2005, Graham & Burghardt 2010), and measuring the costs associated with social play is needed to understand the significance of play behaviour.

Martin (1984) estimated that social play contributes to 2.5 to 15% of the total energy budget, excluding the energy required for growth. Indeed, social play in kittens *(Felis catus)* accounted for 4 to 9% of their daily energy budget (Martin 1984) and 2 to 3% in rats *(Rattus sp.)* (Siviy & Atrens 1992). On the surface, the minimal contribution of play to the overall energy budget suggests that social play is not costly, low priority, and benefits might be low (Martin 1984). However, a low-cost behaviour does not mean that the benefits to such behaviours are also low (Martin 1984, Bekoff & Byers 1985, Martin & Caro 1985). The cost of social play, especially among juvenile animals, might be low, but the long-term benefits may be substantial (Bekoff & Byers 1985, Bekoff & Byers 1992).

Energy budget analyses examining play typically focus on juvenile animals who receive parental care and are not yet responsible for foraging (Martin 1984). The costs of social play among adults could be greater, as adults devote more energy to foraging and reproduction (Martin 1984). For play to continue into adulthood, the benefits gained must outweigh the energetic costs (Caro 1989). Therefore, it is important to measure the energetic costs of social play to further understand the benefits.

I aimed to further our understanding of the energetic costs of adult social play by exploring the use of infrared thermography (IRT) to measure surface temperature changes during play as a proxy for energetic expenditure. In wildlife and veterinary studies, infrared thermography (IRT) has been used to diagnose injury, pregnancy, infectious disease, and to indicate stress levels (Hilsberg 1998, Arenas et al. 2002, Nakayma et al. 2005, Durrant et al.

2006, Dunbar et al. 2009). IRT has also been used to assess heat dissipation from the surface of a mammal to the environment (Klir et al. 1990, Speakman & Ward 1998, Mayle et al. 1999, Kuhn & Meyer 2009, Tattersal & Cadena 2010). The intensity of radiation emitted by an individual is dependent on their surface temperature, which is a combination of the temperature of internal organs and the body surface (Speakman & Ward 1998).

In endotherms, stable body temperature is maintained through heat transfer from the body to the environment (Rezende & Bacigalupe 2015). Heat transfer from the organs to specific body parts is promoted when ambient temperature increases or when metabolic heat production increases with exercise (Andrade 2015). The specific body parts that amplify heat loss are referred to as thermal windows. Thermal windows are areas of the body with little fat or hair (eyes, ears, nose) and areas with a large surface area and a rich vascular bed such as the abdomen (Andrade 2015). Thermal windows allow for the regulation of body temperature by transferring body heat to the environment (Best 1982, Speakman & Ward 1998, Andrade 2015).

Infrared energy emitted from thermal windows is often used to estimate internal body temperature (Zinn et al. 1985, Heath et al. 2001, Dunbar et al. 2009, Johnson et al. 2011, Lu et al. 2018). The eye has been used as an indication of internal temperature because capillary beds in the border of the eyelid and lacrimal caruncle increase in temperature with activity because of changes in blood flow and are therefore indications of brain temperature (internal temperature; Zanghi 2016). For example, thermograms of the eye of mule deer (*Odocoileus hemionus*) were compared to internal temperate, and no significant differences between the two temperature readings were found (Dunbar et al. 2009). Johnson et al. (2011) also compared measurements of body temperature in ponies (*Equus feris caballus)* including rectal, internal microchip and thermograms. Thermographic eye temperatures had a significant correlation with both rectal and microchip temperature readings (Johnson et al. 2011). IRT has been widely used in pig health studies where IRT accurately estimates body temperature by measuring the surface temperature of thermal windows including the eye, ear tip, ear base and vulva (Magnani et al. 2011, Zinn et al. 1985, Warriss et al. 2006, Soerensen & Pedersen 2015).

In another study, thermographic eye temperature and rectal temperature of Angus steers (*Bos taurus)* followed a normal distribution, but the thermographic eye temperature was on average 2ºC lower than rectal temperature (Church et al. 2013). The standard deviation of the IRT measured temperatures was twice as large as the rectal temperature, indicating that IRT may have been an inconsistent measure of surface temperature (Church et al. 2013). The inconsistencies in temperature readings may be due to ambient factors such as humidity and distance to the subject (Church et al. 2013). Researchers using IRT must be fully aware of environmental factors that can increase error in their measurements of surface temperature (Church et al. 2013).

IRT can also be used to detect temperature changes during and after exercise. During exercise, radiation or heat is transferred from the skin to the environment as muscles contract (Shepherd 1987). Kinetic energy is generated and transferred to adjacent tissues and muscles via capillary blood flow and is then dissipated as infrared radiation (Knizkova et al. 2007). For example, muscle temperature in horses (*Equus caballus*) significantly increases as the duration of exercise increases (Lovell et al. 2006). Subsequent studies then found that surface temperature, measured using IRT, increased with muscle contraction (Yarnell et al. 2014). Surface temperature, measured using IRT, also increases during exercise in the human arm (Matsuo et al. 2006). These studies suggest that IRT may be a useful tool to accurately and non-invasively measure surface temperature, and to therefore infer relative internal temperature changes during or after exercise without the need for more invasive methods.

Infrared thermography may also be a useful non-invasive tool to measure heat dissipation after physical exercise, (i.e., social play) exhibited by polar bears (*Ursus maritimus*). Polar bear social play consists of activities including forward advances, rushes, rearing, biting and backward retreats (Latour 1981). Polar bears engage in social play during a period of resource limitation when they are relying on fat stores built up over the previous season (Latour 1981). Any activity that uses stored energy during the ice-free season, including play, can be assumed to be energetically costly. For instance, at ambient temperatures of -40ºC to 0ºC and a walking speed of 4km/hr for 45 minutes, the body temperature of polar bears remains constant at approximately 36ºC, but at increased walking speeds of 7km/hr, body temperature increases to 39ºC (Hurst et al. 1982, Hurst & Øritsland 1982). Normal body temperature in resting polar bears is 36.9ºC +/- 0.5ºC (Best 1982). Between ambient temperatures of -30ºC and 5ºC, basal metabolic rate and body temperature remain constant and independent of ambient temperature (Best 1982), and heat transfer from the body core is equivalent to heat transfer to the environment (Kingma et al. 2014). Therefore, the ice-free season is a period in which polar bears in southern portions of their range may reach or surpass ambient temperatures of 5ºC, and metabolic rate and body temperature may become dependent on ambient temperature and activity level. As ambient temperature increases, polar bear metabolic processes increase due to panting and evaporative cooling (Kingma et al. 2014) resulting in an increase in energy use for thermoregulation that is critical for polar bears to survive the fasting season.

Polar bears have evolved to survive a harsh climate and maintain thermal stability with a dense coat of fur and blubber layer (Pabst et al. 1999), further supporting the assumption that polar bears must rest during the fasting season to conserve energy. When the body temperature of a polar bear increases, blood travels to the thermal windows to dissipate through the skin as heat (Øritsland 1970). Since polar bears are highly insulated, heat loss is restricted to the less insulated areas of the body (Øritsland 1970, DeMaster & Stirling 1981, Best 1982, Stirling 1998). During activity or exercise, heat loss should be most visible from these thermal windows with the use of IRT.

The objective of my study was to determine whether polar bears possess thermal windows that could be used to estimate internal temperature. I measured the surface temperature of the eye, using IRT, during veterinary procedures while each polar bear was immobilized. I compared surface temperature measurements of the eye to internal body temperatures measured by rectal thermometer. I predicted that the eye would be an accurate thermal window to detect internal body temperature, as the surface of the eye has been used to accurately detect the internal temperature of various mammals (Dunbar et al. 2009, Johnson et al. 2011, Valera et al. 2012, Travain et al. 2014, George et al. 2014).

The second objective of my study was to determine whether IRT is a useful tool in accurately measuring the change in the surface temperature of they eye after a bout of social play. In doing so, I will be able to make correlations between anticipated increases in body temperature and energy expenditure. If the eye is a thermal window which accurately depicts internal temperature, I will then be able to use thermography to accurately measure internal temperature before and after play, as a proxy for energy expenditure. In chapter two of this thesis, I found that the occurrence of play increased with the length of the ice-free season. As the length of the ice-free fasting season increases, polar bear energetic demands may increase, increasing the cost of social play. I predict that social play among polar bears is an energetically costly event, therefore, the temperature of thermal windows will be higher directly after play compared to the temperature before play.

To determine energy expenditure during exercise, studies are typically done *in situ* under controlled settings allowing for various metabolic measurements. Currently, we are not able to take metabolic measurements (heart rate, breathing rate, etc.) to quantitatively measure energy expenditure of polar bears in care at Assiniboine Park Zoo (APZ). Therefore, my study will act as a baseline study to determine whether surface temperature changes, within thermal windows, associated with play can be detected through IRT.

Methods

According to the black body radiation law, any object above absolute zero radiates energy transported in the form of electromagnetic waves (Loudon 2000). Energy radiated in the range of 0.39 µm to 0.77 µm is visible by the human eye, but infrared radiation of wavelengths from 2 µm to 15 µm are undetectable. Infrared thermography (IRT) is the use of an infrared thermal imaging camera, allowing for the detection of infrared radiation by measuring the emissivity of surfaces. The lens of the camera focuses the emitted radiation onto a detector that converts the electrical response signal to a digital photo with various colours representing temperature levels of the subject’s surface, called a thermogram. IRT allows us to visualize the surface temperature of an object and estimate the quantity of emitted infrared radiation.

Data Collection

Eye thermograph measurements

Thermographic videos of polar bear eyes were opportunistically recorded during veterinary procedures. While polar bears were immobilized in sternal recumbency position, we took infrared video with a forward-looking infrared (FLIR 4050SC, FLIR Systems Inc., USA) camera from 1 m away, with the eye held open. Previous studies using IRT typically film from approximately 1-3 m away from the subject to get the best-focused thermograms (Dunbar et al. 2009, Faye et al. 2016). The video was taken for a minimum of 10 seconds to capture at least 100 frames for analysis. Internal temperature was determined by rectal thermometer by veterinary staff. Thermographic video of the eye and internal temperature were taken from 20 to 160 minutes of each other.

Social play thermographic measurements

A FLIR camera was used to capture bouts of polar bear play at APZ between October 1 and November 30, 2018. From a rooftop vantage point, I filmed polar bear play bouts from beginning to end. The beginning of a play bout was defined as the start time of the first contact between two polar bears, which included facial contact or paw to body contact. I noted the identity of each polar bear, duration of play and distance from the camera. The end of the play bout was defined as no contact for one minute or more (Byosiere et al. 2016). If the two play partners began playing again after one minute, it was considered a new play bout (Byosiere et al. 2016).

Measures of ambient conditions

Overall atmospheric composition and temperature alter the surface temperature reading of thermograms, as IRT picks up on the infrared radiation emitted by gasses and particles in the lower atmosphere (Minkina & Dudzik 2009, Kuenzer & Dech 2013). I collected measurements of relative humidity, ambient temperature, and distance to the subject, as they are known to influence IRT readings. Environmental conditions can greatly alter surface temperature readings. A critical distance has not been set, although distances from 1-20 m are recommended (Fate et al.

2016). Distance from the subject can affect the temperature reading of thermograms because the surface area of the object within a pixel directly depends on the distance between the object and the sensor (Faye et al. 2016). Increasing the distance from the thermal imaging camera causes an under-estimation of temperature and a spatial homogenization of temperatures from surrounding objects, including the emission of the surroundings reflected by the object and the emission of the atmosphere, especially in outdoor environments (Faye et al. 2016).

IRT studies typically focus on the effects of ambient temperature and relative humidity on surface temperature detection of concrete surfaces (Tran et al. 2017). Studies on concrete (the building material of cement and aggregates) are good example of the issues faced for using IRT in biological studies. With an increase in relative humidity, an increase in convective heat transfer from concrete surfaces occurs (Tran et al. 2017). When emissivity (the ratio of energy emitted from an object and a black body or perfect emitter) and a perfect emitter, distance, and reflected object temperature are corrected for and held constant, detected surface temperature error falls within ± 0.5ºC (Aubrecht et al. 2016). Measures of ambient temperature, relative humidity and distance were therefore used to correct for surface temperature readings in Research IR software (FLIR Systems, Inc. 2015).

Ambient temperature and relative humidity were recorded using a DROP D2 Wireless temperature and humidity data logger (Kestrel Instruments, Boothwyn, PA) or Winnipeg James Armstrong Richardson International Airport weather station data (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html) located 8 km away.

Data Analysis

Eye thermogram analysis

Using Research IR software (FLIR Systems, Inc. 2015), a region of interest (ROI) was placed around the eye (Figure 3.1) and the maximum temperature inside the ROI was plotted for the video. I used maximum temperature instead of mean temperature because the mean temperature would be averaged over a larger number of pixels for distant bears. I assessed the stability in temperature over each video by calculating the cumulative mean of the maximum eye temperatures. Although I collected 100 frames of video, I found that maximum temperature was recorded and held stable over 30 frames. I used a Pearson correlation test and a paired sample t-test to determine any statistical difference between thermographic eye temperature and internal temperature.

Some types of anesthetic drugs are known to alter body temperature (White et al. 1996, Bindu et al. 2017). Due to the nature of veterinary procedures, IRT measurements and internal measurements were not simultaneous. Therefore, I ran a generalized linear model with length of time since the anesthetic drug was administered as the predictor variable and difference in temperature measured with IRT and thermometer as the response variable, with the identity of each bear as a random effect. All statistical analysis was conducted in R (R Core Team 2017).

Social play thermogram analysis

Research IR software (FLIR Systems, Inc. 2015) was used to analyze each infrared video of play, with emissivity set to 0.98 based on the ratio of energy emitted from the pelage of Arctic fauna and a perfect emitter (Hamell 1956). The first frame in which the subject faces towards the camera was used to calculate the initial temperature. At this frame, an ROI was placed around the eye. The maximum temperature within the ROI was recorded. The process was repeated for the other play partner. The process was then repeated at the end of the play bout to determine the final temperature of both play partners. The play bout was considered complete when social play stopped for one minute or more. Change in temperature was calculated by subtracting the maximum temperature at the end of the bout from the maximum temperature at the beginning of the bout.

To test the hypothesis that the duration of social play will influence the magnitude of change in surface temperature from the beginning to the end of the play bout, I used a linear mixed effect model using the lmer function in the lme4 package in R (Bates et al. 2014) with log duration as the predictor variable and the change in surface temperature as the response variable. Identity of each bear was included as a random effect.

Results

The mean difference of 2.68 ± 0.41ºC between thermographic eye temperature (n = 19) and internal temperature (n = 19) was statistically significant (95% CI, $T_{18} = -6.54$, $p \leq 0.001$; Figure 3.2).There was a positive influence of the increase in the length of time since the anesthetic drug was administered on the difference in the eye and internal temperature (n = 19; $R^2 = 0.72$, $T_{12} = 2.30$, p = 0.04; Figure 3.3).

The standard error of the mean difference in eye temperature before and after play increased at distances greater than 30 m (table 3.1). Therefore, I truncated the data to include only surface temperatures from 10 m to 30 m away to remove unreliable measurements at distances greater than 30 m. I used a paired t-test to determine if the surface temperature of the eye of each bear differs before and after play (n=46). I found a significant increase of 1.34ºC ± 0.43ºC (95% CI, T45 = 3.14, p = 0.002) in mean surface temperature after play (figure 3.4).

The duration of social play was on average 3 minutes 9 seconds and ranged from 10 seconds to 12 minutes and 48 seconds in length. I found no significant effect of the duration of social play on the change in surface temperature from the beginning to end of a play bout (n = 72; $R^2 = 0.012$, $T_{70} = 0.957$, $p = 0.342$; Figure 3.5).

Discussion

I found that polar bear surface temperature increases an average of 1.34ºC ± 0.43ºC after engaging in social play. An increase in surface temperature as a result of physical exercise indicates that heat in the form of kinetic energy is being generated and dissipated as infrared radiation (Knizkova et al. 2007). Thus, this study displays the magnitude that surface temperature increases after social play, indicating that there is an energetic cost associated with social play behaviour that can be measured using IRT.

I predicted that the eye would be an indication of internal body temperature, but I found a significant difference between infrared eye temperature and internal body temperature. Previous studies have found a correlation between eye temperature measured with IRT and internal temperature (Dunbar et al. 2009, Johnson et al. 2011, Magnani et al. 2011, Warriss et al. 2006, Soerensen & Pedersen 2015), suggesting that the eye would be the best area of the body to measure temperature using IRT. The standard deviation of polar bear eye temperature in my study was 1.46ºC, whereas the standard deviation of internal temperature was 0.87ºC. Similar to the study by Church et al. (2013), the thermographic eye temperature of polar bears in my study was 2.68ºC ± 0.41ºC lower than the internal temperature.

The main determinate of temperature accuracy of IRT is the distance of the subject to the camera (Johnson et al. 2011, Church et al. 2013). Typically, studies using IRT measure surface temperature from 1-10m away (Johnson et al. 2011, Church et al. 2013). Church et al. (2013) found that from 0.5 to 3m, the IRT temperature readings decreased up to 2ºC, and the least variation occurred at 1m in distance. In my study, distances greater than 30 m from the infrared camera resulted in a larger standard error of the mean surface temperature change after play. When using thermography in the field, a higher resolution camera is needed to increase the reliability of temperature measurements at larger distances. Additionally, the distance of the object needs to be accounted for in IR software, as the distance setting is used to account for infrared radiation from surrounding objects and the atmosphere (Church et al. 2013).

Previous studies that have found the eye to be an accurate thermal window in mammals typically do not measure the eye temperature while the study subject is sedated (Zinn et al. 1985, Heath et al. 2001, Dunbar et al. 2009, Johnson et al. 2011, Lu et al. 2018). After general anesthesia is administered, body temperature declines over time as core body heat redistributes to the surface of the skin and is lost through radiation (Diaz & Becker 2010). Body temperature drops of 1-2ºC are common while under anesthesia in humans (Diaz & Becker 2010). The length of time from sedation to IRT eye measurement in my study was not held constant, as these measurements were taken opportunistically, and the veterinary procedures were top priority. I found that the longer the polar bear was sedated before I took eye temperature measurements, the greater the discrepancy in thermographic eye temperature to internal temperature (Figure 3.3). If possible, eye measurements should be taken as soon as possible after anesthesia to allow for the most accurate measurements. It is possible that anesthetic drugs are a contributing factor to the discrepancy between IRT and internal temperature found in this study.

Most studies that compare the surface temperature of the eye to internal temperature are based on terrestrial animals who do not reside in Arctic environments (Zinn et al. 1985, Heath et al. 2001, Dunbar et al. 2009, Johnson et al. 2011, Lu et al. 2018). These studies typically find no difference in temperature measured by IRT and internal temperature measured by a thermometer (Dunbar et al. 2009, Johnson et al. 2011). The difference in the eye and internal temperature I found in this study, could be due to adaptations of Arctic mammals living in temperature extremes (Denhardt et al. 1998, Ringvold et al. 2003, Hogg et al. 2011).

Arctic regions have high levels of ultraviolet radiation that is reflected and scattered on snow and ice (Weatherhead et al. 2007). Exposure to significant levels of ultraviolet radiation can result in photokeratitis or snow blindness, damaging the cornea and retina (Hemmingsen & Douglas 1970). Arctic mammals have specific adaptations to eliminate the risk of snow blindness (Ringvold et al. 2003). Reindeer (*Rangifer tarandus*) have high concentrations of ascorbate, an ultraviolet radiation absorber, in the epithelium of the eye (Ringvold 1980, Ringvold et al. 2003). The thickness of the epithelium has also adapted to the degree of radiation to protect the basal cell layer (Ringvold et al. 2003). Ringvold et al. (2003) suggest that ultraviolet radiation causes cells to retain a high ascorbate concentration which acts as sunglasses to protect against radiation.

Like reindeer, polar bears are exposed to high levels of ultraviolet radiation in the Arctic. Further research is needed to determine if polar bears also have high concentrations of ascorbate and thick epitheliums to protect themselves against radiation. Adaptations to an Arctic environment may be why my study shows discrepancies between infrared eye temperature and internal temperature, contrary to previous studies on the infrared eye temperature of mammals living in temperate environments (Dunbar et al. 2009, Johnson et al. 2011, Magnani et al. 2011, Warriss et al. 2006, Soerensen & Pedersen 2015). The eye of a polar bear might not be the best place to measure heat dissipation during activity, resulting in a difference in the surface temperature of the eye and internal temperature in this study. Moving forward, studies should focus on other possible polar bear thermal windows such as under the arms, pads of the foot or over the hip (Best 1982).

Despite the perceived benefits associated with social play, the consequences of polar bear social play include energy expenditure and the risk of overheating. In humans, heat strain can occur at ambient temperatures of 30-40ºC (Latzka et al. 1998). Polar bears carry more blubber and insulation than humans and could experience heat stress at even lower ambient temperatures (Best 1982). At ambient temperatures of 5ºC or higher, polar bears surpass their thermoneutral zone and are at a greater risk of overheating with exercise (Best 1982). When social play continues outside of the thermoneutral zone, metabolic processes and evaporative cooling increase to regulate a stable core temperature, further increasing the use of critical energy stores (Kingma et al. 2014).

Polar bears in care at Assiniboine Park Zoo continued to engage in social play in ambient temperatures above 5ºC. However, polar bear social play in the wild (chapter two of this thesis) was not observed at ambient temperatures above 5ºC. Although polar bears in care exhibit similar natural behaviours as their wild counterparts, the stressors they experience differ from wild polar bears. Polar bears in care are fed daily, whereas polar bears in the western Hudson Bay region experience a fasting period during the time social play is observed (Latour 1981). The risk of heat stress above temperatures of 5ºC may outweigh the benefits that polar bears gain from social play. Polar bears in care can engage in more energetically costly activities, as they are not experiencing any food insecurity compared to wild polar bears.

Considering that polar bears will engage in social play more than once per day in the wild (Latour 1981; this study), they are likely expending significant energy during a resource-limited season. There may be a threshold to the amount of energy that can be allocated toward play, and an increase in surface temperature of 1.34ºC ± 0.43ºC may be a signal for polar bears to end the bout and cool off before continuing to play. Additionally, there may be a limit to the duration of play depending on the ambient temperature. To determine the threshold, energy budget analyses should be conducted to determine if there are correlations between daily energy used for play, ambient temperature and surface temperature increase.

Studies thus far have not measured the energetic output of social play among polar bears, but Whiteman et al. (2015) suggested that heat-stress induced from walking onshore is rare. Whiteman et al. (2015) found that wild polar bears rarely walked at speeds of ≥ 1.6 m/s, thus reducing the risk of heat stress. However, social play presumably has greater thermoregulatory stressors than walking, especially at ambient temperatures ≥ 5ºC. The benefits associated with polar bear social play must outweigh the energetic cost and risk of heat stress, or polar bears have not reached the critical threshold of energetic loss through social play.

Overall, IRT can measure heat loss through evaporative cooling during and after exercise, indicating that polar bears are expending kinetic energy during social play. Small discrepancies between internal temperature measurements and IRT measurements are common (Church et al. 2013). The mean difference between the two measurements (2.68ºC in the case of my study) can be used to correct IRT temperature readings in the field. The discrepancies I found between eye temperature measured using IRT and the internal temperature of handled bears, can be used to correct the readings of surface temperature measured during activity. For example, the true change in temperature may be corrected by adding the mean difference of 2.68ºC between surface eye temperature and internal temperature to the eye temperature measured in the field.

As previous studies have suggested, thermographic measurements of the eye can be an indication of internal body temperature but should not be the sole method used (Dunbar et al. 2009, Valera et al. 2012, Travain et al. 2014, George et al. 2014, Zanghi 2016). IRT is beneficial in that it is a non-invasive and quick way to obtain continual temperature readings. IRT is especially useful in measuring the temperature of large, dangerous animals that would otherwise need to be sedated and instrumented to measure their internal temperature. My study acts as a baseline study to investigate the use of IRT in measuring surface temperature as a proxy for energy expenditure. IRT may be a useful tool in measuring the surface temperature of polar bears during activity. Polar bear social play is an energetically costly event that continues to occur during a resource-limited time (Latour 1981; this study) and additional research is needed to fully understand its fitness benefit. IRT has the potential to accomplish this task and to be a non-invasive tool to accurately measure temperature and heat dissipation in the study of energetics in wild species.

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Table 3.1. The mean surface temperature change after social play at distances from 10 to 64 meters away from the infrared camera.

Distance (m)	**Mean surface temperature change (ºC)**	**Standard error**	**n**
10 to 20	1.1	0.44	30
21 to 31	3.51	0.39	16
32 to 42	-1.63	0.86	5
43 to 53	-0.34	0.64	14
54 to 64	1.1	1.25	6

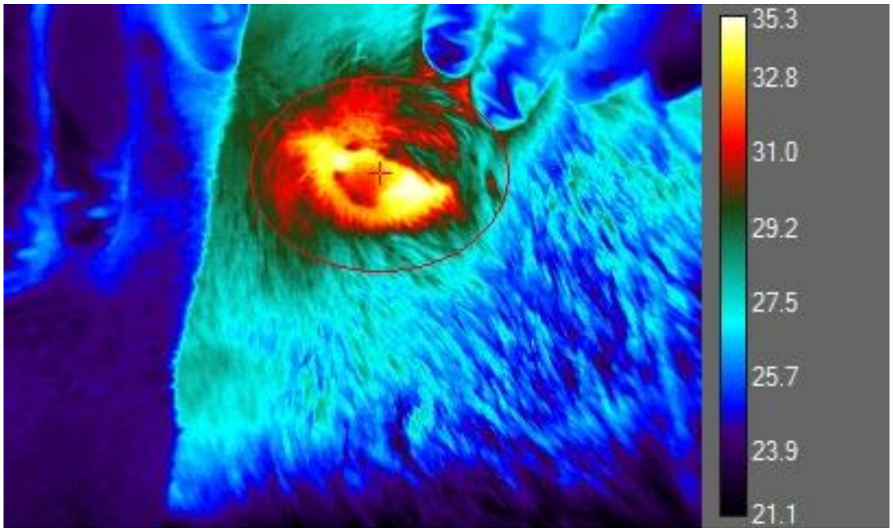

Figure 3.1. A region of interest (ROI) placed around the entirety of the eye of a polar bear.

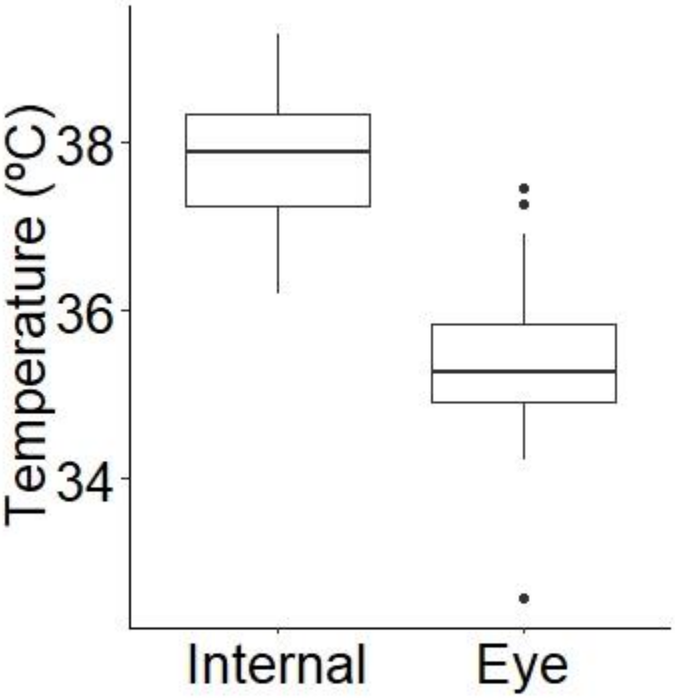

Figure 3.2. A difference of 2.68ºC ±0.41ºC (p=<0.001) between thermographic eye temperature and internal temperature measured on sedated polar bears (n = 19).

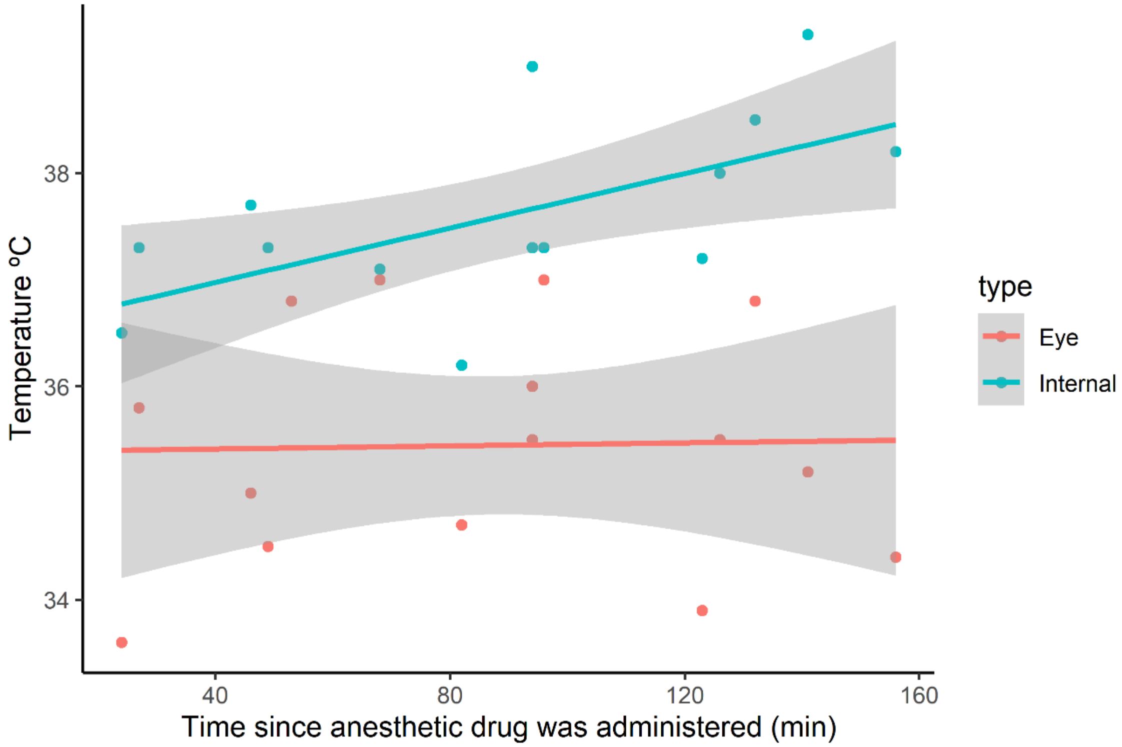

Figure 3.3. The relationship between the length of time since the anesthetic drug was administered and temperature measurements (internal and thermographic eye temperature) of polar bears. A positive relationship between the length of time since the anesthetic drug was administered and the difference in internal and thermographic eye measurements (n = 15, p=0.04).

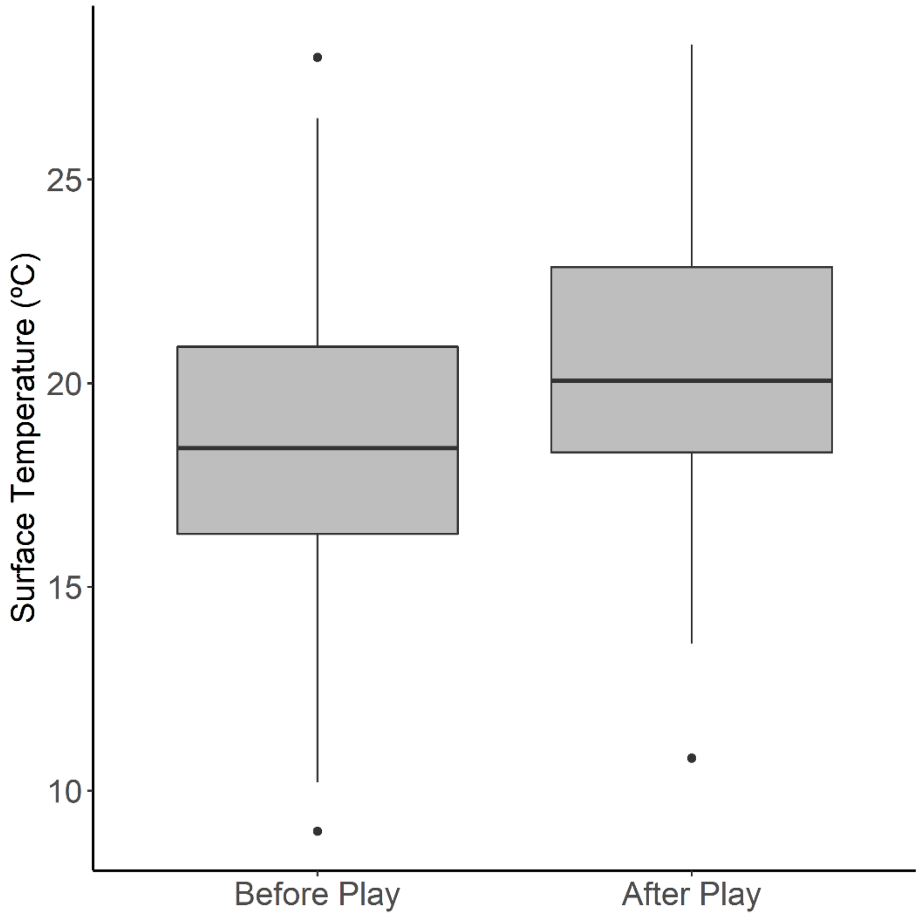

Figure 3.4. Thermographic surface temperature of the eye before (n = 46) and after (n = 46) polar bear social play (p=0.002).

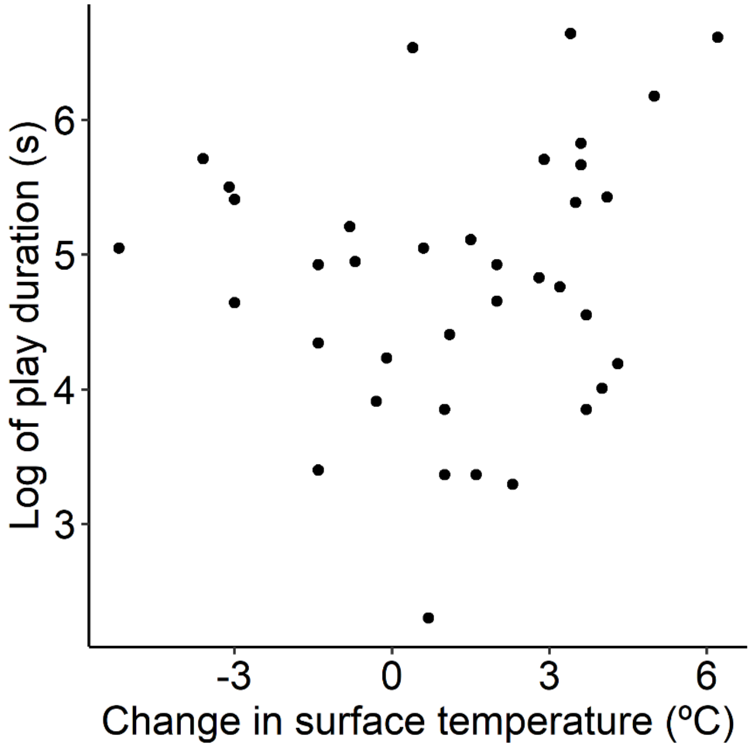

Figure 3.5. The relationship between the change in the surface temperature of polar bear eyes before and after a bout of social play and the duration of the play bout (log-transformed) ($p = 0.34$).

Chapter 4 Thesis Conclusion

Adult polar bear social play is an anomaly, as the hypotheses explaining the occurrence of social play in mammals focus on juvenile play and periods of abundant resources (Burghardt 2001, 2005, Graham & Burghardt 2010). Chapter two of this thesis showed that adult polar bear social play occurs during a resource-limited time in Western Hudson Bay. Despite my prediction that occurrences of polar bear social play per day would decrease as the fasting period lengthened, the frequency of polar bear social play increased. Factors such as sampling effort, social congregation as ice forms and ambient temperature could influence this frequency, however, this result shows that social play occurred among adults in an increasingly resource limited time.

I did not have the appropriate data to analyze each of the proposed benefits associated with social play in this thesis. However, I speculate that the fine-tuning-through-repetition-and-training and the motor training hypothesis may be the best hypotheses to explain the value of adult social play. Adults can benefit from exercise and continuing to fine-tune repeated movements used in competition. Additionally, continuing to train-for-the-unexpected into adulthood must be beneficial in avoiding or escaping harmful situations. Adult brains and muscles have completely developed; however, adults may benefit from continuing to develop muscle mass, also supporting the motor-training hypothesis.

The benefits of play, whether immediate or delayed, vary greatly with the sex and age of the players (Palagi 2018). The age and sex-class of polar bears in my study may have a role in supporting the fine-tuning-through-repetition-and-training and the training-for-the-unexpected hypothesis. The long-term dataset used in this study consisted of play observations of adult and sub-adult male polar bears. Male polar bears reach sexual maturity at approximately five years old, however, they reach asymptotic body mass at 13 years old (Derocher et al. 2005). A male polar bear’s first reproductive event may be delayed well beyond age-at-maturity, and older males typically have a competitive advantage over younger males for access to receptive females (Ramsay & Stirling 1986). Sub-adult and adult male bears may continue to play to train for competition later in their adult life. Behaviours used in polar bear social play are similar to those used during competitive events, excluding the risk of severe injury (Latour 1981). Social play may be beneficial in fine-tuning the muscles used in competition to become stronger competitors (Nowicki & Armitage 1979). Play can expose polar bears to scenarios in which they can practice regaining control after falling or being overtaken by a competitor. The delayed benefits of fine-tuning-through-repetition-and-training and training-for-the-unexpected outweigh the energetic demands of play in the years sampled in this study.

As social play continues into the sub-adult and adult life stages, polar bear social systems may demand more refined socio-cognitive skill to assess competitive abilities (Smaldino et al. 2019). In species with pronounced and well-established dominance hierarchies, social play is less apparent in the adult life stage, as formal dominance displays are enough to maintain social hierarchy (Smaldino et al. 2019). Polar bears are considered a solitary species and do not form social groups outside of the formation of male groups during the ice-free season and family groups (Nowak 1999), indicating a less pronounced, or absent, social hierarchy. Polar bears may use social play to assess the strength and skill level of their play partner, as they may compete against each other in the future. Overall, the social cohesion hypothesis is the least likely hypothesis to explain polar bear social play, as polar bears are solitary for most of the year (Nowak 1999).

To assess the benefits of adult polar bear social play, future studies should focus on tracking individual bears through time. Tracking individuals would allow us to find whether bears who were in better body condition during the ice-free season or bears who played more often, are more successful in the feeding and mating season. Thus, supporting the hypotheses which indicate that play is a form of training. Tracking individuals would also assess whether dominance hierarchies are formed through play. If dominance hierarchies are formed through play, polar bears who played in a bout with a larger bear should be submissive to the larger bear in the hunting and mating season.

Although the benefits of social play are largely unknown, polar bears continue to exert energy towards play as body condition declines. In chapter 3, I assessed whether infrared thermography (IRT) could be a useful tool to measure temperature increases after bouts of social play, to then infer energy use. Infrared thermography proved to be a useful tool in measuring surface temperature increases after polar bear social play. Average increases of 1.3ºC suggest that social play is energetically costly – certainly more so than resting or walking – and although direct energetic expenditure was not measured, I conclude that IRT could be a valuable tool to understand this specialized behaviour.

Several validation steps need to be resolved before IRT temperature measurements can be used in the field. Factors such as distance from the camera, relative humidity and ambient temperature need to be accounted for to obtain the most accurate surface temperature measurements. As well, understanding the relationship between surface temperature and energetic expenditure will be critical and perhaps a valuable role for polar bears in human care. Nonetheless, IRT is a useful method to measure surface temperature changes and can be used non-invasively in the field.

Polar bear social play is a unique behavioural adaptation that is energetically costly, but which has been maintained in the Western Hudson Bay subpopulation. In the face of climate change and overall declines in polar bear body condition, it is uncertain if this trait will persist, or if the cost to the animals will become too high and it will be lost. If social play is maintained because it serves an important fitness function, there is uncertainty about where the resources to maintain this behaviour will come from for individual bears. Nonetheless, an important area of research will be to monitor and understand social play behaviour as environments change. Is social play the canary in the coal mine, in that when or if it disappears will signify a major change in the ecosystem?

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