JZAR JOURNAL OF ZOO AND AQUARIUM RESEARCH
www.jzar.org

JZAR Research article

OPEN ACCESS

Research article

Reproductive trends of captive polar bears in North American zoos: a historical analysis

E. Curry[1*], S. Safayi[2], R. Meyerson[3] and T.L. Roth[1]

[1]*Center for Conservation and Research of Endangered Wildlife (CREW), Cincinnati Zoo and Botanical Garden, 3400 Vine St., Cincinnati, OH, 45220, USA*
[2]*Department of Veterinary Clinical Sciences, College of Veterinary Medicine, Iowa State University, 1600 S. 16th Street, Ames, Iowa, 50011, USA*
[3]*Toledo Zoo, 2 Hippo Way, Toledo, OH, 43609, USA*
**Correspondence: erin.curry@cincinnatizoo.org*

Keywords:
captive breeding, endangered species, reproduction, studbook, *Ursus maritimus*

Article history:
Received: 31 March 2015
Accepted: 9 July 2015
Published online: 23 July 2015

Abstract

Despite the fact that nearly all captive polar bears (*Ursus maritimus*) are recommended for breeding, very few cubs are born each year and the rate of neonatal mortality is high. Animal caretakers tend to rely on anecdotal reports regarding reproductive events, such as timing of parturition, litter size and cub survival. To objectively document trends in polar bear reproduction during their tenure in North American zoos, this analysis utilised 99 years of records in the Polar Bear Studbook to characterise patterns in reproduction and cub survival. Factors evaluated included latitude, year of birth, parental demographics (age, origin (captive-born or wild-caught) and litter size), sex, survival, litter size and litter order. Between 1912 and 2010, 697 individuals (456 litters) were born at latitudes ranging from 25.90 to 52.94 ºN. The average number of litters produced per year was 4.60 ± 0.51 with a range of zero to 18. The polar bear birth season lasted 106 days with mean and median birth dates of 29 November. Litter size was unaffected by any of the variables analysed: 52.7% of litters were singletons, 44.9% were twins and 2.4% were triplets. Older sires produced a higher proportion of male offspring than younger sires ($P < 0.05$). More than half of all individuals died prior to 30 days of age and 30.4% reached adulthood (four years). Cubs of captive-born parents lived longer than those of wild-caught parents ($P < 0.05$). Individuals born in litters of multiples were more likely to die as neonates than those born as singletons ($P < 0.01$) and individuals born to multiparous dams lived longer than those born to primiparous dams ($P < 0.02$). This study represents the largest analysis of captive polar bear reproduction conducted to date and may serve as a reference for individuals involved in the management and care of captive polar bears.

Introduction

Despite their worldwide popularity in zoos and aquaria, little is known about the reproductive processes of the polar bear (*Ursus maritimus*). In North America, polar bear exhibition dates back to the first wild-caught individual maintained at the Philadelphia Zoo in 1876. In 1912, the first captive-bred cub was produced at the National Zoo in Washington, D.C., but it was not until seven years later that a captive-born cub survived to adulthood after being born at the Milwaukee County Zoo (Meyerson 2010). From 1950 to 1980, the numbers of polar bear cubs born in North American zoos increased and the captive population reached its peak of 229 individuals in 1975 (Fig. 1A) as a result of both increased births and wild imports. However, due to limited space and the desire to provide larger, naturalistic exhibits, the demand for polar bears declined. Animal managers were advised against breeding, so many individuals were sterilised or contracepted, causing the population numbers to wane.

Over the past decade, the zoo polar bear population has been decreasing by approximately 4% each year, while the demand for exhibit bears is increasing but can no longer be met (Meyerson and Long 2010; Meyerson and Thompson 2012). Concurrently, threats facing wild polar bears gained national and international attention leading to the 2008 official listing of polar bears as a species threatened with extinction by the U.S. Fish & Wildlife Service (U.S. Fish & Wildlife Service Endangered Species Act 2013) and their 2006 classification as Vulnerable by the IUCN Redlist. Despite this added measure of protection, the future of wild polar bears is uncertain given their dependence on sea ice and its imminent disappearance in a warming climate (Stirling et al. 1999; Molnár et al. 2011).

The need for a robust captive population is three-fold: 1) zoo visitors enjoy seeing these magnificent, charismatic animals; 2) zoo staff can be more effective in delivering their message about climate change using polar bears as the flagship species; and 3) captive individuals can be utilised as a model to study the unique physiology of a species difficult to study *in situ*.

In 2000, the first Population Management Plan (PMP) for captive North American polar bears was completed. Three years later, the population was upgraded to a Species Survival Plan (SSP) with the intent of developing a sustainable population for zoo exhibition (Meyerson and Long 2008). Unfortunately, by the time the SSP was officially established, the captive polar bear population had decreased to potentially unsustainable numbers without the addition of individuals from other countries or wild imports. In an effort to reverse this trend, the SSP encouraged breeding attempts by participating zoos and, by 2008, recommended that every potentially reproductive female be mated (Meyerson and Long 2008). Regardless of this considerable effort, the population is probably too small and reproductive success too low to return to previous peak numbers (Meyerson and Thompson 2012).

The overall goal of this analysis was to characterise patterns in reproduction and cub survival of polar bears during their tenure in North American zoos as a reference for individuals involved in the management and care of the captive polar bear population. Specifically, we were interested in: 1) determining if reproductive success, defined as the number of cubs produced relative to the total number of captive individuals, is declining; 2) defining the cubbing season of polar bears in captivity so that caretakers can better prepare for impending births; 3) evaluating the effects of latitude on cub births, litter size and survival; and 4) determining the effects of parental age, parental origin, or litter order on litter size and survival.

It was not the purpose of this analysis to create a predictive model of population growth or survival of captive-born polar bears, nor was it to establish cause-and-effect relationships of factors correlated with reproduction and cub survival. Efforts were made to focus on outcomes that are not affected by management or breeding recommendations, but animals living in captivity are inherently subjected to human interference not reflected in zoological records. Identifying factors that may affect timing of parturition, litter size and cub survival may aid in institutional management recommendations, thereby facilitating the development of a self-sustaining captive population.

Methods

The dataset was produced by querying the Polar Bear Studbook (Meyerson 2010) events for 'birth' and filtering for captive-born specimens. Only individuals housed at institutions located in North America were included. A spreadsheet was generated which listed each individual born in captivity as an observation. Fields associated with each observation included mined and calculated data such as date of birth, location and latitude of birth, litter size, sex, parental demographics (age, origin, litter size) and age at death. A second worksheet was created that managed each litter, rather than the individual, as an observation.

Date of birth

Only birthdates that were not defined as estimated were included in analyses. If the year was known, but the day or month was estimated, the individual was included in an analysis involving year, but not in a test involving day of birth within birth season. To define the birth season, the year of birth was ignored and all birthdates were sorted ordinally from the beginning of the birth season through the latest recorded birthing date. To determine if individual females have cubs at the same time each year, the ranges of litter birthdates were calculated for multiparous females that produced six or more litters. Inter-birth intervals were determined by calculating the length of time between birthing dates of multiparous females and then determining the mean.

Litters and dam parity

Because certain analyses were performed more appropriately on a birthing event rather than an individual, a litter dataset was created. Individuals were grouped together as a litter if they were born to the same dam during the same birth season. Litters and individuals were classified as those from either primiparous or multiparous dams. Additionally, litter order was determined by sorting based on dam identification, then litter birthdate.

Parental age

When available, ages of dam or sire were calculated by subtracting the offspring's date of birth from the dam or sire's date of birth. Parental ages were divided into three groups: young (4.00–10.99 years); mature (11.00–17.99) and senior (18.00–26.99). Because breeding dates/day of conception are not recorded in the studbook, parental ages represent age at the time of birthing, not at the time of conception.

Survival

To evaluate cub survival in captivity, four categories were created. An individual was defined as a stillborn if listed by the studbook as living 0.00 years. Neonatal deaths encompassed all live births that died prior to 30 days of age (< 0.08 years). Individuals dying between 30 days and 4.00 years were classified as juvenile deaths. Adulthood was defined as reaching 4.00 years of age.

Analyses

Although a multivariate analysis would be the preferred method to determine covariance among factors, a complete set of variables was available only for 91 litters (20.0%) and 132 individuals (18.9%). In addition to limiting the dataset to cubs born of captive-born parents (for which more information was available), the individuals per group did not yield adequate statistical power for valid interpretation of results.

Statistical analyses were performed using JMP (version 10.0; SAS Institute, Inc., Cary, NC) at a 95% confidence level. To resolve differences between and among groups, Student's t-tests or one-way analysis of variance (ANOVA) were utilised. If ANOVA revealed a significant difference ($P < 0.05$), multiple comparisons of means were performed using the Tukey-Kramer method. Chi square analysis was used to identify differences in proportions of categorical variables. In most instances, litters of triplets were eliminated from litter size analyses due to small (< 5) number of triplet litters per category. Correlation analyses were performed to determine the relationship between the following: the number of litters produced and the number of individuals in captivity; the year and the date of parturition; latitude and day of birth; day of birth within birth season; and age at death. All values are presented as mean ± standard error of the mean (SEM) and all ages are reported in years unless otherwise specified.

Results

Overview

Between 1912 and 2010, a total of 697 individual polar bears born at 56 institutions were analysed: 246 were females, 239 males, and 212 of unknown or unrecorded sex. Six hundred and eighty-seven individuals were assigned into 456 litters based on their parental information and date of birth. The mean number of litters produced in captivity per year was 4.60 ± 0.51, with a median of two, a mode of one, and a range from zero to 18 (Fig. 1B).

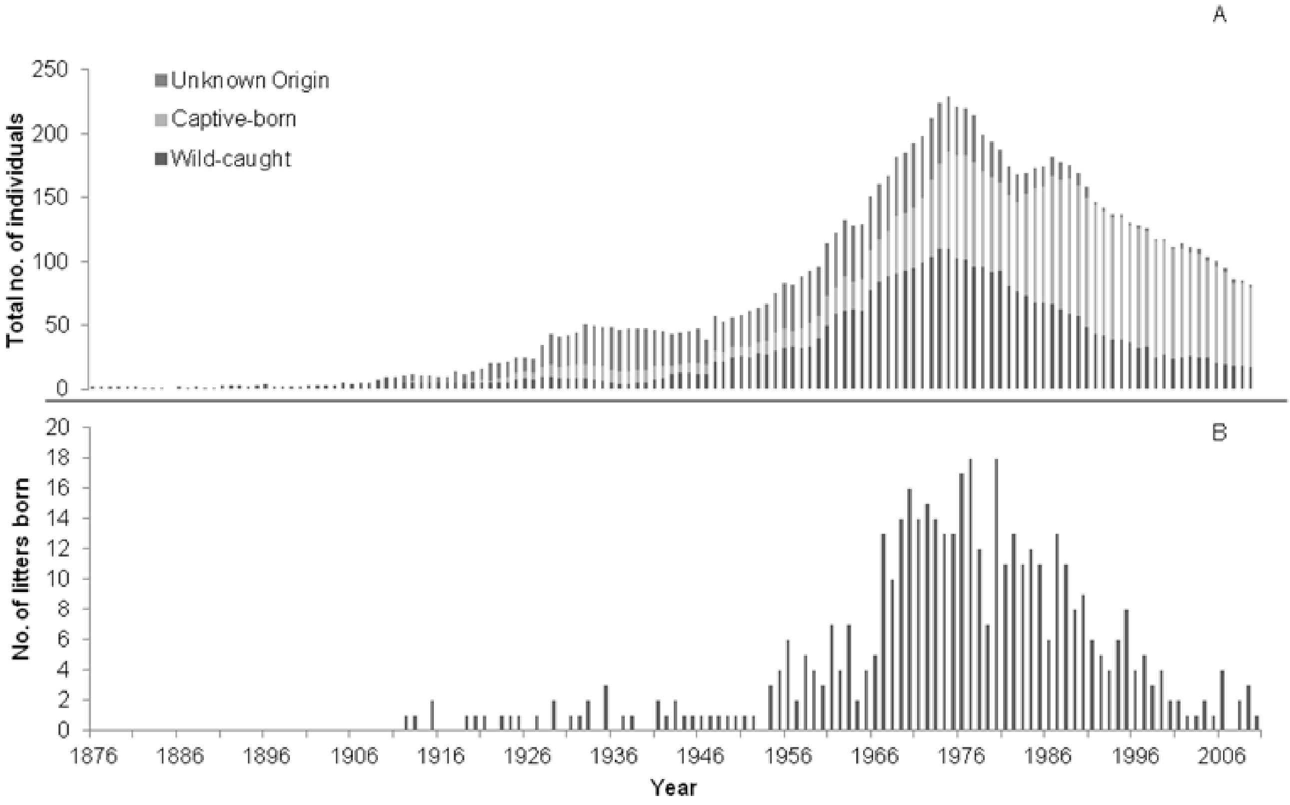

Figure 1. Total number of polar bears living in North American zoos from 1876 to 2010 (Panel A) and the number of litters born in captivity (B) per year.

The latitudes of births ranged from 25.90 to 52.94°N. Overall, the number of litters born per year in captivity was highly correlated with the total number of individuals in captivity (R^2 = 0.891).

Parental demographics

Exact ages of dams and sires were available for 126 and 137 litters, respectively (Table 1; Fig. 2). The mean age at first parturition for a dam was 9.26 ± 0.55 years and a male sired cubs as young as 4.95 and as old as 25.99 years with a median age of 11.92 years. Females had cubs from 4.05 to 26.11 years of age with a median age of 12.77 years. A female produced a maximum of 12 litters and a male sired up to 32 in her/his lifetime in captivity. The parents of the litters born in captivity were both wild-caught and captive-born (Table 1). The mean number of litters produced was the same for captive-born versus wild-caught dams, but wild-caught males sired more litters than captive-born males (P < 0.05). The average inter-birth interval for dams was 2.51 ± 0.13 years with a range of 314 days to 21.09 years.

Birth season

Complete birth-date information was recorded for 446 litters. Based on Grubb's analysis, three litters encompassing six individuals were outliers (26 September, 16 February and 29 March) and were excluded from the birth season analysis. Polar bear birth season in captivity exhibited a normal distribution and was 106 days long, from 11 October through 24 January (Fig. 3). The mean and median litter birth dates were both 29 November while the mode was 23 November. The majority of births (73.8%) occurred between 13 November and 15 December and 95.0% occurred during the months of November and December. Parental age, parental origin, litter size, and litter order did not affect the day of parturition. Correlation analyses failed to show a relationship between year and parturition date (R^2 = 0.001; Fig. 4) or between latitude and parturition date (R^2 = 0.009; Fig. 5). To determine if an individual female had cubs at the same time each year, the litter birthdates were examined for 23 multiparous females that produced six or more litters. The average range of parturition dates for an

Table 1. Parental information for polar bear cubs born in captivity.

	Mean no. of litters(± SEM)	Average age at parturition (± SEM)	Age range	Origin	N	No. of litters	Litters per individual
Dam	3.53 ± 0.25	12.90 ± 0.46	4.05–26.11	Wild	53	209	3.72 ± 0.34
				Captive	44	123	3.05 ± 0.36
Sire	4.56 ± 0.48	12.77 ± 0.43	4.95–25.99	Wild	38	236	6.21 ± 1.04*
				Captive	40	139	3.48 ± 0.36**

*, **Denotes differences in number of litters produced between wild-caught and captive-born sires (P < 0.05).

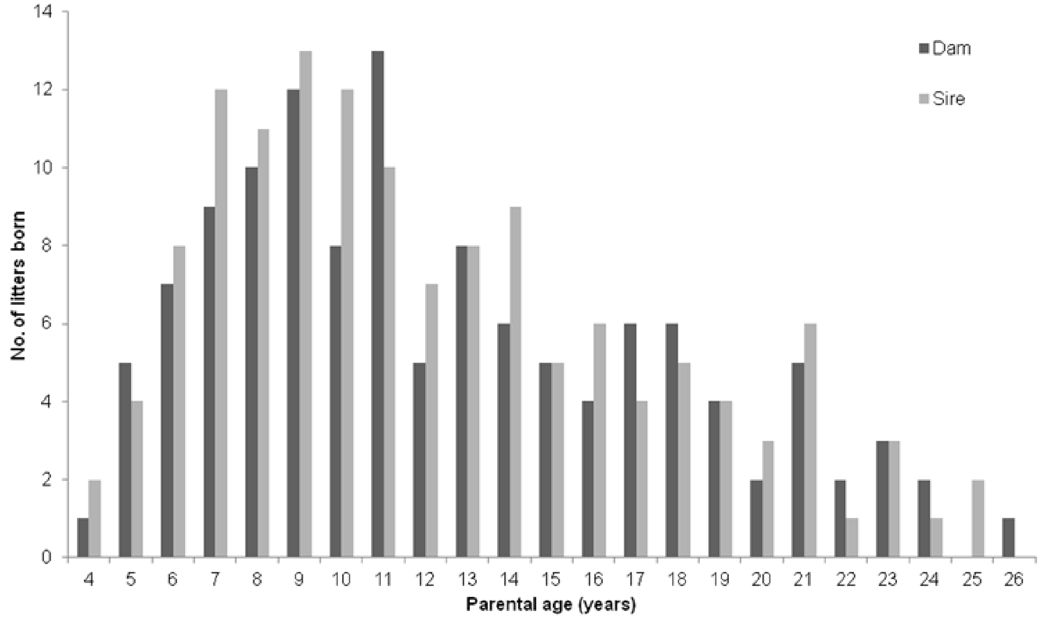

Figure 2. Age distribution of dams and sires at time of litter birth.

individual dam was 34.78 ± 3.58 days, with a median of 35, and range of 7–76 days among dams. These data suggest that the parturition date of a pregnant female cannot be predicted based on her previous parturition dates.

Litter size

Litter information was determined for 687 individuals, which were assigned into 456 litters (Table 2). The mean, median, and mode litter sizes were 1.51, 1, and 1, with a range of 1 to 3. Parental age, parental origin, and litter order did not affect litter size. Dam and sire litter sizes were available for the parents of 48 and 37 litters, respectively: there was no relationship between a parent's litter size and the litter size of his/her offspring, indicating that litter size may not be a genetic trait.

Sex

Sex was reported for 239 males and 246 females born in captivity, a 1.00:1.03 sex ratio, which is not significantly different than the expected ratio of 1.00:1.00. The dam's or sire's age was determined for 133 and 152 individuals, respectively. There was no effect

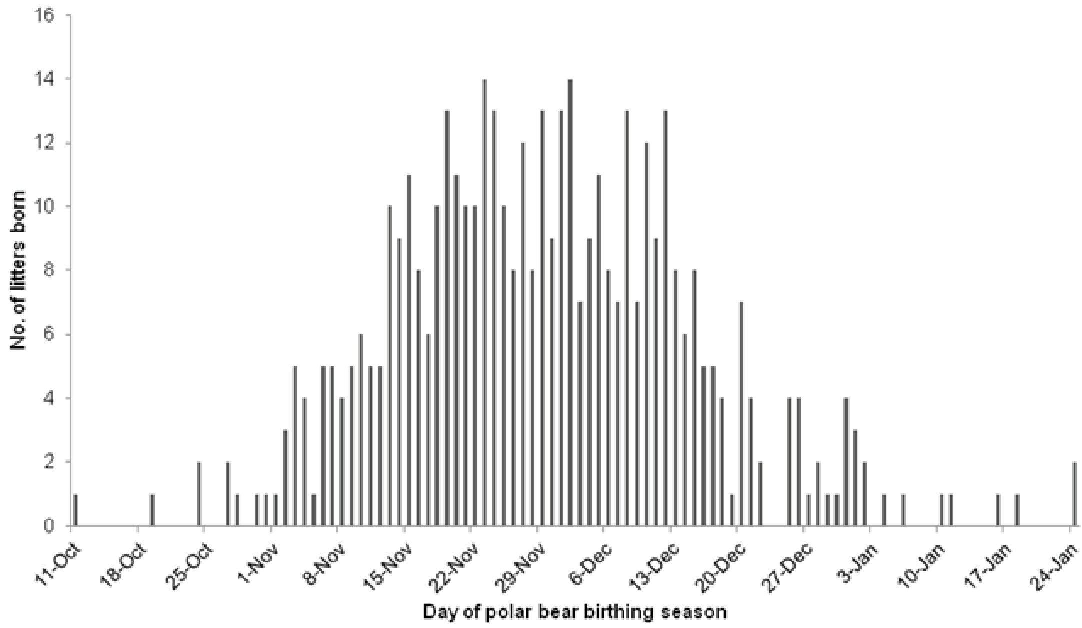

Figure 3. The number of litters born per day of polar bear birth season. The birthdates of 446 litters were analysed to define the birth season. The majority of births occurred in November and December.

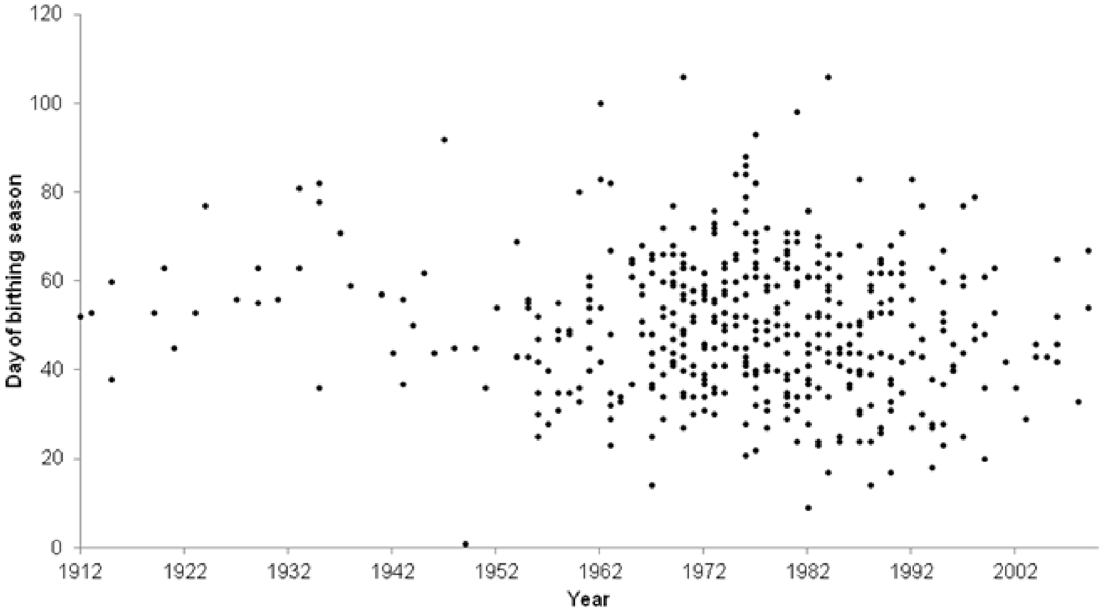

Figure 4. A scatter plot of year (x-axis) by polar bear birthing dates (y-axis) sorted ordinally. There was no significant linear relationship between year and birthing date (R^2 = 0.01) from 1912 to 2010.

of dam's age on the sex of her offspring; however, there was an effect of sire's age (Fig. 6). The senior group (18–25 years) sired a significantly higher proportion of males than the two younger groups (P < 0.05). There was no effect of parental origin or day of birth on offspring sex.

Cub survival

Age at death was obtained for 598 individuals born in captivity. One-hundred and fifty seven were stillborn (26.3%), 181 (30.3%) died as neonates, 78 (13.0%) died between 30 days of age and four years, and 182 (30.4%) lived to adulthood. An individual's sex was related to survival. Although both males and females were equally likely to reach adulthood, a higher proportion of males were recorded as stillborn, whereas a higher proportion of females died between 30 days of age and four years ($P < 0.05$). There was no effect of parental age on offspring survival; however, there was an effect of parental origin. A higher proportion of cubs born to captive-born dams or sires survived to adulthood ($P = 0.003$ and 0.001, respectively). Wild-caught sires produced a higher proportion of cubs recorded as stillborn ($P < 0.01$), but there was

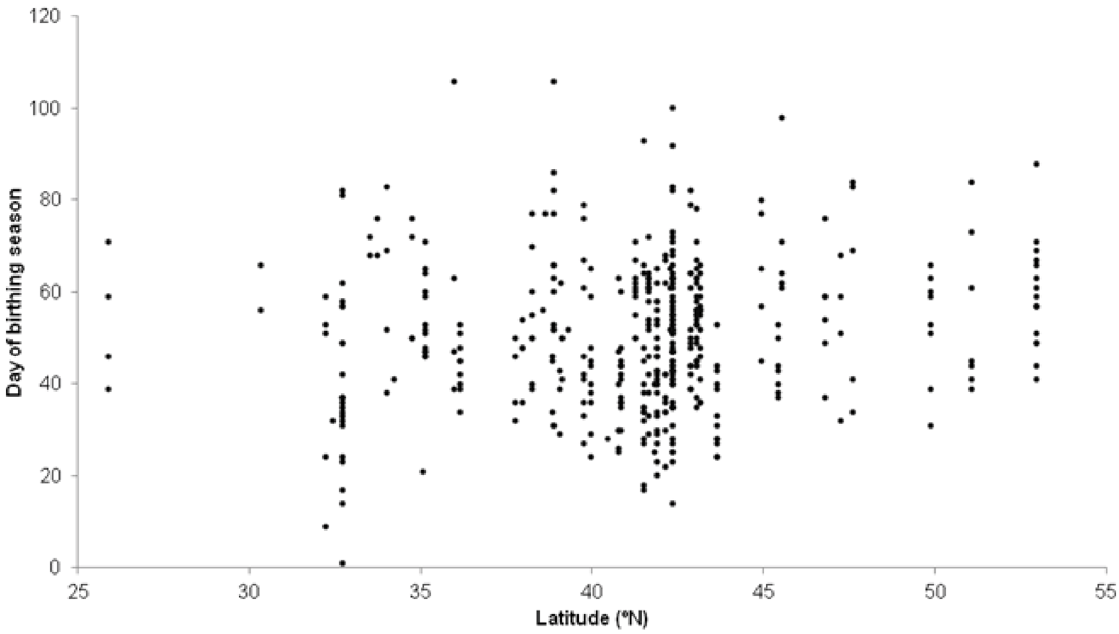

Figure 5. A scatter plot of latitude (x-axis) by polar bear birthing dates (y-axis) sorted ordinally. There was no significant linear relationship between latitude and birthing date (R^2 = 0.01) from 1912 to 2010.

Table 2. Number and percentage of singleton, twin, and triplet litters.

Litter size	No. of litters (%)	No. of individuals (%)
1	236 (51.8)	236 (34.4)
2	209 (45.8)	418 (60.8)
3	11 (2.4)	33 (4.8)

no effect of dam origin on the proportion of stillborns. Also, wild-caught dams or sires produced a higher proportion of cubs that died between 30 days and four years ($P < 0.05$) when compared to captive-born parents.

Cub survival also was affected by maternal parity and litter size. Stillbirths and cub deaths between 30 days and four years of age were more common in primiparous dams ($P < 0.01$) and a trend was observed in which individuals born to a multiparous dam were more likely to reach adulthood ($P = 0.05$); however, survival among individuals born in the second through sixth litters were similar ($P > 0.05$). Individuals born in litters of multiples (twins and triplets) were more likely to die as neonates than those born as singletons ($P = 0.002$) and there was a trend for a higher proportion of singletons to survive to adulthood than those born as multiples ($P = 0.08$).

Age at death was not correlated to latitude ($R^2 = 0.01$), day of birth within the birth season ($R^2 = 0.007$), or to the number of days an individual was born from the mean birthdate of November 29, ($R^2 = 0.01$).

Discussion

This study represents the largest analysis of captive polar bear reproduction and cub survival conducted to date. Regardless of the variation in climates and management practices among institutions and throughout zoological history, this arctic species has been surprisingly consistent in its reproductive patterns and success in captivity. As expected, the overall number of litters born per year is highly correlated with the total number of individuals in captivity, suggesting that the recent decrease in litters produced is largely a function of the declining number of reproductively viable adults in the captive population.

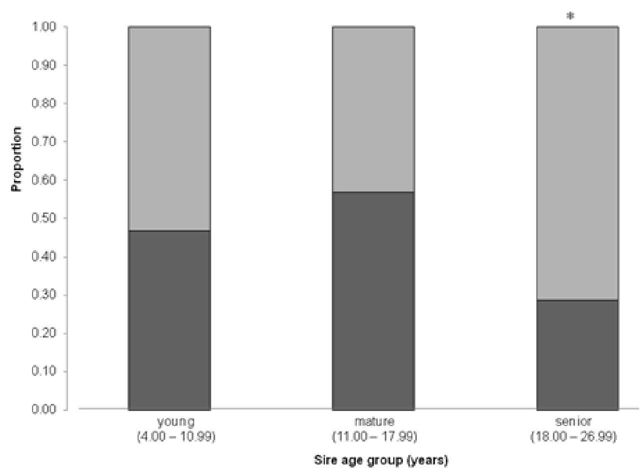

Figure 6. Proportions of male-to-female cubs born to sires grouped by age. Light grey bars = males, dark grey bars = females. * indicates significant difference in proportions.

Parental factors

The data revealed that captive females start producing cubs later in life when compared to wild females. In captivity, the average age at first parturition was 9.26 years, whereas Derocher (1991) reported that the pregnancy rates of wild three- and four-year-old females, based on serum progesterone, were approximately 9% and 80%, respectively. This disparity is probably a result of management recommendations: generally, young females in captivity are not introduced to a sexually mature male until their fifth or sixth year. Ramsay and Stirling (1988) and Derocher (1991) reported the average ages of pregnant females in the western Hudson Bay were 13.6 years and 11.3 years, respectively, with the former study focusing on inland females and the latter on the coastal population. Ramsay also reported inter-year variation in the mean age of pregnant females, ranging from 12.0 years to 15.4 years, which was probably a result of annual fluctuations in food availability and consequently body condition. These ages suggest that the mean age of pregnancy of captive females (12.9 years) was similar to that of the wild population. Additionally, the oldest wild female observed with cubs was 27 years, comparable to the oldest known captive female to produce cubs (26 years). It is entirely possible that females older than 26 years produced cubs in captivity but were not included in the present analysis due to unrecorded or estimated birthdates, particularly for many wild-caught females. The ages at which males sired cubs in captivity were similar to those of parturient females; however, males in captivity are spared from the competition for breeding that wild males confront, so it is likely that males siring most litters in the wild are older, more dominant individuals. The finding that wild-caught sires produced more litters than captive-born sires is almost certainly due to human selection, since a wild-caught individual would be considered a genetic founder and would receive more breeding opportunities.

Birth season

It is generally accepted that delayed implantation evolved to synchronise the timing of parturition with an environment favorable for offspring survival. Accordingly, photoperiod is thought to control timing of implantation in many species that experience obligate embryonic diapause (as reviewed by Lopes et al. 2004). Two separate polar bear births in the southern hemisphere (latitude 34.9°S) occurred on 9 May (2013) and 20 June (1985) and lend support to the assertion that photoperiod is an important regulator of seasonal reproduction in polar bears. However, the lack of a significant linear relationship between latitude (relative to the equator) and birthing date argues against a substantial latitude impact on day of parturition within the geographic range analysed in this dataset.

In a previous study, a considerable variation in the interval from mating to parturition was reported among parturient bears (Stoops et al. 2012), indicating that parturition cannot be predicted based on time of conception. It has been suggested that individual bears are consistent in their timing of parturition regardless of when they conceive. In this analysis, one female gave birth during the same week each year but another produced cubs as early as 27 October and as late as 11 January and the overall average range of cubbing dates per female was slightly greater than one month. Therefore, there does not appear to be an inherent circannual rhythm specific to each individual regarding timing of parturition in captivity. Furthermore, it is improbable that changes in photoperiod are responsible for the large variation observed within an individual because none of these females was moved during her reproductive years. The interplay between photoperiod and the endogenous cues that initiate an embryo's exit from diapause have not been defined in bears and it is possible that other factors, such as body condition and alterations in weather may affect timing of implantation and ensuing parturition.

Average inter-birth intervals of bears born in captivity are presented but are largely dependent on both offspring survival and management influence. A female with surviving cubs will probably spend 2–3 years with the cubs, housed separately from males, whereas a female whose cubs do not survive may be reintroduced to a male immediately after birth season. Although the shortest inter-birth interval in this report was 314 days, in 2011 a captive female housed in Canada produced a litter on 5 January; the cubs did not survive, she mated in early March, and gave birth again on 11 October, only 279 days after her last parturition.

Litter size
Tumanov (2001) reported a mean litter size of 1.76 cubs in an analysis of 50 litters born in a single Russian zoo, which is slightly larger than the value found in this analysis (1.51 cubs/ litter). Our findings were similar to those reported in wild populations (Amstrup and Gardner 1994), with the exception of a remarkably prolific population in the western Hudson Bay with a mean litter size of 1.9 and a 13% incidence of triplets or quadruplets (Ramsay and Stirling 1988). This study found no relationship between latitude and litter size, which is in agreement with a comprehensive summary of the findings in wild populations (Derocher 1999). In the present study, litter size was unaffected by any of the variables examined, including parental litter size, indicating that it may not be an inheritable trait as observed in humans (Lewis et al. 1996) and livestock species (Allan et al. 2009; Davis et al. 1991; Vallet et al. 2005).

Sex ratio
Despite the overall sex ratio of approximately 1:1 for polar bears born in captivity, sires older than 18 years produced a higher proportion of male offspring than the two younger age groups. There is evidence supporting the hypotheses that several factors may affect embryo sex, including parental hormone concentrations (as reviewed by James 2008). Curry et al. (2012) recently reported age-related shifts in testosterone concentrations of male polar bears with levels peaking between 11 and 14 years and starting to decline around 18 years of age. However, there are no data directly linking paternal testosterone concentrations to sex of cubs sired.

Cub survival
Many species of carnivores exhibit a moderate to high rate of neonatal deaths (as reviewed by Clubb and Mason 2006). Although specific causes of death are not recorded in the studbook, likely reasons for the high mortality rate prior to 30 days of age include infanticide, failure to thrive, maternal agalactia or maternal negligence, in addition to stillbirths, which were analysed as a separate category. Data from wild bears indicate that 33% of pregnant females lose all cubs within the first year (Derocher 1991) and that 30–38% of cubs die after exiting the den and prior to weaning (Amstrup and Durner 1995; Ramsay and Stirling 1988). However, these statistics probably underestimate cub mortality because the precise number of wild cubs lost prior to den emergence is unknown. Amstrup and Gardner (1994) reported an average cub number per den on the pack ice of 0.93, indicating that some females failed to produce cubs or that cubs died prior to den emergence. Furthermore, in this study, individuals born in litters of multiples were more likely to die as neonates than those born as singletons, possibly due to lower birth weights and competition for resources. Amstrup and Durner (1995) reported that cub death was independent of litter size, but did not sample individuals in the den, which is where our data indicates that the majority of cub deaths might occur.

Cub survival was also affected by dam parity, but not dam age, suggesting that maternal experience contributes to offspring survival. Interestingly, cubs born to captive-born parents had higher survival rates. It is possible that captive-born parents are better adapted to their environment and, as a result, are calmer, healthier, and in better body condition, all factors that could contribute to offspring more likely to thrive.

Conclusions
1. The recent decrease in the number of litters of polar bears born per year is largely a reflection of the decrease in the total number of individuals in captivity.
2. The majority of births (73.8%) in captivity in North American zoos occur between 13 November and 15 December and 95% occurred during the months of November and December.
3. Latitude, and, by inference, climate did not affect cub survival in captivity within the geographic range analysed, nor did it significantly affect the timing of parturition.
4. Females in captivity start producing cubs later in life compared to wild females.
5. Litter sizes were similar to those observed in wild populations and were not influenced by any of the factors examined; however, cubs born in litters of multiples had lower survival rates.
6. Individuals born to captive-born parents were more likely to survive to adulthood than those born to wild-caught parents.
7. Older males sired a higher proportion of male cubs than younger sires.

Caveats

In addition to the variables analysed in this study, other factors influence reproduction and survival in captivity that are not documented in studbook records. Physiological and husbandry factors such as nutrition, stress, and health may influence litter size, sex, parturition dates and cub survival. Additionally, some cubs were hand-reared, which indisputably impacted cub survival, but this aspect of husbandry was not recorded consistently so could not be evaluated with confidence. The results presented are dependent upon the correctness of the data recorded in the polar bear studbook, which itself relies on the accuracy of input from many individuals at numerous zoos. The under-reporting of stillbirths and neonatal deaths, a prior common practice by facilities, may have impacted results. It also is plausible that year-to-year variations in temperature and weather patterns may affect timing of implantation, birthing dates, and survival, but such evaluation was beyond the scope of this analysis.

Acknowledgements
The authors thank the Shumaker Family Foundation and Rowe and Elizabeth Hoffman for their generous support of CREW's polar bear project, as well as Lynn Blattman for her contributions in building the dataset. The authors report no conflict of interest.

References
Allan M.F., Kuehn L.A., Cushman R.A., Snelling W.M., Echternkamp S.E., Thallman R.M. (2009) Confirmation of quantitative trait loci using a low-density single nucleotide polymorphism map for twinning and ovulation rate on bovine chromosome. *Journal of Animal Science* 87: 46–56.

Amstrup S.C., Durner G.M. (1995) Survival rates of radio-collared female polar bears and their dependent young. *Canadian Journal of Zoology* 73: 1312–1322.

Amstrup S.C., Gardner C. (1994) Polar bear maternity denning in the Beaufort Sea. *Journal of Wildlife Management* 58: 1–10.

Clubb R., Mason G.J. (2006) Natural behavioural biology as a risk factor in carnivore welfare: How analyzing species differences could help zoos improve enclosures. *Applied Animal Behavior Science* 102: 303–328.

Curry E., Roth T.L., MacKinnon K.M., Stoops M.A. (2012) Factors influencing annual fecal testosterone metabolite profiles in captive male polar bears (*Ursus maritimus*). *Reproduction of Domestic Animals* 47: 222–225.

Davis G.H., McEwan J.C., Fennessy P.F., Dodds K.G., Farquhar P.A. (1991) Evidence for the presence of a major gene influencing ovulation rate on the X chromosome of sheep. *Biology of Reproduction* 44: 620–624.

Derocher A.E. (1991) *Population Dynamics and Ecology of Polar Bears in Western Hudson Bay.* Dissertation. Edmonton: University of Alberta.

Derocher A.E. (1999) Latitudinal variation in litter size of polar bears: ecology or methodology? *Polar Biology* 22: 350–356.

James W.H. (2008) Evidence that mammalian sex ratios at birth are partially controlled by parental hormone levels around the time of conception. *Journal of Endocrinology* 198: 3–15.

Lewis C.M., Healey S.C., Martin N.G. (1996) Genetic contribution to DZ twinning. *American Journal of Medical Genetics* 161: 237–246.

Lopes F.L., Desmarais J.A., Murphy B.D. (2004) Embryonic diapause and its regulation. *Reproduction* 128: 669–678.

Meyerson R. (2010) *Polar Bear Studbook (*Ursus maritimus*); North American Population*. Silver Spring, MD: Association of Zoos and Aquariums.

Meyerson R., Long S. (2008) *Polar Bear (*Ursus Maritimus*) Population Analysis and Breeding and Transfer Plan.* Chicago: Association of Zoos and Aquariums Population Management Center, Lincoln Park Zoo.

Meyerson R., Long S. (2010) *Polar Bear (*Ursus Maritimus*) Population Analysis and Breeding and Transfer Plan.* Chicago: Association of Zoos and Aquariums Population Management Center, Lincoln Park Zoo.

Meyerson R., Thompson D. (2012) *Polar Bear (*Ursus Maritimus*) AZA Animal Program Population Viability Analysis Report*. Chicago: Association of Zoos and Aquariums Population Management Center, Lincoln Park Zoo.

Molnár P.K., Derocher A.E., Klanjscek T., Lewis M.A. (2011) Predicting climate change impacts on polar bear litter size. *Nature Communications* 2: 186.

Ramsay M.A., Stirling I. (1988) Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology* 214: 601–634.

Stirling I., Lunn N.J., Lacozza J. (1999) Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52: 294–306.

Stoops M.A., MacKinnon K.M., Roth T.L. (2012) Longitudinal fecal hormone analysis for monitoring reproductive activity in the female polar bear (*Ursus maritimus*). *Theriogenology* 78: 1977–1986.

Tumanov I.L. (2001) Reproductive biology of captive polar bears. *Ursus* 12: 107–108.

U.S. Endangered Species Act (2013) U.S. Fish & Wildlife Service species profile. URL: http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=A0IJ.

Vallet L., Freking B.A., Leymaster K.A., Christenson R.K. (2005) Allelic variation in the erythropoietin receptor gene is associated with uterine capacity and litter size in swine. *Animal Genetics* 36: 97–103.