

SURVIVAL AND REPRODUCTIVE RATES FOR POLAR BEARS AT SVALBARD

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Abstract: Polar bears (*Ursus maritimus*) were captured near Svalbard north of the Norwegian mainland between 1988 and 1993. Only one female older than 15 years was caught. A constant relationship between the number of sampled female bears in consecutive age classes was estimated for females between 2 and 15 years of age at $\phi = 0.96$. If growth rate of the Svalbard population is between 1.00 and 1.03, the age structure estimate of annual female survival rate between ages 2 and 15 years is 0.96–0.99. The lack of females older than 15 years in the catch sample is difficult to explain. Based on data sampled by satellite transmitters on females between 4 and 17 years of age, dates for maternity den entry was between 7 September and 12 December and emergence dates were between 2 March and 27 April. Mean denning duration was 153 days. Reproductive class of females were assessed in 115 cases. The youngest females that had cubs were 5 years old, and mean annual rate of litter production for females between 7 and 17 years was 0.41. Birth success for the same range was 0.82. Annual first year cub survival was 0.55, assuming the mother survived. Survival rate from birth to 2 years was 0.35 and from emergence to weaning was 0.38, assuming the mother survived.

Ursus 10:25–32

Key words: polar bear, population biology, reproduction, satellite telemetry, survival, Svalbard, *Ursus maritimus*.

According to Article II in The International Agreement on the Conservation of Polar Bears, each contracting party shall manage polar bear populations in accordance with sound conservation practices based on the best available scientific data (Anon. 1974). The most important population parameters that must be known to insure scientifically based management of a population of polar bears are distribution, population size, reproductive rate, and survival rate.

The Norwegian population of polar bears is found near Svalbard, about 500 km north of the Norwegian mainland. According to Larsen (1986) the polar bear population in the Svalbard area is a subpopulation of one distributed between eastern Greenland and western Russia. A recent satellite telemetry study concluded that the Svalbard population of polar bears is relatively discrete (Wiig 1995), but the question is further explored (Derocher and Wiig, unpubl. data). The population was totally protected in 1973 and probably doubled in size from 1970 to 1980 (Larsen 1986). Changes in the size of the population since then is not known. Larsen (1986) documented the population biology of polar bears from Svalbard during a decline (1966–70) and increase (1976–1983) in population size. The aim of the present paper is to present data on survival and reproductive rates of polar bears from Svalbard from 1988 to 1993.

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STUDY AREA

Svalbard is a high Arctic archipelago, between 10°E and 35°E and between 74°N and 81°N. It consists of 5 major and several minor islands with a total area of about 62 km². According to the Svalbard Treaty of 9 February 1920, Norway exercises full and unlimited sovereignty over the area. However, citizens of the countries contracting to the Treaty have the same rights as Norwegians to hunt and fish in the area and to conduct maritime, industrial, mining, and commercial operations, provided that they observe the local laws and regulations.

About 50% of the land area of Svalbard is protected as national park or nature reserve by the 1938 Royal Decree "Regulations concerning conservation of the natural environment on Svalbard". The protected areas incorporate most of the important polar bear terrestrial habitat in Svalbard. However, several areas within the protected areas are exempt from the regulations because of established mining rights. The most restricted area in Svalbard in relation to polar bears is Kong Karls Land, where all access is forbidden due to its importance as a denning area.

The archipelago is surrounded by the Greenland Sea to the west and the Arctic Ocean to the north, both with maximum depths of about 3,000 m. The Barents Sea to the east and south has an average water depth of 250 m. The west coast of Spitsbergen has a relatively mild climate caused by the North Atlantic current, which transports warm water masses from the Atlantic Ocean along the western coast before it turns around the north coast and sweeps eastwards (Vinje 1976). A cold current brings drift ice from the Arctic Ocean along the east coast of Svalbard. The eastern waters of Svalbard are covered with drift ice most of the year, with a minimum ice extent around 80°N in September and a maximum extent around

74°N in March. Some ice sweeps around Sørkapp in late autumn and winter, and the western ice edge may extend 40 km from the west coast (Vinje 1981). The average summer and winter temperatures on Spitsbergen's west coast are +5°C and -12°C, respectively. Temperatures may sometimes rise above freezing during winter and even cause rainfall (Hisdal 1985). The average temperatures are 2 to 4 degrees lower in the east. Annual precipitation is normally <400 mm on Spitsbergen's west coast (Hisdal 1985) and less in the eastern part of the archipelago.

As a result of the International Agreement for the Conservation of Polar Bears, polar bear hunting was forbidden in Norwegian areas. The management of polar bears on Svalbard is regulated by The Royal Decree "Regulations concerning the management of game and freshwater fishes on Svalbard and Jan Mayen" enacted in 1978 (Ministry of Environment 1984).

METHODS

Bears were immobilized using remotely injected Zoletil (Haigh et al. 1985, Stirling et al. 1989), as described by Lentfer (1968) and Larsen (1971). Snowmobiles were used for captures during 1988–89; bears were darted from helicopters in subsequent years. Most polar bears were captured in the southern and southeastern Svalbard Archipelago during March and April on land-fast ice; 10 were captured in northern Svalbard. Beginning in 1990 a larger portion of Svalbard was surveyed each spring, and areas of high and low density were determined. All areas were searched each year, but effort was concentrated in high density areas. Adult males were avoided during 1988–92. All sighted bears were captured in 1993.

Females with body weight >100 kg were equipped with satellite transmitters (Telonics Inc., Mesa, Ariz., USA) as described by Harris et al. (1990) and Messier et al. (1992). Transmitters had contact with the satellites every sixth day and provided location, internal transmitter temperature, and short- and long-term activity information. Satellite data were used for females tracked in the period 1988–96. A vestigial premolar tooth was extracted for age determination (Grue and Jensen 1979).

The age distribution was used to evaluate the range of annual survival rates of subadult and adult female bears. If we assume a stable age distribution, the age frequency curve is a function of both age specific survival rates (p_x) and population growth rate (λ) (Caughley 1977). Any standing age distribution at time t gives a measure of the relationship between the number of animals of age x ($N_{x,t}$) and of age $x+1$ ($N_{x+1,t}$); this relationship is called phi, ϕ (Taylor et al. 1987a), so that $N_{x+1,t}/N_{x,t} = \phi_x$. With a stable

age distribution $\phi_x = p_x/\lambda$. By assuming a constant ϕ over the applied age-range, ϕ for females was calculated from the composite age distribution by the Chapman–Robson truncated method based on a maximum-likelihood approach (Chapman and Robson 1960).

The age distributions presented in Larsen (1986:Table 25 male and female bears older than 2 years) of 365 bears caught in the period 1955–70 and 75 bears caught in the period 1977–80 at Svalbard were compared with the female age distribution presented here by pooling the frequencies in 4 age groups with range 3 years (3–5, 6–8, 9–11, 12–14 years).

Female polar bears normally have a 3 year reproductive cycle and mate during spring (Ramsay and Stirling 1988). Cubs are born in late December and remain with their mother until their third spring, when the mother comes into estrous. At first capture, females were classified as with cubs, yearlings, or 2-year-olds or without offspring. The 2 last classes of females were those also classified as available for mating.

Location, temperature, and activity data were used to assess the denning status of each female (Amstrup and Gardner 1994, Messier et al. 1994). A female denning on land has a constant position. I assumed that the transmitter temperature for females in dens was high and activity was low. As criteria for denning I used local position and high temperature. I regarded the activity count only as an additional guide because transition from high to low activity was often unclear. Some females had a local position and high temperature from summer or early autumn to next spring. In many cases, however, the location information ceased before the temperature increased. In those cases the temperature increase was used as indication of date of den entry. A female might open the den in early spring, be out for a short while, go in again for 1 to 2 weeks, then emerge again and stay with the cubs at the den for 1 to 2 weeks (Hansson and Thomassen 1983; Messier et al. 1994; Derocher and Wiig, unpubl. data). Females may even change dens in this period. In spring a drop in transmitter temperature indicated that the female was out of the den; a change in position indicated that she left the denning area. In some cases I observed drops in temperature in January or February, but if the temperature increased again and the female stayed in the same locality, it was taken to indicate continued denning. Time of entrance and emergence from the den was used to assess whether or not a female gave birth.

Only pregnant female polar bears den all winter (Ramsay and Stirling 1988, Messier et al. 1992, Amstrup and Gardner 1994). Age-specific litter production rates were calculated as the fraction of all females at age x that

produced litters based on assessment of satellite telemetry data or by classification when captured. In the latter case only data for those females observed with young were used, because females without young could have lost cubs or yearlings earlier the year they were captured.

Breeding success has been defined as the proportion of available mature females which actually breed in year i (N_i) that emerge with cubs from their dens the following spring (Larsen 1986, Amstrup and DeMaster 1988). In this study, age-specific birth success was estimated as the proportion of females available to mate in spring (age = $x-1$, alone or with 2-year-olds) that presumably produced a litter the following winter (age = x) based on satellite data. Mean birth interval was calculated from the number of years between birth of litters, using females that were followed through at least 2 birth attempts (Ramsay and Stirling 1988).

Individual survival rate from cub to yearling age was calculated from observed litter sizes of cubs and yearlings during March and April (Taylor et al. 1987a). Cub survival was assumed to not vary with litter size (Amstrup and Durner 1995, Derocher and Stirling 1996).

Litter sizes >2 were not observed, and triplets are uncommon in northern populations (Taylor et al. 1987a). Therefore, I assumed that initial and subsequent litter size could only be 1 or 2. Individual survival from yearling to weaning could not be estimated from this method due to lack of observations of litters of 2-year olds. Litter survival rate from birth to the end of the breeding season

was also estimated (Powell et al. 1996). Assuming the individual survival rate for cubs was constant through the first year and that females that lost a litter have the same birth success as other females, litter survival rate was estimated (Taylor et al. 1987a). Since data are used only for females which survive from the year they have cubs to the next year, $\phi = 1$. Total cub survival rate was calculated as the product of individual cub survival rate and litter survival rate (Derocher and Taylor 1994).

The midwinter birth rate, litter survival rate, and birth success were adjusted to 1 April for comparison with rates from other areas. I assumed that individual cub survival was constant through the year and that the litter survival was constant from birth (1 January) to end of breeding season (31 May).

RESULTS

Captured females ranged from 2 to 15 years of age with one 32-year-old (Table 1). The age range for the estimation of mean ϕ (survival $\times \lambda$) was 2–15 years. The estimated ϕ for adult females was 0.96 (SD = 0.03, $n = 83$).

The age distribution differed ($\chi^2_6 = 22.5$, $P < 0.001$, $n = 505$) from that in 1955–70 and 1977–80 (from Larsen 1986). The distribution of numbers in the groups indicated more young animals in the early samples. The proportion of females from 12 to 14 years of age was 0.10 (37/365) in the 1955–70 sample, 0.14 (9/65) in the 1977–80 sample, and 0.24 (18/75) in the 1988–93 sample. The

Table 1. Age distribution and litter size of female polar bears captured at Svalbard, 1988–93.

Age	N Females	Litter size					
		Cubs		Yearlings		2-year olds	
		1	2	1	2	1	2
2	7						
3	7						
4	9						
5	4						
6	9		1				
7	5	1					
8	5		1	1	1		
9	4		1	2	1		
10	7		1	1	1		
11	7		2	2			
12	8	1	2		2		1
13	5			3			
14	5		1		1	1	
15	2		1				
32	1						
Total		2	10	9	6	1	1

current age distribution did not, however, differ from that in 1977–80 ($\chi^2_3 = 3.35$, $P = 0.34$, $n = 140$). In all 3 studies few bears (<5 %) were >15 years of age (15, 3, and 1 respectively), and only 2 were >20 years old.

Reproductive class of females between 4 and 17 years of age were assessed in 115 cases (Table 2). Forty-three females were classified as giving birth, of which 36 were assessed from satellite data; 5 of these were confirmed by observation during the succeeding spring. Temperature changes were the primary indicator used to determine den entrance date (Table 3). Emergence dates were determined from changes in location and increases in temperature. In 14 cases the position data were lost before the temperature increased. In 10 cases the time of entrance of the den was indicated to be as early as between June and August. In 4 cases transmitters ceased in spring before the bear emerged. All were recorded as successful production of litter. For all dens except the summer entries (Jun–Aug), the entry dates were between 7 September and 12 December ($\bar{x} = 7$ Nov, $SD = 25$ days, $n = 26$). Den emergence dates were between 2 March and 27 April ($\bar{x} = 5$ Apr, $SD = 14$ days, $n = 32$). Denning duration was between 90 and 197 days with a mean of 153 days ($SD = 26$, $n = 24$).

Based on the litter production rate estimated from satellite data (Table 2), the earliest age of first litter production was 5 years. For females between 7 and 17 years, the litter production rate was 0.41 ($n = 93$). Birth success for 7- to 17-year-olds, calculated as the proportion of available females in spring that had litters the next win-

ter, was estimated at 0.82 ($n = 28$) (Table 4). Mean interbirth interval was estimated at 2.2 years ($SE = 0.2$, $n = 18$).

Mean spring litter size for cubs was 1.83 ($SE = 0.11$, $n = 12$) and for yearlings, 1.40 ($SE = 0.13$, $n = 15$). Only 2 2-year-old litters were caught. Survival rate from cub to yearling (in spring) was 0.63.

In 4 (14%) of 28 cases females were in maternity dens 2 consecutive winters. By correcting for a birth success rate of 0.82, the litter survival rate to the end of the breeding season (end of May) of the first year was 0.87. The maximum first year survival for cubs was 0.5, assuming the mother survived. Adjusted to spring, litter production rate for 7- to 17-year olds was 0.36, birth success for 7- to 17-year olds was 0.73, and cub survival was 0.60.

DISCUSSION

Capture effort was concentrated in southern Spitsbergen and was not evenly distributed over the population range (Wiig 1995). Small sample sizes can probably not explain why only 1 female >15 years old was caught. It is interesting to note that Larsen (1986) also missed the older age groups in his samples, not only from the time the hunt was still going on in Svalbard (before 1974), but also the years 1979 and 1980. His sample from the early period included a mixture of hunted and marked bears taken all year, while his latter sample was from bears captured in the summer season. Some of the bears he captured were taken farther east and north than the ones I captured.

There are 3 possible explanations for the lack of older bears: (1) incorrect aging, (2) age-related distribution of bears, and (3) bears >15 years old experience differentially higher mortality rates.

Because the determination of age by cementum layering has been done by very experienced people, it is unlikely that the ages were incorrect. Further, visual inspection of tooth-wear at the time of capture confirmed that older bears were missing from the sample.

The lack of individuals born during the time the hunting still went on in Svalbard could reflect that since hunting ceased, there has been a recolonization by younger bears in the area in which bears were captured. In this case older females could be reproducing in the area of Kong Karls Land, which has been protected as denning area since 1939 and is an area in which we have not been allowed to capture bears. Another explanation could be that older females do not reproduce, have different distribution than younger females, and therefore were not available for capture. In 1994–96 we caught 50 adult females

Table 2. Age-specific litter production for female polar bears in the Svalbard area in 1988–96 calculated as the fraction of all females at age x that produced litters based on assessment of satellite telemetry and capture data.

Age	n	Litter production rate
4	4	0.00
5	7	0.29
6	11	0.18
7	10	0.70
8	9	0.33
9	5	0.20
10	8	0.38
11	13	0.46
12	13	0.38
13	11	0.09
14	9	0.67
15	7	0.29
16	6	0.50
17	2	0.50
>30	1	0.00
7–17	93	0.41

Table 3. Number of cases in which the different satellite sensors (L = location, T = temperature, A = activity, C = transmitter ceased) were used to assess den entry and emergence dates for female polar bears at Svalbard, 1988–96.

Activity	L	L,T	L,A	L,T,A	T	T,A	A	C	Total
Den entry	3	6	0	3	19	5	0	0	36
Den emergence	13	10	2	2	2	2	1	4	36

in the southeastern part of Svalbard and found that old females were also missing there (Derocher and Wiig unpubl. data).

It is not likely that females >15 years old have a much higher mortality rate than younger females. If this was true, then the Svalbard population would have a dramatically different survival pattern than that found in other polar bear populations. Therefore it is important to further determine why the older females are not caught.

When calculating survival rates from the Chapman–Robson truncated method, age distribution is assumed to be stable and population size constant. Since the Svalbard population has been protected for >20 years and no difference in age distribution was found between the sample of Larsen (1986) from 1978–80 and the present sample, I assumed that the present age distribution was stable. The population at Svalbard may have changed from an increasing state to a more stable state; however, I did not evaluate this possible bias. Further, it is warranted to use these assumptions for comparison because the same assumptions are made for many other polar bear populations to estimate survival rates (e.g., Derocher and Taylor 1994), where it is clear that the population growth rate must have reacted to variations in hunting pressure.

Table 4. Birth success of female polar bears at Svalbard, 1988–96, estimated as fraction in maternity dens at age x of those available for breeding at age $x-1$, from satellite telemetry and capture data.

Age	Available	Birth success
4	2	0.00
5	7	0.29
6	6	0.17
7	7	1.00
8	4	0.75
9	0	–
10	1	1.00
11	5	0.80
12	3	1.00
13	2	0.50
14	1	1.00
15	1	0.00
16	3	0.67
17	2	1.00
7–17	28	0.82

Larsen (1986) estimated an observed survival rate, ϕ , of 0.825 (SD = 0.021) for the Svalbard polar bear population 3 to 20 years of age during 1954–70, and at 0.906 (SD = 0.05) for bears 3 to 14 years of age during 1977–80, based on the Chapman–Robson truncated method. Using the same method, I estimated that ϕ = 0.96 (SD = 0.03) for females 2 to 15 years of age during 1988–93. For the female age range 3 to 14 years, ϕ = 0.98 (SD = 0.02).

Since the sample size for estimating ϕ was small, I explored the sensitivity of the estimate to changes in the number of animals in the youngest and oldest age classes. The number in age class 2 years was varied from 5–10 and in age class 15 years from 1–5. By using all combinations between these age classes, estimated ϕ varied between 0.947 (using 10 in age class 2 years and 1 in age class 15 years) and 0.987 (using 5 in age class 2 years and 5 in age class 15 years). These values would not change the conclusions of this paper.

Fowler (1981) stated that adult survival is relatively inflexible in large mammals, is subject to error in measurement, and has not been shown to change in many populations. Applying these assumptions, Larsen (1986) assumed a constant natural survival rate in Svalbard polar bears of 0.95 for both sexes between 3 and 20 years. A natural survival rate of 0.95 for adult polar bears has been used in modeling other polar bear populations (Taylor et al. 1987b) and was believed to be the rate after correcting for harvest in Hudson Bay (Derocher 1991).

Annual survival rates for adult females in the high 90 percent range are though to be necessary to sustain population numbers for large mammals with low reproductive potential (Eberhardt 1985). Using telemetry to follow known individuals, Amstrup and Durner (1995) estimated a natural (no harvest mortality) survival rate of adult polar bears aged 3–27 years at 0.996. However, high senescence mortality in the age classes above 20 must occur to truncate the age distribution at about 30 years. They assumed that there could be some bias in their data and suggested that for purposes of simulation, estimates of natural survival rates of 0.969–0.996 should be applied. Polar bears are long-lived animals with low reproductive output and on annual population growth rate which unlikely exceeds 2% (Taylor et al. 1987b). If the growth

rate of the Svalbard population is between 1.00 and 1.03, the estimate of annual survival for bear 3–15 years is 0.96–0.99, similar to the range suggested by Amstrup and Durner (1995).

It is uncertain whether females actually entered dens as early as July or just were in a resting state on the ground. Den entry could be possible because slopes with snow lairs can also be found in summer in many areas of Svalbard. Messier et al. (1994) also had problems with discriminating between den site selection and actual entry into dens. For calculation of mean den entrance date I excluded entrance dates occurring in June–August.

Den entry as early as late August was recorded in the Canadian Arctic Archipelago (Messier et al. 1994); entry in November and December were not regarded as maternity dens. In the Beaufort Sea successful land-denning bears entered dens between 8 October and 24 November, and successful pack-ice denning bears entered dens between 17 October and 13 December (Amstrup and Gardner 1994). The range of entry dates at Svalbard spans these periods.

In the Canadian Arctic Archipelago, bears emerged from the dens between 4 March and 7 April (Messier et al. 1994). In comparison, the Beaufort Sea females emerged between 13 March and 18 April inland and between 4 March and 29 April on the pack ice (Amstrup and Gardner 1994). The emergence dates recorded in my study were from the beginning of March to the end of April. In their detailed study of the behavior of female polar bears after emergence from dens at Kong Karls Land, Svalbard, Hansson and Thomassen (1983) found that the females left the denning area between mid-March and mid-April. Many factors probably were important for timing of female departure from the denning area, in particular the developmental level of the cubs, which varied between family groups and years (Hansson and Thomassen 1982).

In the Canadian Arctic Archipelago, it was regarded as unlikely that dens occupied for <150 days were maternity dens and mean duration of stay within maternity dens was 186 days (Messier et al. 1994). In the Beaufort Sea a mean duration of 147 days for successful land dens and a mean duration of 130 days for successful pack-ice dens was estimated (Amstrup and Gardner 1994). In the present study the shortest duration of den use was 90 days, and 63% (15/24) of the den durations were for >150 days.

To what degree cub mortality in the den triggers den emergence is not known. However, since few such cases were found, early emergence by females that had lost their litter is not believed to have biased the results.

The youngest bears that produced a litter in Svalbard were 5 years old. The maximum rate of litter production did not occur until the age of 7 years. Larsen (1986) used reproductive rates of 0.35 for 4-year olds and 0.6 for bears 5 years and older to model a typical high arctic polar bear population; however, data from Svalbard were not given. Litter production is possible at an age of 4 years but is not common before the age of 6 years in the Beaufort Sea area (Lentfer et al. 1980, Amstrup and Durner 1996). In the Canadian High Arctic, the majority of females were 5-years old when they had their first litter (Stirling et al. 1984). In the Central Canadian Arctic most females started litter production at the age of 6 years (Furnell and Schweinsburg 1984), while in southeastern Baffin Island most females started at 4 years (Stirling et al. 1980). In Hudson Bay the age of first reproduction changed from 4 years in the early 1970s to 5 years in the late 1980s (Ramsay and Stirling 1988, Derocher et al. 1992). The onset of reproduction of polar bears at Svalbard is similar to western Hudson Bay.

The age-specific litter production rate that I observed for females increased between 5 and 7 years of age and was then relatively constant with a mean of 0.41 (0.36 when adjusted to spring) for females between 7 and 17 years of age. With an estimated mean litter size of 1.83 cubs (in spring), the number of cubs produced per female per year was 0.62. Prior to 1988, litter production data for Svalbard was not available. Comparative litter production estimates were calculated to range from 0.51–0.59 (Larsen 1986) based on an average litter size of 1.84 and litter production rates of 0.277–0.321 taken from Lentfer et al. (1980) and DeMaster and Stirling (1983). However, the estimated production rate is larger than that calculated from the Beaufort Sea (0.24; Lentfer et al. 1980, Amstrup and Durner 1996). Comparable spring data from Western Hudson Bay do not exist, but based on autumn data overall litter production rates declined from 0.48 during 1966–79 to 0.34 during 1985–92 (Derocher and Stirling 1995). The shift in rate in Western Hudson Bay reflects a shift in age of offspring at weaning from 1.5 years to 2.5 years.

During 1977–83, 77% of mature and available polar bear females which bred in Svalbard emerged from dens the following spring with a litter (Larsen 1986). Although I used a different approach to calculate birth success, which did not exclude females that lost cubs in the den, the adjusted value of 0.73 was similar to that found by Larsen (1986). In Alaska and Canada, 30–60% of adult female polar bears available to breed either do not breed or are not impregnated (Lentfer et al. 1980, Tay-

lor et al. 1987b) and in western Hudson Bay 33% of females pregnant in the autumn were without cubs in the following year (Derocher et al. 1992). They assumed the reason for the apparent reproductive failure include neonatal mortality, failure to implant, or spontaneous abortion.

Birth interval in polar bears is highly dependent on litter loss. Females that lose their cubs during spring may come into estrous and mate the same spring (Derocher et al. 1992, Garner et al. 1994). Although few such cases have been documented in Svalbard, I observed 4 cases in which females were assumed to be in maternity dens during 2 consecutive winters.

A 2-year breeding interval was observed in 6 cases and might either indicate that the cubs were weaned during the spring of their second year or that they died. A breeding interval of 2 years is well known from the western Hudson Bay (Ramsay and Stirling 1988). If that also occurred at Svalbard (as suggested by Lønø 1970), many lone yearlings and few 2-year-olds with their mothers should have been observed in early spring. No lone yearlings were observed. Although I captured only 3 females with 2-year-olds in spring, they likely left their mother after the capture period.

The birth interval for polar bears in Alaska was 3.1–3.6 years (Lentfer et al. 1980), while an interval of 3.2 years was reported from western Hudson Bay (Ramsay and Stirling 1982). The relatively short interval between cub production found at Svalbard is partly the result of data collection by satellite during mid-winter, while other studies were based on observations made during spring. However, the short interval at Svalbard could also reflect high cub mortality and indicate that females often lose their litters and breed again during the first spring after litter loss.

Litter sizes in spring for cubs (1.83) and yearlings (1.40) observed during 1988–93 are similar to those estimated from Svalbard during 1977–83 by Larsen (1986). Mean cub litter size from 8 management units in North America was between 1.64 and 1.89 (Derocher and Taylor 1994) and in the Beaufort Sea was 1.6 (Amstrup and Gardner 1994).

Larsen (1986) estimated individual cub survival between 4 and 12 months at 0.67, similar to the individual rate of 0.63 for age 4 to 16 months estimated here, based on spring observations. In the Canadian High Arctic, individual cub survival rates were between 0.830 and 0.980 (Derocher and Taylor 1994). In western Hudson Bay the survival rate was 0.532 between spring and autumn (Derocher and Stirling 1996).

The timing of mortality in polar bear cubs is poorly documented (Derocher and Stirling 1996). It is possible

that the loss of whole litters is most pronounced during the first months of life (Larsen 1986). Most of the whole litter loss seems to occur before the end of the breeding season (Derocher et al. 1992, Derocher and Stirling 1996). In the Beaufort Sea most mortality of young occurred during the first year of life (Amstrup and Durner 1995). My estimate of total annual cub survival (0.60 in spring, assuming the mother survives) is a maximum rate because it is based on the assumption that whole litter loss occurred before the end of the breeding season. If the rate of litter loss is constant through the first year, cub survival rate would be less than I estimated.

Survival of yearlings cannot be estimated from my data, but the rate must be between 0.55 (cub survival) and 0.96 (adult survival). For purposes of comparison with other populations, I estimated cub survival of 0.63, based on total cub survival without whole litter survival. This gave a total survival from birth to 2 years of 0.35 and from emergence to weaning of 0.38, assuming mothers survived.

Larsen (1986) estimated total survival from birth to 2 years as 0.34 for bears at Svalbard during 1976–83. In this estimate he accounted for survival rates of mothers, but did not include whole litter loss. Thus, my estimate is similar to Larsen's (1986) estimate. Amstrup and Durner (1995) estimated the survival from emergence to weaning as 0.676 in the Beaufort Sea. Annual cub survival from data pooled from across Canada is 0.77 (Derocher and Taylor 1994), which also is higher than in Svalbard. The cub survival in western Hudson Bay has not been estimated for a comparable period, but it is as low as 0.44 between 3 and 11 months (Derocher and Stirling 1996). In any case, the cub survival of polar bears at Svalbard is less than in most other populations, but not as low as in western Hudson Bay.

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