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Survival rates of radio-collared female polar bears and their dependent young

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Abstract: Polar bears (*Ursus maritimus*) are hunted throughout most of their range. In addition to hunting, polar bears of the Beaufort Sea region are exposed to mineral and hydrocarbon extraction and related human activities such as shipping, road building, and seismic testing. As human populations increase and demands for polar bears and other arctic resources escalate, reliable estimates of survivorship of polar bears are needed to predict and manage the impacts of those activities. We used the Kaplan–Meier model to estimate annual survival (with 95% confidence intervals) for radio-collared female polar bears and their dependent young that were followed during a 12-year study in the Alaskan Beaufort Sea. Survival of adult female polar bears was higher than had been previously thought: $\hat{S} = 0.969$ (range 0.952–0.983). If human-caused mortalities were deleted, the computed survival rate was 0.996 (0.990–1.002). Survival of young from den exit to weaning was 0.676 (0.634–0.701). Survival during the second year of life, 0.860 (0.751–0.903), was substantially higher than during the first year, 0.651 (0.610–0.675). Shooting by local hunters accounted for 85% of the documented deaths of adult female polar bears. Conversely, 90% of documented losses of young accompanying radio-collared females were not directly caused by humans. Deaths of dependent young were independent of litter size ($P = 0.36$), indicating that parental investment in single cubs was not different from investment in litters of two or more. Precise estimates of the survival of independent juveniles and adult males still need to be developed.

Résumé : Les Ours blancs (*Ursus maritimus*) sont la cible des chasseurs dans presque toute l'étendue de leur répartition. En plus de subir la chasse, les Ours blancs de la région de la mer de Beaufort sont exposés à l'extraction de minerais et d'hydrocarbures et aux activités humaines qui lui sont reliées, transport maritime, construction de routes, tests sismiques. Avec l'augmentation de la population humaine et de la demande pour les Ours blancs et autres ressources arctiques, des estimations justes de la survie des ours s'imposent pour pouvoir évaluer l'impact de ces activités et en assumer la gestion. Nous avons utilisé le modèle Kaplan–Meier pour estimer le taux annuel de survie (avec des intervalles de confiance de 95%) de femelles munies d'un collier émetteur et de leurs petits, suivis pendant 12 ans dans la mer de Beaufort sur la côte de l'Alaska. La survie des femelles adultes s'est avérée supérieure à ce que l'on croyait : $\hat{S} = 0,969$ (0,952–0,983). En ne tenant pas compte des mortalités causées par l'activité humaine, le taux calculé de survie était de 0,996 (0,990–1,002). La survie des jeunes de la sortie du repaire au sevrage était de 0,676 (0,634–0,701). La survie au cours de la deuxième année, 0,860 (0,751–0,903), était considérablement plus élevée qu'au cours de la première année, 0,651 (0,610–0,675). La mortalité due aux chasseurs locaux a expliqué 85% des cas de mortalité chez les femelles adultes. En revanche, 90% des cas connus de mortalité de jeunes accompagnant des femelles porteuses d'émetteurs n'étaient pas causés par l'activité humaine. La mort de petits encore dépendants n'était pas reliée au nombre de petits dans la portée ($P = 0,36$), ce qui indique que l'investissement des parents dans l'élevage d'un seul petit ne diffère pas de l'investissement alloué aux portées de 2 petits ou plus. Une méthode d'estimation précise de la survie des juvéniles indépendants et des mâles adultes reste à mettre au point.

[Traduit par la Rédaction]

Introduction

Compared with most mammals, polar bears are slow to mature, have long interbirth intervals, and small litters (DeMaster and Stirling 1981; Amstrup and DeMaster 1988). Some specifics of polar bear population dynamics, however,

remain unknown. Production of cubs by polar bears, for example, has often been underestimated (Stirling et al. 1975; Lentfer et al. 1980; DeMaster and Stirling 1983; Amstrup et al. 1986). Undersampling of cubs can preclude accurate descriptions of age structures and prohibit estimates of survival. In polar bears and other animals that are constrained by their evolutionary history to long delays in maturation, adult survival is the parameter that has the greatest impact on population growth (Eberhardt and Siniff 1977; Eberhardt 1985; Taylor et al. 1987). However, obtaining useful estimates of survivorship is one of the most difficult challenges

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in population analysis (Eberhardt 1985). Annual survival rates for adult females in the high 90 percentile range are thought to be necessary to sustain population numbers for large mammals with low reproductive potential (Eberhardt 1985). Previous estimates of survival rates for polar bears, which were derived from age-structure or mark and recapture data, were between 80 and 94% (DeMaster and Stirling 1981; Furnell and Schweinsburg 1984; Amstrup et al. 1986; Amstrup and DeMaster 1988; Ramsay and Stirling 1988; Derocher 1991) and, in most cases, these are insufficient to maintain polar bear populations if existing estimates of recruitment are accurate. For polar bears, the only useful estimates of age structure are subject to many limitations because they are composites constructed from multiyear data (Spinage 1972; Amstrup et al. 1986). Similarly, heterogeneity in mark and recapture data has reduced the accuracy and precision of survival estimates derived from them (Amstrup et al. 1986; Amstrup and DeMaster 1988). We hypothesized that survival rates of polar bears must be higher than indicated by previous estimates.

Polar bears are hunted throughout most of their range. In addition to hunting, polar bears of the Beaufort Sea region are exposed to mineral and hydrocarbon extraction and related human activities such as shipping, road building, and seismic testing. As human populations increase and demands for polar bears and other arctic resources escalate, reliable estimates of survivorship and reproduction of polar bears are needed to predict and manage the impacts of these activities. The objective of this study was to develop reliable estimates of the survival of adult and juvenile polar bears in the Beaufort Sea.

Materials and methods

Field procedures

We captured and marked polar bears each spring between 1982 and 1992, except for 1990. Bears were also captured in the autumn of 1981–1986, 1988, and 1989. Autumn captures occurred each year in October and November and spring captures between March and May. We captured polar bears throughout the Alaskan Beaufort Sea, which extends from Point Barrow, Alaska, at approximately 157°W, to the Canadian border, at 141°W, and in bordering areas to the east and west. We immobilized polar bears by injecting drugs (phencyclidine hydrochloride (Sernylan®, Park, Davis and Co.), etorphine hydrochloride (M-99®, Lemmon Co.), and tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Co.)) with projectile syringes fired from helicopters (Larsen 1971; Schweinsburg et al. 1982). Capture and marking protocols were approved by an independent animal care and welfare committee.

Each year, we collared a limited number ($\bar{x} = 27$) of adult females with radio transmitters. We attached very high frequency (VHF) radio collars to polar bears between 1981 and 1985 and relocated them approximately 4 times per year with aircraft (Amstrup and Gardner 1994). After autumn 1985, we mostly deployed ultra high frequency platform transmitter terminals (PTTs) that were relocated by satellite. Sensors on the PTTs recorded the temperature of the collar and 2 indices of activity. Positions of collared animals were determined by sensors on the satellite that interpreted

frequency-shift patterns caused by changes in relative positions of the satellites and animals (Fancy et al. 1988). Collars carrying PTTs also carried VHF beacons that we located with aircraft. Survival of radio-collared bears was determined by periodic reobservations from aircraft and by movement and activity patterns discernible from sensors on PTTs. PTTs provided data at least weekly. We attempted to reobserve radio-collared polar bears by aircraft every 2–3 months. Reobservations were not always evenly distributed in time, however, and were most frequent during spring and autumn, when the combination of ice conditions and daylight were most suited to visual observations. Hence, we divided reobservations into spring (January–June) and autumn (July–December) time intervals.

Analyses

Cementum annuli from extracted premolar teeth were counted to estimate ages of radio-collared animals (Hensel and Sorensen 1980; Stirling et al. 1980). Counts were performed at the Laboratory of Polar Bear and Seal Research, University of Alberta, Edmonton, Alberta, Canada. Survival rates for adult females and the young accompanying them were estimated by following radio-collared polar bears and determining their fate. Data were analyzed using Pollock et al.'s (1989) staggered-entry modification of Kaplan and Meier's (1958) survivorship model. We chose this method because of (i) its elegant simplicity (computations are similar to those used in life tables), (ii) the ease with which the model deals with censored animals (animals that disappear from the study and for which neither subsequent death nor continued life can be documented), and (iii) the broad basis in survival theory. Pollock et al. (1989) censored animals (deleted them from numbers at risk) during the first time period in which they were missed by the search effort. Because our time intervals were long (e.g., 2 periods per year) we decided to censor animals during the period in which they were last observed rather than waiting for the first period in which they were not observed. This resulted in lower estimates of survival. With the variation in our reobservation intervals and the long time periods used, however, we felt that the more conservative estimates were safer. Numerous animals left the study when they shed their radios or when their radios failed and then reentered the study as new animals at risk when they were recaptured and fitted with new radio collars. Some animals were censored and then found dead several time periods later. These deaths provided information on mortality patterns, but because of the need to be consistent in reporting whether animals died or were censored, we could not use them in calculating mortality rates.

Pollock et al.'s (1989) model estimates a survival rate and confidence interval on that rate for the telemetry study duration, in our case 12 years. We converted survival estimates for the whole study to the parameter of interest, annual survival, by taking the 12th root of the point and interval estimates. "Total" and "natural" survival were calculated. Computations of total survival included all documented deaths. Natural survival was estimated by censoring animals that died as a result of human causes rather than recording them as deaths.

We also calculated survival of young between the ages of

Table 1. Kaplan–Meier estimates of survival rate calculated from female polar bears of all ages that were radio-collared in the Beaufort Sea of Alaska and Canada in 1981–1992.

Year and season	No. of new radios applied	Total no. at risk (r_j)	No. censored	No. of deaths (d_j)	Survival ^a (\hat{S}_t)	Mortality ^b (\hat{M})	Var(\hat{S}_t)	95% interval on \hat{S}_t	
								Min.	Max.
1981									
Spring	15	15	13	0	1.000	0.000	0.000	1.000	1.000
Autumn	14	16	1	0	1.000	0.000	0.000	1.000	1.000
1982									
Spring	14	29	6	0	1.000	0.000	0.000	1.000	1.000
Autumn	5	28	6	0	1.000	0.000	0.000	1.000	1.000
1983									
Spring	24	46	7	0	1.000	0.000	0.000	1.000	1.000
Autumn	6	45	12	0	1.000	0.000	0.000	1.000	1.000
1984									
Spring	24	57	20	1	0.982	0.018	0.000	0.949	1.016
Autumn	1	37	10	1	0.956	0.027	0.001	0.891	1.021
1985									
Spring	42	68	8	2	0.928	0.030	0.001	0.869	0.987
Autumn	4	62	8	0	0.928	0.000	0.001	0.866	0.990
1986									
Spring	16	70	24	2	0.901	0.029	0.001	0.835	0.968
Autumn	1	45	11	0	0.901	0.000	0.002	0.819	0.984
1987									
Spring	14	48	15	0	0.901	0.000	0.002	0.821	0.981
Autumn	0	33	2	1	0.874	0.031	0.003	0.768	0.980
1988									
Spring	15	45	9	2	0.835	0.045	0.003	0.736	0.934
Autumn	28	62	2	0	0.835	0.000	0.002	0.751	0.920
1989									
Spring	10	70	13	1	0.823	0.014	0.002	0.742	0.904
Autumn	27	83	17	0	0.823	0.000	0.001	0.749	0.898
1990									
Spring	0	66	23	6	0.748	0.095	0.002	0.658	0.839
Autumn	0	37	3	0	0.748	0.000	0.004	0.627	0.869
1991									
Spring	14	48	11	1	0.733	0.021	0.003	0.626	0.840
Autumn	0	36	7	1	0.712	0.028	0.004	0.588	0.837
1992									
Spring	23	51	16	2	0.684	0.040	0.003	0.579	0.790
Autumn	0	33	33	0	0.684	0.000	0.004	0.553	0.816
Total	297								
Annual survival rate					0.969			0.952	0.983

^aStaggered entry of new animals into the study and calculation of the finite survival rate (\hat{S}_t) were handled according to Pollock et al. (1989).

^bInstantaneous mortality in each period, calculated as $\log_e(\hat{S}_t)$ (Krebs 1989).

0–1 and 1–2 with the procedure of Trent and Rongstad (1974). That procedure is simply a comparison of the observed losses with binomial expectations (e.g., for the i th period of monitoring, the mean survival rate is

$$\bar{S}_i = \frac{x_i - y_i}{x_i}$$

where x_i represents the number of animals monitored in the i th period and y_i represents the numbers of animals dying in the i th period). For dependent young, we examined 2 time periods: (1) when young were aged “0–1,” and (2) when

young were aged “1–2.” We modified Trent and Rongstad’s (1974) procedure by assuming that censored animals died at the same rate as noncensored animals. Those assumed deaths were then added to deaths (y_i) actually observed. For example, if $\bar{S}_i = 0.8$, then 20% of censored animals were assumed to have died and that 20% was added to the number of known mortalities. Also, rather than estimating confidence intervals from a published table of approximations (Trent and Rongstad 1974), we generated individual binomial distributions with the binomial probability function in SAS version 6.07 (SAS Institute Inc., Cary, N.C.) to establish our interval estimates. We reported survival as “point

Table 2. Kaplan–Meier estimates of survival rate calculated from female polar bears aged 3–10 years that were radio-collared in the Beaufort Sea of Alaska and Canada in 1981–1992.

Year and season	No. of new radios applied	Total no. at risk (r_j)	No. censored	No. of deaths (d_j)	Survival ^a (\hat{S}_t)	Mortality ^a (\hat{M})	Var(\hat{S}_t)	95% interval on \hat{S}_t	
								Min.	Max.
1981									
Spring	11	11	10	0	1.000	0.000	0.000	1.000	1.000
Autumn	9	10	5	0	1.000	0.000	0.000	1.000	1.000
1982									
Spring	10	15	4	0	1.000	0.000	0.000	1.000	1.000
Autumn	3	14	5	0	1.000	0.000	0.000	1.000	1.000
1983									
Spring	16	25	4	0	1.000	0.000	0.000	1.000	1.000
Autumn	4	25	8	0	1.000	0.000	0.000	1.000	1.000
1984									
Spring	14	31	16	1	0.968	0.033	0.001	0.907	1.029
Autumn	1	15	7	1	0.903	0.069	0.005	0.761	1.045
1985									
Spring	25	32	7	0	0.903	0.000	0.002	0.806	1.001
Autumn	3	28	5	0	0.903	0.000	0.003	0.799	1.007
1986									
Spring	8	31	8	2	0.845	0.067	0.004	0.728	0.962
Autumn	1	22	10	0	0.845	0.000	0.005	0.706	0.984
1987									
Spring	9	21	10	0	0.845	0.000	0.005	0.703	0.987
Autumn	0	11	1	0	0.845	0.000	0.010	0.648	1.042
1988									
Spring	12	22	6	1	0.807	0.047	0.006	0.658	0.955
Autumn	20	35	3	0	0.807	0.000	0.004	0.689	0.924
1989									
Spring	5	37	12	0	0.807	0.000	0.003	0.692	0.921
Autumn	9	34	18	0	0.807	0.000	0.004	0.687	0.926
1990									
Spring	0	16	10	2	0.706	0.134	0.009	0.518	0.893
Autumn	0	4	1	0	0.706	0.000	0.037	0.331	1.081
1991									
Spring	6	9	6	0	0.706	0.000	0.016	0.456	0.956
Autumn	0	3	1	0	0.706	0.000	0.049	0.273	1.139
1992									
Spring	9	11	5	1	0.642	0.095	0.013	0.415	0.869
Autumn	0	5	8	0	0.642	0.000	0.030	0.305	0.978
Total	175								
Annual survival rate					0.964			0.906	0.998

^aFor details of calculations see Table 1.

estimate or mean” followed by 95% confidence interval, when interval estimates were available.

Results

Survival was estimated from attachment of 297 radio collars to adult female polar bears between 1981 and 1992 (Table 1). We estimated survival, \hat{S} , over the 12-year study period as 0.684 (0.553–0.816). This 12-year survival rate translated into a constant annual survival rate of 0.969 (0.952–0.983). Radio-collared females ranged in estimated age from 3 to 27 years. Survival estimates for females aged 3–10 were 0.964 (0.906–0.998) (Table 2). For ages 11–27, the estimates were 0.962 (0.933–0.984) (Table 3). Although fewer

animals died between the ages of 3 and 10 years than from 11 to 27, the 95% confidence intervals around the estimates for each age group overlapped extensively, suggesting that the difference was not significant. Deletion of mortalities caused by humans resulted in an estimated natural survivorship of 0.996 (Table 4) with a 95% confidence interval that overlapped unity (0.990–1.002).

Only 26 deaths of radio-collared adult female polar bears were documented during the 12 years of monitoring: 3 bears died of natural causes, 1 by consuming ethylene glycol from an unknown source (Amstrup et al. 1989), and 22 (85% of the detected mortality) were shot by coastal hunters. Six of these deaths (1 natural death plus 5 hunting mortalities) could not be included in Kaplan–Meier calculations because they

Table 3. Kaplan–Meier estimates of survival rate calculated from female polar bears aged 11–27 years that were radio-collared in the Beaufort Sea of Alaska and Canada in 1981–1992.

Year and season	No. of new radios applied	Total no. at risk (r_j)	No. censored	No. of deaths (d_j)	Survival ^a (\hat{S}_t)	Mortality ^a (\hat{M})	Var(\hat{S}_t)	95% interval on \hat{S}_t	
								Min.	Max.
1981									
Spring	2	2	1	0	1.000	0.000	0.000	1.000	1.000
Autumn	5	6	0	0	1.000	0.000	0.000	1.000	1.000
1982									
Spring	6	12	4	0	1.000	0.000	0.000	1.000	1.000
Autumn	2	10	3	0	1.000	0.000	0.000	1.000	1.000
1983									
Spring	8	15	4	0	1.000	0.000	0.000	1.000	1.000
Autumn	2	13	3	0	1.000	0.000	0.000	1.000	1.000
1984									
Spring	10	20	7	0	1.000	0.000	0.000	1.000	1.000
Autumn	1	14	2	0	1.000	0.000	0.000	1.000	1.000
1985									
Spring	19	31	3	3	0.903	0.102	0.003	0.804	1.002
Autumn	1	26	4	0	0.903	0.000	0.003	0.795	1.011
1986									
Spring	11	33	13	0	0.903	0.000	0.002	0.807	0.999
Autumn	0	20	3	0	0.903	0.000	0.004	0.780	1.026
1987									
Spring	4	21	7	0	0.903	0.000	0.004	0.783	1.023
Autumn	0	14	0	1	0.839	0.074	0.008	0.662	1.015
1988									
Spring	3	16	4	1	0.786	0.065	0.008	0.608	0.964
Autumn	8	19	2	0	0.786	0.000	0.007	0.623	0.950
1989									
Spring	7	24	2	1	0.754	0.043	0.006	0.604	0.903
Autumn	7	28	4	0	0.754	0.000	0.005	0.615	0.892
1990									
Spring	6	30	9	3	0.678	0.105	0.005	0.541	0.816
Autumn	1	19	1	0	0.678	0.000	0.008	0.505	0.851
1991									
Spring	10	28	5	1	0.654	0.036	0.005	0.511	0.796
Autumn	1	23	6	0	0.654	0.000	0.006	0.497	0.811
1992									
Spring	9	26	10	1	0.629	0.039	0.006	0.482	0.776
Autumn	0	15	14	0	0.629	0.000	0.010	0.435	0.823
Total	123								
Annual survival rate					0.962			0.933	0.984

^aFor details of calculations see Table 1.

were not discovered by radiotelemetry and the animals had been censored, because of radio failure, long before their death. Two of the natural deaths of radio-collared polar bears apparently were caused by fights with other bears. The cause of the third natural mortality was not determined, owing to bad weather and the long distance to the site of death; however, human intervention seemed unlikely. During the course of the study we also were able to determine the causes of death of three unmarked bears that were serendipitously found dead. One of these, a large male, died of gastric dilatation and volvulus (Amstrup and Nielsen 1989), one adult female died of complications arising from blockage of the bile duct by gallstones, and a third was apparently killed and

eaten by a large male. Hence, agonistic behavior was the apparent cause of 3 of the 5 natural deaths we observed.

Survival of young from den exit through the time of weaning was 0.676 (0.634–0.701; Table 5). Most mortality of young occurred during the first year of life (Table 6), when the annual survival rate was 0.651 (0.610–0.675). Survival during the second year of life, 0.859 (0.751–0.903), was much higher (Table 7). Binomial estimates of cub ($\bar{x} = 0.710$, 0.627–0.821) and yearling ($\bar{x} = 0.870$, 0.850–0.930) survival (Trent and Rongstad 1974) were higher than Kaplan–Meier estimates.

The deaths of five cubs or yearlings were associated with the harvest of their radio-collared mothers. We concluded

Table 4. Kaplan–Meier estimates of the natural survival rate calculated from female polar bears of all ages that were radio-collared in the Beaufort Sea of Alaska and Canada in 1981–1992.

Year and season	No. of new radios applied	Total no. at risk (r_j)	No. censored	No. of deaths (d_j)	Survival ^a (\hat{S}_t)	Mortality ^a (\hat{M})	Var(\hat{S}_t)	95% interval on \hat{S}_t	
								Min.	Max.
1981									
Spring	15	15	13	0	1.000	0.000	0.000	1.000	1.000
Autumn	14	16	1	0	1.000	0.000	0.000	1.000	1.000
1982									
Spring	14	29	6	0	1.000	0.000	0.000	1.000	1.000
Autumn	5	28	6	0	1.000	0.000	0.000	1.000	1.000
1983									
Spring	24	46	7	0	1.000	0.000	0.000	1.000	1.000
Autumn	6	45	12	0	1.000	0.000	0.000	1.000	1.000
1984									
Spring	24	57	21	0	1.000	0.000	0.000	1.000	1.000
Autumn	1	37	10	1	0.973	0.027	0.001	0.921	1.025
1985									
Spring	42	68	10	0	0.973	0.000	0.000	0.935	1.011
Autumn	4	62	8	0	0.973	0.000	0.000	0.933	1.013
1986									
Spring	16	70	26	0	0.973	0.000	0.000	0.936	1.010
Autumn	1	45	11	0	0.973	0.000	0.001	0.926	1.020
1987									
Spring	14	48	15	0	0.973	0.000	0.001	0.928	1.018
Autumn	0	33	3	0	0.973	0.000	0.001	0.918	1.028
1988									
Spring	15	45	11	0	0.973	0.000	0.001	0.926	1.020
Autumn	28	62	2	0	0.973	0.000	0.000	0.933	1.013
1989									
Spring	10	70	14	0	0.973	0.000	0.000	0.936	1.010
Autumn	27	83	17	0	0.973	0.000	0.000	0.939	1.007
1990									
Spring	0	66	28	1	0.958	0.015	0.001	0.911	1.005
Autumn	0	37	3	0	0.958	0.000	0.001	0.895	1.021
1991									
Spring	14	48	12	0	0.958	0.000	0.001	0.903	1.014
Autumn	0	36	8	0	0.958	0.000	0.001	0.894	1.022
1992									
Spring	23	51	18	0	0.958	0.000	0.001	0.904	1.012
Autumn	0	33	33	0	0.958	0.000	0.001	0.891	1.025
Total	297								
Annual survival rate					0.996			0.990	1.002

Note: Natural survival rates were calculated by censoring animals that were killed by humans rather than including them as deaths.

^aFor details of other calculations see Table 1.

the two yearlings accompanying the radio-collared bear that died of ethylene glycol poisoning also died, but because they were not radio-collared, their remains were not found. The 61 other documented deaths of young of radio-collared females were due to unidentified natural causes. Fifty of 68 documented deaths of young were from litters of two. We recorded 20 deaths of single young from litters of two, and the loss of 15 whole litters of two. Rates of disappearance of young as singles or as whole litters were not significantly different ($\chi^2 = 0.83$, $df = 1$, $P = 0.36$). Likewise, the rate of loss of litters of single cubs (16 of 102 litters) did not

differ from the rate of loss of litters of twin cubs (15 of 106) ($\chi^2 = 0.072$, $df = 1$, $P = 0.79$).

Discussion

Annual variability in adult mortality (Tables 1–3) mainly resulted from annual variation in numbers of bears killed by hunters. Hunter kill was regulated by the availability of bears near coastal settlements. Proximity of radio-collared bears to the coast, and hence their vulnerability to harvest, varied with weather and sea-ice conditions among years. The polar

Table 5. Kaplan–Meier estimates of survivorship between den emergence and weaning for young of female polar bears that were monitored with radiotelemetry in the Beaufort Sea in 1981–1992.

Year and season	Total no. at risk (r_j)	No. censored	No. of deaths (d_j)	Survival ^a (\hat{S}_t)	Mortality ^a (\hat{M})	Var(\hat{S}_t)	95% interval on \hat{S}_t	
							Min.	Max.
1981								
Spring	3	3	0	1.000	0.000	0.000	1.000	1.000
Autumn	10	5	3	0.700	0.357	0.015	0.462	0.938
1982								
Spring	10	3	1	0.630	0.105	0.015	0.392	0.868
Autumn	10	4	1	0.567	0.105	0.014	0.336	0.798
1983								
Spring	6	4	0	0.567	0.000	0.023	0.268	0.866
Autumn	3	0	0	0.567	0.000	0.046	0.145	0.989
1984								
Spring	20	9	4	0.454	0.223	0.006	0.307	0.601
Autumn	8	3	2	0.340	0.288	0.010	0.149	0.532
1985								
Spring	10	3	2	0.272	0.223	0.005	0.128	0.416
Autumn	7	1	2	0.194	0.336	0.004	0.065	0.324
1986								
Spring	23	2	5	0.152	0.245	0.001	0.095	0.209
Autumn	16	3	1	0.143	0.065	0.001	0.078	0.207
1987								
Spring	24	13	1	0.137	0.043	0.001	0.086	0.187
Autumn	10	0	7	0.041	1.204	0.000	0.016	0.066
1988								
Spring	14	4	2	0.035	0.154	0.000	0.017	0.053
Autumn	34	4	4	0.031	0.125	0.000	0.021	0.041
1989								
Spring	42	12	9	0.024	0.241	0.000	0.017	0.032
Autumn	48	6	2	0.023	0.043	0.000	0.017	0.030
1990								
Spring	46	27	10	0.018	0.245	0.000	0.013	0.024
Autumn	13	4	4	0.013	0.368	0.000	0.006	0.019
1991								
Spring	23	5	3	0.011	0.140	0.000	0.007	0.015
Autumn	17	6	1	0.010	0.061	0.000	0.005	0.015
1992								
Spring	34	17	4	0.009	0.125	0.000	0.006	0.012
Autumn	13	13	0	0.009	0.000	0.000	0.004	0.014
Annual survival rate				0.676			0.634	0.701

^aFor details of calculations see Table 1.

bear's evolutionary strategy of long life suggests that variations in mortality of adults caused by natural factors will occur infrequently and irregularly, and that annual survival of adults should be treated as a constant (Eberhardt 1977). Hence, an estimate of annual mortality calculated over a period of several years is more useful than shorter term measurements that are influenced by serendipity.

These are the first estimates of survival of polar bears that were obtained by following known individuals over time. Hence, they are not subject to a variety of assumptions (e.g., stable age structure, equal probability of capture) that can be violated when other methods are relied upon. Estimates based on age-structure analyses can be reliable if the assumptions are met (Caughley 1966, 1967, 1977). However, such

methods have dealt with "synthetic cohorts" and are subject to many questions (Spinage 1972) to which we seldom have answers. DeMaster and Stirling (1983) and Larsen (1985) used changes in numbers and sizes of litters seen to estimate survival of young. Age-structure estimates are particularly dubious for cubs because new cubs in the spring, the first group in the age structure, may be undersampled (Amstrup and DeMaster 1988). Other published estimates of survival of young have been based on mark–recapture data. The reliability of both age-structure and mark–recapture data from polar bear studies is usually limited by small sample sizes and heterogeneity of the capture samples.

This study has shown that survival rates of polar bears are higher, at least in the Beaufort Sea, than previous estimates

Table 6. Kaplan–Meier estimates of survivorship between den emergence and age 1 year for the young of female polar bears that were monitored with radiotelemetry in the Beaufort Sea in 1981–1992.

Year and season	Total no. at risk (r_j)	No. censored	No. of deaths (d_j)	Survival ^a (\hat{S}_t)	Mortality ^a (\hat{M})	Var(\hat{S}_t)	95% interval on \hat{S}_t	
							Min.	Max.
1981								
Spring	3	3	0	1.000	0.000	0.000	1.000	1.000
Autumn	10	5	3	0.700	0.357	0.015	0.462	0.938
1982								
Spring	10	3	1	0.630	0.105	0.015	0.392	0.868
Autumn	10	4	1	0.567	0.105	0.014	0.336	0.798
1983								
Spring	6	4	0	0.567	0.000	0.023	0.268	0.866
Autumn	3	0	0	0.567	0.000	0.046	0.145	0.989
1984								
Spring	17	6	4	0.434	0.268	0.006	0.278	0.589
Autumn	8	3	2	0.325	0.288	0.009	0.140	0.510
1985								
Spring	10	3	2	0.260	0.223	0.005	0.121	0.399
Autumn	7	1	2	0.186	0.336	0.004	0.062	0.310
1986								
Spring	21	0	5	0.142	0.272	0.001	0.085	0.198
Autumn	16	3	1	0.133	0.065	0.001	0.072	0.193
1987								
Spring	15	4	1	0.124	0.069	0.001	0.065	0.183
Autumn	10	0	7	0.037	1.204	0.000	0.015	0.060
1988								
Spring	11	1	2	0.030	0.201	0.000	0.013	0.048
Autumn	34	4	4	0.027	0.125	0.000	0.018	0.036
1989								
Spring	37	7	9	0.020	0.279	0.000	0.014	0.027
Autumn	48	6	2	0.019	0.043	0.000	0.014	0.025
1990								
Spring	27	8	10	0.012	0.463	0.000	0.008	0.017
Autumn	13	4	4	0.008	0.368	0.000	0.004	0.013
1991								
Spring	20	2	3	0.007	0.163	0.000	0.004	0.010
Autumn	17	6	1	0.007	0.061	0.000	0.004	0.010
1992								
Spring	27	10	4	0.006	0.160	0.000	0.004	0.008
Autumn	13	13	0	0.006	0.000	0.000	0.003	0.009
Annual survival rate				0.651			0.610	0.675

^aFor details of calculations see Table 1.

have indicated. Estimated survival rates of adult bears approached 1 when they were unperturbed by humans. These estimates were sufficient to confirm the growth in the population that has been observed in recent years (S.C. Amstrup, unpublished data). Also, these estimates corroborate the conclusions of Eberhardt (1985) that marine mammal populations can be sustained only if survival of adults is in the high 90% range. Even the lower extremes of our interval estimates fall within the range prescribed by Eberhardt (1985)!

Two caveats concerning our estimates of survival rate for adults should be considered. First, if a disproportionate number of censored subjects were undiscovered deaths, our survivorship estimates could be biased upward. Second, the

difference between our estimates of total and natural survival does not include the possibility of density-dependent compensation.

We believe that our search efforts were successful in preventing survival estimates from becoming significantly biased. If animals dying of natural causes tended to sink, preventing subsequent transmissions, or if all radios quit at the time of death, a bias could have emerged. We discovered many premature failures of the radio hardware, and we discovered many cases of bears shedding their radios at various times after attachment. Simultaneous death and radio failure appeared highly unlikely, and, in our experience, bears that die of natural causes are not likely to sink. Bears that were

Table 7. Kaplan–Meier estimates of survivorship between ages 1 and 2 years for young of female polar bears that were monitored with radiotelemetry in the Beaufort Sea in 1981–1992.

Year and season	Total no. at risk (r_j)	No. censored	No. of deaths (d_j)	Survival ^a (\hat{S}_t)	Mortality ^a (\hat{M})	Var(\hat{S}_t)	95% interval on \hat{S}_t	
							Min.	Max.
1981								
Spring	3	3	0	1.000	0.000	0.000	1.000	1.000
Autumn	1	1	0	1.000	0.000	0.000	1.000	1.000
1982								
Spring	6	3	1	0.833	0.182	0.019	0.561	1.106
Autumn	4	4	0	0.833	0.000	0.029	0.500	1.167
1983								
Spring	5	3	0	0.833	0.000	0.023	0.535	1.132
Autumn	3	0	0	0.833	0.000	0.039	0.448	1.218
1984								
Spring	10	9	1	0.750	0.105	0.014	0.518	0.982
Autumn	1	1	0	0.750	0.000	0.141	0.015	1.485
1985								
Spring	5	3	1	0.600	0.223	0.029	0.267	0.933
Autumn	3	1	0	0.600	0.000	0.048	0.171	1.029
1986								
Spring	14	2	1	0.557	0.074	0.010	0.363	0.751
Autumn	11	2	0	0.557	0.000	0.012	0.338	0.776
1987								
Spring	19	13	1	0.528	0.054	0.007	0.365	0.691
Autumn	5	0	2	0.317	0.511	0.014	0.087	0.546
1988								
Spring	6	4	1	0.264	0.182	0.009	0.083	0.445
Autumn	7	2	0	0.264	0.000	0.007	0.096	0.432
1989								
Spring	28	12	2	0.245	0.074	0.002	0.166	0.324
Autumn	22	3	0	0.245	0.000	0.002	0.156	0.334
1990								
Spring	40	27	6	0.208	0.163	0.001	0.151	0.266
Autumn	7	4	0	0.208	0.000	0.005	0.071	0.346
1991								
Spring	15	3	2	0.181	0.143	0.002	0.098	0.263
Autumn	10	2	1	0.162	0.105	0.002	0.070	0.255
1992								
Spring	19	14	0	0.162	0.000	0.001	0.096	0.229
Autumn	5	5	0	0.162	0.000	0.004	0.032	0.293
Annual survival rate				0.859			0.751	0.903

^aFor details of calculations see Table 1.

sick sought a firm substrate on which to rest and ultimately die (Amstrup et al. 1989; Amstrup and Nielsen 1989; S.C. Amstrup, unpublished data). If many more animals were dying during this study, we would have found them!

If animals were illegally killed and their collars destroyed they would have been undetected. We are confident that "illegal kills" were not common. The taking of a polar bear is a big event in the coastal villages of the Beaufort Sea and difficult to keep secret. Also, polar bear hunters in the Beaufort Sea make a concerted effort to police themselves (Treseder and Carpenter 1989). Hence, we believe that the vast majority of our censored animals disappeared because of shed radios or radio failure and were not undetected deaths, and we feel that our estimate of total survival is largely unbiased.

Some compensation in mortality of polar bears in the Beaufort Sea seems likely. S.C. Amstrup (unpublished data) reported strong evidence of a density response involving survival of young and stature of adult females. With a population size lower than 2000 and a harvest of approximately 80 (Amstrup et al. 1986; Nageak et al. 1991; S.C. Amstrup, unpublished data), density responses involving even small numbers could noticeably alter estimated rates. Hence, for purposes of simulation, estimates of the natural survival rate between 0.969 and 0.996 should also be considered.

We are more confident in the Kaplan–Meier estimates than in our binomial (Trent and Rongstad 1974) estimates because of the systematic method by which censored animals are incorporated. Our treatment of censored animals in the binomial model was sensible but "ad hoc."

Survivorship of dependent young was independent of the size of litter of which they were a part. This implies that parental investment does not diminish for single-cub litters as suggested by Tait (1980). Polar bears breed in the spring, implantation occurs in the autumn, and birth occurs in mid-winter (Ramsay and Stirling 1988). The altricial young must then be nurtured for months inside a birth lair, and then for up to 2 years following emergence (Ramsay and Dunbrack 1986). During any reproductive cycle, therefore, many physiological and ecological unknowns could intervene between conception and birth and between birth and weaning. A bear with a litter of any size has overcome many of the hurdles it faced in attempts to reproduce. It would make no sense for such a bear, assuming that sufficient resources are available to raise the cub, to make a decision to abandon or otherwise reduce investment in a single cub. The next cycle, after all, may be worse from the standpoint of the opportunity for foraging, snow cover for denning, or even the opportunity to encounter an acceptable mate. Furnell and Schweinsburg (1984) concluded that mortality of dependent young occurred primarily through the loss of whole litters. Females that cannot care for two young, they reasoned, cannot care for one. Our data refute that conclusion also. Events that lead to loss of a portion of a litter do not necessarily result in loss of all litter members. In fact, often it may be the case that a female is inadequately nourished to provision multiple young, but could provide for a single cub.

Eberhardt (1977) observed that juvenile marine mammals were most vulnerable to a relative scarcity of resources. Young and Ruff (1982) demonstrated that for black bears, social interactions can directly influence recruitment of young to adulthood even when food resources are not in short supply. We observed that survival of dependent polar bears improved with age. We were unable, however, to examine survival of independent juveniles (aged 2–3) with radio telemetry. We have observed juvenile bears scavenging kills of more experienced animals, and Stirling (1974) and Smith (1980) presented evidence of the potential importance of such scavenging to recruitment. We have also observed that larger bears often chase smaller bears away from kills, and sometimes even kill them. This suggests that successful foraging by independent juveniles, and their survival, may be influenced by social factors as well as availability of seals.

Male polar bears cannot be followed by radiotelemetry for extended periods because their necks are larger than their heads and radio collars do not stay attached. Hence, we have no radiotelemetry data on survivorship of adult males. Adult males are, of course, necessary for population maintenance. Males also may be vectors of population regulation (McCullough 1981; Young and Ruff 1982). The population dynamics of polar bears will be fully understood only with the aid of better estimates of survival of independent juveniles and adult males, and clarification of the possible roles played by males in regulating population size.

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