

## Reproductive biology and ecology of female polar bears (*Ursus maritimus*)

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(With 1 plate and 5 figures in the text)

Data on age-specific natality rates, litter size, interbirth interval, age of first reproduction, reproductive senescence, age of weaning and cub survival were determined for a free-ranging population of polar bears inhabiting Hudson Bay, Canada, near the southern limit of the species range. Serum progesterone levels were also determined for females at different stages of their reproductive cycle to provide corroborative support for the reproductive parameters described. Animals were live captured using immobilizing drugs and each animal uniquely marked for future identification. First parturition occurred at four or five years of age and the age-specific natality rate increased with age until approximately 20 years, after which it dropped markedly. At least 40% of adult females displayed two-year interbirth intervals and 55% of cubs in their second year were independent of their mother. Mean size of cub litters in spring was 1.9 and 13% of litters had three or more cubs. The natality rate for 5–20-year-old females was estimated as 0.9, higher than that reported for any more northerly polar bear populations where two-year interbirth intervals are rare, fewer than 5% of yearling cubs are weaned and triplet litters occur with less than 1% frequency. Cub mortality was initially high and declined with age. Although cubs in western Hudson Bay were weaned at a younger age and a lighter weight than their counterparts in more northern populations, cub mortality rates were similar. The reason for the marked differences in reproductive parameters in the western Hudson Bay population is not known. We speculate that sea-ice conditions may be sufficiently different to allow weaned bears at a lighter body weight to hunt seals more successfully there than further north.

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### Introduction

Bears (Ursidae) are prominent members of the mammalian fauna wherever they are found and include the largest of the Carnivora as well as some of the largest of terrestrial mammals (Nowak & Paradiso, 1983). They are, or were recently found, on all continents except Australia and Antarctica. Yet, in spite of their conspicuousness and ubiquity, many details of their reproductive biology are incompletely known. Questions relating to changes in reproductive parameters with age and concomitant effects on lifetime reproductive success, effects of environmental perturbations on subsequent reproductive effort, energetic costs of reproduction, and strategies of energy accumulation and storage relative to reproductive effort are, at best, only partly answered.

As would be expected for a large, long-lived organism (Calder, 1984), bears display low reproductive rates. As a consequence, they are slow to recover from population reductions. Three major factors influence reproductive rates: litter size, age of first reproduction, and interbirth interval (Knight & Eberhardt, 1985). Both age of first reproduction and size of litters for bears are within the expected range for animals of their size, however, the interval between successive births is relatively long (Bunnell & Tait, 1981; Wootton, 1987). The long interbirth interval is proximally mediated by a long period of association with cubs. The presence of unweaned young appears to inhibit oestrus and the initiation of a new reproductive cycle (Baker, 1912; Erickson & Nellor, 1964; LeCount, 1983). Entire populations of bears are also known to experience complete or partial reproductive failure in years when food resources are significantly reduced (Jonkel & Cowan, 1971; Martinka, 1974; Rogers, 1976; Stirling, Pearson & Bunnell, 1976; Picton, 1978). The availability and abundance of food resources appear to exert a strong effect on realized reproductive rates for all species of bears for which data are available. After weaning, young bears are independent for one or more years before they reach reproductive maturity, a time during which they often attain considerable somatic growth.

Mating occurs in the spring for all species of Holarctic bears (brown, *Ursus arctos*; black, *U. americanus*; and polar, *U. maritimus*), but implantation of blastocysts is delayed until autumn (Wimsatt, 1963; Asdell, 1964; Hensel, Troyer & Erickson, 1969; Lønø, 1970, 1972). At about the time of implantation, females cease feeding and enter dens in which they spend the winter without food and water. The length of time spent in an overwinter den varies among populations of both brown and black bears, generally being longer with increasing latitude (Johnson & Pelton, 1980). Active gestation and early post-partum lactation occur while the mother is fasting. No other mammals, except some of the large mysticete cetaceans, go without food and water for extensive periods during gestation (Frazer & Huggett, 1973). Similarly, only the bears, some cetaceans, and some phocid pinnipeds fast through part or all of the lactation period (Lockyer, 1981; Fedak & Anderson, 1982). The period of gestation is very short for bears and cubs are born in an immature state, significantly smaller relative to their mother than predicted for eutherian neonates (Leitch, Hytten & Billewicz, 1959; Frazer & Huggett, 1974; McKeown, Marshall & Record, 1976). The period of lactation is correspondingly longer with extended postnatal bonding. The pattern of relatively short foetal development and relatively extended lactation is more characteristic of a metatherian reproductive strategy than that of a eutherian (Renfree, 1983; Lee & Cockburn, 1985). Ramsay & Dunbrack (1986) have proposed that physiological constraints associated with

undertaking gestation and lactation while fasting have necessitated such a metatherian-like convergence in bears.

Although most bears have secondarily adopted an omnivorous or herbivorous diet, polar bears, recently evolved from brown bear ancestors (Erdbrink, 1953; Kurten, 1964), have reverted to a carnivorous feeding mode (Hylander, 1978), preying primarily on ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*). Polar bears have also evolved to live on the sea-ice of the Arctic Ocean, an environment qualitatively different from the terrestrial habitats exploited by other bears. One of the most significant environmental differences experienced by polar bears results from the labile nature of sea-ice which leads to spatial and temporal variability in access to resources, primarily seals and mates (Stirling & McEwan, 1975; Smith & Stirling, 1978; Smith, 1980; Ramsay & Stirling, 1986a). Although long-term average sea-ice conditions and productivity are generally predictable, local conditions may vary significantly both within and among seasons (Jacobs & Newell, 1979; Catchpole & Faurer, 1983). Polar bears are therefore obliged repeatedly to search out anew areas of sea-ice habitat where seals are abundant and accessible. In some years, these searches may entail movements of considerable distance (Schweinsburg, Lee & Latour, 1982; Lentfer, 1983). Consequently, neither male nor female bears maintain discrete home ranges as do black and brown bears (Amstrup & Beecham, 1976; Young & Ruff, 1982; Servheen, 1983).

A preliminary study indicated that the population of polar bears inhabiting western Hudson Bay differed in several reproductive parameters from other polar bear populations (Ramsay & Stirling, 1982). Specifically, the mean litter size appeared larger, mean interbirth interval shorter, and overall natality rate higher in western Hudson Bay than in other populations studied. In this paper we describe, using a larger sample size of bears and in greater detail than hitherto, the reproductive productivity of female polar bears from western Hudson Bay. A primary intent was to determine the reproductive characteristics of this population and to generate testable hypotheses to account for differences among populations. Because nutritional status appears to play a major role in regulating the reproductive performance of all species of bears, we paid particular attention to body weight as a possible indicator of nutritional condition. When possible, comparison of measured parameters was made between the bears of western Hudson Bay and those from more northern Canadian populations. Research was based primarily on field studies and samples of bears were captured each year over a six-year-period. In addition to being able to generate cross-sectional reproductive parameters on the population, we also obtained partial reproductive histories of some females, thus generating information on interbirth intervals, cub mortality and pregnancy rate.

The polar bears of western Hudson Bay were initially chosen for detailed study because the region contains the densest concentration of overwintering female bears known in Canada and a traditional denning area that has been known to have been active for at least 200 years (Hearne, 1795; Jonkel, Kolenosky, Robertson & Russell, 1972). At the time we began our research, some information had already been collected for this population from various studies conducted over the preceding 15 years (Stirling, Jonkel, Smith, Robertson & Cross, 1977). These data, although collected with different objectives than in the current study, provided baseline information to assist in planning studies, as well as comparative historical background information. Finally, field logistics from the town of Churchill, Manitoba are less expensive than if conducting similar research at any other potential sites in the Canadian Arctic.

Preliminary descriptions of the reproductive life-history of females in the study population have been given by Stirling *et al.* (1977) and Ramsay & Stirling (1982). Aspects of the behaviour of females using the Manitoba denning region in winter and spring were described by Jonkel *et al.*

(1972), Ramsay & Stirling (1984), and Ramsay & Andriashek (1986). Several studies have reported on some features of the reproductive biology of female polar bears in other populations, particularly those features relating to population dynamics (e.g. Lønø, 1970; Uspenski & Kistchinski, 1972; Stirling *et al.*, 1976; Stirling, Calvert & Andriashek, 1980, 1984; Lentfer, Hensel, Gilbert & Sorensen, 1980; Hansson & Thomassen, 1983; Furnell & Schweinsburg, 1984; Larsen 1985).

## Methods

### *Study populations*

Most captures of polar bears were made on land in the Hudson Bay lowlands of north-eastern Manitoba, Canada. This region lies at the boreal forest-tundra ecotone and is characterized by long, cold winters and short, cool summers (Thompson, 1968; Maxwell, 1986). Hudson Bay freezes entirely each winter, with the exception of an offshore lead system (Lardner, 1968; Danielson, 1971). In summer, all the sea-ice melts (Markham, 1986), forcing bears ashore in a relatively restricted area (Stirling *et al.*, 1977). This results in a high density of bears on land during summer and autumn and allows researchers a relatively high catch-per-unit-effort. Logistic centres for field operations were based at the town of Churchill, Manitoba or in temporary field camps to the south and east of Churchill and within 150 km. Except where noted, all captured bears were located north of the Nelson River at 57° N latitude and south of 58° N latitude. Prior to 1977, most animals handled were captured at or near the town of Churchill as part of a regional bear management programme (Stirling *et al.*, 1977). After 1977, and especially after 1980 when our field work began, most bears were handled away from human habitation.

Capture programmes were carried out during 3 seasons, each determined by the seasonal movements and activities of the bears (Fig. 1). During February and March, 1980–1984 (spring season) adult females with their cubs-of-the-year were handled each year soon after they emerged from overwinter maternity dens. The second sampling period occurred in later July and August, 1981–1985 (summer season) at or soon after the time that all bears were forced ashore from the melting sea-ice of Hudson Bay. The third sampling period was in October and early November, 1980–1983 (autumn season) just before Hudson Bay refroze and all bears, except pregnant females, returned to the sea-ice.

In the spring field seasons, searches were made for bears or their tracks in snow by flying along water courses and lake shores (Ramsay & Andriashek, 1986). The ability to locate bears in spring varied greatly with weather conditions. Field work was discontinued when wind chill values exceeded 2200 watts/m<sup>2</sup> or when visibility while flying was limited. Bears, or their tracks in snow, were most visible on calm, sunny days immediately following a fresh snowfall. Overcast skies or blowing snow made it considerably more difficult to track and locate bears. All bears observed were captured except those few seen too late in the day to allow complete handling before nightfall. Because spring searches were predominantly conducted on land, usually only adult females and their cubs-of-the-year were available for capture. Consequently, males and females one year of age and older, except for females with new-born cubs, were rarely sampled then and only during searches made on the sea-ice.

During the summer and autumn field seasons, all age and sex classes were available for capture. Helicopter searches were then made throughout most of the study region. The population tends to segregate by sex in those seasons, with most males near the coastline and most females and juveniles distributed inland (Stirling *et al.*, 1977; Lunn & Stirling, 1985). In summer, some bears could not be captured because they were found in areas too wet to allow safe immobilization. Most bears sighted were captured, however, although some bias against sampling adult males occurred because of the importance of obtaining as large a sample of females as possible and the distributional differences between sexes resulting in the need to spend more time searching for each female located. We have assumed, however, that female bears of all age and reproductive classes in

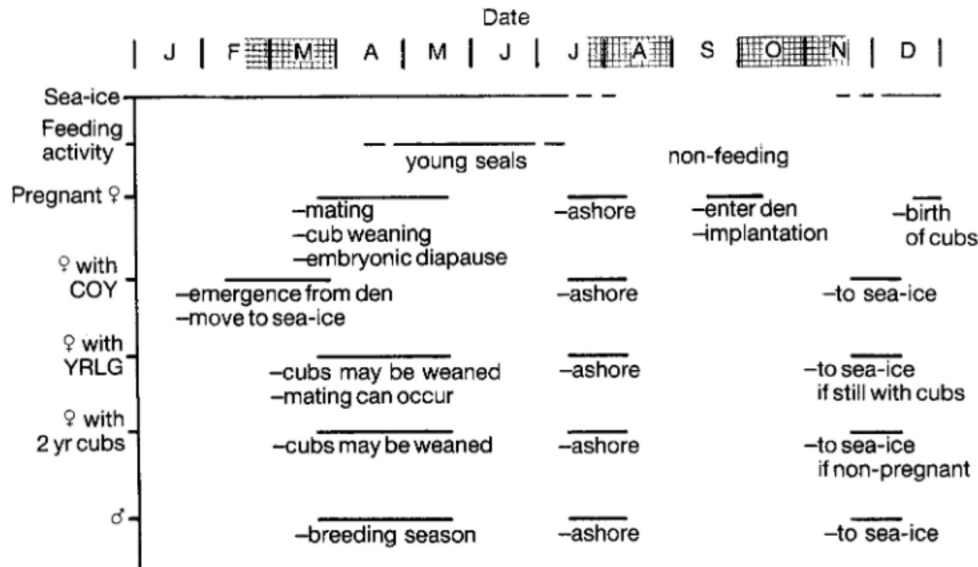


FIG. 1. Schematic view of seasonal activities of polar bears in western Hudson Bay, by reproductive class. Horizontal bars indicate approximate intervals of duration of activities. Seasonal sampling periods are shaded (■) and the presence of sea-ice is approximately indicated. The seasonal occurrence of young, naive ringed seals of the year corresponds with a period of intense feeding by polar bears. COY = cubs-of-the-year; YRLG = yearling cubs.

both summer and autumn were sampled at approximately their frequency in the female component of the population and have pooled samples from these 2 seasons in most of the analyses except for comparisons of body weight.

Calculation of age-specific reproductive rates were made following modifications of the techniques used by Stirling *et al.* (1980) and Furnell & Schweinsburg (1984). Only females with cubs-of-the-year were used to estimate the number of females producing litters in a given year as many females in western Hudson Bay abandon their yearling cubs before the summer sampling period (Ramsay & Stirling, 1982, 1986a). Therefore, inclusion of females with yearlings in estimates of relative cub production in the year of the cubs' birth would bias estimates of reproductive parameters downward because it is not possible to differentiate solitary females that had recently abandoned yearling cubs from females that had not given birth to cubs in the previous year.

The age-specific rate of litter production (LP) was calculated by the formula:

$$LP_x = \frac{\text{No. of females of age } x \text{ with cubs-of-the-year}}{\text{No. of females of age } x}$$

The age-specific mean litter size (LS) was calculated by the formula:

$$LS_x = \frac{\text{No. of cubs-of-the-year accompanying females of age } x}{\text{Total no. of cub-of-the-year litters with females of age } x}$$

An estimate of age-specific natality rate is the product of these 2 reproductive parameters. Stirling *et al.* (1980) calculated LP for females in the year they conceived, whereas we have calculated it for the year they gave birth. The results are comparable, although those presented in Stirling *et al.* (1980) are shifted back one age-class relative to those presented here. Furnell & Schweinsburg (1984) also only considered females with cubs-of-the-year when calculating LP but they do not break their sample up by age-class.

Data collected from live-handled polar bears from more northerly populations in the Canadian Arctic are presented for purposes of comparison or to augment data that could not be collected within the study population because of logistic constraints. These supplementary data were collected as part of other research programmes conducted by the Canadian Wildlife Service and the Northwest Territories Wildlife Service and some have not been published previously. Descriptions of these study regions and methods used to capture bears there are described in DeMaster, Kingsley & Stirling (1980), Stirling *et al.* (1980, 1984), Schweinsburg *et al.* (1982), Furnell & Schweinsburg (1984), and Amstrup, Stirling & Lentfer (1986).

#### *Capture and handling*

Bears were captured alive using standard chemical immobilization methods (Lentfer, 1968; Larsen, 1971). Most animals were located during search operations carried out in a Bell 206B helicopter and subsequently shot from the air with darts containing immobilizing drugs. Bears located in the vicinity of the town of Churchill were captured in baited snares or culvert traps and subsequently drugged, or were shot with immobilizing darts fired from a motor vehicle. Immobilizing drugs used and specific handling details varied somewhat over the 20 years (1966–1985) that data were collected (Ramsay & Stirling, 1986b).

Once safely immobilized, each bear was assigned a permanent and unique identifying number on its first capture by which it could be identified on any subsequent recapture. The identifying number was applied as a tattoo on each upper lip and on a plastic or metal tag attached in each ear (Stirling *et al.*, 1977). Each bear's sex and the age and sex of accompanying bears was recorded. Morphometric measurements were taken and a first premolar tooth extracted for age determination through counts of cementum annuli (Stirling *et al.*, 1977; Grue & Jensen, 1979). A temporary number was painted on the pelage of the back and/or sides using a hair dye. This facilitated identification of individuals from afar during the season of capture. Selected adult females were fitted with radio transmitter collars in the 164 MHz range to facilitate relocation or recapture of the animals when desired. Weights of cubs-of-the-year in spring less than 6 months old were determined to the nearest 100 g using a spring scale. A spring scale was also used to determine body weights, to the nearest kilogram, of a representative sample of bears; these data were then used to generate a best-fit axillary girth-body weight regression (Nagy, Kingsley, Russell, Pearson & Goski, 1984). All body weights of bears reported in this paper, except cubs in spring, were estimated using the regression formula. Axillary girth was measured when the bears were in a sternally recumbent position with limbs extended away from the body and along the longitudinal axis. A cord was passed under the body in the axillary region and the smallest body circumference recorded during an exhalation of the bear. A tension of approximately 600 g was maintained on the cord during measurement.

Not all measurements could be obtained for every bear and some radio-tagged animals were sighted on occasion but not handled. Consequently, for each age and sex class of bear, not all sample sizes were the same for each parameter measured.

Two cubs-of-the-year found dead in spring were kept frozen and air freighted to Edmonton, Alberta. There they were necropsied by Dr D. Onderka of Alberta Agriculture. Standard anatomical and histological necropsy procedures were used.

Blood samples were obtained from free-ranging female bears older than 6 months of age by femoral venipuncture using a 50 ml syringe. Whole blood was immediately transferred to sterile vacutainers and stored at approximately 0 °C until the evening of the day collected. Samples were then centrifuged and the serum removed and frozen at –20 °C until analysis. Serum levels of progesterone were determined at the Reproductive Endocrine Laboratory of the University of Saskatchewan using antisera prepared in rabbits (Foresman & Daniel, 1983; Rawlings, Jeffcoate & Rieger, 1984). All samples were run in duplicate against known standards. Bears were divided into seasonal, age and reproductive classes for comparison of progesterone levels. Those 4 years of age and older were considered adults; those younger than 4 years were considered juveniles. Adult bears were further subdivided by whether they were accompanied by cubs of any age. Juvenile bears were never accompanied by their own cubs. The seasonal strata were the same as those used for other analyses.

All statistical calculations were made using MIDAS (Statistical Research Laboratory, The University of Michigan) or BMDP (Department of Biomathematics, The University of California, Los Angeles) statistical software.

## Results

### *Population description*

Eight-hundred-and-ninety-five individual females including 230 cubs-of-the-year and 90 yearling cubs were captured in the population studied between 1966 and 1985 (Table I). Seventy percent of these females (626/895) were handled between 1980 and 1985, the major years of this study. Eight-hundred-and-thirty-five males have also been captured since 1966, including 205 cubs-of-the-year and 90 yearling cubs. Because bears were handled in three discrete annual field seasons (Fig. 1), an individual could be captured or observed more than once in a single year. Before 1980, and especially prior to 1977, most bears were handled in autumn at or near Churchill, Manitoba as part of a bear monitoring programme (Stirling *et al.*, 1977). Bears near Churchill were significantly younger than bears in the study population captured away from human habitation (Stirling *et al.*, 1977; Lunn & Stirling, 1985). Hence, the apparent absence of older bears in the annual samples prior to 1977 is probably due to biases introduced by the sampling method and does not represent missing age classes from the population in those years.

TABLE I

*Age structure of female polar bears captured in Zone A1, by year in spring and summer/autumn (1966–1985). Bears handled only once in any season. U = unknown age*

Year	Age																								U	Total		
	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23			24+	
1966		1																								1	2	
1967			3							1																	3	7
1968	2	2		2																							6	12
1969	2	6	3	1				1	1	1									1								3	19
1970	1	3	2	3	2			2	2		1				1												7	24
1971	6	3	5	3	4			2				2															5	30
1972	2	3		2	1	1		1																			3	13
1973	1	4	1	1	2			1						1														11
1974	5	5	1	2	1	3		1			1				1												3	23
1975	2	1	2		2	1	1	1	1	1			1														2	15
1976	7	6	2	2	1			3		1		1	1					1									2	27
1977	7	3	6	5	1	2	3	1	1		1	1	1		1	1	1	1			1						4	41
1978	3	1	3	7	1	2	1	2		1		1	1		2				1			1				1	4	31
1979	3	1	3					1		1		1			1				1			1					1	14
1980	22	5	3	1	5	1	3	4		2	2	3		5	2	4	4	3			2	1						72
1981	42	3	3	1	1	1	7	3	5	2	5	4	5	4	4	2	2	5	5			1		1				106
1982	25	15	6	3	1		2	2	1	4	1	3	3	1	3	2	4	4	2	3	2	2		1				90
1983	60	17	13	4	8	6	4	4	7	2	5	5	5	5	10	5	3	5	7	5	8	1	2	2	2			195
1984	31	11	8	3	3	4	1	7	13	1	3	3	1	4	3	2	3	2	3	2	3	2	1	2				111
1985	9		11	5	3	1	1	3	2	1	1		2		4	2	3	1					1			2		52
Total	230	90	75	45	36	22	24	38	34	17	21	23	20	21	31	18	21	24	17	10	16	8	2	4	5	43	895	

*Weight estimation*

Scale weights and axillary girths were available for 138 bears ranging in age from cubs-of-the-year to 18 years. Weights of bears in this sample ranged from 36 to 409 kg and axillary girths ranged from 48 to 165 cm. For both sexes pooled, the best fitting polynomial regression model was:

$$\ln \text{SWT} = 0.02 + (0.062 \cdot \text{AXG}) - (0.000165 \cdot \text{AXG}^2); \quad r_2 = 0.98$$

where  $\ln \text{SWT}$  = the logarithm of scale weight in kg and  $\text{AXG}$  = axillary girth in cm. All weights presented, other than those for cubs-of-the-year in spring, were calculated using this model.

*Age-specific reproductive parameters*

One-hundred-and-eighteen adult females with accompanying cubs-of-the-year and eight solitary adult females were handled in spring in the inland denning region of north-western Manitoba between 1980 and 1984 (Table II). The mean age of females with cubs-of-the-year was 13.6 years (S.E. = 0.44, median age = 14.0 years), significantly younger than that of solitary adult females ( $\bar{x}$  age = 18.0 years, S.E. = 2.4; Mann-Whitney  $U = 276$ ,  $P = 0.05$ ). Inter-year differences in the mean age of bears with cubs varied little (Kruskal-Wallis  $H = 6.61$ ,  $d.f. = 4$ ,  $P = 0.16$ ), ranging between 15.4 (S.E. = 1.1) years in 1982 to 12.0 (S.E. = 1.1) years in 1984. There were significant differences, however, in the mean ages of females with differing sized litters (Kruskal-Wallis  $H = 6.07$ ,  $d.f. = 2$ ,  $P = 0.05$ ). Females with litters of three or four cubs ( $\bar{x}$  age = 16.3 years, S.E. = 0.9) were older, on average, than females with twin cubs ( $\bar{x}$  age = 13.0 years, S.E. = 0.5,  $t_{115} = 2.4$ , Bonferroni  $P = 0.05$ ). There was no significant difference between the mean ages of females with litters of one ( $\bar{x}$  age = 14.3 years, S.E. = 1.2) and two ( $t_{115} = 1.2$ , Bonferroni  $P = 0.7$ ) or three or four ( $t_{115} = 1.2$ , Bonferroni  $P = 0.7$ ) cubs. More than two-thirds of females with litters of three or four cubs were older than the median age. The increased incidence of these largest sized litters in older age classes accounts for the general increase in mean litter size with age.

During summer and autumn, a total of 129 adult females were captured while accompanied by cubs-of-the-year and a further 46 while accompanied by yearling cubs (Table III). No adult females were ever seen accompanied by cubs older than yearlings during these seasons. The average age of females with cubs-of-the-year ( $\bar{x}$  age = 11.4 years, S.E. = 0.4, median age = 11.0 years) did not differ from the age of females with yearling cubs ( $\bar{x}$  age = 11.6 years, S.E. = 0.6, median age = 11.0 years) (Mann-Whitney  $U = 2867$ ,  $P = 0.85$ ). In addition, the average age of females with cubs-of-the-year did not differ from that of females with yearlings in the years that their cubs were born (Mann-Whitney  $U = 1762$ ,  $P = 0.25$ ). The ages of females with different-sized litters did differ significantly, however, for those with cubs-of-the-year (Kruskal-Wallis  $H = 13.5$ ,  $d.f. = 2$ ,  $P = 0.001$ ) but not for those with yearling cubs (Kruskal Wallis  $H = 1.1$ ,  $d.f. = 2$ ,  $P = 0.58$ ). The mean age of females with single cubs-of-the-year ( $\bar{x}$  age = 10.1 years, S.E. = 0.5) was less than that of females with two cubs ( $\bar{x}$  age = 12.4 years, S.E. = 0.6,  $t_{124} = 3.1$ , Bonferroni  $P < 0.01$ ) and three cubs ( $\bar{x}$  age = 14.0 years, S.E. = 0.9,  $t_{124} = 2.6$ , Bonferroni  $P < 0.05$ ).

The average age of females with cubs-of-the-year in summer and autumn was younger than that observed in spring (Mann-Whitney  $U = 9768$ ,  $P < 0.001$ ). Twelve percent (14/118) of the bears with cubs-of-the-year in spring were 20 years or older and 28% (33/118) were 10 years or younger. By summer/autumn, these proportions were 4% (5/129) for bears 20 years or older and 47% (61/129) for those 10 years or younger.



TABLE II

*Age structure of adult females captured in spring in the denning region of north-eastern Manitoba (1980-1984), ordered by number of accompanying cubs-of-the-year. \* Indicates age class of female with quadruplet litter. No females younger than five years of age were seen with cubs in spring when on land*

Age of female with cubs	Age-specific mean litter size for females	Accompanying cubs			
		1 cub	2 cubs	3 or 4 cubs	None (solitary)
5	1.8	1	5		
6	1.7	2	6		
7	1.3	2	1		1
8	1.9	1	6		
9	2.0	1	2	1	
10	1.6	2	3		
11	2.0		3		1
12	2.0		6		
13	1.9	2	5	1	1
14	2.1	1	10	3	
15	2.0	1	5	1	
16*	2.4		7	3	
17	2.0	1	6	1	
18	1.8	3	5	1	
19	2.2		5	1	
20	2.2	1	3	2	1
21	1.3	3	1		1
22	1.0	2			
23	1.5	1	1		1
24					1
25					1
Total	1.9	24	79	15	8

The age structure of female subadult and adult bears handled in the western Hudson Bay in summer and autumn (Table III) allowed calculation of age-specific reproductive parameters for the population (Table IV). Onset of cub production was age-specific and sudden. No three-year-olds and only 5% of four-year-olds were with cubs in summer and autumn, whereas almost 50% of bears aged five years and older had accompanying cubs. Onset of reproductive senescence appeared similarly sudden. No bears older than 20 years in summer and autumn had accompanying cubs even though bears older than 20 years were known to have cubs with them in spring (Table II). Although sample sizes were small, females older than about 20 years apparently experienced higher levels of cub loss before summer than did younger bears.

TABLE III

*Age and litter size of cubs accompanying adult female polar bears, by age class, handled in north-eastern Manitoba in summer and autumn (Aug.-Nov.), 1966-1985*

Age of female	Total no. in each age class	No. with cubs	Cubs-of-the-year			Yearlings		
			1	2	3	1	2	3
2	73	0						
3	46	0						
4	38	2	2					
5	16	8	6	1		1		
6	15	9	4	3		2		
7	34	21	7	7		1	6	
8	28	19	8	5		3	3	
9	13	10	4	6				
10	17	13	5	3		2	3	
11	17	13	3	4	2		4	
12	12	9	5	1	1	2		
13	12	12	3	4	1	1	2	1
14	16	14	6	5		2		1
15	12	10	2	3	2	2	1	
16	12	7	1	5		1		
17	15	11	3	5	1	1	1	
18	9	9		4	1		4	
19	3	1	1					
20	8	7		5			2	
21	2	0						
23	1	0						
24	1	0						
25	1	0						
30	1	0						
Total	402	175	60	61	8	18	26	2
Proportion of total			0.47	0.47	0.06	0.39	0.57	0.04

As both the rate of litter production and mean litter size tended to increase with age, from first parturition to reproductive senescence, overall natality rates also increased with age. The inverse of rate of litter production is the interbirth interval or time between successive litters. The clustering of litter production rates around 0.5 for all productive age classes suggests that a two-year interbirth interval is common.

#### *Interbirth interval and age of weaning*

Sixty-six times in the western Hudson Bay population, adult females were captured on two separate occasions, each time with cubs of different litters (Table V). The mean maximum interval

TABLE IV

*Age-specific rate of litter production, mean litter size, and natality rate for female polar bears calculated using females with cubs-of-the-year in north-eastern Manitoba captured in summer and autumn (August–November), 1966–1985. Methods of calculation of reproductive parameters given in text. Summary statistics for combined age groups listed at bottom of table. Sample sizes in parentheses*

Age of female in year cub born	Age-specific rate of litter production	Age-specific mean litter size	Age-specific natality rate
3	0.0 (46)	0.0 (0)	0.0
4	0.1 (38)	1.0 (2)	0.1
5	0.4 (16)	1.1 (7)	0.5
6	0.5 (15)	1.4 (7)	0.7
7	0.4 (34)	1.5 (14)	0.6
8	0.5 (28)	1.4 (13)	0.6
9	0.8 (13)	1.6 (10)	1.2
10	0.5 (17)	1.4 (8)	0.7
11	0.5 (17)	1.9 (9)	1.0
12	0.6 (12)	1.4 (7)	0.8
13	0.7 (12)	1.7 (8)	1.2
14	0.7 (16)	1.5 (11)	1.0
15	0.6 (12)	2.0 (7)	1.2
16	0.5 (12)	1.8 (6)	0.9
17	0.6 (15)	1.8 (9)	1.1
18	0.6 (9)	2.2 (5)	1.2
19	0.3 (3)	1.0 (1)	0.3
20	0.6 (8)	2.0 (5)	1.3
20+	0.0 (6)	0.0 (0)	0.0
5–9	0.5 (106)	1.4 (51)	0.7
10–14	0.6 (74)	1.6 (43)	0.9
15–19	0.5 (51)	1.9 (28)	1.0
20–24	0.4 (12)	2.0 (5)	0.8
5–20	0.5 (239)	1.6 (127)	0.9

TABLE V

*Maximum interbirth intervals (years) and the minimum mean natality rate for female polar bears captured on two or more occasions with cubs of different litters in north-eastern Manitoba (1966–1985). Proportion of cycles for each time interval in parentheses*

No. of cycles for each interbirth interval						Total no. of cycles observed	Total no. of bear years	Total no. of cubs	Natality rate
1	2	3	4	5	6				
2 (0.03)	26 (0.39)	21 (0.32)	12 (0.18)	2 (0.03)	3 (0.05)	66	193	123	0.6

TABLE VI

*Number of yearling cubs captured in north-eastern Manitoba during summer-autumn (August–November), 1966–1984, by sex and weaning status. Proportion of total number of cubs that were alone shown in parentheses*

Weaning status of yearlings at capture	Sex		
	Female	Male	Both
With mother	37	39	76
Alone	49	44	93
Total	86 (0.57)	83 (0.53)	169 (0.55)

between successive litters, calculated from these longitudinal observations, was 2.9 years. Because some intervening litters were likely undetected, especially during the longer intervals, the actual mean interbirth interval was probably lower. The most striking aspect of these data is that almost 40% of the cycles observed were two years in length. In contrast, of 26 interbirth intervals recorded from more northerly Canadian populations, only five (19%) were two years in length. A female with a two-year interbirth interval would have to mate in the spring of the year when her cubs were about 16 months old (yearlings). Adult females apparently abandon cubs from previous litters before entering their maternity dens, as none in dens has ever been recorded accompanied by cubs of different ages. Cubs would therefore have to be abandoned as yearlings for a female to have a two-year interbirth interval.

Consistent with a high proportion of females having two-year interbirth intervals, 55% of all yearlings captured in the western Hudson Bay population during summer or autumn were independent of their mothers (Table VI). Independent yearling cubs from western Hudson Bay in summer and autumn appeared to have at least as great a probability of survival to two years-of-age or older ( $39/93 = 0.42$ ), a minimum estimate of survival rate, as did yearling cubs still with their mother ( $25/76 = 0.33$ ) (log-likelihood ratio test,  $G = 1.5$ ,  $d.f. = 1$ ,  $P = 0.23$ ). There was no significant difference between sexes in the proportion of yearlings that were independent when captured ( $G = 0.27$ ,  $d.f. = 1$ ,  $P = 0.60$ ). In more northern populations, independent yearlings are rare; only seven out of 210 (3%) were independent in spring. Even the proportion of two-year-old cubs that were independent in spring in those populations, 42% ( $92/225$ ), was lower than that of yearling cubs during summer/autumn in western Hudson Bay.

#### *Body weight of adult females*

Adult females lost weight through summer and autumn, when they were on land and without access to seals (Table VII). Solitary females showed the least change ( $-8\%$ ,  $F_{1, 56} = 1.92$ ,  $P = 0.17$ ), females with cubs-of-the-year the greatest ( $-20\%$ ,  $F_{1, 81} = 40.7$ ,  $P < 0.001$ ), while females with

yearling cubs showed an intermediate weight loss between those seasons ( $-11\%$ ,  $F_{1,31}=6.1$ ,  $P=0.02$ ). Solitary females were significantly heavier than females with cubs in both summer ( $F_{2,81}=20.5$ ,  $P<0.001$ ) and autumn ( $F_{2,87}=49.9$ ,  $P<0.001$ ); females with cubs-of-the-year and yearling cubs were not significantly different in weight, even in autumn ( $t_{87}=1.84$ , Bonferroni  $P>0.05$ ).

The sample of solitary females handled in summer and autumn probably included both pregnant and non-pregnant females. Sixteen adults that were known to be pregnant were captured in the autumn period. Their mean weight was 234 kg (S.E. = 8.2), about 47% (75 kg) greater than that of females with cubs-of-the-year in spring; a difference that presumably represents the average cost of producing and nursing cubs as well as their own maintenance over winter until feeding is resumed.

Adult females from western Hudson Bay in spring, with cubs-of-the-year, weighed an average of 159 kg (Table VII), ranging from 94 to 233 kg. Older females tended to be heavier than younger females:

$$WT = (2.2 \cdot AGE) + 128; \quad r^2 = 0.20$$

where WT represents body weight in kg and AGE is in years. An even stronger weight:age relationship was detected among solitary adult females in autumn, the reproductive class that includes all pregnant females. Once again, older bears tended to be heavier than younger adults

$$WT = (6.5 \cdot AGE) + 171; \quad r^2 = 0.43.$$

Three solitary females that were  $\geq 20$  years of age had a mean weight in autumn of 157 kg (S.E. = 12), about one-half that expected from the weight:age regression for younger adults, and were not used in the regression. It would appear that the sudden onset of reproductive senescence among bears older than 19 years is correlated with a notable drop in body weight. No similar weight:age relationship was apparent for females with cubs-of-the-year or yearling cubs in either summer or autumn (all  $r^2 < 0.02$ ).

Because most sampling in western Hudson Bay was done in the late summer and autumn while in other regions of the Arctic it was done in the spring, comparisons of body weight of animals of different age and sex classes among populations are difficult. The limited comparative data available, however, indicate little difference in seasonal weights between the two regions. Four known pregnant bears from western Hudson Bay that were handled in summer had a mean weight of 274 kg (S.E. = 27); six known pregnant females handled in summer from more northerly populations had a mean weight of 257 kg (S.E. = 8), a difference that was not significant ( $t_8=0.7$ ,  $P=0.5$ ). Females with cubs-of-the-year in the northern populations had a mean weight of 218 kg (S.E. = 12,  $n=18$ ) in summer and 208 kg (S.E. = 14,  $n=4$ ) in autumn; females with yearling or two-year-old cubs had a mean weight of 210 kg (S.E. = 8,  $n=17$ ) in summer and 195 kg (S.E. = 15,  $n=7$ ) in autumn. Females in spring with cubs-of-the-year in the northern populations had a mean weight of 161 kg (S.E. = 2,  $n=191$ ), no different from their counterparts in western Hudson Bay ( $t_{307}=0.5$ ,  $P=0.62$ ).

The greatest increase in weight occurred between the spring and summer sampling periods, with the largest gains achieved by pregnant females. Unfortunately, there were few spring weights for breeding females from the western Hudson Bay population. Twenty-four females from the northern populations were known to have bred in the year of their sampling, at or about the time of their oestrus. They had a mean weight of 166 kg (S.E. = 26), little different from the weight of females with cubs-of-the-year in those populations, but significantly lower than that of known

TABLE VII

*Mean calculated weights (kg)  $\pm$  1 S.E. of female polar bears older than four years captured in north-eastern Manitoba during the on land period, but not captured in the vicinity of the town of Churchill or its garbage dump, (1970-1984). Sample sizes in parentheses. Arrows indicate the weight changes in reproductive classes with time, assuming no losses of litters occurred between seasons*

Accompanying bears	Summer (Jul.-Aug.)	Autumn (Oct.-Nov.)	Spring (Feb.-Mar.)
None	249 $\pm$ 11 (22)	230 $\pm$ 7 (40)	199 $\pm$ 10 (6)
Cubs-of-the-year	190 $\pm$ 5 (46)	152 $\pm$ 4 (37)	159 $\pm$ 2 (118)
Yearling cubs	191 $\pm$ 6 (16)	170 $\pm$ 6 (17)	



PLATE I. Pregnant female polar bear in July, weighing 410 kg. Object on crown of head is a radio-transmitter glued to the fur.

pregnant females in summer/autumn ( $t_{28} = 8.0$ ,  $P < 0.001$ ). Although the sample is not from western Hudson Bay, it would appear that the annual period of peak weight gain for pregnant females occurs after they have mated. Weight gains experienced by pregnant bears during spring hyperphagia can be large. Solitary, and presumed pregnant, females in summer were often obese to the point of inhibiting locomotion (Plate I). One 17-year-old female from western Hudson Bay with three cubs-of-the-year was handled in November, 1983 when she weighed 99 kg. The following July she was without cubs, probably pregnant, and weighed 410 kg, a four-fold weight change in eight months.

In autumn, 1983 known pregnant females were significantly lighter in weight ( $\bar{x}$  weight = 216 kg, S.E. = 9.8,  $n = 8$ ) than were known pregnant bears handled in autumn of other years ( $\bar{x} = 253$  kg, S.E. = 9.5,  $n = 8$ ;  $t_{14} = 2.7$ ,  $P = 0.01$ ). For all other reproductive classes of adults in western Hudson Bay in both summer and autumn weights were lower, but not significantly so, than in other years sampled. However, bears of all age and sex classes in the summer and autumn of 1983 appeared to us, at the time of capture, to be, on average, in poorer condition than at equivalent seasons in the years previous and subsequent. Some qualitative behavioural observations corroborated this view. During autumn, 1983, the town of Churchill recorded a larger number of bears feeding at its dump (Lunn & Stirling, 1985) than in the previous three years and a higher number of human-bear incidents than in any year of the previous decade. Three cubs-of-the-year were found abandoned by their mothers in autumn and near starvation, something seen in no other year.

There were significant differences in mean weights in spring among years ( $F_{4, 113} = 2.4$ ,  $P = 0.05$ ) but not among bears with differing sized litters ( $F_{2, 115} = 1.6$ ,  $P = 0.20$ ). Females with cubs-of-the-year in spring, 1984 were lower in weight ( $\bar{x}$  weight = 145 kg, S.E. = 5.9) than in any other year sampled. The differences among years were significant, however, only between bears handled in 1984 and 1982 ( $\bar{x}$  weight = 171 kg, S.E. = 4.3,  $t = 3.0$ , Bonferroni  $P < 0.05$ ).

#### *Litter size and cub survival*

Litters of two were predominant in western Hudson Bay in spring (Fig. 2) and one litter of four was observed. The mean size of litters in spring was 1.9 (S.E. = 0.05) with little inter-year variation and no significant difference in size among years ( $F_{4, 113} = 0.23$ ,  $P = 0.92$ ). Sizes of litters in spring generally increased with the age of the mother until age 20 years and then declined (Table II). The proportion of females that had litters of two cubs remained relatively constant at about 0.7 for all age-classes between five years and 19 years ( $\geq 20$  years—0.4), whereas the increase in frequency of litters of three or four cubs in the mid-range of age classes was coupled with a decline in frequency of females with litters of one cub in the same age classes.

By summer/autumn (Fig. 2), the mean size of cub-of-the-year litters had declined to 1.6 (S.E. = 0.05), a 17% decline and significantly different from that in spring ( $F_{1, 245} = 18.9$ ,  $P < 0.001$ ). The mean size of yearling-cub litters in summer/autumn was 1.7 (S.E. = 0.05), not significantly different from that of cubs-of-the-year then (Table III). Between spring and summer/autumn, the proportion of triplet and twin cub-of-the-year litters decreased and that of singles increased. Females that had lost their entire litter during that period were not considered when calculating summer/autumn mean litter size, consequently, early cub loss would have been even greater than that indicated by differences in mean seasonal litter size. An approximate estimate of entire loss of cub-of-the-year litters was determined from 19 females captured and two females with radio

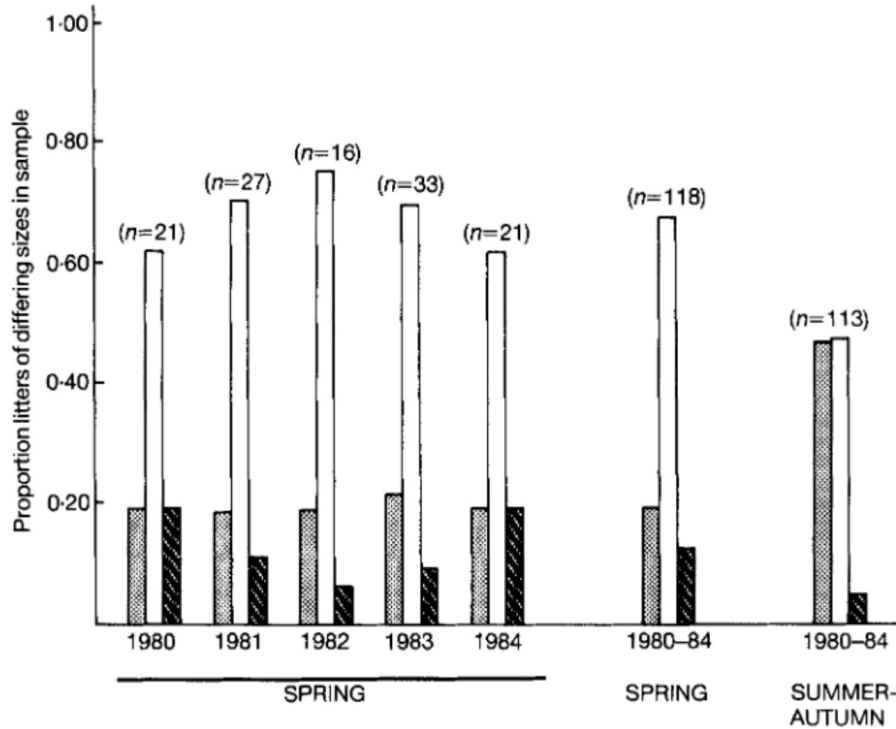


FIG. 2. Frequency of cub-of-the-year litters of differing sizes observed in spring (1980-84) and summer/autumn (1980-85) samples from north-eastern Manitoba. □-Litters of one, ▨-litters of two, ▩-litters of three or four.

TABLE VIII

*Proportion of bears in north-eastern Manitoba initially handled as cubs-of-the-year (1966-1984) and recaptured at least one year later (1967-1985), as a function of litter size or sex and season. Differences in totals result from sex being unknown for some animals*

Size of litter or sex of cubs when initially handled	Proportion recaptured (cubs initially handled in spring)	Proportion recaptured (cubs initially handled in summer/autumn)
1	3/21 = 0.14	14/54 = 0.26
2	11/134 = 0.08	19/94 = 0.20
3 or 4	5/34 = 0.15	9/21 = 0.43
Total	19/189 = 0.10	42/169 = 0.25
Female	7/93 = 0.08	23/95 = 0.24
Male	12/96 = 0.13	19/69 = 0.28

collars sighted in spring that were recaptured or resighted the subsequent summer or autumn. Four (19%) lost their entire litter before the cubs were one year old.

The marked drop in mean cub-of-the-year litter size between spring and summer/autumn



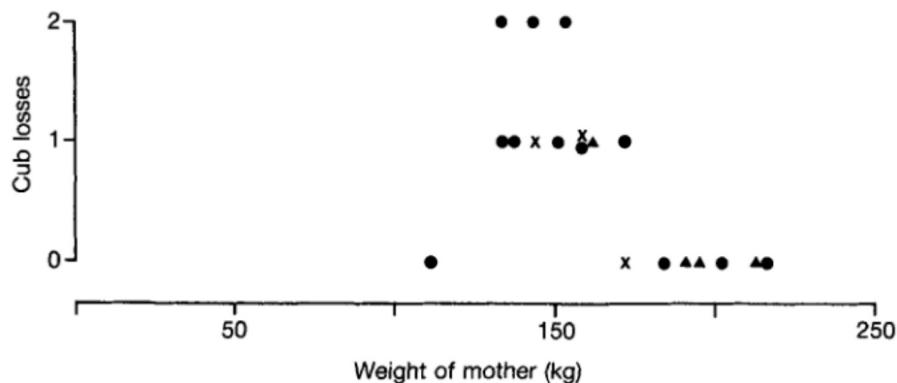


FIG. 3. Number of cubs-of-the-year lost from litters between spring and summer/autumn, 1980–1984 relative to the weight of adult females in spring in north-eastern Manitoba. Females with single (▲), twin (●) and triplet (×) litters in spring.

indicates that considerable cub mortality occurred in the first few months after emergence from dens. The number of cubs initially marked that were subsequently relocated in a later season gives a minimum estimate of cub survival. Absence of a resighting is not confirmation of death, but a resighting is confirmation of survival. Presumably, the longer the interval since initial capture, the greater the opportunity for survivors being resighted. Forty-one (18%) cubs-of-the-year initially captured in spring were recorded alive the following summer or later, at least five months after capture. There was no difference in the proportion of cubs that survived by sex ( $G=0.39$ ,  $d.f.=1$ ,  $P=0.75$ ) or litter size in spring ( $G=3.0$ ,  $d.f.=2$ ,  $P=0.22$ ). No differences in minimal survival rates were found between male and female cubs-of-the-year for either season of capture (in spring  $G=1.3$ ,  $d.f.=1$ ,  $P=0.25$ ; in summer/autumn  $G=0.23$ ,  $d.f.=1$ ,  $P=0.63$ ). Cubs-of-the-year handled in summer/autumn were 2.5 times as likely to be resighted one year or more later than those initially handled in spring (Table VIII), a difference that is highly significant ( $G=14.0$ ,  $d.f.=1$ ,  $P<0.001$ ) and a further indication of extensive cub mortality before summer of their first year. For these analyses, however, cubs handled in spring had a longer interval until the first opportunity for resighting than did cubs handled in summer/autumn.

The estimated survival rate of cubs continued to increase with age. For yearling cubs handled in summer or autumn (1966–1984) the minimum survival rate, to at least the next year, was 0.38 (64/169); that for two-year-old cubs was 0.53 (71/134). Data that are directly comparable to these are unavailable from more northerly polar bear populations as so few animals were captured there in summer and autumn. For bears handled in spring in those populations, however, the minimum rate of survival to at least the next year was 0.16 (53/340) for cubs-of-the-year, 0.21 (38/182) for yearling cubs, and 0.28 (56/197) for two-year-old cubs, suggesting that cub survival rates may be higher in western Hudson Bay than in other Canadian populations for all age-classes of cubs.

A direct measure of early cub mortality in western Hudson Bay was obtained from the 19 adult females that were handled in spring with cubs-of-the-year and subsequently recaptured in summer/autumn of their year of capture. Eleven of these females lost cubs, including four that lost their entire litter, for a net cub mortality of 38% (14/37) (Fig. 3). Females that lost no cubs were significantly heavier in spring ( $\bar{x}$  weight = 185 kg, S.E. = 11.7) than were females that lost at least

one cub ( $\bar{x}$  weight = 150 kg, S.E. = 3.8, Mann-Whitney  $U = 76.5$ ,  $P = 0.007$ ). Females that lost two cubs were similar in weight to those that lost one. The age of the mother appeared to be a less important factor than did weight in predicting cub mortality as there was little difference in age between females that lost no cubs ( $\bar{x}$  age = 13.4 years, S.E. = 1.4) and those that did ( $\bar{x}$  age = 11.4, S.E. = 1.5, Mann-Whitney  $U = 55.5$ ,  $P = 0.34$ ).

Few cubs that died of natural causes were found in western Hudson Bay. Two adult females, aged seven and 11 years, were captured at their dens in spring, each with a single dead cub-of-the-year. These were the two youngest solitary females listed in Table II. Laboratory necropsies on their cubs did not reveal cause of death in either case. The carcass with the younger mother was much lighter in weight (3.2 kg) than the mean weight of living cubs from litters of one (14.2 kg), and, in fact, lighter than any cub captured alive. Time of death relative to parturition was not known, however, and the cub may have died before the sampling period when cub weights would have been lower. The heavier of the dead cubs was of similar weight (12.2 kg) to cubs captured alive. Both carcasses had internal and subcutaneous fat reserves, especially evident in the larger cub. The smaller cub's digestive tract was devoid of ingesta while the larger had milk residues in the intestines. All tissues were found to be negative for *Trichinella* spp. larvae, no significant bacteriological infections were detected, no sign of other internal parasites were found, and no visible lesions were seen. The lighter cub's death may have been a result of the mother being analactic; her mammae were undeveloped and no milk could be expressed. If her cub's death occurred well before our discovery, however, mammary regression would be expected. Analactia seems a less likely explanation for the death of the heavier cub as its mother's anterior pair of mammae were enlarged and milk could be easily expressed.

Wolves (*Canis lupus*) were documented in spring harassing polar bears, and in one case killed a cub of a family travelling to Hudson Bay (Ramsay & Stirling, 1984). One dead cub was found in October, 1982 near Churchill. Necropsy revealed thoracic puncture wounds and haemorrhaging from the liver. The wounds were of a size and conformation that they could have been inflicted by a wolf or a subadult bear.

Some cubs may be abandoned or become prematurely separated from their mother. A single cub-of-the-year was found walking alone in March, 1981. No adult female was found in the vicinity, although tracks of an adult with one cub passed nearby. Ambient temperatures at the time of location were about  $-30^{\circ}\text{C}$  and, to still be alive, the cub must have nursed within a relatively short time prior to discovery (Blix & Lentfer, 1979).

The total number of cubs born each year in the western Hudson Bay population is not known. Assuming no immigration, a minimum estimate of a cohort's size would be the total number of bears, on their first capture, from that cohort during the expected lifespan of its members. The number captured must be an underestimate because of cumulative mortality and because some bears would remain uncaptured. Of the cohorts born between 1980 and 1984 inclusive, 72 bears have been captured to 1985 from the 1980 cohort, 90 from those born in 1981, 93 from those born in 1982, 115 from those born in 1983, and 63 from those born in 1984. We note that 54% of all bears captured from the 1980, 1981, 1983 and 1984 cohorts were first captured as cubs-of-the-year in spring of their birth year, while the comparable figure for 1982 was 33%.

#### *Weight and sex of cubs*

Weights of living cubs-of-the-year in spring from western Hudson Bay ranged between 3.4 kg for a triplet cub in 1981 and 24.5 kg for a single cub in 1980 with an overall mean weight over five

years of 10.9 kg (Table IX). Mean cub weights differed significantly among years ( $F_{4, 210} = 5.35$ ,  $P < 0.001$ ). Cub weights in 1984 were significantly lower than in 1981 ( $t_{210} = 4.5$ , Bonferroni  $P < 0.001$ ) and 1983 ( $t_{210} = 3.3$ , Bonferroni  $P < 0.05$ ) and marginally lower than in 1982 ( $t_{210} = 2.6$ , Bonferroni  $P < 0.1$ ).

Cubs from litters of one in spring were about 30% heavier than were individual cubs from a litter of two and a twin cub about 30% heavier than was a cub from a litter of three (Table IX). Thus, the ratio of mean weight of cubs from adjacent-sized litters was close to 1.3, a pattern consistent for all years save 1982 when the ratio for mean single cub weight to twin weight was 1.0 and that of mean twin weight to triplet weight was 1.8. As expected with a volumetric relationship of 1.3, the straight-line length of cubs varied significantly among litters of differing sizes by a ratio of 1.1 ( $F_{2, 219} = 34.3$ ,  $P < 0.001$ ; single cubs  $\bar{x}$  length = 79.8 cm, S.E. = 1.7; twin cubs  $\bar{x}$  length = 74.5 cm, S.E. = 0.4; and triplet cubs  $\bar{x}$  length = 66.4 cm, S.E. = 1.5). The total weight of cubs from a litter of two was almost 60% greater than that of a single cub and the total weight of cubs from a litter of three was about 80% greater. The total weight of a litter of three was about 10% greater than that of a litter of two.

Cubs from western Hudson Bay that were initially handled in spring and known to have survived to at least one year were significantly heavier ( $\bar{x}$  weight = 12.4 kg, S.E. = 0.5) than those that were not resighted at age one year or older ( $\bar{x}$  weight = 10.6 kg, S.E. = 0.2,  $F_{1, 213} = 10.5$ ,  $P = 0.001$ ). Cubs in spring, 1984, were, on average, lighter in weight than were cubs in other years and had the least opportunity to be resighted, hence they could bias the weight downward of bears never resighted. When only cubs tagged in the springs of 1980 through 1983 were considered, there was still a significant difference in weight between the two classes ( $F_{1, 179} = 6.7$ ,  $P = 0.01$ ).

Even in spring, sexual dimorphism in weight was apparent and female cubs were about 8% lighter than male cubs ( $t_{213} = 1.9$ ,  $P = 0.06$ ) (Table IX). Although the sex ratio of the samples of cubs in spring, including those not weighed, varied among years, from 0.82 to 1.33, it was unity

TABLE IX  
Mean scale weights (kg)  $\pm$  S.E., by litter size and sex in year of capture, of cubs-of-the-year in spring (February–March) in north-eastern Manitoba. Sample sizes in parentheses

Litter size or sex	Year					
	1980	1981	1982	1983	1984	1980–1984
1 cub	14.6 $\pm$ 3.8 (4)	15.5 $\pm$ 1.6 (6)	11.8 $\pm$ 1.6 (3)	14.9 $\pm$ 1.3 (7)	12.0 $\pm$ 3.0 (3)	14.2 $\pm$ 0.9 (23)
2 cubs	10.6 $\pm$ 0.4 (26)	12.2 $\pm$ 0.3 (34)	11.7 $\pm$ 0.6 (24)	11.2 $\pm$ 0.4 (46)	9.3 $\pm$ 0.4 (22)	11.1 $\pm$ 0.2 (152)
3 or 4 cubs	8.5 $\pm$ 0.8 (9)	9.6 $\pm$ 1.2 (9)	6.4 $\pm$ 1.1 (4)	8.7 $\pm$ 0.9 (9)	7.7 $\pm$ 1.0 (9)	8.4 $\pm$ 0.5 (40)
Total	10.6 $\pm$ 0.5 (39)	12.2 $\pm$ 0.4 (49)	11.0 $\pm$ 0.6 (31)	11.2 $\pm$ 0.4 (62)	9.1 $\pm$ 0.5 (34)	10.9 $\pm$ 0.2 (215)
Females	9.3 $\pm$ 0.5 (17)	12.2 $\pm$ 0.7 (26)	10.9 $\pm$ 0.7 (14)	10.7 $\pm$ 0.5 (32)	8.5 $\pm$ 0.8 (17)	10.5 $\pm$ 0.3 (106)
Males	11.5 $\pm$ 0.8 (22)	12.1 $\pm$ 0.5 (23)	11.2 $\pm$ 0.9 (17)	11.7 $\pm$ 0.6 (30)	9.7 $\pm$ 0.5 (17)	11.4 $\pm$ 0.3 (109)

TABLE X  
 Mean calculated body weights (kg)  $\pm$  S.E., by season and sex, of cubs-of-the-year and yearling cubs in north-eastern Manitoba. Sample sizes in parentheses

Age of cub and sex	Season	
	Summer	Autumn
Cub-of-the-year	53 $\pm$ 2	42 $\pm$ 2
Female	(38)	(36)
Cub-of-the-year	59 $\pm$ 3	48 $\pm$ 3
Male	(30)	(23)
Cub-of-the-year	56 $\pm$ 2	44 $\pm$ 2
Total	(68)	(59)
Yearling cub	119 $\pm$ 7	92 $\pm$ 5
Female	(14)	(33)
Yearling cub	133 $\pm$ 9	117 $\pm$ 4
Male	(14)	(31)
Yearling cub	126 $\pm$ 6	104 $\pm$ 4
Total	(28)	(64)

(114 males:114 females) for the combined five years of sampling. The lowest sex ratio occurred in 1984, the year that cub weights were also lowest; however, the sex ratio was also low in 1981 (0.89), the year with the highest mean weight of cubs. No difference in spring sex ratio was discernible among litters of differing sizes ( $G=3.0$ ,  $d.f.=2$ ,  $P=0.22$ ). The sex ratio for cubs-of-the-year captured in summer and autumn was 0.72, and that for yearlings 0.96.

If polar bear twins are primarily dizygotic, then the expected frequency of sex composition of litters of two should be 1:2:1 for all female, mixed sex, and all male litters, respectively. In contrast, if twins are primarily monozygotic, then a 1:1 frequency of all female and all male litters of two would be expected. The observed sex composition of litters of two in spring was 21 all female, 30 mixed sex, and 27 all male, not significantly different from the expected pattern for dizygotic twins ( $\chi^2=5.1$ ,  $d.f.=2$ ,  $0.1 > P > 0.05$ ). Litters of three did not vary significantly from the 1:3:3:1 frequency of sex composition expected if the litters were trizygotic; four all female litters, five with two females and one male, four with one female and two males, and one all male ( $\chi^2=3.5$ ,  $d.f.=3$ ,  $P > 0.1$ ).

Between spring and summer, cubs-of-the-year showed a five-fold increase in weight and then, like adult females, showed a significant decline in weight between summer and autumn during the on-land period (Table X). Yearling cubs showed a similar weight loss during the on-land period. The mean summer to autumn weight loss was about 20% for cubs-of-the-year ( $F_{1,125}=21.4$ ,  $P < 0.001$ ) and 18% for yearlings ( $F_{1,90}=11.1$ ,  $P=0.001$ ). Females were lighter in weight than were males for both age-classes and seasons of sampling, although sexual dimorphism was less pronounced in summer (for cubs-of-the-year  $F_{1,66}=2.3$ ,  $P=0.14$ ; for yearlings  $F_{1,26}=1.6$ ,  $P=0.22$ ) than in autumn (for cubs-of-the-year  $F_{1,57}=3.5$ ,  $P=0.07$ ; for yearlings  $F_{1,62}=14.3$ ,  $P < 0.001$ ). No significant differences were detected among years in the summer or autumn mean weights of cubs of either age.

Yearlings that were known to survive to at least two years of age tended to be heavier ( $\bar{x}$  weight = 119.0 kg, S.E. = 5.2,  $n = 32$ ) than were bears that were not seen again ( $\bar{x}$  weight = 107.1 kg, S.E. = 3.6,  $n = 82$ ;  $t_{112} = 1.8$ ,  $P = 0.08$ ). Solitary yearling females were not significantly lighter in weight ( $\bar{x}$  weight = 88.0 kg, S.E. = 6.3,  $n = 29$ ) than yearling females still with their mothers ( $\bar{x}$  weight = 105.2 kg, S.E. = 5.0,  $n = 27$ ;  $t_{110} = 2.2$ , Bonferroni  $P > 0.05$ ). Similarly, solitary yearling males were little different in weight ( $\bar{x}$  weight = 123.5 kg, S.E. = 4.7,  $n = 34$ ) from those still with their mother ( $\bar{x}$  weight = 125.0 kg, S.E. = 5.5,  $n = 24$ ;  $t_{110} = 0.2$ , Bonferroni  $P > 0.5$ ).

Although a much higher proportion of yearling cubs were independent of their mothers in western Hudson Bay relative to more northerly populations, weights of cubs differed little between the two regions. Yearling females from the northern populations had a mean weight of 114 kg (S.E. = 7,  $n = 14$ ) in summer and male yearling cubs had a mean weight of 130 kg (S.E. = 10,  $n = 10$ ), neither value significantly different from their counterparts in western Hudson Bay (for females  $t_{21} = 0.5$ ,  $P = 0.61$ ; for males  $t_{22} = 0.3$ ,  $P = 0.80$ ).

A crude index of the extent of female investment in cubs is the ratio between weight of litters and weight of mother. This is not an ideal measure of reproductive investment as it does not consider allometric metabolic costs that would be associated with cubs of differing sizes, nor possible differences in foetal growth rates with increasing litter size. We chose to use this simple statistic, however, because: 1) litter sizes varied little among years, even in years with significant differences in cub weights; 2) it is an easily obtained measure that permits comparison to be made among populations; and 3) more detailed information on energetics of polar bears is needed before a better measure of reproductive investment can be applied. In western Hudson Bay, the ratio of litter weight to mother weight was 0.13 (S.E. = 0.004) with little inter-year variation ( $F_{4, 106} = 1.07$ ,  $P = 0.37$ ). Ratios among females with differing litter sizes, however, varied greatly ( $F_{2, 108} = 54.2$ ,  $P < 0.001$ ). Females with one-cub litters had the lowest mean ratio ( $\bar{x} = 0.08$ , S.E. = 0.004), significantly lower than that for females with twins ( $\bar{x} = 0.14$ , S.E. = 0.003,  $t = 8.5$ ,  $d.f. = 108$ , Bonferroni  $P < 0.001$ ) or triplets ( $\bar{x} = 0.16$ , S.E. = 0.007,  $t = 8.5$ ,  $d.f. = 108$ , Bonferroni  $P < 0.001$ ). Females with twins and triplets were more similar ( $t = 2.3$ ,  $d.f. = 108$ , Bonferroni  $P < 0.1$ ).

#### *Serum progesterone concentrations*

Clear differences in the seasonal pattern of serum progesterone (Fig. 4) were observed for solitary females four years of age and older ( $F_{2, 74} = 37.0$ ,  $P < 0.001$ ), with an increase in levels from spring ( $\bar{x} = 1.1$  ng/ml,  $n = 63$ ) through summer ( $\bar{x} = 5.3$  ng/ml,  $n = 19$ ) and autumn ( $\bar{x} = 15.7$  ng/ml,  $n = 28$ ). Little seasonal change was apparent, however, for juveniles (spring  $\bar{x} = 0.3$  ng/ml,  $n = 17$ ; summer  $\bar{x} = 0.4$  ng/ml,  $n = 20$ ; autumn  $\bar{x} = 0.4$  ng/ml,  $n = 34$ ;  $F_{2, 68} = 0.9$ ,  $P = 0.41$ ) or females with cubs (spring  $\bar{x} = 0.5$  ng/ml,  $n = 90$ ; summer  $\bar{x} = 0.4$  ng/ml,  $n = 30$ ; autumn  $\bar{x} = 0.7$  ng/ml,  $n = 34$ ;  $F_{2, 128} = 2.2$ ,  $P = 0.12$ ). Six anomalously low values were recorded for solitary bears in summer and autumn. Two of these bears were from the youngest adult age class (four years) and two were from amongst the oldest (21 years). The remaining two were 12 and 16 years of age. A single 10-year-old female with one yearling cub showed an anomalously high progesterone level in autumn, as did a single three-year-old juvenile. The anomalous female with yearling cub was characterized, at handling, by a swollen and inflamed vulva with copious mucoid vaginal discharge. No other female handled was observed with similar symptoms.

Fifteen adult females in summer and autumn were known to have been pregnant at the time of sampling and all had serum progesterone levels greater than 2 ng/ml. All were solitary when

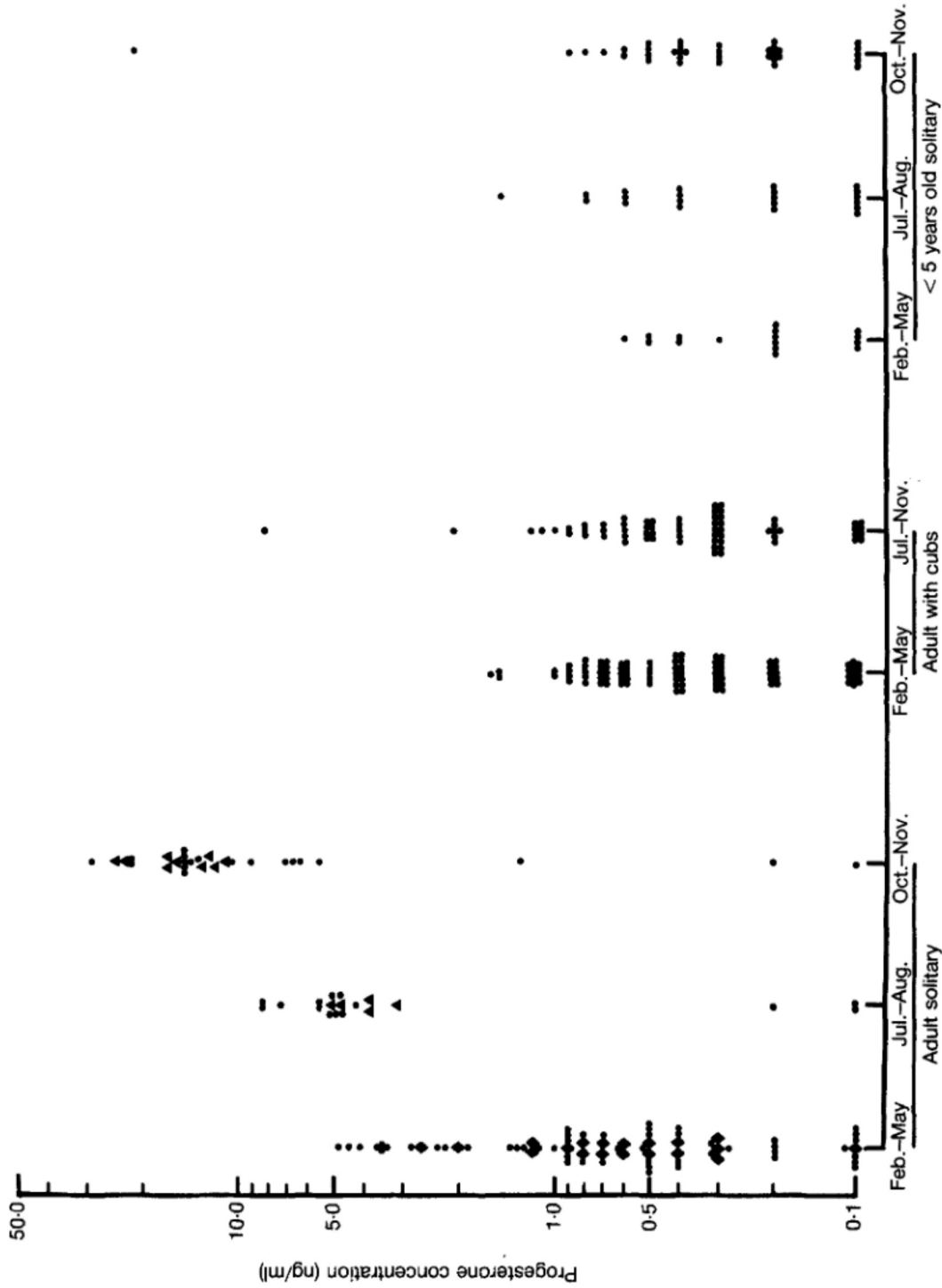


FIG. 4. Serum progesterone concentration (ng/ml) for female polar bears handled in the Canadian Arctic, 1982-1985. Bears ordered by season, age class and reproductive category. Individual samples marked (●) except those of known-pregnant (▲) and known-breeding (✕) females. Note logarithmic scale of serum progesterone concentration.

captured and their progesterone levels were similar to those of most other solitary adult females captured at the same season but whose reproductive status was not known. Eighteen adult females that were without cubs and sampled in spring ( $18/63 = 0.29$ ) were with an adult male consort when captured (Fig. 4). Only one of these females had serum progesterone levels greater than 2 ng/ml, although six other solitary females had levels ranging between 3 and 5 ng/ml, as high as those of known pregnant bears in summer (Fig. 4).

A more fine-scale resolution of temporal changes in serum progesterone levels of solitary adult females within and between seasons is shown in Fig. 5. If the six anomalously low progesterone values of summer and autumn are not considered, then the coefficient of the best-fitting linear regression is 0.8. The spring samples with progesterone values greater than 2 ng/ml tend to be clustered higher than the other spring samples. Samples with these moderately elevated values occur throughout the same period when consorting pairs were observed.

One four-year-old solitary female was captured in September near Churchill, as part of that town's bear deterrent programme, and held in captivity for 51 days until release. Blood samples were obtained in late October on days 42, 46, 49 and 51 of captivity. Serum progesterone levels declined over the sampling period, from 15.0 to 6.4 ng/ml, suggesting that, if pregnant, she may have aborted during captivity and repeated handling. An adult female with two cubs-of-the-year, also temporarily held in captivity, was sampled on the same dates and showed consistently low serum progesterone levels ranging between 0.1 and 0.2 ng/ml.

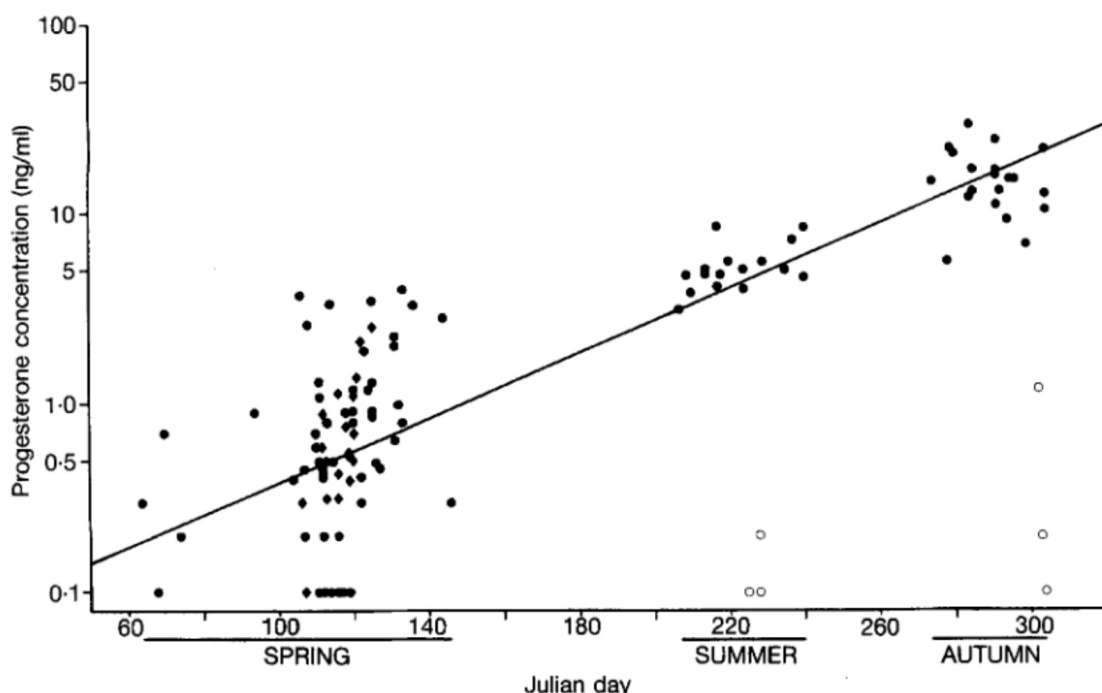


FIG. 5. Serum progesterone values for solitary adult females by day of year. Span of each season of sampling is indicated by a horizontal bar. Six anomalously low values (○) were considered outliers and not used in calculating the regression:

$$\ln y = 0.020 x - 2.94, r^2 = 0.79.$$

### Discussion

Female polar bears inhabiting western Hudson Bay differ from their counterparts in other Canadian populations in a number of important reproductive characteristics. Interbirth intervals of two years are the most common in western Hudson Bay (39%), whereas in other populations they occur with about one-half that frequency (Ramsay & Stirling, 1986a). A two-year breeding interval requires that a female weans her current litter during the spring of the cubs' second year. The high proportion of independent yearling cubs observed in the western Hudson Bay population, relative to other populations, is consistent with that observation. That these independent yearlings have survival rates similar to yearlings still with their mothers shows that a two-year breeding interval is also a viable reproductive strategy. In contrast, independent yearlings are almost totally absent (< 1%) from northern populations, suggesting that most of the females from those populations with two-year interbirth intervals lost their litters before weaning. After premature loss of a litter, a female would be available to mate again in the next breeding season (Ramsay & Stirling, 1986a).

Striking differences in the size of litters also exist between northern and southern polar bear populations. Triplets made up 12% of the cub-of-the-year litters observed in spring from western Hudson Bay, and even one quadruplet litter was captured. In contrast, triplet litters are rare in other Canadian populations; occurring with a frequency of less than 1% (Stirling *et al.*, 1980, 1984; Furnell & Schweinsburg, 1984). The mean litter size of western Hudson Bay litters in spring was between 6% and 15% greater than that of any other Canadian polar bear population recorded (Stirling *et al.*, 1976, 1980, 1984; Furnell & Schweinsburg, 1984).

As would be expected from such major differences in reproductive parameters among populations, the mean natality rate of females in western Hudson Bay was 37–51% greater than that reported in the other populations. There are two major points, however, that must be considered before natality rates calculated in our study can be compared to those of other populations. First, our calculations were made from data collected in summer/autumn whereas, in all other studies, estimates of population reproductive parameters have been determined using data collected in spring. Because cubs are known to die between spring and summer/autumn of their first year, our estimated rate of natality in western Hudson Bay was lower than if spring data had been used for the calculations. Secondly, simple consideration of changes in mean litter size among seasons can only give a minimum estimate of cub loss as the actual extent of loss among seasons depends on how mortality rates vary with litter size (Bunnell & Tait, 1985). This is indicated by comparing different estimations of mortality rate for western Hudson Bay cubs-of-the-year between spring and summer/autumn of their first year. Calculated from the change in mean litter size, the rate of cub mortality was 17%, whereas, based on sequential captures of known families, the cub mortality rate was estimated to be more than twice as great (38%).

A further consideration is that our method for the calculation of the age-specific rate of litter production was somewhat different from that used in other studies. We did not incorporate females with accompanying yearling cubs in our calculation, as was done in most of the other studies reported, because of the high proportion of females in western Hudson Bay that abandoned their cubs in the spring of their second year. Clearly, inclusion of females with yearling cubs into the numerator of our estimate would have underestimated cub production. However, even if, for purposes of comparison, we included females with yearlings in the calculation of age-specific reproductive parameters, the western Hudson Bay population still has an estimated 14% to 33% greater rate of litter production than that reported in other Canadian populations.



Over an intermediate time frame (i.e./ $10^1$ - $10^2$  years), the natality and mortality rates of a mammalian population must balance unless the carrying capacity of the environment changes. A population with a higher natality rate and similar or lower mortality rate than another must necessarily be increasing relatively faster or declining less rapidly. There is not sufficient information at present to determine the stability or rate of growth of any Canadian polar bear population. Consequently, we cannot say whether the western Hudson Bay population is in a phase of positive growth, although that is possible. For a population to sustain long-term growth, one of two conditions, that are not mutually exclusive, must be met. If a population was reduced in the past and the causal agent was no longer in effect, then the population would be expected to recover to its approximate pre-decline level. In the second case, the environment must undergo a change such that a greater number of animals can exist in a particular locale than previously. Without knowledge of historical demographics of the populations, however, differentiating between these two conditions is not possible.

Comparison of reproductive parameters of the western Hudson Bay polar bear population with those from populations that are known to have been reduced in size by heavy hunting might be instructive. In the Svalbard archipelago, hunting was entirely eliminated in 1973 after several decades of heavy hunting and the polar bear population has since been increasing in size (Larsen, 1985). Unfortunately, data collection methods differ between Svalbard and western Hudson Bay and direct comparison of most results is difficult. None the less, the reported mean litter size of cubs-of-the-year in spring (1.83), as well as the frequency of litters of one (0.21), two (0.76), three (0.02) and four (0.01) cubs, was similar to that found in western Hudson Bay and are almost identical to those reported for bears from south-eastern Baffin Island (Stirling *et al.*, 1980), another population thought to have experienced heavy hunting pressure. Determination of interbirth intervals in the Svalbard population is a parameter that would allow additional comparison with other Canadian populations.

Bunnell & Tait (1981) demonstrated an inverse relationship between mean litter size in spring and latitude for 12 polar bear populations, although the populations were not identified. They imply that the increased productivity of vegetation on land in the more southern latitudes is likely to be the critical factor influencing litter size. Two observations run counter to their claim. First, family groups in northern Manitoba appear to spend little time in spring foraging for vegetation (Ramsay & Andriashek, 1986). Even during summer and autumn when the nutritive quality of vegetation would be far superior to that found in spring, bears spend little time feeding and all lose weight, except those few with access to human refuse tips (Knudsen, 1978; Lunn & Stirling, 1985). Secondly, individual growth rates in the more southerly Canadian populations appear little different from those of bears further north, suggesting that the nutritive planes are similar in both. If food for polar bears were more abundant in western Hudson Bay than elsewhere, then one might expect to see increased growth rates of individuals there.

Limited comparative data suggest that body weights, when stratified by season, age and reproductive class, are very similar for polar bears in western Hudson Bay and the more northern Canadian populations. It follows that somatic growth rates are likewise similar between these populations. Thus, cubs that are weaned as yearlings in western Hudson Bay were no heavier than were yearling cubs in the northern populations, virtually none of which were successfully weaned.

At present there is little information on the timing and causes of mortality in young bears. A typical mammalian pattern of juvenile mortality, however, appeared to apply; mortality rates were greatest for young cubs-of-the-year and declined with age until adulthood (Caughley, 1966). Although the actual mortality agents are incompletely described, they appear to affect

preferentially lighter weight individuals.

Clearly, a female could increase her fitness if she were able to reduce her interbirth interval or increase the size of litter that could be weaned without sacrificing her own future reproductive effort, the survival of her post-weaning cubs to reproductive age, or their reproductive success (Altmann, 1983). Unfortunately, problems associated with measuring such costs of reproduction are formidable (Bell, 1980; Clutton-Brock, Guinness & Albon, 1983). Although the life-time reproductive success of any female polar bear remains to be determined, the present data warrant consideration. Female polar bears in western Hudson Bay had a higher mean natality rate than their counterparts in other populations and their cubs appeared to have similar or even lower rates of mortality.

A related issue is whether the behavioural and developmental characteristics of cubs that are weaned as yearlings are different from cubs with a longer period of association with their mother. Increased mortality does not appear to result from early weaning in western Hudson Bay. Perhaps females from there are able to wean cubs as yearlings, not because of more abundant prey, but because the prey are more accessible to yearling cubs (Stirling & Latour, 1978; Ramsay & Stirling, 1982). During spring, and perhaps in winter as well, polar bears capture seals by breaking through a snow crust over seal dens and breathing holes (Stirling & Latour, 1978; Smith, 1980). The density and compression strength of that overlying snow might set a lower limit to the weight a polar bear can be before it can break through to capture prey. A weight limit of this form would effectively constrain cubs that weighed less to dependence on their mothers for food. The polar bears of Hudson Bay live further south than do those of any other population. One consequence is that they are limited to exploiting only annual sea-ice that melts completely each summer. Snow and ice conditions on Hudson Bay may be sufficiently different from that in other Arctic marine habitats to allow successful independence of cubs at an earlier age than in more northerly regions. If our hypothesis is correct, then a principal reproductive parameter, interbirth interval, is regulated by a mechanical feature of the environment; the thickness and compression strength of snow cover.

A prediction of this hypothesis is that the force necessary to break into a subnivean seal construction should be lower in Hudson Bay than in other regions of the Arctic. Further, the compressive force that can be generated by a yearling cub should be sufficient to break into a seal lair in Hudson Bay but insufficient to do so elsewhere. To date, experimental testing of our prediction has not been carried out.

Climatic oscillations of relatively great biological significance and of intermediate duration (i.e./  $10^1$ – $10^2$  years) are a regular feature of the Arctic (Dansgaard, Johnsen, Reeh, Gundestrup, Clausen & Hammer, 1975; review by May, 1979). Such oscillations can have profound effects on marine productivity as well as on the extent and composition of sea-ice (Vibe, 1967; Cushing, 1982). The impact of these environmental changes on mammalian populations, including polar bears, can be profound (Dansgaard *et al.*, 1975; Stirling *et al.*, 1976). If early abandonment of cubs as yearlings is a polymorphic behavioural or physiological trait that occurs in even a small fraction of a polar bear population, then any environmental change that increased the probability of cub survival after abandonment could result in a rapid increase of that trait within the population. The demographic consequences of a reduction in interbirth intervals from three to two years, effected over the 15-year reproductive life of an adult female, would be pronounced. Too little is known of the dynamics of cub abandonment and cub mortality and of climatic fluctuations that may have occurred in Hudson Bay to speculate further.

That nutritional status and food availability are primary constraints on reproductive

performance in mammals is well documented (Sadleir, 1969; McNab, 1980, 1983). The long period of fasting undertaken by bears during gestation and early lactation and the concomitant period of hyperphagia prior to that fast should make the relationship between nutrition and reproduction particularly critical for them. Pregnant females, therefore, might be expected to be most stressed in years of restricted food availability (Rogers, 1976; Stirling *et al.*, 1976). The low mortality rate of adult bears and their long reproductive span suggests that females that experience nutritional stress should adopt a bet-hedging, iteroparous strategy of allocating limited resources to their own maintenance and abandon or limit any current reproductive effort, and increase the likelihood of surviving to reproduce again in the future (Millar, 1977; Rubenstein, 1982). It is reasonable to assume that the amount of stores that a pregnant bear can accrue prior to fasting will dictate the reproductive partitioning of those resources (Woodside, Wilson, Chee & Leon, 1981).

Overwinter weight losses of adult female polar bears in dens were similar to those reported for black bears (Tietje & Ruff, 1980). Females with cubs in spring weighed 31% less than pregnant females in autumn, while females that didn't have accompanying cubs in spring weighed 13% less.

Worthy of note is the temporal pattern of weight changes experienced by female polar bears relative to the timing of oestrus and ovulation. A human female must attain a minimum percentage body fat before menstruation can be initiated and maintained (Frisch, 1984). The caloric content of that fat approximates the energetic costs of pregnancy and early lactation (Frisch & McArthur, 1974). Such a feedback mechanism ensures that a female does not undertake the additional costs of reproduction without sufficient nutrient reserves to ensure her own survival. Similar feedback controls on fertility are well documented in other mammalian species and are regularly exploited in animal husbandry through the practice of 'flushing' (Sadleir, 1969; Clutton-Brock *et al.*, 1983). Bears seemingly follow a different pattern of nutritional feedback in that oestrus occurs before the season of weight gain or maximum attained weight and, hence, prior to the assessment of fat stores available for gestation and lactation. Bears may have shifted the 'decision' on whether to undertake a gestation forward in time from ovulation to implantation. Rogers (1976) proposed that female bears with insufficient body reserves would fail to achieve implantation of blastocysts in the autumn and thus forgo reproduction that winter.

Although the data on body reserves in polar bears are limited, they are consistent with the hypothesis of lowered reproductive investment in some years. No data are available that would support total abandonment of reproductive effort in years of lowered resource availability. In 1983, pregnant females in north-eastern Manitoba were, on average, lighter in weight than in other years of the study. The mean weight of cubs in spring the next year, 1984, was markedly lighter than in other years, while the mean weight of adult females was only marginally lighter. Although it is yet too soon to detect, the 1984 cohort may be relatively absent from future demographic samples because of the increased mortality experienced by cubs of lower than average weight in spring. Sizes of cub litters were no different in 1984 than in other years. Thus, females that did give birth to cubs did not alter the size of their litters in response to reduced nutrient stores. There was no indication that a notably high proportion of pregnant females abandoned their pregnancy in 1983-1984, although if pregnant females did not enter dens in 1983 or abandoned them prior to our spring field season in 1984, they probably would not have been detected.

Polar bears older than 20 years had notably lower natality rates than did younger adults and their cubs may also have experienced higher rates of early mortality than did cubs of younger mothers. Females without cubs found in the Manitoba denning region in spring were often old animals and they frequently displayed atypical behaviours (Ramsay & Andriashek, 1986). During

autumn, the few solitary and hence potentially pregnant, adult females older than 19 years weighed considerably less than would be expected from a simple extrapolation of the body weight:age relationship shown by younger adult females. All these data suggest that reproductive senescence occurs at about 20 years of age in polar bears, contrary to the suggestion of Bunnell & Tait (1981) that females maintain reproductive competency almost throughout their life. Although reproductive senescence is a well known phenomenon in human and laboratory populations, it has rarely been demonstrated in wild populations of mammals as most individuals are removed by various mortality factors before senescence occurs (Talbert, 1977; Rubenstein, 1983; Gouzoules, Fedigan, Gouzoules & Fedigan, 1984). One consequence of large body size, however, is a lowered mortality rate of juveniles and adults, allowing senescence to enter into the dynamics of a population (Calow, 1977). Even so, an increase in mortality rate appears coincident with the onset of reproductive senescence; polar bears older than 20 years were proportionately less frequently found than were younger age classes. About 5% (19/376) of all females older than four years are older than 20 years, although they comprise about 20% of all adult age classes. Functionally, therefore, female polar bears inhabiting western Hudson Bay have a reproductive span of about 15 years, from about five to 20 years of age, similar to that found in other populations (Stirling *et al.*, 1980, 1984; Furnell & Schweinsburg, 1984).

Natality rate was positively correlated with age of mother, at least until 20 years of age. Why this should be so is less clear. Two general hypotheses, not necessarily exclusive, have been proposed to account for such a life-history pattern, common in birds and mammals. The first posits that parents gain experience in acquiring resources and raising offspring with each successive reproductive bout and thus improve their reproductive output with time (Curio, 1983). The second proposes that a female should invest progressively more reproductive effort with age as her future reproductive potential declines (Clutton-Brock, 1984). A suitable measure of reproductive costs in polar bears has, however, not been developed to allow the testing of either hypothesis. It is noteworthy that Kingsley, Nagy & Russell (1983) found that proportional changes in body weight of brown bears over winter increased with age for adult females, even as total body weight increased as well. Older females thus put both absolutely and relatively greater amounts of resources into reproduction than did younger animals.

Bears, like most carnivores, have a zonyary and endotheliochorial placenta (Wimsatt, 1974). Characteristic of this form of placentation is that circulating levels of progesterone during pregnancy are primarily of luteal origin (Levasseur, 1983; Hodges, Bevan, Celma, Hearn, Jones, Kleiman, Knight & Moore, 1984). Lønø (1972) noted that the corpus luteum of the post-implantation polar bear shows extensive histological change and a greater degree of vascularization than does the pre-implantation structure. Although not confirmed, it is tempting to speculate that the elevated serum progesterone levels observed in some solitary adult females in spring reflects production from newly formed corpora lutea of pregnancy. If correct, then systemic progesterone concentration rises rapidly after conception to about 5 ng/ml and stays at that level throughout the pre-implantation period. Implantation occurs in autumn (Wimsatt, 1963; Lønø, 1972) coincident with a 2-3 fold increase in serum progesterone concentration. For late summer and autumn, a similar pattern in serum progesterone levels was noted in two pregnant captive black bears (Foresman & Daniel, 1983).

Eighty-seven percent (41/47) of solitary adult females sampled in summer and autumn showed elevated serum progesterone levels. Four of the solitary bears with anomalously low levels were in the youngest (4 years old) or oldest (> 20 years old) age-classes of adults, both of which are known to have relatively low rates of cub production. The progesterone data suggest that a high

proportion of the potentially pregnant bears in summer and autumn were indeed pregnant. With only two exceptions, serum progesterone levels of females with cubs and juvenile females remained low in all seasons and non-cyclic, suggesting that few, if any, bears in these age-classes were pregnant. This is consistent with serum progesterone levels observed for non-pregnant black bears (Foresman & Daniel, 1983) and support the suggestion by Ramsay & Stirling (1986a) that pregnant females are not accompanied by cubs. Instead, cubs are abandoned by their mothers before or soon after oestrus and mating.

Because polar bears show delayed implantation and enter dens at about the time of implantation, pregnancy can rarely be diagnosed using criteria based on foetal development (e.g. foetal heartbeat detection using doppler ultrasound or rectal palpation for gravid uteri) (Follis & Spillet, 1974; Barrett, 1981). The presence of an ovarian bursa in bears also limits the usefulness of field laparotomy techniques for diagnosing pregnancy (Bush, Wildt, Kennedy & Seager, 1978) because they require ovarian or uterine dissection that might jeopardize the female or her future reproductive performance. A single serum sample, however, obtained in July or later, appears to offer a relatively simple and non-invasive means of diagnosing pregnancy in polar bears. This could be of use in future ecological studies where knowledge of the reproductive status of a free-ranging bear is desired, and also to staff of zoological gardens who attempt to breed polar bears in captivity. The method may also be useful for diagnosis of pregnancy even earlier in the year, soon after mating has occurred. Confirmation of the latter possibility will require endocrine information from bears handled immediately following the breeding season and then subsequently followed to determine whether they had bred and produced cubs the following year.

A rise in luteal progesterone levels in spring, soon after mating, may have nutritional ramifications. Circulating progesterone during pregnancy can affect the rate of weight gain, body composition, and control of lipogenesis in female mammals (reviewed in Hervey & Hervey, 1981). Pregnant female polar bears undergo a large weight gain between the time of oestrus in spring and implantation in the autumn. The nutrient stores represented by the weight gain are the reserves required to maintain the female and her offspring as well as support cub growth during her winter fast. Elevated progesterone levels of pregnant bears during the period of weight gain may proximally mediate storage tissue composition and final weight achieved.

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