ECOPHYSIOLOGICAL STUDIES OF BODY COMPOSITION, BODY SIZE AND REPRODUCTION IN POLAR BEARS.

A Thesis Submitted to the College of
Graduate Studies and Research
in Partial Fulfilment of the Requirements
for the Degree of Doctor of Philosophy
in the Department of Biology
University of Saskatchewan
Saskatoon

By
Stephen Noel Atkinson
Spring 1996

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SUMMARY OF DISSERTATION

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of the requirements for the

DEGREE OF DOCTOR OF PHILOSOPHY

by

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Spring 1996

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ECOPHYSIOLOGICAL STUDIES OF BODY COMPOSITION, BODY SIZE AND REPRODUCTION IN POLAR BEARS (*URSUS MARITIMUS*).

The nutritional ecology of polar bears is characterised by wide annual variation in rates of food intake, ranging from hyperphagia to prolonged periods of fasting. A fundamental adaptation to fasting, thought to be well developed in bears and in particular polar bears, is an ability to minimize the net catabolism of body protein whilst relying upon lipids as a source of energy. Data are presented, however, which suggest that the efficiency of protein sparing in polar bears is not fixed, but varies according to the body composition of individuals at the on-set of a fast. As a simple consequence of their obesity, fatter bears are able to derive a lower proportion of their energy demands from protein catabolism. These findings are discussed with reference to previous studies of fasting in other bear species.

Due to their 'feast-or-famine' existence, female polar bears are one of the few mammals known to regularly fast for extended periods during reproduction. Maternal body condition (fat content) is thus shown to exert a particularly strong positive influence on reproductive performance during such fasts. In addition, maternal age is found to be positively associated with reproductive performance, both indirectly through its relationship to maternal condition and also directly. Evidence that lactational performance is affected by age, independent of condition, is consistent with the hypothesis that reproductive effort increases with age.

As polar bears are polygynous and sexually dimorphic, relative body size probably plays an important role in male mating success. Consequently, theory predicts that mothers in good condition should invest more in male than female offspring, to produce males that are large as adults. Differences in size arising during early life (when cubs are largely dependent on their mothers for nutrition), however, are shown to be a much weaker determinant of relative adult size among males than females. It is proposed that the prolonged growth period of males, relative to females, predisposes growth in males to a greater degree of environmentally mediated variation and thus reduces the potential for mothers to influence the adult size of male offspring through a strategy of sex-biased investment.

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ABSTRACT.

For the polar bear (*Ursus maritimus*), a terrestrial carnivore on the highest trophic level in the Arctic marine ecosystem, periods of nutritional restriction or fasting are a characteristic feature of an annual cycle. The overall objective of my thesis was to examine some of the effects of such a 'feast-or-fast' feeding pattern on the body composition, body size and reproductive performance of this Holarctic ursid.

As a reproductive strategy, pregnant polar bears occupy maternity dens for up to 6 months between late summer and spring. While in dens, maternal nutrient stores meet all maintenance energy requirements and sustain the nutritional demands of gestation and early lactation. Bears are the only terrestrial mammals that, as a normal feature of their life history, are known to go without food during gestation or for significant portions of lactation. I therefore quantified the nutritional costs of this prolonged 'reproductive fast' in polar bears and examined the effects of variation in maternal body condition on reproductive performance. In general, pregnant females were obese prior to entering maternity dens, some individuals containing as much as 1 kg of fat per kg of lean body mass (LBM). Among bears, LBM was positively associated with body fat mass, suggesting that accumulation of lean tissue may be necessary in-order to transport the large fat stores required for fasting. While fasting, body mass decreased by 43% and of the change in body energy content 93% was attributable to loss of fat. Maternal fat content exerted a particularly strong influence on reproductive performance during the denning period. For example, the body weight of cubs when they emerged from dens in spring was very closely related to the size of maternal fat stores. Bears that were fatter prior to denning produced heavier cubs, which would be more likely to survive. Much of the variation in body condition prior to denning was accounted for by age, older females being in better condition. Whether due to the fact that foraging success improves

with experience or that bears of poor quality and condition die at a younger age, reproductive performance within the observed age range (4-21) should thus be highest among older bears.

In general, lactation is the most energetically expensive phase of reproduction. As a result, milk production will be particularly sensitive to food intake and body condition, but may also be affected by other factors such as maternal age. Being among the few species that produce milk while fasting, studies of lactation in bears may provide some unique insights into the trade-offs between maternal condition and reproductive expenditure that dictate reproductive strategies. Besides denning, late summer and autumn is one such period when lactation coincides with fasting in polar bears. The absence of sea-ice during these warmer months denies bears access to their marine mammal prey. Using an index of milk quality that was closely related to daily milk energy yield, I investigated the independent effects of maternal body condition and age on lactation during this ice-free season. In the early stages of fasting, variation in milk quality among females was highly dependent upon percent body fat, but unaffected by total body weight or age. As fasting progressed, declining condition was accompanied by a reduction in milk quality. By the later stages of fasting, however, variation in milk quality was found to be dependent upon maternal age rather than body condition. Irrespective of condition, older bears tended to produce higher quality milk. While lactation in polar bears is clearly sensitive to body condition, these results also provide strong support for an age-specific increase in reproductive effort among females.

Body size is typically a strong determinant of male reproductive success in polygynous mammals such as polar bears. Consequently, theory predicts that mothers in good condition should invest more in male than female offspring in-order to produce large adult males. An underlying assumption of this theory, however, is that early differences in body size among male offspring, such as those apparent by the end of maternal care, will affect their relative adult body size. I tested the validity of this assumption in polar bears and found that, in comparison to females, variation in body size among 2-year-old males was a weak determinant of adult size. I suggest that, in comparison to females, a longer period of growth after maternal care may predispose the adult size of males to a greater degree of environmentally mediated variation. This lack of persistence in relative body size would limit the ability of mothers to affect the adult size of their male offspring, and thus reduce the effectiveness of sex-biased maternal investment as a reproductive strategy in polar bears.

One of the principle physiological adaptations enabling animals to go without food for prolonged periods seems to be a heightened ability to minimize the net catabolism of body protein. Relative to most species, bears, and in particular polar bears, are thought to be highly efficient at avoiding a net loss of protein during their prolonged seasonal fasts. Most data supporting this idea, however, originate from studies in which captive black bears apparently maintained a constant lean body mass while fasting. To further test this proposal, therefore, I quantified changes in the body composition of free-ranging polar bears during the ice-free season. For a sample of 10 adult and sub-adult male polar bears, body condition at the start of the study ranged from 0.12 - 0.58 kg of fat per kg of LBM. Subsequently, over an interval of 79 days, losses of LBM and fat varied considerably among individuals. In contrast to previous studies on fasting bears, catabolism of protein appeared to meet a significant proportion of maintenance energy demands in some individuals. When converted into energetic units, between 74 - 99 % of the observed losses in body energy content were attributable to the catabolism of body fat. Furthermore, bears that derived the highest proportion of their energy needs from lipid stores, were those that were relatively fat when first captured. I suggest that in polar bears, and ursids in general, the previously noted ability to minimize protein loss during extended fasts is in part dependent upon the extraordinary magnitude of fat stores that some individuals can accumulate in seasons when food is abundant.

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1. GENERAL INTRODUCTION.

The polar bear (*Ursus maritimus*) is a large quadrupedal mammal that has evolved to exploit the productivity of a marine ecosystem. The most carnivorous of the ursid species, polar bears spend a majority of their lives on the sea-ice of Arctic and sub-Arctic regions where they prey upon marine mammals, primarily ringed seals (*Phoca hispida*) (Smith 1980; DeMaster and Stirling 1981). The distribution and abundance of seals, and their vulnerability to predation, however, is subject to considerable short- and long- term variation due to factors such as ecosystem productivity and sea-ice conditions (Stirling, Archibald and DeMaster 1977a; Smith and Stirling 1978; Hammill and Smith 1989; Hammill and Smith 1991). As a result, the nutritional ecology of polar bears is characterised by wide variation in rates of food intake, ranging from hyperphagia to prolonged periods of fasting. The overall objective of my research was to investigate the effects of such a 'feast-or-fast' existence on the body composition, growth and reproductive performance of polar bears.

Each year, food availability for polar bears reaches a peak in spring (April/May) when large numbers of naive young seals, in their birth lairs, are particularly susceptible to predation (Stirling and Archibald 1978; Hammill and Smith 1991). Polar bears feed extensively during this season and are thought to deposit large nutrient stores essential for survival later in the year when food is less abundant (Watts and Hansen 1987; Ramsay and Stirling 1988; Messier, Taylor and Ramsay 1992). In late summer, for example, most bears have little or no access to seals due to the break-up and melting of the sea-ice.

No where is this 'ice-free season' more prolonged, and the reduction in availability of prey so complete, than at the warmer lower latitudes of the polar bears' geographical range. In sub-Arctic regions such as western Hudson Bay, where research for this thesis was conducted, all bears are forced onto land as the sea-ice melts completely in late July (Stirling et al. 1977bb; Derocher and Stirling 1990). While on land, bears have little or no access to food and are thus obliged to fast for up to 4 months, until late October or early November, when most individuals return to the newly formed sea-ice to feed (Derocher, Andriashek and Stirling 1993b; Ramsay and Hobson 1991). Even after returning to the sea-ice, food availability during the winter may be low and bears are thought to feed infrequently (Messier et al. 1992).

Like many sexually dimorphic mammals, polar bears appear to have a polygynous mating system and parental care is provided exclusively by females (Ramsay and Stirling 1986; Ramsay and Stirling 1988). In contrast to most mammals, however, a significant proportion of maternal investment occurs at times when, or locations where, food is not available. Unlike other ursid species, only pregnant polar bears over-winter in dens (Ramsay and Stirling 1988; Messier, Taylor and Ramsay 1994). While other bears (including females with cubs) return to sea-ice at the end of the ice-free season, pregnant bears enter dens where they remain until spring. During denning, adult females fast whilst also expending nutrients on gestation and early lactation. Other than some mysticete whales, bears are the only species known to fast during gestation (Frazer and Huggett 1973; Ramsay and Dunbrack 1986) and the only terrestrial mammals that go without food for an extended period during lactation (Oftedal 1993). Among marine mammals, some phocid seals and mysticete whales do not feed for all or significant part of lactation (Oftedal 1993). Ironically, therefore, the reproductive cycle of female polar bears has some key features in common with the reproductive patterns of their marine mammal prey.

Current knowledge about the nutritional costs, constraints and adaptive strategies associated with attempts to reproduce while fasting stems largely from studies of marine mammals (see reviews by Iverson 1993; Oftedal 1993). Relatively little is known about the 'reproductive fasts' of bears (Watts and Hansen 1987; Derocher, Andriashek and Arnould 1993a; Oftedal et al. 1993; Arnould and Ramsay 1994; Samson and Huot 1995). Chapter 3 of my thesis focuses on the early stages of reproduction in polar bears, when pregnant females occupy dens. I quantify the size of nutrient stores that pregnant bears accumulate prior to denning and investigate some of the factors that affect the accumulation of these nutrients. The nutritional costs of this prolonged fast are also estimated and the impact of variation in maternal condition on reproductive performance is examined. Sitting at the highest trophic level of the arctic food web, polar bears have no predators except man. Adult mortality is low and females may live for more than 20 years (Ramsay and Stirling 1988; Derocher 1991). The long reproductive life span of females introduces the potential for age and experience to exert a considerable influence on reproduction (Pianka 1976; Clutton-Brock 1984; Derocher and Stirling 1994). Chapter 3 considers the effects of age, in particular, as a factor affecting maternal body condition and reproductive performance in pregnant bears.

After emerging from dens in spring, female polar bears may continue to lactate until cubs are as old as 2-3 years (Ramsay and Stirling 1988). This long lactation period may thus encompass several ice-free seasons, during which females continue to lactate while fasting. Chapter 4 looks at variation in lactational performance during the ice-free season. Specifically, this section of the thesis attempts to tease apart the independent effects of maternal condition and age on milk production. Based on predictions derived from life-history theory, about reproductive strategies in iteroparous species (Gadgil and

Bossert 1970; Pianka and Parka 1975; Pianka 1976), evidence of an adaptive age related change in maternal reproductive effort is sought.

After becoming independent of their mothers, polar bears continue to grow for a number of years before attaining adult body size (Kingsley 1979; Derocher 1991). It is these juvenile years between independence and adulthood that are the subject of chapter 5. In polygynous mammals such as the polar bear, the reproductive success of males is dependent largely on factors, such as relative body size, which determine competitive ability in intra-sexual contests for access to mates (Clutton-Brock, Albon and Guinness 1988; Le Beouf and Reiter 1988; Haley, Deutsch and Le Beouf 1994). Under these circumstances, maternal investment theory predicts that mothers in good condition should invest more in male than female offspring, in-order to produce males that are large and reproductively successful (Maynard-Smith 1980; Charnov 1982; Clutton-Brock and Albon 1982; Frank 1990). One of the fundamental assumptions of this theory is that differences in body size apparent in early life (such as might result from variation in the level of nutrition received from mothers) persist over the juvenile years and into adulthood. This assumption, however, has rarely been tested in studies of polygynous mammals (Clutton-Brock, Guinness and Albon 1982; Green and Rothstein 1993). Given the level of sexual dimorphism, current knowledge of their mating system and access to a set of longitudinal data on changes in the body size of individuals, polar bears are an ideal species in which to address this question.

One of the principle adaptations enabling any animal to go without food for extended intervals is the ability to minimize catabolism of the body's protein reserves (Castellini and Rea 1992). Relative to many other species, bears, and in particular polar bears, are thought to be highly efficient at conserving protein when fasting (Nelson 1987; Ramsay, Nelson and Stirling 1991). However, data documenting rates of fat and protein catabolism in fasting polar bears, have yet to be presented in support of this proposal. In-order to assess the efficiency of protein sparing in polar bears, chapter 6 quantifies changes in the body composition of fasting male bears, in which there are no confounding nutrient expenditures on gestation or lactation. The use of free-ranging bears as subjects, also provides insight into natural variation in the effectiveness of this physiological adaptation to fasting.

2. STUDY SITE AND GENERAL METHODS.

Data collection for the research took place near the town of Churchill, Manitoba (Canada), in an area bordered by the Churchill and Nelson rivers and the western-coast of Hudson Bay (57°00' to 58°50'N latitude and 92°25' to 94°15'W longitude (Fig. 2.1). In comparison with other parts of western Hudson Bay, polar bears can be found at high densities in this area when they come ashore for the ice-free period each year (Stirling et al. 1977b; Derocher 1987). In addition, an inland portion of the study site is known to be an area where pregnant polar bears have traditionally denned in relative proximity to one another (Ramsay and Stirling 1990). The study site was therefore selected as the most cost effective location at which to sample bears.

The study site is situated in a transitional zone (ecotone) where the northern edge of the boreal forest meets the tundra and coastal plains (Ritchie 1960). The inland habitat consists of sparse woodland intermingled with lichen covered tundra, peat bogs, numerous shallow ponds, and creeks or small rivers. Nearer the coast, gravel beach ridges and grassy sand dunes predominate. In late-summer, bears that have just come off the receding sea-ice are usually concentrated along the coastal habitats. As the ice-free season progresses, the distribution of bears changes and exhibits some degree of segregation by age and sex. In particular, adult females, either solitary or with cubs, tend to move inland while adult males remain on the coast (Derocher and Stirling 1990). Towards the end of the ice-free season (late October), most bears that are inland (except pregnant females) return to the coast as the sea-ice starts to reform. Pregnant females

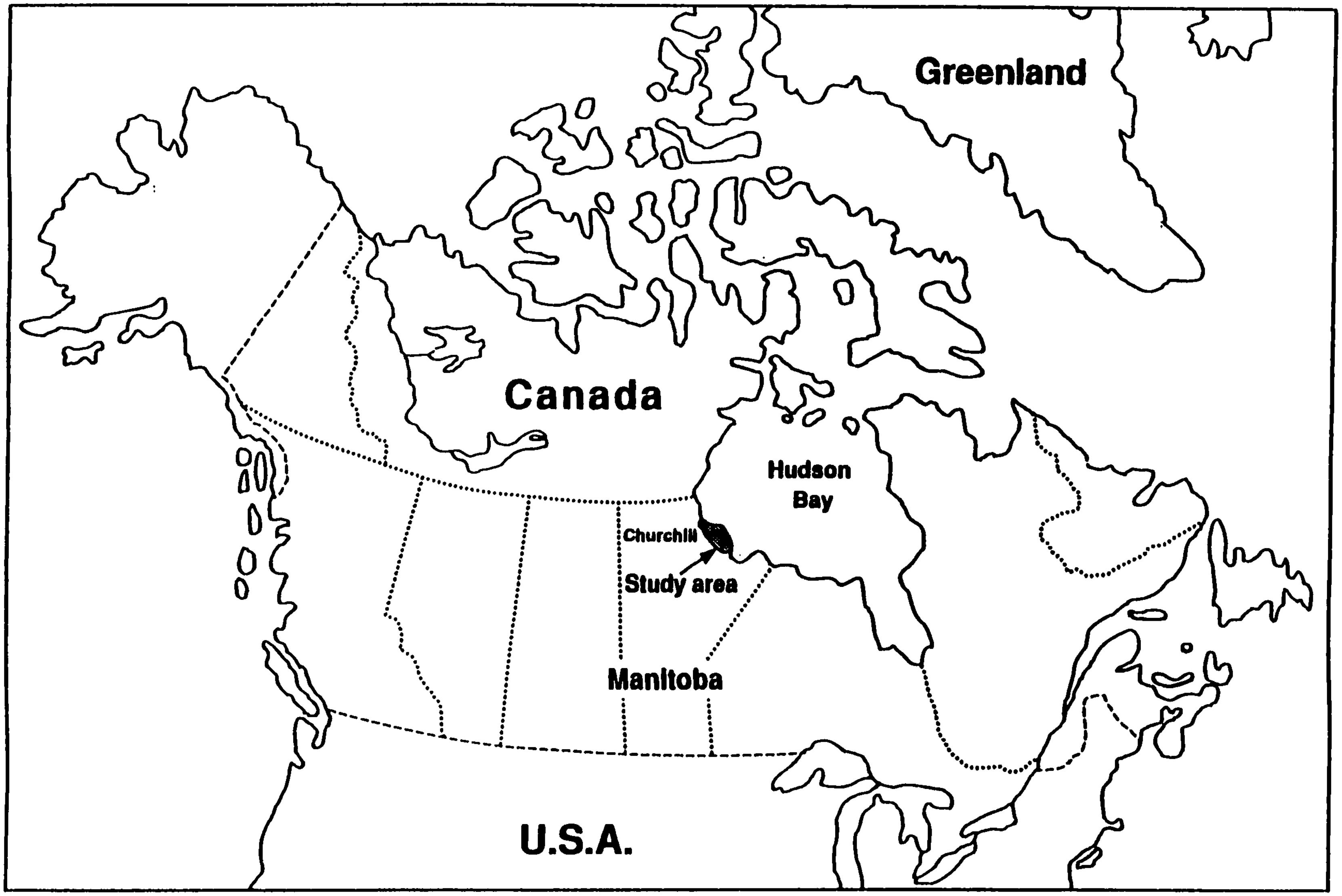

Figure 2.1. A map indicating the location of the study site.

remain in the inland denning area where they overwinter (Ramsay and Stirling 1988; Ramsay and Stirling 1990).

2.1 Location and capture of bears.

Bears were located during aerial searches of the study area in a Bell 206B helicopter. Once sighted, each animal was immobilized using the drug Telazol administered at a dose of approximately 8 mg/kg of estimated body mass (Stirling, Spencer & Andriashek 1989). In the case of bears > 12 months of age, the drug was delivered via injection from a projected dart. Most cubs < 12 months (cubs-of-the-year) were drugged by means of a syringe attached to a pole, but some larger individuals were darted. Additional doses of Telazol were administered as required during the handling procedure.

2.2 Marking and identification.

For subsequent identification, each bear was assigned a unique number. This number was printed on a set of tags that were attached to the ears and was also applied as a green lip tattoo on both the left and right sides of the upper lip. Many bears in the study area had been handled in previous years by other researchers and were already marked with identifying numbers. Consequently, it was not necessary to mark these recaptured bears when handled in the present study.

2.3 Estimation of age.

Data on the ages (years) of bears at time capture were collected. Since all polar bear cubs are born around early December (Derocher, Andriashek and Stirling 1992; Messier, Taylor and Ramsay 1994), cubs-of-the-year were easily distinguishable from older cubs by their body size and patterns of tooth eruption. For some bears older than 12 months, age was known because they had been previously captured as cubs-of-the-year. In other cases, a vestigial premolar tooth was extracted. The tooth was then thin sectioned and age was determined by counting annuli in the cementum (Grue and Jensen 1979). The accuracy of this technique has been verified by counting annuli in teeth from known age bears (Calvert and Ramsay in press).

2.4 Weighing.

At some point during handling, each bear was placed in a nylon net and weighed (±450g) by means of an electronic load cell (Senstek, Saskatoon) suspended from an aluminium tripod.

2.5 Body composition.

For many bears, body composition at time of capture was measured on the basis of a two compartment model in which body mass is composed of fat and fat-free or lean body mass (LBM). Following the protocol detailed by Farley and Robbins (1994) for determination of body composition in bears, total body water (TBW) pool size was determined *in vivo* using the isotopic dilution technique (Reilly and Fedak 1990; Rumpler, Allen and Ullrey 1987). Immediately upon capture, a catheter was inserted into either the sub-lingual or jugular vein and a blood sample (10 ml) was taken in-order to establish background isotope concentrations in the bears' body water. At a dose of approximately 0.5g/kg of body mass, a measured (±10mg) amount of deuterated water (^2H_2O) of 99.9% purity (Isotec Inc. Miamisburg, OH, USA) or 99.85% (Aldrich Chemicals) was then administered intra-venously via a syringe connected to the catheter. The syringe and catheter were back washed with blood to ensure that all the isotope was flushed into the vein. A second blood sample was subsequently taken at 130-220 minutes post-injection, after the isotope had equilibrated with body water (Farley and Robbins 1994).

All blood samples for TBW determination were collected in evacuated tubes without anticoagulants and kept cool until they could be centrifuged for ten minutes. Serum fractions were then pipetted into cryogenic vials and frozen at -20°C within 12 hours of blood collection. Samples were later stored at -70°C until analysis. Upon returning to the laboratory, serum was sublimated under high vacuum (Byers 1979) and the resulting water fraction collected. The concentration of deuterium in serum water was determined by infra-red spectrophotometry using a Miran 1FF IR analyser (Foxboro Co., East Bridgewater, MA, USA). The TBW pool size (kg) of each bear was then calculated according to the following equation;

$$TBW = [M_i \div D_i] \times [I_i \div (E_{bw} - B_{bw})] \times 10^{-3} \qquad \text{(Eqn. 2.1)}$$

Where M_i is the mass of isotope injected (g), D_i the density of the isotope injected, B_{bw} the background concentration (measured in parts per million; PPM) of the isotope in bear water prior to injecting the dose of isotope, I_i the concentration of isotope injected, and E_{bw} the concentration of isotope in bear water at equilibration.

Estimates of total body water derived from dilutions were expressed as a percentage of total body mass (TBM) and applied to a regression equation (2.2) which describes the inverse relationship between percent total body water (PBW) and percent body fat (PBF);

$$PBF = 96.85 - [1.33 \times PBW] \qquad \text{(Eqn. 2.2)}$$

This equation (2.2) was derived by calibration of the dilution technique with whole body chemical extractions on black (*U. americanus*) and brown bears (*U. arctos*) (Farley & Robbins 1994). In these two species, isotopic dilutions are known to estimate PBF with a standard error of 2.7 %. A similar accuracy was assumed for polar bears. Values for PBF were also expressed in kilograms with the remainder of body mass being accounted for by LBM.

2.6 Statistics.

Data were analyzed using a combination of parametric and non-parametric statistics, following procedures outlined in Sokal and Rohlf (1981) and Siegel and Castellan (1988). Statistical tests were performed using either SAS (SAS Institute 1988) or SPSS statistical software. Unless stated, tests were two-tailed and values of $p < 0.05$ were considered significant. Means are presented in text and tables with one standard error.

3. THE EFFECTS OF PROLONGED FASTING ON THE BODY COMPOSITION AND REPRODUCTIVE PERFORMANCE OF PREGNANT FEMALE POLAR BEARS (*URSUS MARITIMUS*).[1]

3.1 Introduction.

As part of their annual cycles, many animals experience seasonal periods of fasting or nutritional restriction when food resources are scarce or unavailable (King and Murphy 1985). Some of the longest and most nutritionally demanding fasts, however, are those seen in species such as bears, penguins and seals, which occur when reproductive activities coincide with seasons of low food availability, or are intense enough to preclude foraging (Mrosovsky and Sherry 1980; Costa et al. 1986; Robin et al. 1987; Deutsch, Haley and Le Boeuf 1990; Boyd and Duck 1991; Oftedal 1993). For example, most Holarctic bears (genus *Ursus)* enter dens in autumn where they remain until the spring (Johnson and Pelton 1980). Although bears do not have access to food while over-wintering in dens, females that are pregnant will give birth to and suckle offspring (Oftedal et al. 1993). Thus, at a time when all nutritional requirements are met from body stores, adult females must sustain the additional costs of gestation and the first two to three months of lactation. Consequently, reproductive performance will be largely dependent upon the magnitude of nutrient stores that female bears are able to deposit during bouts of extensive feeding prior to denning.

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[1] *A version of this chapter has been published. Atkinson, S.N. and Ramsay, M.A. (1995). Functional Ecology 9:559-567.*

Perhaps one of the longest 'reproductive fasts', not only among ursids but mammals in general, is that experienced by pregnant polar bears at the lower latitudes of this species geographical range. Unlike other ursid species, only pregnant polar bears regularly occupy dens over the winter (Ramsay and Stirling 1988; Messier, Taylor and Ramsay 1994). In areas such as the study site in western Hudson Bay (Chapter 2), pregnant polar bears commence fasting in late summer (when forced ashore by the melting of the sea-ice), enter maternity dens in the autumn (Sept/Oct) and eventually emerge in spring (March) with their new cubs (Chapter 1). In total, therefore, these parturient females may fast for up to 8 months, including a 2-3 month pre-denning period and 5-6 months of denning.

Little is known about the nutritional costs that pregnant polar bears must incur in-order to fast for such a prolonged period and still reproduce successfully (Watts and Hansen 1987). The objectives of the present study, therefore, were to; (1) Compare the magnitude of nutrient stores in pregnant bears with those of females at later stages of the reproductive cycle, (2) Examine some of the factors (ecological and physiological) which affect the accumulation of these nutrient stores, (3) Quantify changes in the body composition of pregnant females over their pre-denning and denning fast, (4) Assess the impact of variation in maternal condition on reproductive performance at this early stage of the reproductive cycle.

3.2 Methods.

Field work was conducted at the study site in western Hudson Bay (Chapter 2) between 1989 and 1994. From late July through early November (the ice-free period), adult females either solitary (and suspected of being pregnant) or accompanied by offspring were located and immobilized using standard techniques (Chapter 2). Solitary females were handled before they had entered maternity dens. Once fully immobilized, all bears were ear-tagged, lip tattooed, weighed and if necessary a tooth was extracted for aging (Chapter 2).

3.2.1 Determination of body composition.

The body composition of each bear was determined by isotopic dilution as previously described (Chapter 2). In addition, between 1991 and 1993, body composition in some bears (including all solitary females) was also determined by a secondary technique known as bioelectrical impedance analysis or BIA (Kushner 1992). For BIA, bears were kept well anaesthetized and placed on a plastic sheet to reduce the loss of electrical current into wet ground. Each individual was positioned in a sternally recumbent position and the snout-vent length (SVL) measured as the distance between the tip of the nose and the base of the tail, while following the dorsal contours of the body. Whole body resistance (WBR) was then measured with a Model 101A impedance meter (RJL Systems, Detroit, MI), using the snout to tail electrode configuration described by Farley and Robbins (1994). This arrangement of electrodes minimized potential errors resulting from variation in the placement and movement of limbs. Values for SVL and WBR were then applied to a regression equation to estimate TBW (kg);

$$TBW = -1.86 + [0.231 \times (SVL^2 \div WBR)] + [0.074 \times TBM] \qquad \text{(Eqn. 3.1)}$$

This equation (3.1) was obtained by calibration of the BIA technique with estimates of TBW derived from isotopic dilutions on polar bears (Farley and Robbins 1994). The results of equation 3.1 were then applied to equation 2.2 to estimate PBF. The accuracy of bioelectrical impedance analysis is affected by a number of factors that are difficult to standardize, such as depth of anesthesia, extremes of ambient temperature, moisture (rain/humidity) and operator experience. When examining body composition data, therefore, values obtained from isotopic dilutions were used in preference to values derived from BIA.

3.2.2 Pregnancy determination.

Like some other carnivores, polar bears delay implantation (Wimsatt 1963). Mating takes place in the spring (April-May) but, in the study population, blastocysts do not implant until late September through early October (Derocher, Stirling and Andriashek 1992). Pregnancy in solitary adult females can, however, be diagnosed prior to implantation by examination of serum progesterone levels (Ramsay and Stirling 1988; Derocher et al. 1992). For each solitary bear, therefore, a blood sample was drawn from the femoral vein prior to injection of deuterated water. Blood was kept cool until it could be centrifuged for ten minutes. Serum was then removed and frozen within 12 hours of blood collection. Samples were later stored at -70°C until analysis. Serum progesterone concentrations were determined by radioimmunoassay (Rawlings, Jeffcoate and Reiger 1984) at the Department of Veterinary Physiological Sciences, W.C.V.M., University of Saskatchewan. Bears with progesterone levels exceeding 2.5 ng/ml were considered to have been pregnant at time of capture (Derocher et al. 1992).

3.2.3 Relocation and recapture of bears after denning.

Each spring, around the time of den emergence (March), efforts were made to locate bears that had been solitary the previous ice-free season. In particular, during both 1992 and 1993, each solitary adult female captured during the ice-free period was fitted with a radio-collar (Telonics Inc., Mesa, Az.). I then attempted to relocated and recaptured these bears, along with their 3 month old cubs, as they emerged from dens in March of the following years. In addition, a number of adult females not previously handled in the study were captured while leaving dens during March of 1994. All adult bears were weighed and their body composition determined by isotopic dilution or BIA, as previously described. The litter size and body mass (±450 g) of cubs accompanying each mother was noted.

3.3 Results.

3.3.1 Body composition during the ice-free period.

Body composition was determined by isotopic dilution for a total of 63 adult female polar bears captured during the ice-free period. Of these, 24 were solitary and 39 were accompanied by offspring. From progesterone levels, four of the solitary females were diagnosed as non-pregnant and excluded from further analyses. Body composition data for the remaining 59 animals are summarized with reference to their reproductive status (pregnant or with cubs) in Table 3.1. Mean julian day of capture was not significantly different between pregnant females and those with offspring ($t = 1.178$, $d.f. = 57$, $P > 0.2$). Pregnant bears were significantly heavier in fat, lean (LBM) and total body mass (TBM), and were also relatively fatter than females with offspring (Table 3.1).

Animals ranged in age from 4 to 24 years. Age data were log transformed to approximate a normal distribution. When age was used as a covariate in analyses of body composition, it was found to interact significantly with reproductive status (TBM, $F = 20.25$, $d.f. = 1$, $P < 0.001$: LBM, $F = 5.21$, $P < 0.03$: Fat, $F = 24.66$, $P < 0.001$). TBM, LBM and fat all increased significantly with age in pregnant females ($n = 20$, $r^2 = 0.60$, $P < 0.001$; $r^2 = 0.49$, $P < 0.001$; $r^2 = 0.64$, $P < 0.001$: Figs. 3.1a-c

Table 3.1. Body composition of adult female polar bears captured during the ice-free season (Aug-Oct) in western Hudson Bay (as determined by isotopic dilution). Means were compared with two-tailed student *t*-test after testing for homogeneity of variances.

Body component	Pregnant females ($n = 20$)	Females with offspring ($n = 39$)	t	P
Total body mass (kg)	286.0 ±13.3	217.2 ±5.8	5.51	<0.001
Lean body mass (kg)	169.4 ±6.7	150.6 ±3.4	2.79	<0.010
Total body fat (kg)	116.6 ±7.9	66.6 ±3.7	6.50	<0.001
Relative fatness (fat per unit of LBM [kg/kg])	0.68 ±0.04	0.44 ±0.02	5.59	<0.001

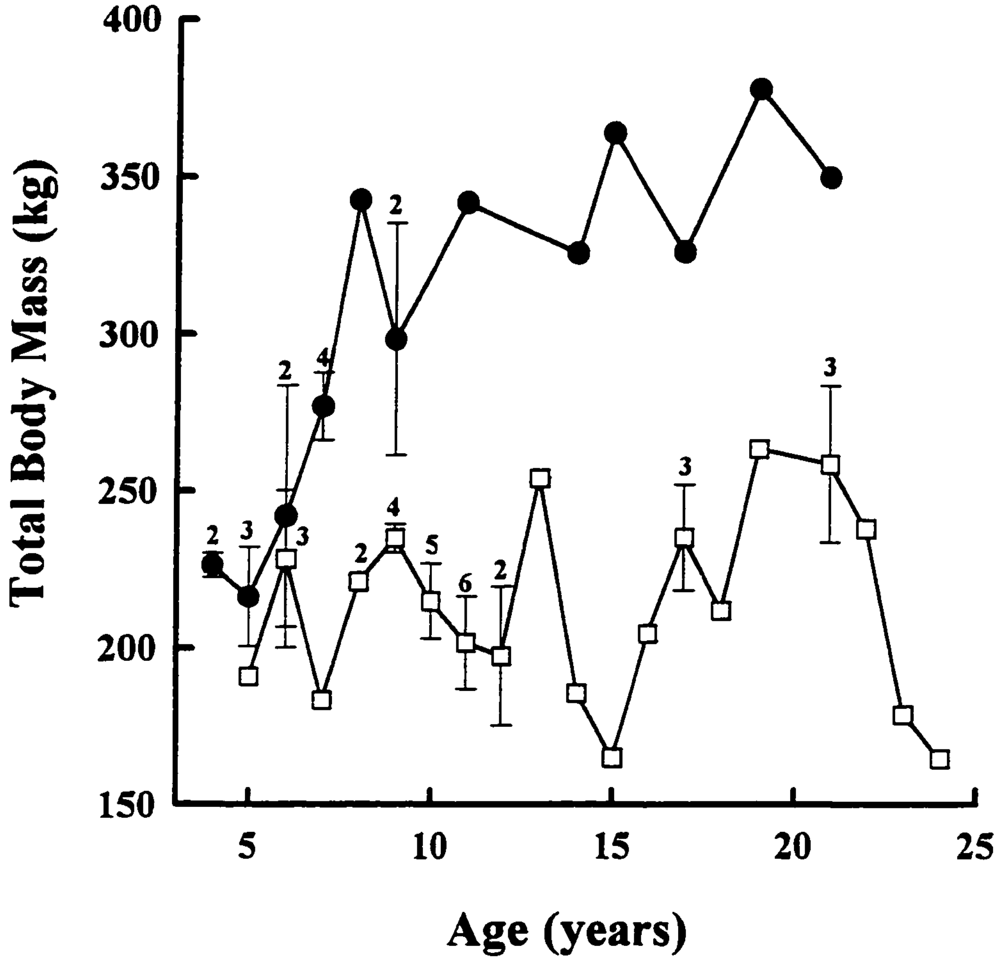

Figure 3.1a. The relationship between total body mass (kg) and age in adult female polar bears that are pregnant (circles) or accompanied by cubs (squares) during the ice-free season in western Hudson Bay. Where > 1, samples sizes are displayed above symbols.

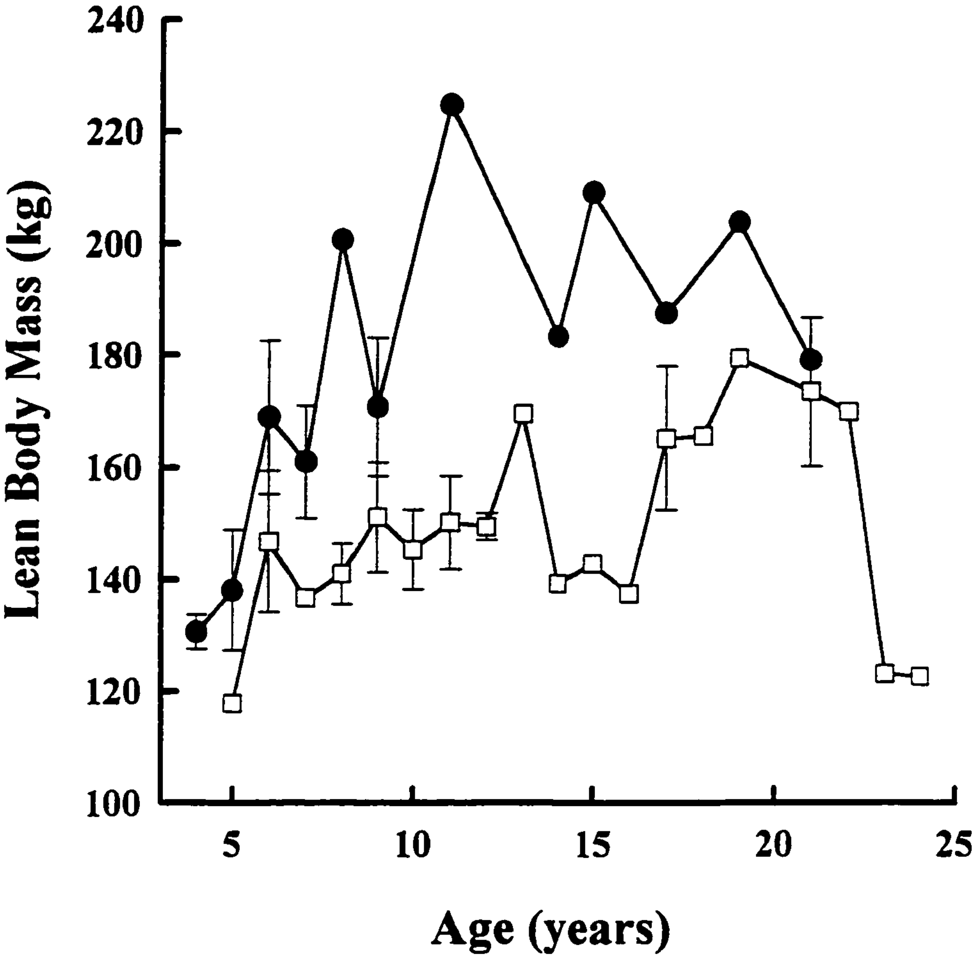

Figure 3.1b. The relationship between lean body mass (kg) and age in adult female polar bears that are pregnant (circles) or accompanied by cubs (squares) during the ice-free season in western Hudson Bay. See figure 3.1a for samples sizes.

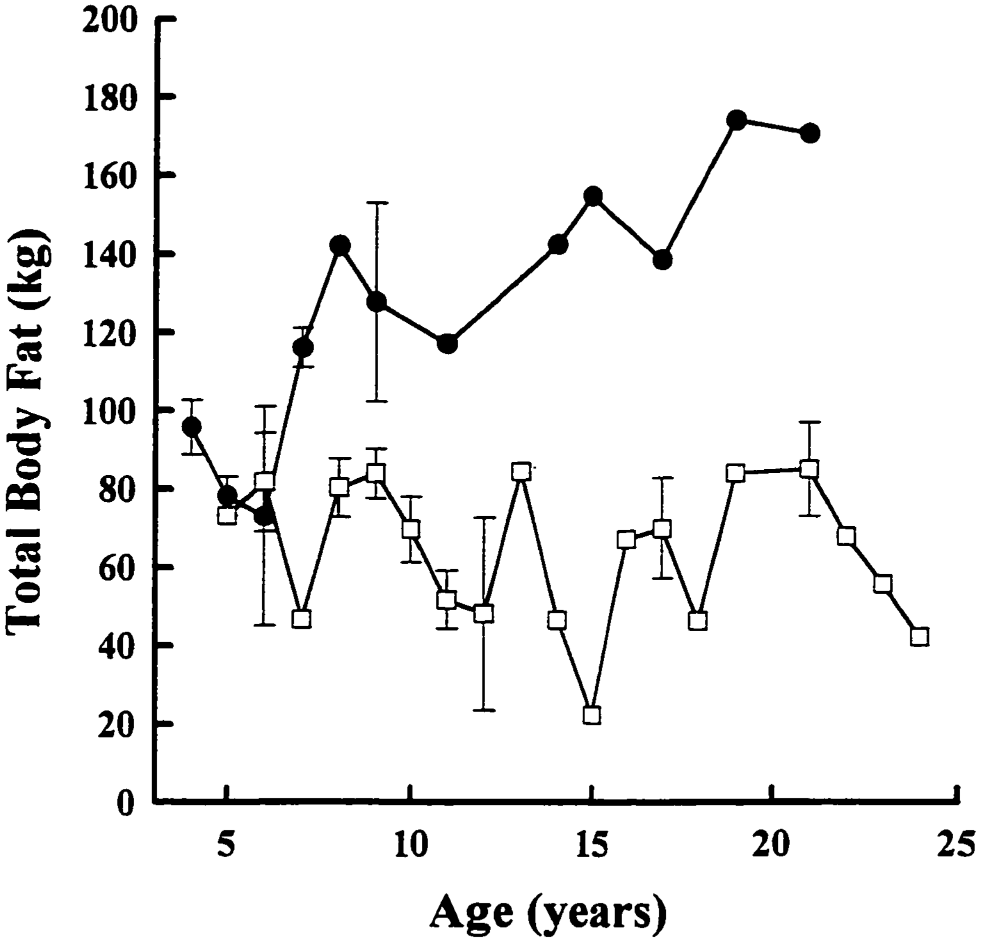

Figure 3.1c. The relationship between body fat content (kg) and age in adult female polar bears that are pregnant (circles) or accompanied by cubs (squares) during the ice-free season in western Hudson Bay. See figure 3.1a for samples sizes.

respectively), but not in females with offspring ($n = 39$, $r^2 = 0.02$, $P > 0.4$; $r^2 = 0.09$, $P > 0.07$; $r^2 = 0.01$, $P > 0.6$: Figs. 3.1a-c respectively). Pregnant females also tended to increase in relative fatness with age ($r^2 = 0.22$; $P < 0.04$), while females with offspring did not ($r^2 = 0.08$, $P > 0.07$).

The relationships between the two components of TBM are shown in Figure 3.2. LBM increased with fat mass in pregnant females but displayed only a weak tendency in females with offspring ($r^2 = 0.46$, $P < 0.002$; $r^2 = 0.09$, $P > 0.06$: respectively).

3.3.2 Denning and cub production.

In spring, during searches of the traditional denning area (Ramsay and Stirling 1990), 14 of the 20 pregnant females handled during the ice-free seasons were either recaptured or resighted shortly after emerging from maternity dens with their cubs. Table 3.2 compares body composition data, collected during the ice-free period, from bears that were or were not relocated in spring. Although the sample of six bears that were not relocated may include individuals that did produce cubs, bears in this group were on average lighter in fat, LBM and TBM. Bears not relocated were also relatively less fat around the time of den entry than those subsequently found with offspring.

Eight of the 14 females relocated in spring were recaptured. The body composition of these bears before and after denning was thus known. During the ice-free period body composition was determined by both isotopic dilution and BIA. For logistical reasons, however, composition after denning was determined by isotopic dilution for only 2 of the 8 bears and by BIA for the remaining 6. To maintain consistency, changes in the body composition of individuals between the pre- and post-denning periods were calculated using data derived when the same technique (dilution or BIA) was applied at both capture and recapture. On average, bears lost 137 kg (43%)

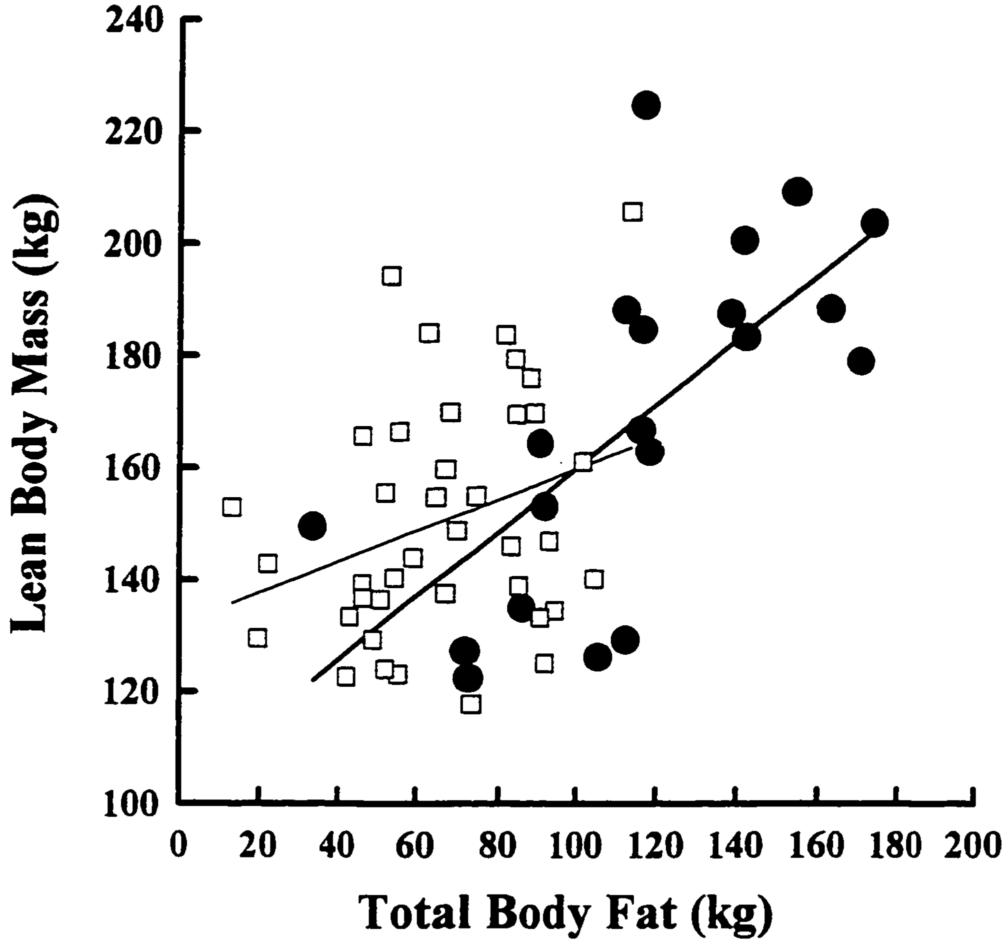

Figure 3.2. The relationship between lean body mass (kg) and body fat content (kg) in female polar bears that are pregnant (circles) or accompanied by cubs (squares) during the ice-free season in western Hudson Bay.

Table 3.2. A comparison of the summer/autumn body composition of pregnant polar bears that were or were not relocated with cubs the following spring. Means were compared with two-tailed student *t*-test after testing for homogeneity of variances.

Body Component	Females relocated with cubs ($n = 14$)	Females not relocated ($n = 6$)	t	P
Total body mass (kg)	310.6 ±11.5	228.7 ±21.7	3.72	<0.010
Lean body mass (kg)	178.7 ±5.6	147.6 ±14.5	2.48	<0.050
Total body fat (kg)	131.9 ±7.1	81.1 ±11.0	3.98	<0.001
Relative fatness	0.74 ±0.03	0.56 ±0.07	2.96	<0.010

of body mass over a pre- to post- denning period of 192 days (Table 3.3). This loss, which includes mass lost as a result of cub production, consisted of 49 and 88 kg of LBM and fat respectively. During the study, two bears captured during the ice-free season of 1992, while accompanied by offspring, were recaptured in 1993 when pregnant. Interestingly, the LBM and fat of these bears had increased between these years by 55 kg (±3.8) and 68 kg (±2.6) respectively. These increases in mass were not significantly different from the average decreases in LBM and fat that occurred over the pre- to post-denning period ($t = 1.404$, *d.f.* = 8, $P > 0.1$; $t = 1.808$, *d.f.* = 8, $P > 0.1$, respectively).

Assuming a value of 22.2 % for the protein content of lean tissue in bears (Farley and Robbins 1994), and energy equivalents of 23.6 MJ/kg and 39.3 MJ/kg for protein and fat, respectively (Blaxter 1989), changes in body composition over the pre- to post-denning period were converted into energetic units (Table 3.3). Including energy transferred to cubs in the form of fat and protein during gestation or lactation, bears lost 3722 MJ (±225) of body energy at a rate of 19.4 MJ/day (±1.1). Loss of body fat accounted for 93.1% (±0.5) of this change in body energy content over the fasting period. When expressed as MJ/kg of body mass$^{0.75}$/day (body mass being calculated as the average of TBM at capture and recapture), the resulting mass specific rates of energy loss were on average 1.07 (±0.05) times the predicted value for basal metabolic rate in animals of the same body mass as these polar bears (Kleiber 1947).

Six of the eight females recaptured in spring had produced two cubs each, the remaining two producing one cub each (Table 3.3). For litters of two, total spring litter weight was significantly related to maternal body fat (Fig. 3.3: $r^2 = 0.92$, $P < 0.01$) and TBM ($r^2 = 0.83$, $P < 0.03$) around the time of den entry, but not to LBM ($r^2 = 0.42$, $P > 0.1$). Taking into account differences in metabolic body mass, and hence maternal

Table 3.3. Changes in the body composition of eight pregnant adult female polar bears between the summer/autumn ice-free period and emergence from maternity dens in spring.

	Mass lost (kg)	LBM lost (kg)	Fat lost (kg)	Energy# equivalent of mass lost (MJ)	Percentage of energy loss derived from fat	Capture interval (days)	Litter size	Litter weight (kg)
	99.7	29.6	70.1	2909.0	94.6	202	1	12.5
	105.9	32.6	73.3	3050.5	94.4	166	2	17.7
	112.7	47.9	64.8	2797.9	91.0	149	2	20.2
	146.8	51.9	94.9	4001.3	93.2	210	1	13.2*
	148.6	43.2	105.4	4367.5	94.8	168	2	25.2
	151.4	56.1	95.3	4039.2	92.7	218	2	24.0
	163.6	63.7	99.8	4256.7	92.1	216	2	21.7
	167.7	65.6	102.1	4357.3	92.1	204	2	25.0*
Mean	137.1	48.9	88.2	3722.4	93.1	192	1.75	19.9
S.E.	8.9	4.4	5.3	225.3	0.5	9	0.15	1.7

* Bears for whom body composition was determined by isotopic dilution at both initial and recapture. All other data based upon BIA. # Assuming protein content of LBM is 22.2% (Farley & Robbins 1994), and protein and fat contain 23.6 and 39.3 MJ/kg (Blaxter 1989).

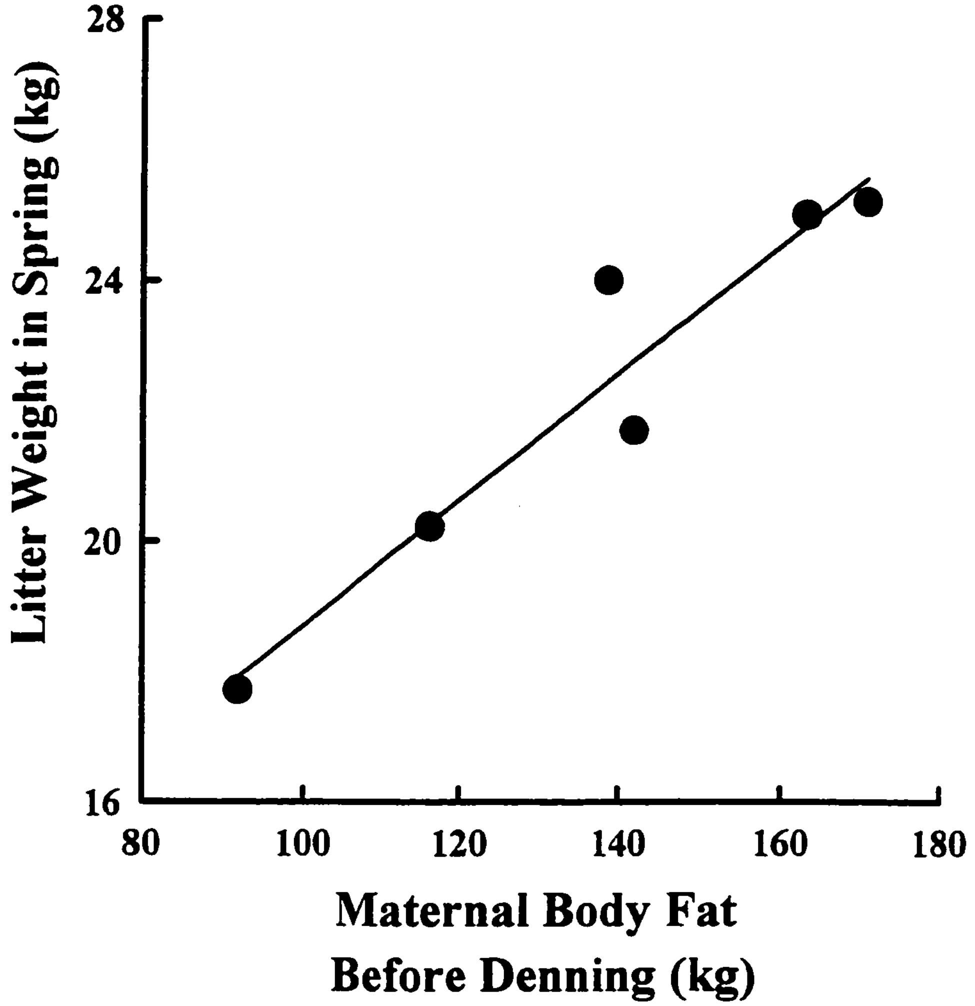

Figure 3.3. The effect of pre-denning body fat content in pregnant polar bears on the weight of their litters in spring. Litters of two cubs only.

maintenance requirements, variation in spring litter weight was also examined with respect to changes in maternal body composition over the pre- to post- denning period. Litter weight (for all 8 litters) was weakly related to the TBM specific rate of maternal energy loss (MJ/kg$^{0.75}$/day; $r^2 = 0.42$, $P = 0.08$). Differences in maternal maintenance energy requirements in relatively obese animals such as female polar bears, however, will be largely the result of variation in LBM rather than TBM (Segal et al. 1989). Consequently, litter weight was more closely related to the lean mass specific rate of maternal energy loss (MJ/kg of LBM/day; $r^2 = 0.53$, $P = 0.04$).

In addition to the eight females recaptured in spring, post-denning body composition was determined for a 5 other adult females. For these 13 bears, post-denning fat, LBM, total body mass and relative fatness were all unrelated to age ($r^2 = 0.02$, $P > 0.6$; $r^2 = 0.05$, $P > 0.4$; $r^2 = 0.002$, $P > 0.8$; $r^2 = 0.10$, $P > 0.3$: respectively).

3.4 Discussion.

3.4.1 Nutrient stores of pregnant polar bears.

Spring (April/May) is a time when ringed seals (*Phoca hispida*), one of the primary prey species of polar bears, become particularly vulnerable to predation (Stirling and Archibald 1977; Hammill and Smith 1991). Bears may become hyperphagic during this window of opportunity and deposit a majority of the body stores necessary for fasting later in the year (Watts & Hansen 1987; Ramsay & Stirling 1988; Messier, Taylor & Ramsay 1992). Hunting seals, however, may be a skill that requires not only large body size but also considerable experience in locating and catching prey (Stirling and Latour 1978). Consequently, in the first 1-2 years of life, polar bears may be almost entirely dependent upon their mothers for nutrition. As a result of food sharing, adult females who are accompanied by cubs during the spring will thus undoubtedly be limited in the extent to which they can accumulate energy and other nutrient stores.

Spring is also an important period in the reproductive cycle of polar bears, when adult males and some females engage in mating activities (Ramsay and Stirling 1986). In western Hudson Bay, females that do mate will subsequently need to accumulate body stores sufficient to endure up to eight months of fasting and also sustain the nutritional demands of reproduction. Among females engaging in mating activities in a given year, therefore, selection should favour individuals that abandon offspring from their last reproductive cycle before the spring period of high food availability. Indeed, previous studies have suggested that polar bear cubs do become independent around the time of the mating season (Ramsay and Stirling 1988). The predicted effects of such a strategy (if in operation) are consistent with differences in body composition between pregnant bears and females with offspring, that were observed in the present study (Table 3.1).

During the ice-free season in western Hudson Bay, pregnant polar bears are on average 31.7% heavier than females with offspring. Most (73%) of this difference in body mass is accounted for by fat. Pregnant females may reach extremely obese proportions, attaining as much as 49% body fat in this study. Nevertheless, there is also a notable difference in LBM between females with cubs and pregnant females (Table 3.1). The accumulation of body fat in pregnant bears appears to be accompanied by a proportional increase in LBM (Fig. 3.2). Such a 'companionship' of fat and LBM during weight gain has been reported in other species (Harris, Kasser and Martin 1986; Forbes 1987, 1993; Lindstrom and Piersma 1993) but the function of this dynamic relationship between body components is not clearly understood (Marsh 1984; Evans et al. 1992; Forbes 1993). In the case of pregnant polar bears, accretion of lean tissue may occur for several reasons. Polar bears are known to range over extremely large areas while foraging on the sea-ice (145,000-351,000 km^2; Garner, Knick and Douglas 1990). An increase in LBM, particularly muscle mass, may thus be necessary to transport and structurally support the large, heavy fat deposits required for up to 8 months of fasting. While not exclusive to pregnant bears, this 'weight training' effect would be most detectable among these individuals because they undergo the largest relative increases in body mass. More obviously, a rise in LBM concomitant with fat deposition would also provide an available pool of protein and minerals essential for the growth and maintenance of offspring during the denning period (Ramsay and Dunbrack 1986).

3.4.2 Changes in body composition and energy expenditure over the pre- to post-denning period.

While denning, female polar bears are relatively inactive (Messier, Taylor and Ramsay 1994). Any 'excess' muscle tissue, accumulated during fat deposition, may thus be the first or only lean tissue used as a source of protein to meet nutritional requirements. In the present study, pregnant females lost significant quantities of LBM over the pre- to post- denning fast (Table 3.3). From the limited data available, it seems that this loss of lean tissue was indeed approximately equivalent to that which may be gained when adult females deposit fat in preparation for denning.

Because the quantity of nutrients that mothers transferred to offspring was unknown, the relative contributions of fat and protein catabolism to maternal maintenance metabolism during fasting could not be calculated. Of the total loss in maternal body energy content, however, most (93%) was attributable to depletion of fat stores (Table 3.3). Studies of fasting in pinnipeds and penguins have yielded comparable values for the contribution of fat metabolism to either total or maintenance energy expenditure (Table 3.4). Pregnant polar bears thus appear to conform to the pattern of nutrient

Table 3.4. Estimates of the contribution (%) of fat metabolism to energy requirements during fasting in various animal species.

Species	Circumstances & duration of fast	Percentage of energy derived from body fat	Source
Northern elephant seal (*Mirounga angustirostris*)	Pups, 8-12 weeks of post-weaning period.	98	Pernia, Hill & Ortiz (1980)
Emperor penguin (*Aptenodytes forsteri*)	Adult males, 17 weeks, courtship and incubation.	96	Robin *et al.* (1987)
Antarctic fur seal (*Arctocephalus gazella*)	Adult males, 4 weeks of mating period.	92	Boyd & Duck (1991)
Harbour seal (*Phoca vitulina*)	Adult females, 3-4 weeks of lactation period.	90*	Bowen *et al.* (1992)
Rat# (*Rattus norvegicus*)	Adults, laboratory test, 2 weeks.	83	Belkhou *et al.*(1991)

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*This value includes fat (and protein) drawn from maternal stores for milk production. # Included as an example of a species that does not typically experience prolonged fasts under natural circumstances.

metabolism seen among other species that are adapted to prolonged fasting (also see chapter 6).

In typically obese mammals, such as seals, fasting metabolic rates (FMR) among adults have been found to range from 2.4 to 3.3 times the interspecifically predicted resting metabolic rates (RMR) (Kleiber 1947; Boyd and Duck 1991; Boyd, Arnbom and Fedak 1993). In contrast, among adult female polar bears, average rates of body energy loss over the pre- to post- denning period (Table 3.3) were exactly equal to predicted RMRs, suggesting that maternal maintenance requirements were less than the predicted RMR. Although these bears were handled before and after, rather than during denning, approximately 86% of the time between first and second handling (Table 3.3) would have been spent in maternity dens (assuming 5.5 month denning period). The comparatively low rate of energy expenditure, therefore, probably reflects the effectiveness of maternity denning (and its associated degree of inactivity), as a strategy of over-winter energy conservation (Watts and Hansen 1987; Messier et al. 1992). Furthermore, studies of denning energetics in captive, reproductively inactive black and grizzly bears, have estimated rates of energy expenditure to be between 68% and 73% of predicted RMR (Watts and Jonkel 1988; Farley 1994). Assuming similar (if not higher) values for polar bears under natural denning conditions, and taking into account a higher rate of energy expenditure during those portions of the sampling period bears were not in dens, it would seem that maintenance is by far the largest component of the maternal energy budget during this long reproductive fast.

3.4.3 Age and body composition.

While structural growth in female polar bears is completed by about 4 or 5 years of age (Kingsley 1979; Derocher 1991), body mass in adults fluctuates depending on season and reproductive status. Overlaying these seasonal and reproductive cycles, body mass may also vary among animals of different ages. In agreement with a previous study that used estimates of body mass only (Derocher et al. 1992), my results indicate that, within the observed range of ages, the average body mass of pregnant female polar bears increases with age (Fig. 3.1a). Additionally, the data show clearly that body fat is the primary component of this effect (Fig. 3.1c), although LBM also tends to change with age (Fig. 3.1b).

There are a number of possible explanations for such a positive association between age and body condition. Older females may tend to have longer inter-birth intervals, encompassing years of reproductive inactivity or failure. The reduced rate of reproduction would permit individuals to allocate a greater proportion of their annual food intake to nutrient stores and hence be in better condition for their next reproductive cycle. In large, long-lived mammals the lowest fecundities and longest inter-birth intervals are often seen among very young or old animals (Clutton-Brock, Guinness and Albon 1983; Huber 1987; Green 1990). Indeed, pregnancy rates among polar bears in western Hudson Bay appear to decline in bears that are particularly old (>20 years) (Ramsay and Stirling 1988; Derocher et al. 1992). Given the relatively young age range (<22 years) of bears in the present study, however, reproductive senescence is unlikely to account for the observed age-specific pattern in body mass and composition. Pregnancy rates for bears within the age range of this study are relatively constant suggesting that older adult females do not increase their inter-birth intervals by deferring mating. Furthermore, declining pregnancy rates among old bears are concurrent with decreasing rather than increasing body mass (and probably condition) (Derocher et al. 1992).

An alternative explanation for the age-specific increase in condition is that, for some carnivores, practice and experience may play an important role in the success of foraging. In the case of polar bears, hunting seals which are patchily distributed and often concealed within lairs under sea-ice (Smith and Stirling 1978; Hammill and Smith 1989) may, in particular, be a skill that improves significantly with age (Stirling and Latour 1978). Older bears may, therefore, be more successful at accumulating resources in preparation for fasting.

While it is interesting to speculate about changes in the body condition of individuals over time, caution should nevertheless be exercised when drawing conclusions from cross-sectional data. A positive relationship between age and body condition could also arise if animals that are of poor quality, with respect to factors such as hunting ability, die at a younger age than better quality individuals (Curio 1983; Clutton-Brock 1991). Within a given cohort, the average quality and body condition of female bears would thus increase with age. From the data, therefore, I am limited to concluding that body condition prior to denning was, on average, better among older bears than younger individuals.

In contrast to pregnant bears, body condition was unrelated to age in female polar bears accompanied by cubs during the ice-free season (Fig 3.1a-c). This suggests that over the period between pregnancy and the weaning of cubs, bears that are older or in better condition before denning lose larger quantities of nutrients, which are presumably transferred to their offspring. Age-specific annual survival rates for females in the study population do not differ between the ages of 3 to 21 years (Derocher 1991). Any increase in reproductive expenditure among older or higher quality bears, therefore, does not appear to significantly affect adult survival. Consequently, this greater energetic expenditure cannot necessarily be viewed as greater maternal investment or effort because the costs of reproduction (in terms of survival and future reproduction) may not differ among bears of varying age or condition (Williams 1966; Tuomi, Hakala and Hukioja 1983; Clutton-Brock 1984; Part, Gustaffson and Moreno 1992).

3.4.4 Body composition and reproductive performance.

In mammals, nutritional deficiency can result in the impairment of all reproductive processes including conception, gestation and lactation (eg. Bauman and Curry 1980; Loudon and Kay 1984; Albon et al. 1986; Lochmiller, Hellgren and Grant 1986; Lonnerdal 1986; Ramsay and Dunbrack 1986; Oftedal 1993). For species such as bears in which reproduction is intimately associated with fasting or nutritional restriction, reproductive success may, therefore, be particularly dependent upon maternal body condition (Rogers 1987; Eiler, Wathen and Pelton 1989; Elowe and Dodge 1989). Data presented in the present study illustrate clearly the impact that maternal energy stores have on the success of a reproductive attempt. Bears that entered dens in autumn with the smallest fat stores, either absolutely or relative to LBM, were those least likely to be seen with cubs the following spring (Table 3.2). Poor body condition prior to denning may have resulted in the failure of embryonic implantation, foetal abortion, or abandonment and consumption of cubs after birth (Tait 1980; Hellgren et al. 1991). Furthermore, among females that successfully produced cubs, litter weight at den emergence was remarkably sensitive to the size of maternal fat stores prior to denning, and may, to a lesser extent, have been affected by other nutrient stores (Fig. 3.3). Bears with larger fat stores before denning produced heavier cubs. In turn, heavier cubs are more likely to survive the trials of their first spring to summer period out on the sea-ice (Ramsay and Stirling 1988).

As body condition varies with age among pregnant polar bears, reproductive performance during the denning period should follow a similar pattern. In a study of polar bear denning ecology, Messier, Taylor and Ramsay (1994) found that middle-aged females (those in the upper half of the age range in my study) spent less time in maternity dens than young or old bears but still tended to emerge with the heaviest cubs. They attributed this effect to the possibility that these 'prime-age' females were in better physical condition prior to denning than bears in other age classes. My results strongly support their view but without further research it is unclear whether age itself is an important determinant of reproductive performance. In particular, there is a need to distinguish between two hypotheses. Differences in body condition and reproductive performance, between young and prime-age females, could arise if; (1) the condition of individuals improves with age because experience affects foraging skill, or (2) bears that are of poor quality and body condition die at a younger age than better quality individuals. These hypotheses infer that variation either within or among female polar bears affects body condition and reproduction. Long-term data on the body composition and survival of individuals are required to test these alternatives.

4. THE SENSITIVITY OF LACTATION IN POLAR BEARS (*URSUS MARITIMUS*) TO MATERNAL BODY CONDITION AND AGE.

4.1 Introduction.

For mammals in general, lactation is the most nutritionally demanding phase of reproduction (Oftedal 1985; Gittleman and Thompson 1988; Oftedal and Gittleman 1989). Amongst carnivores, for example, maternal energy requirements at the peak of milk production are estimated to be somewhere between 150 to 300% greater than those of non-lactating individuals (Oftedal and Gittleman 1989). Considering the nutritional costs it is hardly surprising that in many species lactation is particularly sensitive to food availability and maternal body condition (Vernon and Flint 1984; Garnsworthy 1988; Oldham and Friggens 1989; Rasmussen 1992). Nevertheless, other factors such as litter size (Knight, Maltz and Docherty 1986; Hammond and Diamond 1992; Rogowitz and McClure 1995) and maternal age (Clutton-Brock 1984; Stewart 1986; Green 1990; Sydeman et al. 1991) may also exert considerable influence on the process of milk production.

Interspecifically, there is wide variation in the extent to which mammals rely upon endogenous nutrient stores to sustain lactation (Sadleir 1984). Bears (family: *Ursidae*), like phocid seals and mysticete whales, are extreme examples of such variation. In many species of these 3 taxa, mothers fast for all or a significant proportion of the lactation period (Oftedal 1993). During these fasts, milk is thus synthesised from body nutrient stores which must also provide all the energy necessary to support maternal maintenance metabolism. Under such opposing constraints, the proportion of available nutrients allocated to lactation should reflect strongly the optimal trade-off between maternal condition (and probability of survival) versus reproductive expenditure. Study of these 'lactational fasters' may therefore provide some unique insights into the life history strategies governing reproduction in iteroparous mammals. To date relatively little is known about the factors that are responsible for variation in lactational performance in bears, seals or whales (eg Iverson et al. 1993; Derocher, Andriashek and Arnould 1993a; Arnould and Ramsay 1994).

Like other ursid species, polar bears exhibit an exceptionally long lactation cycle in comparison to most terrestrial carnivores (Oftedal and Gittleman 1989). Cubs may continue to nurse until well into their 3rd year of life (Ramsay and Stirling 1988). The first 2 to 3 months of lactation occur while mothers are fasting in over-winter dens (Watts and Hansen 1987; Atkinson and Ramsay 1995). After emerging from dens in the spring, food availability is highly seasonal and lactation may encompass several additional time periods when mothers do not have access to food, such as the ice-free season (Chapter 1). No where is the ice-free season more prolonged, and the reduction in access to prey so complete, than at the southern limits of the polar bears' geographical range, such as the study site in western Hudson Bay (Fig. 2.1). For adult females in this sub-arctic region, production of milk during the 3-4 month ice-free fast may have a significant impact on body condition whilst being essential for the survival of cubs (Derocher et al. 1993a; Arnould and Ramsay 1994).

Unlike bears in maternity dens, polar bears on-land in late summer and autumn are relatively easy to locate and capture thereby presenting an ideal opportunity to investigate the factors affecting lactation in fasting bears. On this basis, I initiated a study designed to examine the sensitivity of lactation to maternal body condition and age during the ice-free season in western Hudson Bay. Females suckling offspring less than a year old (often referred to as cubs-of-the-year) were of particular interest because these young cubs appear to be most dependent upon milk for survival (Arnould and Ramsay 1994).

4.2 Methods.

4.2.1 Capture and handling.

From 1992 to 1994, research activities at the study site were centred around two distinct periods during the ice-free seasons; in late July to mid-August (late summer) and mid-October to early November (autumn). Respectively, these two intervals represent early and late stages of the on-land fast. During each stage, adult females and their accompanying cubs-of-the-year were located and chemically immobilized. Upon capture, mothers and cubs were weighed, ear tagged, lip tattooed and when necessary a tooth was extracted for aging purposes (Chapter 2). Litter size and the sex of each cub were also noted.

4.2.2 Maternal body condition.

Maternal body condition at time of capture was expressed as either total body mass (TBM) or percent body fat (PBF). Measurement of PBF followed the protocol previously described for isotopic dilution (Chapter 2).

4.2.3 Lactational performance.

Adult females were injected intra-muscularly with 2.5 ml of oxytocin (25 UI/ml). Approximately 5 minutes later, after cleaning nipples to remove debris, milk was manually expressed from the mammary glands into cryogenic vials. Individual mammary glands were evacuated as extensively as possible without repeated administration of oxytocin. Based on the reported similarity of milk from different mammae on individual females (Arnould 1990; Derocher et al. 1993a), milk collected from different glands was pooled into a single sample for each bear. Milk samples were kept cool until they could be frozen at -20°C. For analysis, frozen samples were allowed to thaw at room temperature and were then heated on a steam bath for 10-20 minutes. To determine the dry matter content of milk, each sample was agitated and two sub-samples (2-4g) taken. Sub-samples were dried at 90°C until they attained a constant mass. The dry matter content of milk was expressed as a percentage of wet weight (total solids content %). Variation in total solids content (%) between sub-samples of the same milk sample was found to be minor (0.58% ±0.1) and mean values were used in statistical analyses.

Data on the dry matter content of milk were used as a means of assessing the lactational performance of each adult female around the time of capture. As in other species which secrete highly concentrated milks, such as seals (eg Iverson et al. 1993), a majority of variation in the solids content of polar bear milk is accounted for by fat, the most energy dense component (Arnould 1990; Derocher et al. 1993a). During the ice-free season in western Hudson Bay the fat content (g/100g) of polar bear milk averages 28% but may be as high as 46% and accounts for approximately 78% of the gross energy in milk transferred to cubs. Consequently, variation in the total solids content of milk corresponds closely to the gross energy content (Fig. 4.1) and therefore provides a good index of the energetic quality of milk that female polar bears produce and cubs consume.

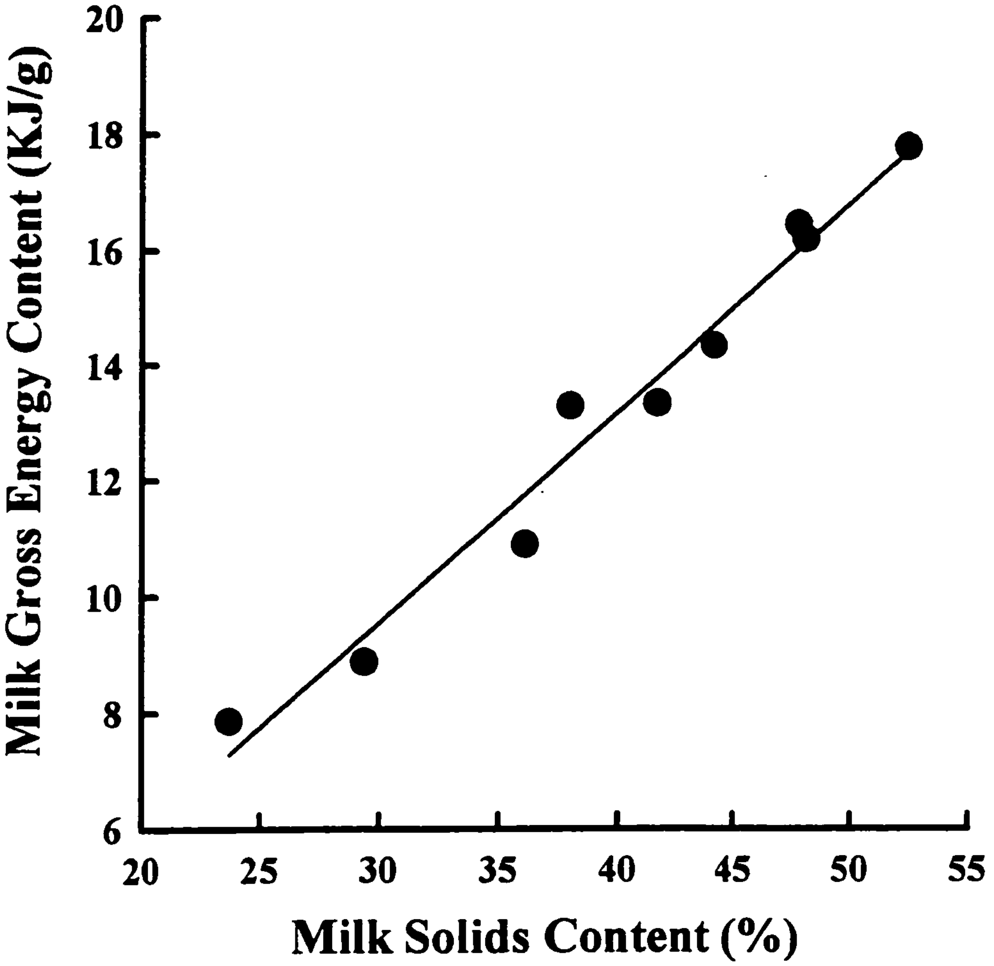

Figure 4.1. The relationship between the gross energy (KJ/g) and total solids content of polar bear milk. Data from Arnould (1990).

Variation in the total solids content of milk may also reflect variation in the rate at which energy is transferred from mothers to offspring. Milk yields among polar bears during the ice-free season in western Hudson Bay were estimated in a previous study (Arnould 1990; Arnould and Ramsay 1994) using the hydrogen isotope transfer method (Holleman, White and Luick 1975). Examination of these data (Fig. 4.2) suggests that the total solids content of milk provides a useful index of daily milk energy yield (MJ/day). As expected a high milk solids content is generally associated with a high daily milk energy yield. Further support for the use of total solids is provided by changes observed in the body masses of lactating bears that were captured and recaptured during the ice-free season (Fig. 4.3). Females producing the most concentrated milks exhibited the highest rates of mass loss (Arnould and Ramsay 1994; Ramsay unpublished data). Although some of the residual variation around these curves (Fig. 4.2 and 4.3) will reflect measurement error, an unknown proportion may be accounted for by differences in litter size. For this reason, litter size was incorporated into analyses in the present study as a control rather than a means of providing insight into the effects of litter size on milk yield.

4.2.4 Potential biases in measurement of milk solids content.

There are a number of potential biases in the collection of milk for total solids determination. The solids content of successive milk samples from a mammary gland may vary significantly (reviewed by Oftedal 1984). As a result, incomplete evacuation of mammae may bias values for total solids content. Recent studies on bears and seals, however, have found little or no variation in sequential samples from the same mammae (Iverson et al. 1993; Derocher et al 1993; Arnould and Ramsay 1994; Oftedal et al. 1987). In the present study, variation from this source was thus assumed to be minimal.

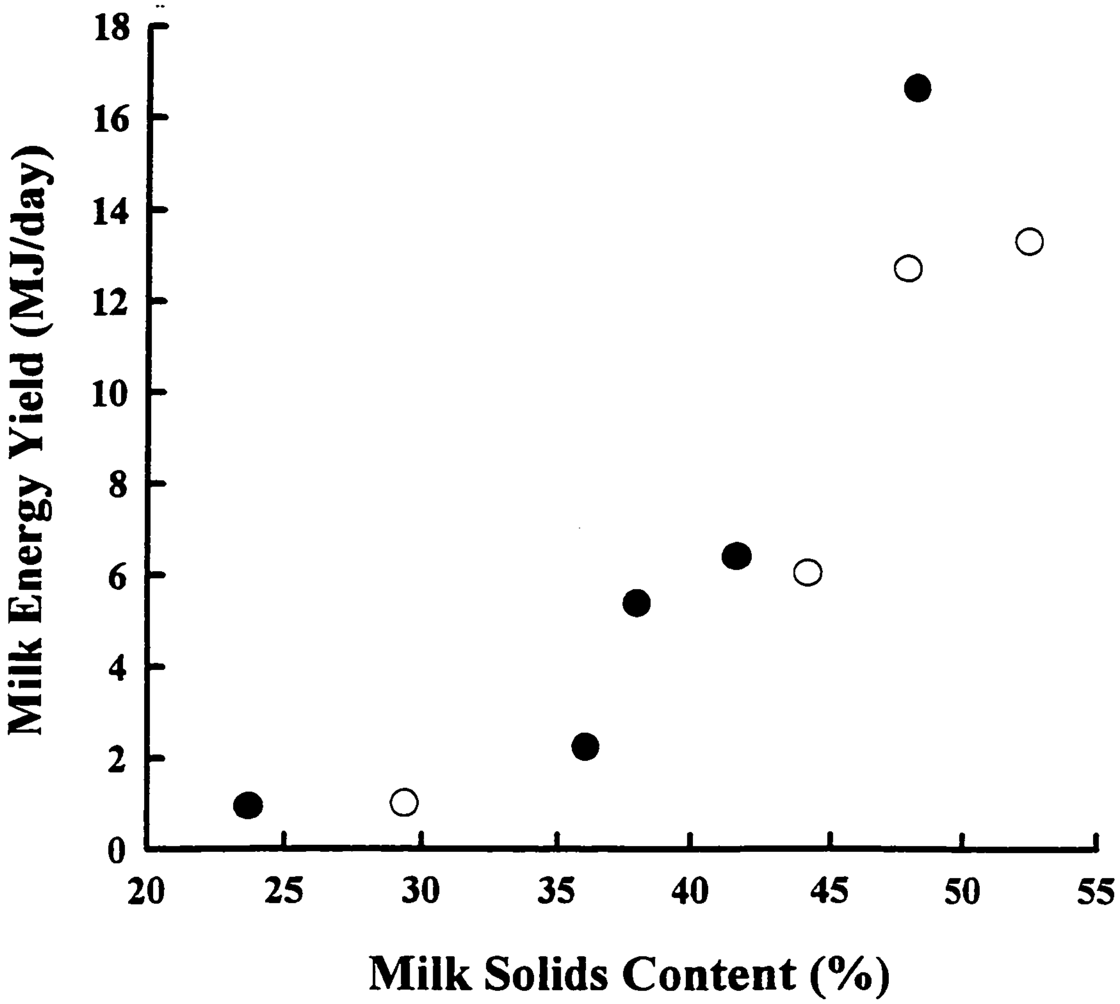

Figure 4.2. A plot of daily milk energy yield (MJ/kg) against milk solids content (%) for polar bears lactating during the ice-free fast in western Hudson Bay. Open and filled circles represent females accompanied by litters of 1 or 2 cubs, respectively. Data from Arnould (1990) and Arnould and Ramsay (1994).

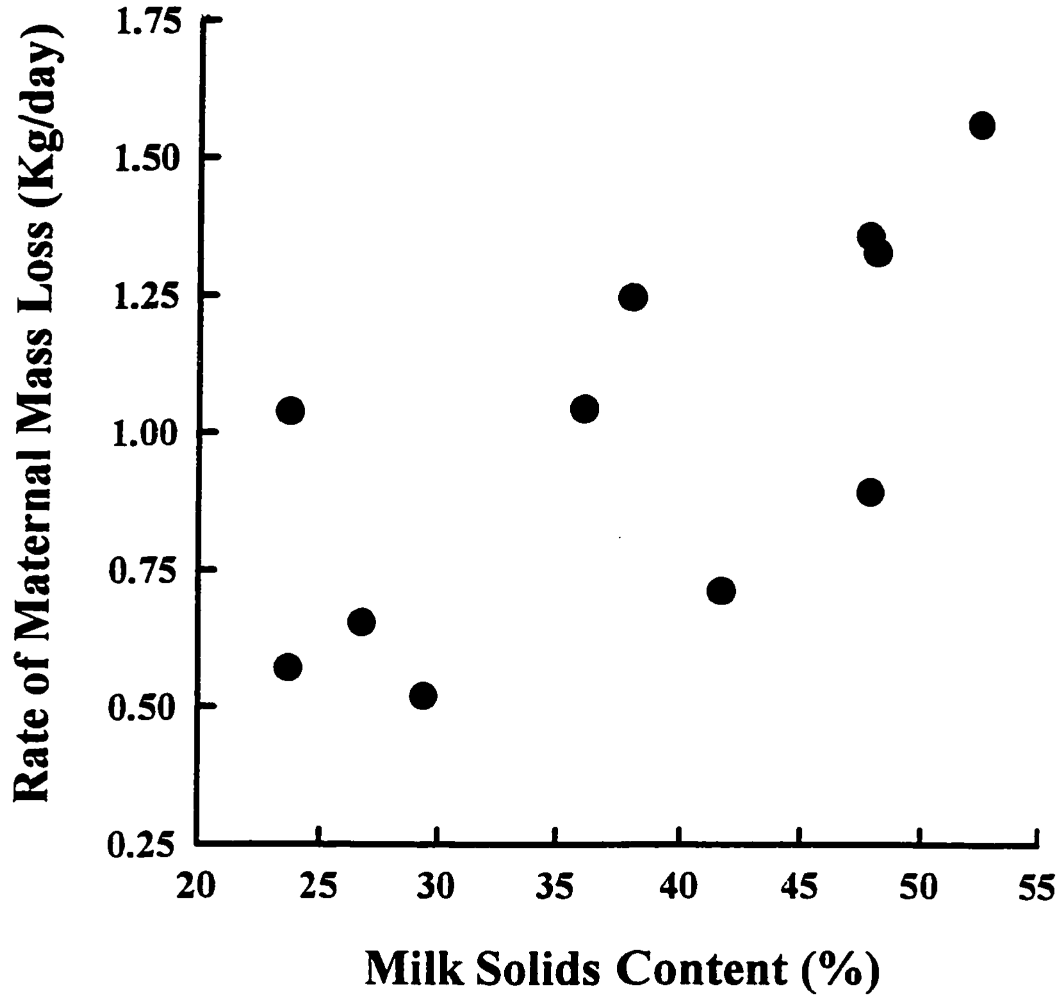

Figure 4.3. Relationship between rate of mass loss (Kg/day) and milk solids content (%) in lactating polar bears during the ice-free fast in western Hudson Bay. Data from Arnould (1990) and Ramsay (Unpublished data).

The length of time since cubs last nursed may also affect the composition of milk that is expressed from mammary glands. For some species, residual milk in the mammae of mothers that have recently nursed their offspring tends to be higher in solids content (Oftedal 1984). Although I was unable to control for this potential source of variation, mothers that had recently nursed cubs would be expected to have relatively little milk in their mammae. While collecting milk samples, however, it was very obvious that the volume of milk in the mammary glands was positively associated with the milk's solids content (Personal observation).

In most mammals lactation can generally be divided into three distinct stages; early, mid (peak) and late (Oldham and Friggens 1989). Depending upon the species each stage may be defined by differences in milk yield and/or composition (Oftedal 1984). The use of data on milk composition may therefore be biased by variation in the stage of lactation at which each milk sample was collected. In bears, the early to mid stages of lactation are thought to be complete before or shortly after emergence from the maternity den in spring (Gittleman and Oftedal 1987). During the ice-free season, female polar bears with cubs of any age are considered to be in the late phase of lactation (Derocher et al. 1993a; Arnould and Ramsay 1994). Consequently, in the present study, potential variation in milk solids content resulting from differences in stage of lactation was minimized by limiting sampling to late lactation. Potential biases were further minimized by only comparing milks collected from mothers that were suckling cubs of approximately equivalent age (cubs-of-the-year).

4.2.5 Statistical analyses.

All data originally expressed as percentages (total milk solids and body fat) were arcsin transformed prior to analyses. Other parameters such as age and body mass were log transformed.

4.3 Results.

During the ice-free seasons of 1992 to 1994, data on maternal body mass, body composition, age, milk total solids content, litter size and cub body mass were collected from 35 lactating polar bears and their cubs-of-the-year. Of these family groups, 18 and 17 were handled during late summer and autumn respectively (Table 4.1). On a Julian day basis the late summer and autumn sampling periods centered around days 229 (±1.9) and 297 (±2.7) of each year and were thus separated by approximately 2 months. Maternal body condition (as measured by either body mass or fat content) was significantly poorer among bears in the autumn relative to those handled in late summer. This drop in maternal condition as fasting progressed was accompanied by decreases in the total solids content of milk and the body mass of cubs. Although not significant, lactating females handled in late summer tended to be younger than those handled in autumn. Comparison of maternal age as presented in Table 4.1 was unbiased by date of capture because age was rounded down to the nearest year. For example, any female in her 11th year of life was assigned an age of 10 years.

Variation in the quality of milk that adult females produced while fasting on-land was examined with respect to maternal body condition and age by means of unique sums of squares 2-way analysis of covariance (2-way ANCOVA). Separating the late summer and autumn samples, ANCOVA models were constructed using milk total solids content as the dependent variable, litter size as a categorical factor, TBM or PBF as an index of condition, and maternal age. To reduce imbalances in design, data for 3 bears accompanied by litters of triplet cubs were excluded from analyses (2 from late summer and 1 from autumn) but are presented in graphical figures.

Table 4.1 A comparison of the characteristics of lactating polar bears (mass, condition, age, milk quality), and their accompanying offspring (litter size and cub mass), between the late summer and autumn stages of the ice-free season in western Hudson Bay. Means were compared by one-way ANOVA after testing for homogeneity of variances.

	Early fast (July/Aug) (n = 18)	Late fast (Oct/Nov) (n = 17)	P
Total body mass (kg)	230.2 ±4.8	172.1 ±3.8	<0.001
Body fat (%)	28.5 ±1.1	22.0 ±1.2	<0.006
Age (yrs)	10.9 ±0.9	13.9 ±1.4	>0.080
Milk solids (%)	45.2 ±1.5	36.2 ±2.9	<0.015
Litter size	1.5 ±0.17	1.5 ±0.15	--
Body mass of female cubs (kg)	60.0 ±2.9	49.8 ±4.0	<0.050
Body mass of male cubs (kg)	70.5 ±4.6	55.3 ±3.8	<0.020

In late summer milk quality among bears was clearly more sensitive to variation in maternal PBF than to variation in total body mass (Figs. 4.4a & b). An ANCOVA model incorporating PBF, maternal age and litter size accounted for a significant proportion of the observed variation in milk quality among bears ($F_{[3, 15]} = 4.59$, $P < 0.025$). Controlling for the effects of litter size and maternal age, PBF exerted a strong independent effect on milk quality ($t_{slope} = 3.55$, $d.f. = 14$, $P < 0.005$). Fatter bears produced milk with a higher solids content irrespective of age or litter size. Litter size ($F_{[1, 15]} = 0.67$, $P > 0.400$) and maternal age ($t_{slope} = 0.84$, $d.f = 14$, $P > 0.400$) had no significant independent effects on milk quality.

Unlike bears in late summer, milk quality in the autumn appeared to be insensitive to variation in maternal body condition (Figs. 4.5a & b). An ANCOVA model incorporating litter size, PBF and maternal age explained a significant proportion of the variation in milk quality ($F_{[3, 15]} = 4.02$, $P < 0.035$). Examining each parameter while controlling for the effects of others in the model, PBF and litter size had no significant independent effects on milk quality (PBF, $t_{slope} = -1.56$, $d.f = 14$, $P > 0.140$; Litter size, $F_{[1, 15]} < 0.01$, $P > 0.940$). In contrast milk quality was strongly influenced by maternal age (Fig. 4.6). Older mothers produced milk with a higher solids content ($t_{slope} = 3.07$, $d.f. = 14$, $P = 0.010$).

In addition to the 17 lactating bears, five other females accompanied by cubs were handled during the autumn but milk could not be expressed from their mammary glands. The lack of milk in the mammae of these "dry" bears may have arisen either as a result of low rates of milk production combined with recent suckling by cubs, or complete involution of mammary glands such that lactation had ceased. Without additional information it was not possible to distinguish clearly between these two alternatives, although the nipples of dry bears showed few signs of recent suckling and their

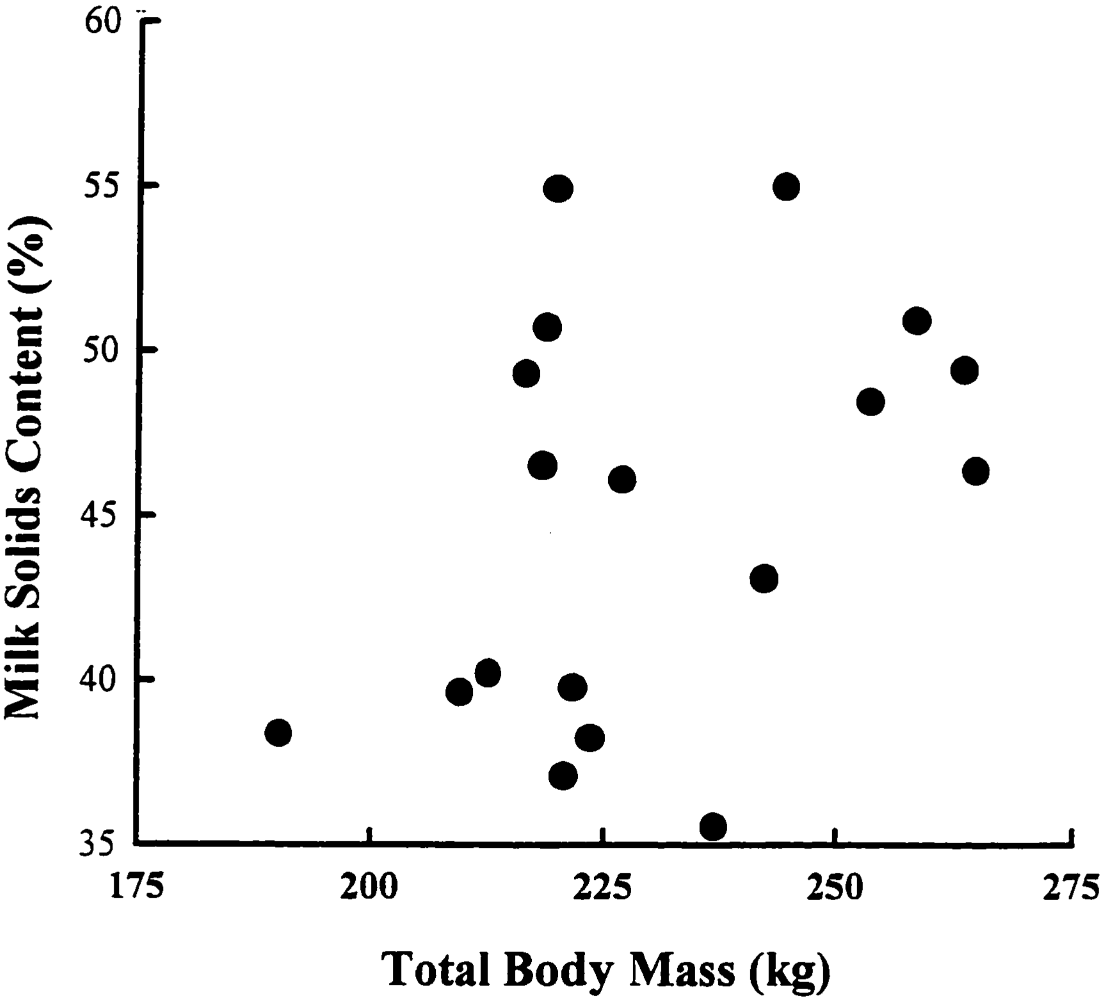

Figure 4.4a. Variation in milk solids content (%) in relation to body mass (kg) among lactating polar bears during the summer stage of the ice-free period in western Hudson Bay.

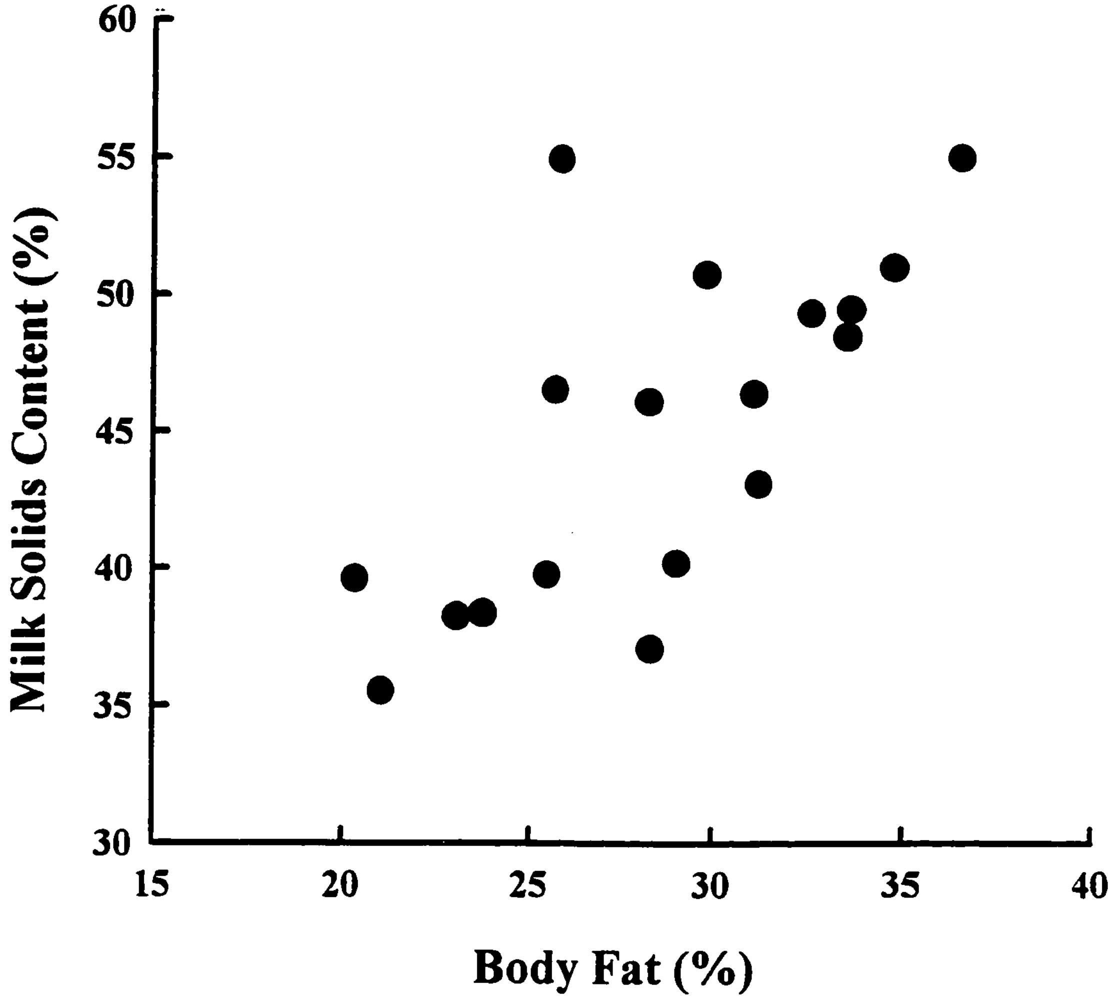

Figure 4.4b. Variation in milk solids content (%) in relation to body fat content (%) among lactating polar bears during the summer stage of the ice-free period in western Hudson Bay.

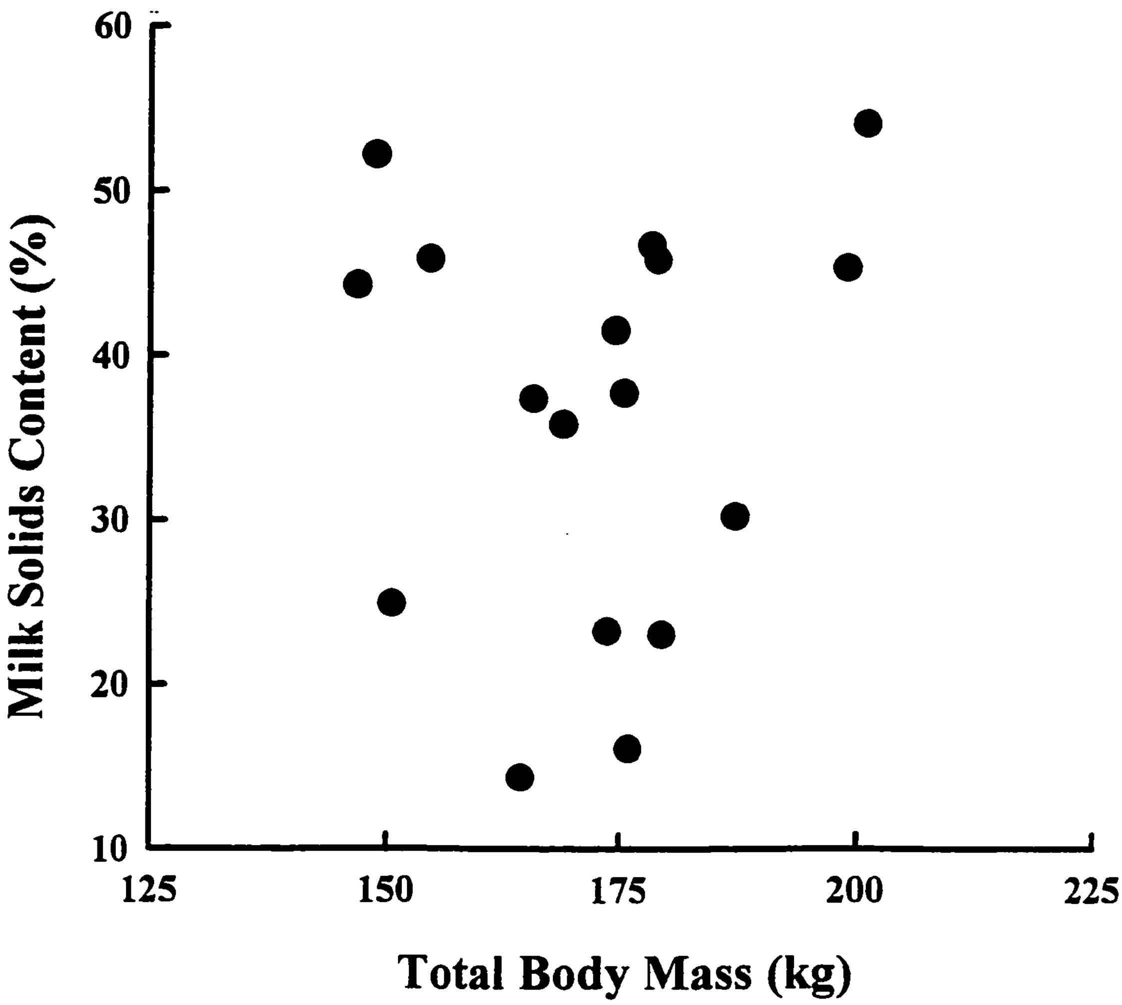

Figure 4.5a. Variation in milk solids content (%) in relation to body mass (kg) among lactating polar bears during the autumn stage of the ice-free period in western Hudson Bay.

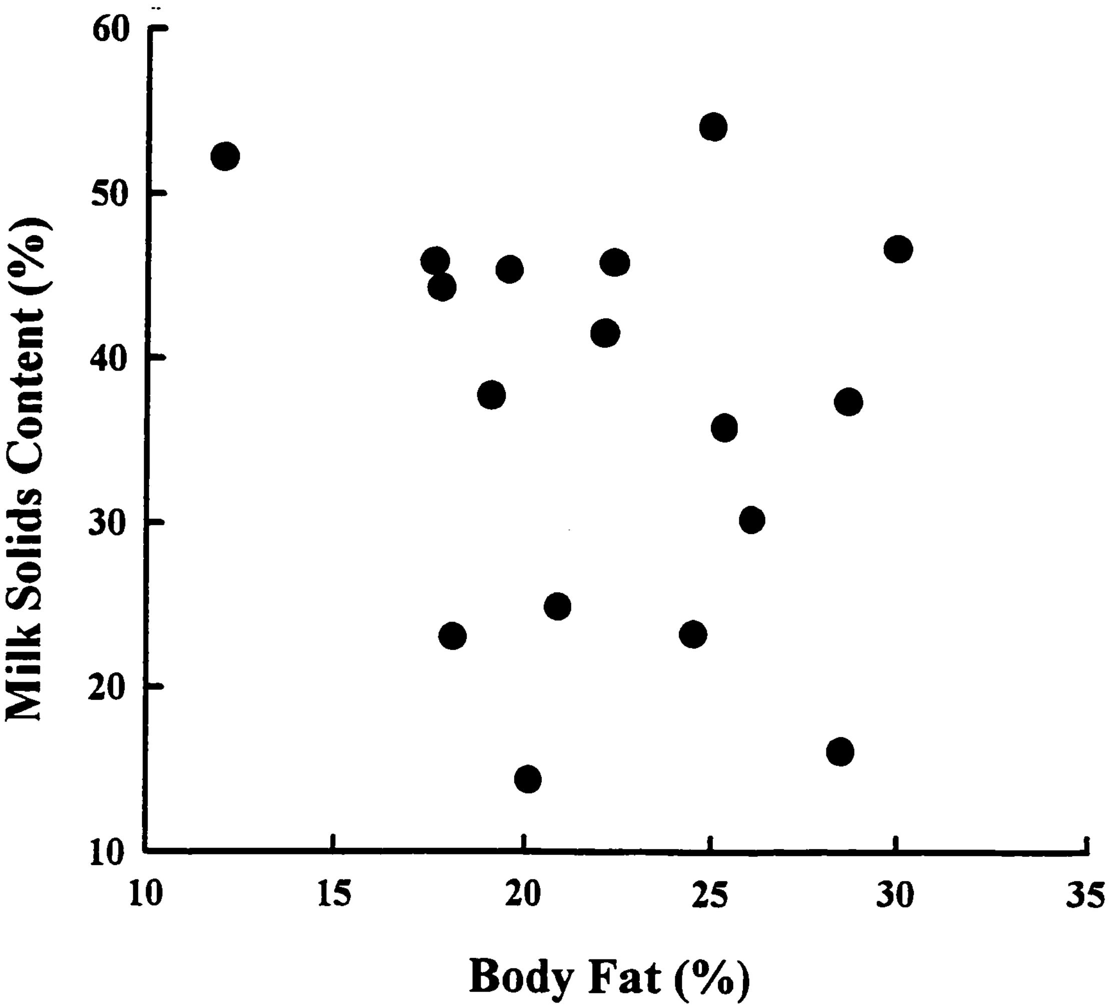

Figure 4.5b. Variation in milk solids content (%) in relation to body fat content (%) among lactating polar bears during the autumn stage of the ice-free period in western Hudson Bay.

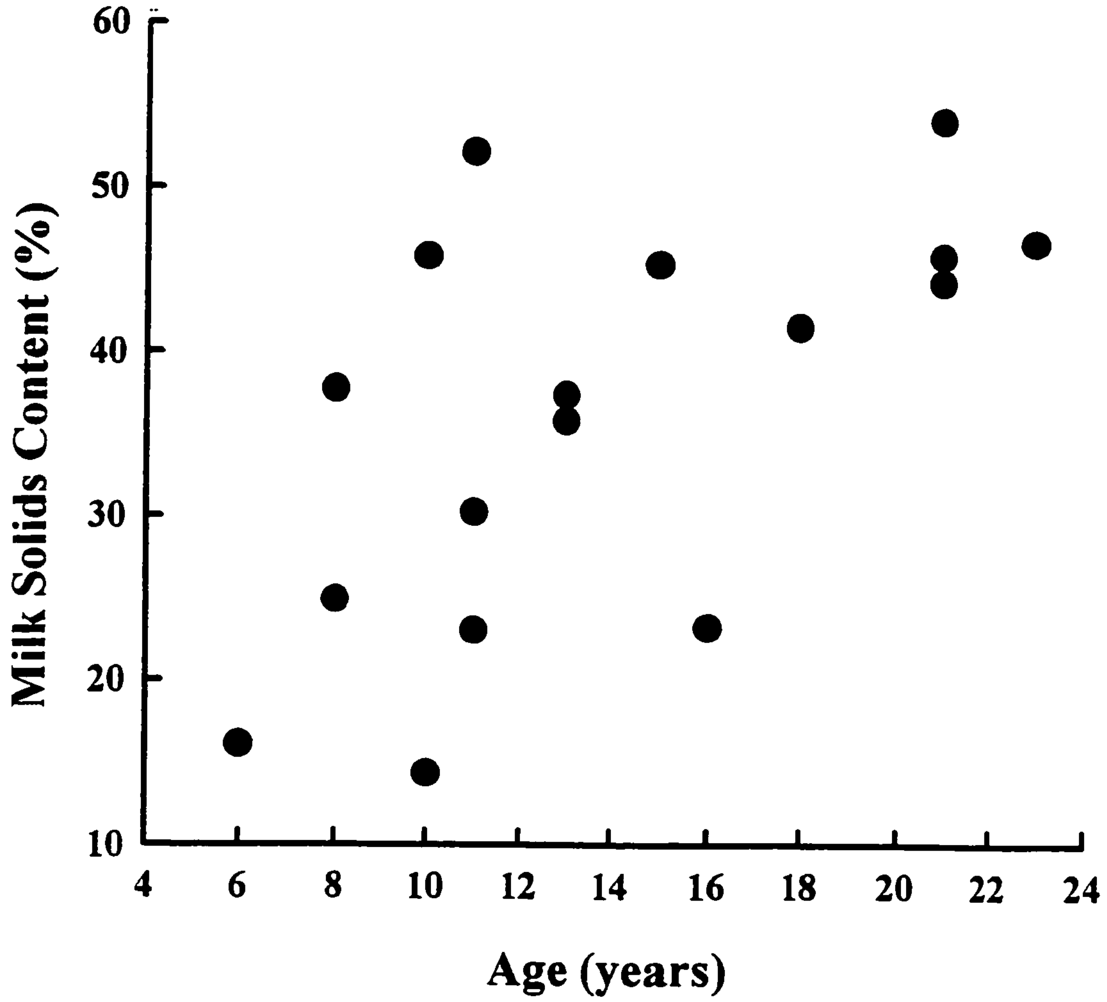

Figure 4.6. Variation in milk solids content (%) in relation to age (years) among lactating polar bears during the autumn stage of the ice-free period in western Hudson Bay.

mammae appeared to be regressed or reduced in size relative to bears known to be lactating. Comparing the characteristics of mothers from which milk could and could not be expressed did not reveal any significant differences in maternal body mass, PBF or age (Table 4.2). Of the females from which milk samples were obtained, nine, seven and one were accompanied by one, two and three cubs respectively. In comparison, of the dry females, one had two cubs while the other four each had a single cub. After pooling litters of two and three cubs into a single category (multiple cub litters), there was no significant difference in the relative frequencies of single and multiple cub litters between milked and unmilked mothers (Fisher's exact test, $P > 0.35$).

4.4 Discussion.

4.4.1 Body condition and milk quality.

The link between nutrition and lactation has been examined extensively in a variety of mammals such as livestock, rodents and humans (eg Bauman and Currie 1980; Oldham and Friggens 1989; Rasmussen 1992; Pine, Jessop and Oldham 1994a). The results of many of these studies have suggested that during lactation, nutritional restriction, fasting or poor body condition does not compromise milk composition but rather affects only milk yield (g/day) (see Oftedal 1985; Jensen 1989; Chan-McLeod, White and Holleman 1994). In contrast, other studies have demonstrated that milk composition does in fact change significantly in response to maternal nutritional status (Rook and Witter 1968; Lonnerdal 1986; Pine, Jessop and Oldham 1994b). Based on the similarity of milk secretion processes among all mammals, Iverson (1993) suggested that in species such as seals, whales and bears, that are highly adapted to producing milk while fasting, milk composition is unlikely to be affected by variation in maternal condition. Milk composition may remain relatively constant while yield changes in

Table 4.2. A comparison of the characteristics of adult female polar bears from which milk could (Lactating) or could not (Dry) be expressed during the autumn stage of the ice-free season in western Hudson Bay. Means were compared by one-way ANOVA after testing for homogeneity of variances.

	Dry (n = 5)	Lactating (n = 17)	P
Total body mass (kg)	169.0 ±11.9	172.1 ±3.8	>0.700
Body fat (%)	20.8 ±1.1	22.0 ±1.2	>0.600
Age (yrs)	15.2 ±2.3	13.9 ±1.4	>0.600

response to body condition. Very little is known, however, about variation in milk composition in mammals which fast during lactation (Oftedal 1993).

During late lactation the fat (and hence total solids) content of polar bear milk fluctuates from relatively high levels (averaging 33%) while mothers are feeding in spring and early summer, to lower levels (25%) during the ice-free period (Derocher et al. 1993a). Over the course of an ice-free season milk fat content tends to decrease gradually and ranges from 46.3 to 4.9% (Derocher et al. 1993a). Derocher et al. (1993) postulated that these reductions in milk quality during fasting reflected decreases in milk energy yield which occur as maternal fat reserves become exhausted. Similar ideas have also been put forward to explain large decreases (7%) in the fat content of northern fur seal (*Callorhinus ursinus*) milk during periods when lactating females are fasting on-land (Costa and Gentry 1986). This hypothesis that milk composition during fasting is sensitive to maternal condition is supported strongly by the results of the present study. During the late summer stage of the ice-free season variation among bears in milk quality is largely explained by differences in maternal condition, as measured by PBF but not total body mass (Figs. 4.4a & b).

While fasting, the fat stores of lactating polar bears provide precursors for the synthesis of fat rich milk but are also the primary source of fuel for metabolic maintenance of lean tissue (Atkinson, Nelson and Ramsay in press). It is hardly surprising, therefore, that variation in milk solids content is so strongly attuned to a measure of the relative fat content of the body, such as PBF, rather than total body mass. Since both body fat mass and LBM may differ among individual bears, variation in total body mass does not necessarily reflect fat content. Similarly, in other species that fast while producing fat rich milk, maternal mass may be an inadequate index of body condition when attempting to explain variation in lactational performance. In at least two recent of studies of lactation in seals, the use of total body mass rather than PBF may account for the failure to find significant relationships between maternal condition and milk composition (Kretzmann, Costa and Higgins 1991) or indices of milk yield (Hindell, Bryden and Burton 1994). In other studies, observed relationships between body condition and indices of lactational performance may have been significantly improved by the use of PBF (Anderson and Fedak 1987; McCann et al. 1989; Kovacs, Lavigne and Innes, 1991; Arnbom et al. 1993; Iverson et al. 1993).

4.4.2 Body condition and milk energy yield.

The pronounced effect of maternal body condition on the total solids content of polar bear milk (Fig. 4.4b) probably translates into a similar effect on daily milk energy yield. Crudely interpolating between the relationships shown in figures 4.2 and 4.4b provides some idea as to the overall sensitivity of lactation to maternal condition in late summer. For example, on an approximate basis, a decline in maternal PBF of 5% would result in a 30% reduction in milk energy yield. With a current late summer average of 230kg for total body mass, of which 65.5kg (28.5%; Table 4.1) is body fat, a 5% drop in PBF would be accounted for by a 15kg reduction in the body fat content of lactating females (50.5*100/[230-15]). Placing this rough figure (15kg) in context with documented variation in body mass, one can speculate about the impact that density-dependent or environmentally induced changes in maternal condition would have on lactation during late summer. For example, estimates of body mass suggest that between the mid 1960's and the early 1990's the average mass of adult female polar bears during the ice-free season in western Hudson Bay may have decreased by as much as 30kg (Derocher and Stirling 1992). If this long-term change in mass were due largely to bears accumulating less fat prior to coming ashore, lactational performance should, according to the findings of the present study, have declined substantially over the last three decades. Cubs-of-the-year, in particular, appear to be dependent upon milk during the ice-free season because they probably possess insufficient energy stores to endure prolonged fasts (Ramsay and Stirling 1988; Arnould and Ramsay 1994). It is easy to see from my results how lowered milk production, on a scale that would result from a 30kg reduction in maternal body mass, could have contributed to the reduction in survival among cubs-of-the-year that has been observed in this population (Derocher and Stirling 1992).

4.4.3 Age and lactation.

Even during the early stages of the ice-free season in western Hudson Bay, the quantity of milk produced by female polar bears is insufficient to prevent cubs from catabolizing their own body nutrient stores (Arnould and Ramsay 1994). By the autumn, after 2-3 months of food restriction, cubs have lost a significant amount of body mass (Table 4.1) and their nutritional dependency on milk may thus have increased considerably. Over the same period, maternal body mass and condition also declines (Table 4.1) such that by autumn the nutrient stores available for sustaining lactation may be approaching exhaustion in many individuals. In contrast to late summer however, and despite body fat contents at least as low as 12% in some lactating females, maternal body condition does not appear to be the strongest determinant of milk production during the autumn (Fig. 4.5). Instead, maternal age is most apparent as a factor affecting variation in lactational performance (Fig. 4.6). Independent of body condition, older bears tend to produce higher quality milks thereby implying greater milk energy yields.

4.4.3.1 Age-specific patterns of reproduction.

Numerous species of birds and mammals exhibit age-specific changes in reproductive performance (reviewed by Clutton-Brock 1984). In many instances, however, age per se is not the underlying cause of these reproductive patterns but rather is correlated with some aspect of 'quality' that affects an individual's ability to reproduce successfully. Quality may include such factors as social status, defence of offspring, foraging efficiency and body condition or size (Nur 1984; Albon et al. 1986; Ozoga and Verme 1986; Nol and Smith 1987; Green 1990; Wooller et al. 1990; Pyle et al. 1991; Sydeman et al 1991; Lunn and Boyd 1993; Arnbom, Fedak and Rothery 1994). Within a population or social group, variation in quality and reproductive performance across age classes may result from changes within individuals over time (ie experience, growth and senescence), or because poor quality individuals die at a younger age thus increasing average quality amongst survivors (Curio 1983; Coulson and Porter 1985; Nol and Smith 1987).

When examining age-specific reproductive patterns, seperating the effects of quality from age may prove difficult if quality is determined by a wide range of factors. In fasting polar bears, however, the only obvious measure of maternal quality that is associated with age and might affect lactation is body condition. Amongst adult females, average body mass (Derocher and Stirling 1994) and condition (Atkinson and Ramsay 1995) increases up to about 15 years of age and tends to decline in older bears. Consequently, many reproductive parameters such as litter size and weight follow a similar trend to age (Ramsay and Stirling 1988; Derocher and Stirling 1994). Having essentially controlled for body condition in my analyses, age itself still seems to exert some influence on reproduction. So, to what can such condition independent but age dependent lactational performance be attributed?

4.4.3.2 Reproductive effort.

Reproductive effort is defined as the proportion of available resources, such as time and energy, that an individual allocates to reproduction (Emlen 1970; Pianka and Parka 1975; Tuomi, Hakala and Haukioja 1983; Clutton-Brock 1984). In iteroparous animals, expectation of future reproduction, or residual reproductive value (Pianka 1976), may decline with advancing age. Under these conditions, life history theory predicts that reproductive effort should increase with age in order to promote the success of current reproduction (Gadgil and Bossert 1970; Pianka and Parka 1975). This shift in the trade-off between current and future reproduction, is most likely to occur in species that experience low adult mortality and some form of senescence towards the end of life, as indicated by deteriorating body condition and rising mortality (Emlen 1970; Charlesworth and Leon 1976; Curio 1988; Part, Gustafsson and Moreno 1992). Reasonable certainty of survival during adult life, and cues to aging, enable individuals to judge their residual reproductive value with some degree of accuracy and adjust reproductive effort accordingly.

Few studies have been able to provide convincing evidence of an increase in reproductive effort with age in mammals (Clutton-Brock 1984; Sydeman 1991; Bowen et al. 1994). Female polar bears, however, might well be expected to exhibit age-related changes in reproductive effort because they have a long lifespan (>20 years), low adult mortality and what appears to be a senescent decline in survival (Derocher 1991), body weight (Derocher and Stirling 1994) and probably condition (Atkinson and Ramsay 1995) in later life. Indeed, the results of the present study provide strong evidence that reproductive effort increases with age (at least up to 23 years). Among females of equal body condition in the late stages of the ice-free season, older individuals would apparently show the best lactational performance. Thus, at time when maternal condition is relatively poor and cubs are perhaps most dependent upon milk, older females appear to make a greater effort to sustain lactation than do younger mothers.

4.4.3.3 Costs of reproduction.

Underlying any discussion of reproductive effort is the assumption that by allocating more resources to reproduction an individual runs a higher risk of mortality and loss of future reproductive opportunities (Tuomi et al. 1983; Clutton-Brock 1984; Part et al. 1992). Such costs of reproduction, however, may be subtle and often hard to quantify (Reznick 1985). For example, it has been hypothesised (Partridge 1987), and empirical evidence suggests (Bradley et al. 1989; Sydeman et al. 1991), that senescence is not necessarily a simple consequence of aging and limits on lifespan. Declining physical condition and reproductive performance, such as that seen in female polar bears during later life, may in part reflect the gradual cumulative costs of successive reproductive attempts. The condition independent lactation apparent in the present study is exactly the type of expenditure that would contribute to some form of 'accelerated senescence' (Partridge 1987) or reproductive 'burn-out'. Unfortunately, detailed long-term data on the reproductive histories of individual bears are not yet available to test this proposal.

4.4.3.4 Effect of parity on lactation.

The mammary glands of many mammals do not cease to develop at the on-set of sexual maturity (Knight 1984). Continued cell proliferation during early reproductive life may lead to differences in secretory activity and lactation patterns among animals of varying age or, more importantly, parity (Oldham and Friggens 1989). Evidence from dairy cattle and pigs suggests that, despite receiving food *ad libitum*, the extent to which body nutrient stores are mobilized to sustain milk production increases over the first four lactation cycles. With increasing parity females are more tolerant of a negative energy balance during lactation (Neilson, Crawford and Oldham 1988; Yang et al. 1989). Whether a similar effect occurs in wild species such as polar bears, that have not been subject to intense selection by man for high productivity, is unknown. Discussion from this perspective does, however, provide a potential physiological basis for the observed association between age and lactation in polar bears: Lactation in bears that are older and of higher parity being less sensitive to fasting.

4.4.4 Cessation of lactation: Age or condition dependent?

Personal observations and those of previous investigators (Derocher et al. 1993a) suggest that some (22%) bears stop lactating during the ice-free season in western Hudson Bay. Comparing the characteristics of a small number of these analactic bears with those of lactating bears did not reveal any obvious differences in body mass, condition or age (Table 4.2). Given a larger sample size, an analyses of lactating vs non-lactating bears might well reveal an interaction between both age and body condition. On the basis of my results, one prediction arising is that older females will stop lactating at a lower level of condition than younger individuals.

The cessation of lactation during the ice-free season is an event that could mark the end of the weaning process and initiate the break up of family groups. The age at which polar bear cubs become independent of their mothers varies considerably both among and within populations. The western Hudson Bay population is especially notable because a significant number of cubs become independent at an earlier age (end of their first year) than in more northerly populations (Ramsay and Stirling 1988). It is conceivable that the longer ice-free season in western Hudson Bay and other southern populations, such as James Bay, might cause more mothers to stop lactating thereby promoting the independence of cubs at a relatively young age. Two predictions of this hypothesis would be that: (1) In years following ice-free seasons when maternal condition was poor, or the duration of fasting long, the frequency of independent yearling cubs would increase. (2) Older mothers would tend to wean their cubs later than younger mothers. What factors determine when a mother stops producing milk is a question that remains unanswered by this study but one that clearly merits further investigation.

5. GROWTH IN EARLY LIFE AND RELATIVE ADULT BODY SIZE AMONG POLAR BEARS (*URSUS MARITIMUS*).[2]

5.1 Introduction.

Among mammalian species, the occurrence of sexual size dimorphism is typically associated with a polygynous mating system (Ralls 1977; Alexander et al. 1979). In some cases adult males may be more than twice the size of adult females. The polar bear is a prime example. In this highly sexually dimorphic carnivore, adult males weigh approximately twice as much as females and are 20% greater in length (Ramsay and Stirling 1986; Derocher 1991). This size dimorphism is largely the result of the longer growth period of males relative to females (Kingsley 1979; Derocher 1991). Females attain adult body length at around 5 years of age, shortly after they commence breeding (Ramsay and Stirling, 1988; Derocher 1991), while males do not reach adult body length until 8 years of age.

For species which exhibit extreme sexual dimorphism, variation in life-time reproductive success is usually greatest amongst males (Clutton-Brock 1988). Male mating success is largely dependent upon relative body size and other traits which determine competitive ability in intra-sexual contests for access to mates (Parker 1974; Maynard-Smith and Parker 1976; Clutton-Brock, Albon and Guinness 1988; Le Beouf and Reiter 1988; Haley, Deutsch and Le Boeuf 1994). Among male polar bears,

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competition for matings is thought to be particularly intense because the number of oestrous females available in any mating season is limited. Some females can remain anoestrous for up to 2-3 years while rearing cubs (Ramsay and Stirling 1986; 1988). Furthermore, unlike other species of Ursidae, polar bears do not occupy discrete home ranges or defend territories. As a result, dominance hierarchies may have little opportunity to form and the outcome of male-male interactions is often determined by fighting, as indicated by the high incidence of wounding and broken canines found in adult males but not in females (Ramsay and Stirling 1986). Structural size, therefore, should be a particularly important determinant of reproductive success in male polar bears but less so in females (Latour 1981; Ramsay and Stirling 1986).

In any polygynous mammal, the adult body size that an individual attains will be dependent, to varying degrees, on a number of factors including the level of nutrition received during maternal care and food availability during the juvenile years after maternal care. For species such as the polar bear, in which body size affects male reproductive success, maternal investment theory predicts that adult females in good nutritional condition should tend to allocate a greater proportion of their resources to individual male rather than female offspring (Maynard-Smith 1980; Charnov 1982; Clutton-Brock and Albon 1982; Frank 1990). By biasing nutrition toward males, mothers may produce males that are relatively large and eventually grow to become reproductively successful. A fundamental assumption of this theory is that the success of growth in early life exerts a strong influence on the eventual adult body size of males. Whether differences in body size that are apparent at an early age (as might result from variation in nutrition provided by mothers or food availability in the environment after independence) persist to adulthood, however, is a question that has rarely been addressed in studies of large, long-lived mammals in the wild (Clutton-Brock, Guinness and Albon

1982; McCann, Fedak and Harwood 1989; Green and Rothstein 1993).

Examining data on the persistence of relative body size among polar bears, I attempted to test the hypothesis that body size in early life (but after the period of maternal care) influences the relative adult body size that individuals eventually attain. Although actual data on maternal expenditure or investment are not presented, the implications of the results for strategies of maternal investment in polar bears are briefly discussed.

5.2 Methods.

5.2.1 Data collection.

Data for the study were collected between 1965 and 1993 from bears captured on-shore in summer and autumn (the ice-free period) at the study site in western Hudson Bay. This area of northern Manitoba, is an ideal location for investigation of long term changes in body size because the high density and degree of philopatry of bears in this region increases the probability that tagged individuals will be repeatedly captured over a number of years, albeit at irregular intervals. Bears were captured using standard immobilization techniques and each animal was ear tagged, lip tattooed and sexed. Animals were aged using records of past captures or when necessary a tooth was extracted (Chapter 2).

Previous studies of polygynous mammals, have used body weight and/or body length as indices of body size (eg Clutton-Brock, Albon and Guinness 1988; Le Boeuf and Reiter 1988; Haley et al 1994). In polar bears, fat may account for anywhere from 10 to 50% of total weight (Atkinson and Ramsay 1995). Consequently, body weight is particularly sensitive to seasonal changes in food intake and reproductive status, whilst also being dependent upon age and sex (Ramsay, Mattacks and Pond 1992). In contrast, body length is primarily dependent upon age and sex, and is therefore a more appropriate measure of structural size than weight. On this basis, length rather than weight was used in analyses of relative body size. Body length (cm) was measured as the straight line distance from the tip of the nose to the end of the last tail vertebra when each bear was placed in a sternally recumbent position. It is important to note that, as length is a linear measure, a difference in body length will translate, by some cubic function, into a much larger difference in structural mass.

5.2.2 Selection of data for analyses.

Polar bears in their first (cubs-of-the-year) and second (yearlings) years of life receive varying quantities milk during the ice-free period and may grow in length at rates ranging from 0.06 to 0.34 and 0.00 to 0.13 % per day, respectively (Arnould and Ramsay 1994). As a result, any analysis of observed variation in body length among cubs-of-the-year or yearlings would undoubtedly be confounded to some extent by differences in date of capture (over the 4 month annual sampling period).

The timing of independence in young polar bears (i.e., when offspring become nutritionally and socially independent of their mothers) varies both within and among populations. In western Hudson Bay (Canada), independence is thought to occur some time around spring in either the second or third year of life, when offspring are approximately 1.4 (yearlings) or 2.4 (2-year-olds) years of age (Ramsay and Stirling 1988). During the ice-free period, therefore, any bear in its third year of life or more is independent and not receiving milk. Although juveniles (immature bears that are independent) may feed on berries and other vegetation for brief periods over the ice-free season, stored fat deposits meet a majority of energy requirements (Ramsay and Hobson 1991; Derocher et al. 1993b). In these nutritionally restricted or fasting animals, body weight steadily declines (Derocher 1991; Atkinson, Nelson and Ramsay in press) and any structural growth may be inhibited to a greater degree than in cubs-of-the-year or yearlings. Consequently, body length in juvenile bears may be less sensitive to date of capture over the annual sampling period. Following this line of reasoning, only juvenile and adult polar bears were included in analyses.

5.2.3 Birth year effects.

Since 1965 there has been a gradual linear decline in the body weight of bears in the study population (Derocher 1991). As data for this study were collected over 28 years, any similar long-term trends in body length might affect analyses of relative body length. To test for such trends, year of birth was used to distribute animals according to the years they were growing rather than their year of capture. Defining adult bears as those females >5.0 and males >8.0 years of age, the relationship between adult body length and birth year was examined for male and female bears using least-squares regression analyses (SAS Institute, 1988). Based upon these results, birth year was used as a covariate in subsequent analyses of relative body length.

5.2.4 Persistence of relative body size among males and females.

To investigate the effects of early growth on adult body size in polar bears, males and females that were captured as 2-year-olds (after the maternal care period) and later recaptured as adults were included in analyses. Two-year-olds were defined as animals in their third year of life and were therefore between 2.6 and 2.9 years of age at the time of initial capture. Many individuals captured as 2-year-olds were captured several times as adults. For each of these bears, average adult body lengths were calculated. In analyses, data on body length were then weighted according to the number of times each animal was captured as an adult.

Animals were separated by sex and an 'among-individuals' mean body length calculated for each sex-by-age category (males or females, as 2-year-olds or adults). These group means were then subtracted from the body lengths of each bear in the relevant groups, to give the deviation from the mean or relative body length of each individual. The relationship between the relative body length of 2-year-olds and their subsequent relative adult body length was tested by partial correlation analysis with birth year as a covariable.

In another analysis, the body lengths of 2-year-old bears recaptured as adults were compared with the lengths of 2-year-olds that were not recaptured as adults. To eliminate the possibility that bears born in later years were not recaptured as adults simply because they had not yet reached adulthood, only females born before 1988 and males before 1985 were included in this analysis.

5.3 Results.

5.3.1 Birth year effects.

Adult body length declined with increasing birth year in females (Fig. 5.1a; $n = 344$, $r^2 = 0.08$, $P < 0.001$) but not males (Fig. 5.1b; $n = 151$, $r^2 = 0.004$, $P > 0.4$).

5.3.2 Growth in early life and adult body size.

A total of 42 females and 30 males were handled as 2-year-olds and then recaptured at least once as adults (>5.0 and >8.0 years respectively). The adult females were recaptured on a total of 109 separate occasions and males on 73 occasions. The ages of adults ranged from 5.6 to 26.8 years for females and 8.6 to 24.8 years for males. On average, females increased in length by 11% from 2-year-olds to adulthood while

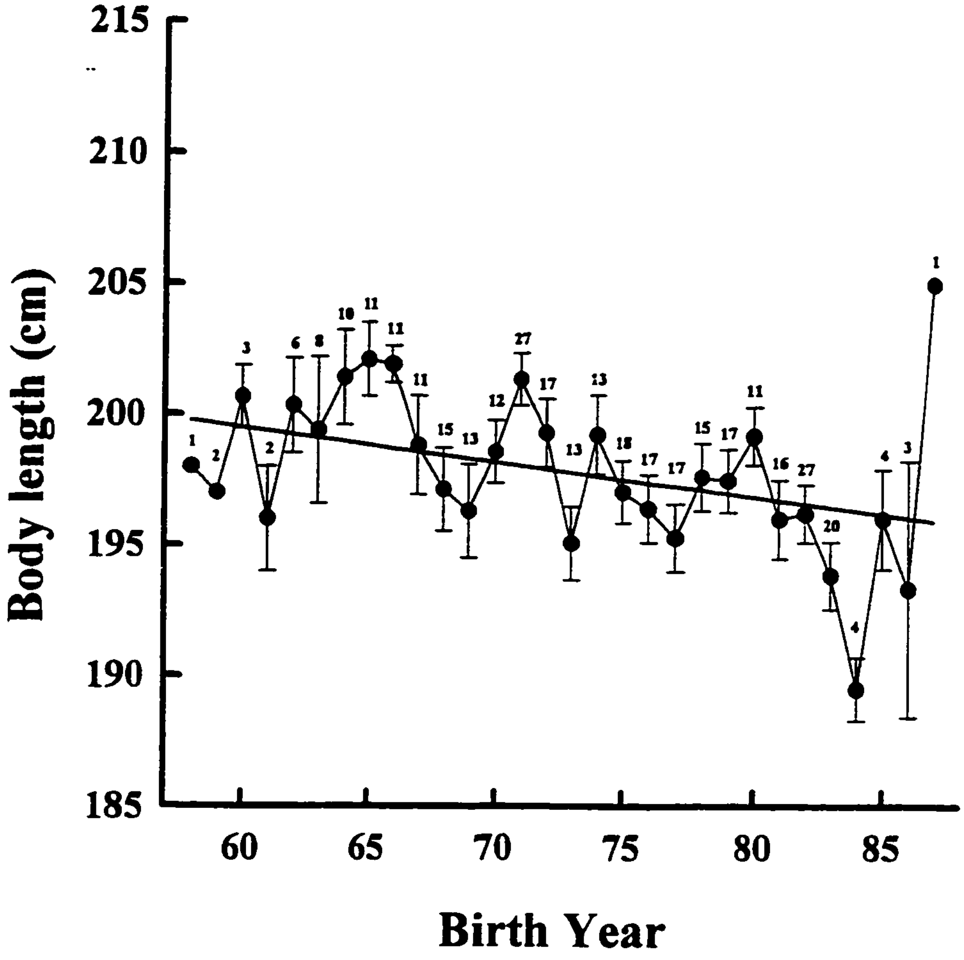

Figure 5.1a. The relationship between mean body length (cm) and birth year in adult female polar bears (>5 years). Bars represent ±1SE. Samples sizes indicated above points.

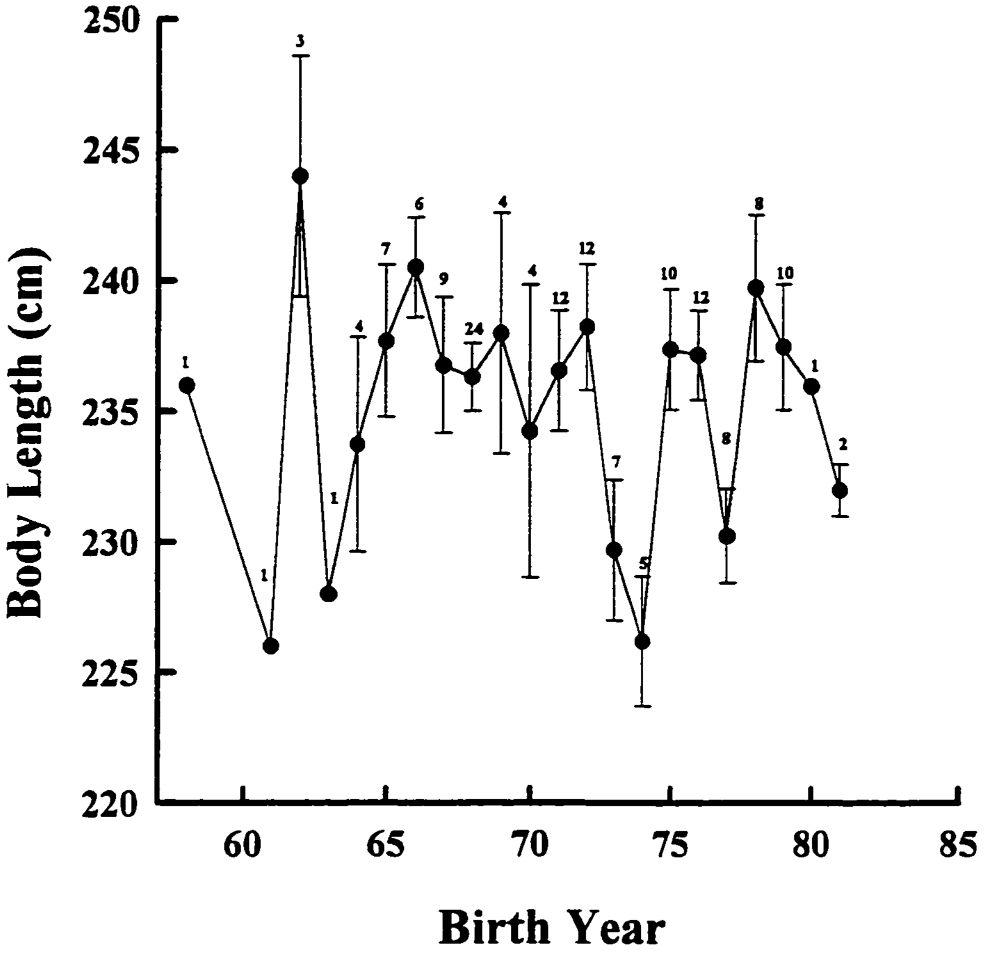

Figure 5.1b. The relationship between mean body length (cm) and birth year in adult male polar bears (>8 years). Bars represent ±1SE. Samples sizes indicated above points.

males grew by 23% (Table 5.1). For both sexes, the range of these growth increments was wide.

Relative adult body length for females was significantly related to relative length as a 2-year-old (Fig. 5.2a; $r_{\text{partial}} = 0.41$, $P < 0.01$). Larger 2-year-old females tended to become relatively large as adults. In contrast, relative adult male body length was weakly related to relative length as a 2-year-old (Fig. 5.2b; $r_{\text{partial}} = 0.33$, $P > 0.07$). Relatively large 2-year-old males did not necessarily grow to be relatively large as adults. Birth year had no significant effect on either sex.

To eliminate the possibility that younger adult bears had not quite reached their maximum body size when recaptured, the minimum adult ages for inclusion of bears in the analyses were arbitrarily increased by 2 years. Of the 42 females captured as 2-year olds, 31 were recaptured when >7.0 years of age. For this sample, relative adult body length was again related to relative length as a 2-year-old ($r_{\text{partial}} = 0.46$, $P < 0.0075$). Larger 2-year old females tended to be relatively large adults. Of the 30 adult males captured as 2-year olds, 21 were recaptured at >10.0 years of age. Relative adult male body length was again unrelated to relative body length as a 2-year-old ($r_{\text{partial}} = 0.32$, $P > 0.15$).

Comparing the body lengths of 2-year-olds that were either recaptured or not recaptured as adults (Table 5.1), revealed no significant differences between these two groups (Females; $t = 0.41$, *d.f.* = 56, $P > 0.5$. Males; $t = 0.31$, d.f = 61, $P > 0.5$). Thus I conclude, the 2-year-olds used in the recapture analyses (Fig. 5.2) were representative of the population.

Table 5.1. Body length (cm), and changes in body length (%), of polar bears that were captured as 2-year-olds and later recaptured as adults (>5 yrs and >8 yrs for females and males respectively). For comparison, body lengths of bears that were handled only as 2-year-olds are also presented. Sample sizes are in parentheses (*n*).

		Recaptured animals		
	2-year-olds captured only once	2-year-olds	Adults	Mean [and range of] increase (%) in body length
Females	177.5 ±1.6 (16)	178.3 ±0.8 (42)	198.5 ±0.9 (42)	11.3 [3.1-17.9]
Males	192.1 ±1.5 (33)	191.4 ±1.3 (30)	235.2 ±1.4 (30)	22.9 [12.3-37.2]

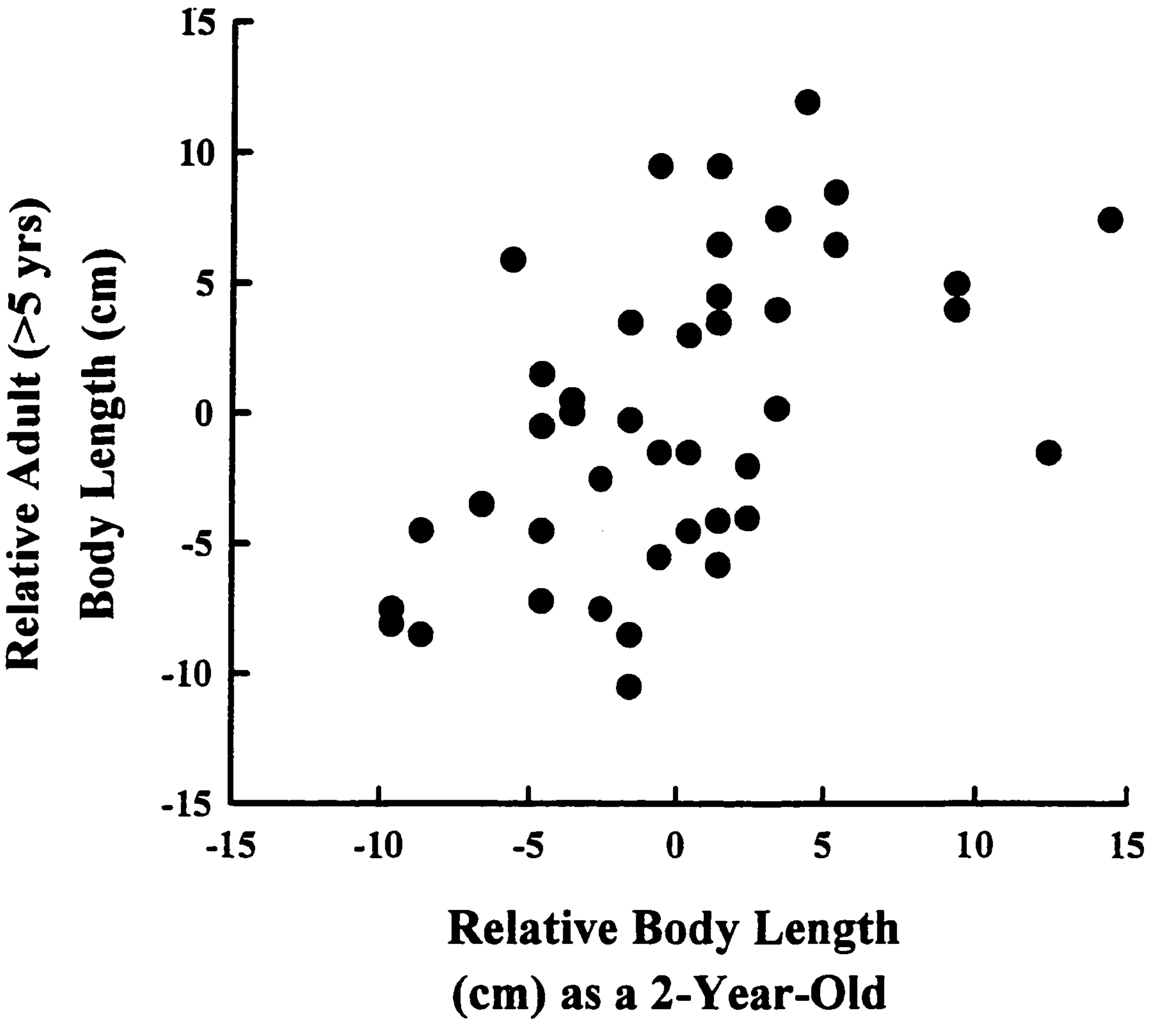

Figure 5.2a. The relationship between relative mean adult body length and relative juvenile body length in female polar bears.

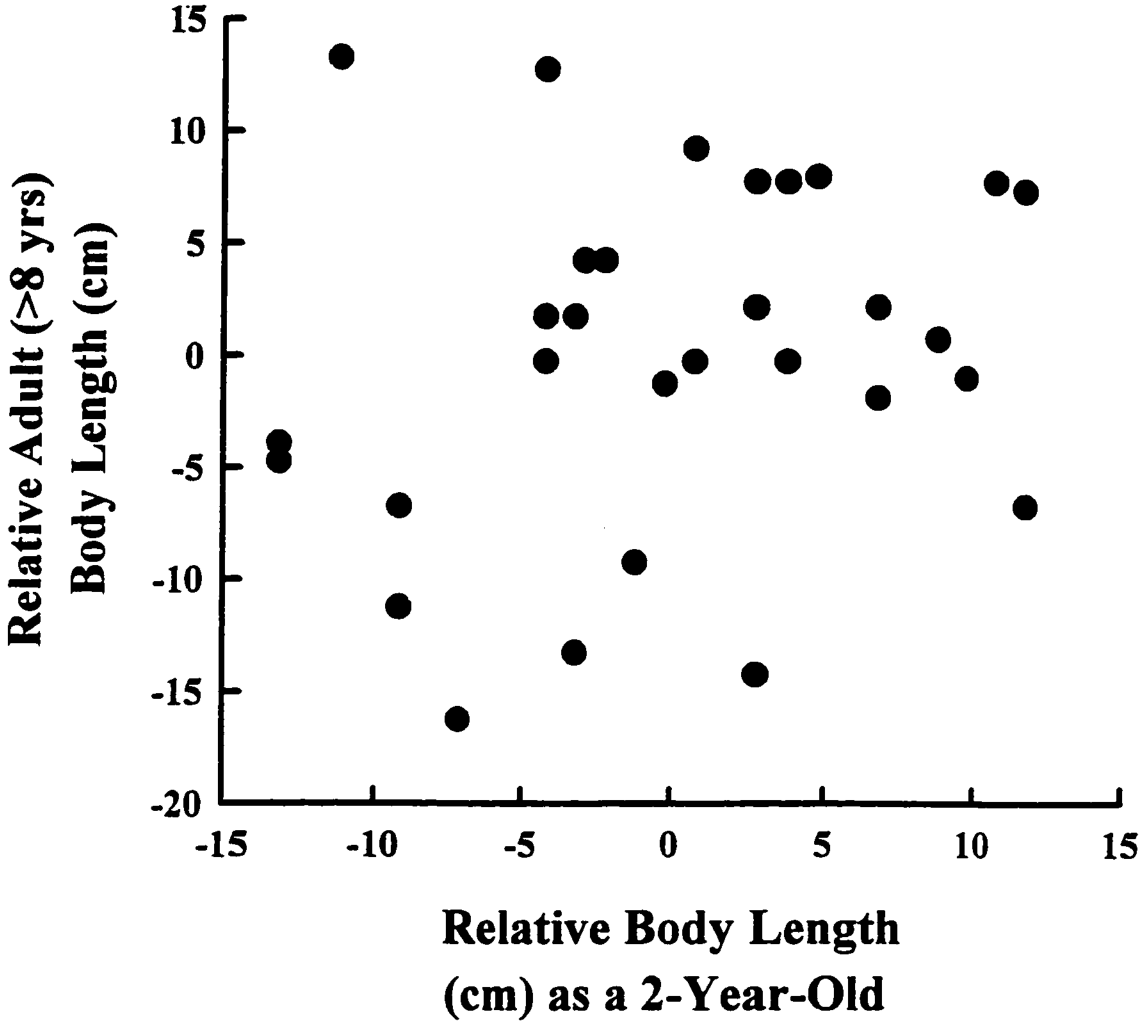

Figure 5.2b. The relationship between relative mean adult body length and relative juvenile body length in male polar bears.

5.4 Discussion.

5.4.1 Long-term trends in body size.

For males in particular, adult body size in species such as polar bears is a trait that may be closely associated with fitness and is thus predicted to exhibit relatively low heritability (Mousseau and Roff 1987; Leamy and Bradley 1988). In mammals, with their determinate growth patterns, variation in body size in wild populations may be largely dependent upon nutrition (eg East and Lockie 1964; Ralls and Harvey 1985) rather than genetics. Nevertheless, adult body size will reflect the effects of both genetical and environmental influences on growth (Stearns 1992; Bernardo 1993). Changes within, or variation among, populations in body size may arise in response to changes in selection pressures (Ralls and Harvey 1985; Leamy and Bradley 1988; Millar and Hickling 1990), level of inbreeding (Berger and Peacock 1988), and density dependent or environmentally induced variation in food availability (Bryden 1968; Kingsley, Nagy and Reynolds 1988; Fowler 1990; Albon, Clutton-Brock and Langvatn, 1992).

The body size of polar bears in the western Hudson Bay population appears to be responding to some sort of change in conditions, either nutritional or genetical. From birth year analyses, it is apparent that over the interval of data collection, since 1965, the average body length of adult females has gradually declined (Fig. 5.1a). No such trend, however, is seen among males (Fig. 5.1b). While the relatively small sample size for adult males compared to females (151 vs 344) may account for this difference in body length trends between the sexes, I offer a second explanation. Body length is a measure of the cumulative growth which occurred over the years prior to sampling each animal. In male polar bears, the relatively long growth period means that successive cohorts of offspring will overlap considerably with respect to the years during which they were growing. All males born within an 8 year period will have experienced some degree of similarity in environmental conditions and population densities during their years of growth. Consequently, the subtle effects of gradually declining resource availability (or natural selection) on growth rates and body size may be hard to detect in adult males. In contrast, adult females have a much shorter growth period and, as a result, less overlap will occur among cohorts in terms of conditions experienced during years of growth. I suggest, therefore, that long-term changes in mean adult body size may become evident earlier in adult females than males.

Unlike my results for body length, Derocher (1991) found that when analyzed by year of capture, estimated body weight has declined within all sex and age categories of polar bears in western Hudson Bay, including adult males. Polar bears experience large annual fluctuations in body weight and composition due to periods of hyperphagia and fasting (Watts and Hansen 1987; Ramsay et al. 1992). As a result, body weight will be more sensitive than length as an indicator of changes in food availability. The effects on adult males of subtle or gradual changes in food availability may thus be more apparent in their body weight than in body length.

5.4.2 Growth in early life and adult body size.

In western Hudson Bay, 2-year-old polar bears that are captured during the ice-free season have been independent of their mothers for approximately 1.2 to 1.5 or 0.2 to 0.5 years. Observed variation in body size among 2-year-olds, can therefore be attributed to variation in the level of nutrition received during maternal care and, to some extent, foraging success after independence. Having reached this juvenile stage of development, 2-year-old females subsequently increase in length by only 11.2 %, on average, before attaining adult body size at around 5 years of age (Table 5.1). Not surprisingly, therefore, differences in relative body length apparent among 2-year-old females tend to persist and are reflected in relative adult body length (Fig. 5.2a). Large 2-year-old females generally become large adults. In contrast, a relatively large proportion of growth in the body length of males occurs during the juvenile years (after maternal care) (Table 5.1) over a period approximately twice as long as that of females (5 - 6 versus 2 - 3 years). Unlike females, the body size that males have attained by the time they are 2-year-olds does not appear to exert a particularly strong influence on their eventual adult body size (Fig. 5.2b).

For polar bears in any population, the juvenile years represent a period during which rates of food intake may vary considerably. Hunting skills may take time to reached adult standards (Stirling and Latour 1978) and maternal resources, such as milk or killed seals, no longer buffer young bears from environmental variability. Polar bears prey upon marine mammals, primarily ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*), that are unevenly distributed both temporally and spatially (Smith and Stirling 1978; Smith 1980; Hammill and Smith 1989). As a result, foraging success and hence growth rates may vary widely and unpredictably both within and among juvenile bears. Relative to females, prolonged growth period beyond the time of family break-up may, consequently, predispose the growth rates of males to a greater degree of environmentally mediated variation. Under these conditions, differences in body size that are established at an early age (such as in 2-year-olds) would be weaker determinants of relative body size among adult males than females.

5.4.3 Maternal investment strategies in polar bears.

Derocher (1991) found that the relative body length of polar bear cubs in their first year of life was positively associated with length in their second year. Furthermore, cub and yearling lengths were also related to maternal weight thereby suggesting that maternal condition may strongly influence offspring body size (at least during the period of maternal care). On the basis of my results (Fig. 5.2a and b), however, I propose that for males in particular, differences in relative body size apparent by the end of maternal care are unlikely to persist to adulthood. If this were the case, any bias in the allocation of maternal resources in favour of male offspring would not necessarily be an effective strategy of parental investment. The level of investment male cubs received would not determine, with a high degree of certainty, their eventual adult size and reproductive success. A similar lack of persistence in the relative body size of male offspring has been reported or proposed for two other large, long-lived polygynous mammals, the bison (*Bison bison*) and the southern elephant seal (*Mirounga leonina*) (McCann et al. 1989; Green and Rothstein 1991; 1993). Interestingly, in both species evidence of sex-biased maternal investment is weak. It remains to be seen whether this is the case for polar bears.

6. CHANGES IN THE BODY COMPOSITION OF FASTING POLAR BEARS (*URSUS MARITIMUS*): THE EFFECT OF RELATIVE FATNESS ON PROTEIN CONSERVATION.[3]

6.1 Introduction.

Many animals experience regular periods of fasting either as a result of seasonal declines in food availability or when intense reproductive activities prevent foraging (Mrosovsky and Sherry 1980; King and Murphy 1985; Cherel, Stahl and Le Maho 1987; Ryg, Smith and Øritsland 1990; Boyd and Duck 1991). Despite being able to mobilise considerable energy stores in the form of fat during these fasts, death may nevertheless result if a significant amount of body protein is lost (Cherel et al. 1992). One of the fundamental adaptations which permits animals to fast for particularly extended intervals, therefore, is a heightened ability to minimize the catabolism of body protein while relying upon large stores of body fat to meet maintenance energy requirements (Belkhou et al. 1990; Castellini and Rea 1992).

Even among species that are adapted to fasting, Holarctic bears of the genus *Ursus* are notable for their ability to go without food for prolonged periods (Nelson 1987; Castellini and Rea 1992). For two species in this taxa, black (*U. americanus*) and grizzly (*U. arctos*) bears, denning for the duration of a 5-month over-winter fast is a strategy of energy conservation that is adopted by most individuals (Johnson and Pelton 1980; Watts

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[3] *A version of this chapter has been accepted for publication. Atkinson, S.N., Nelson, R.A., and Ramsay, M.A. Physiological Zoology 69:000-000.*

and Jonkel 1988). While denning, fasting bears are able to rely almost exclusively on their fat stores there by avoiding the net catabolism of protein, net production of urine and thus maintaining a relatively constant lean body mass (LBM) (Lundberg et al. 1976; Nelson 1980). The remarkable effectiveness of this protein-sparing adaptation is, however, thought to be limited to the over-winter denning period as black bears that are denied access to food during the summer are apparently unable to attain a similar protein-sparing state (Nelson et al. 1975).

In a third species of Holartic ursid, the polar bear, the ability to endure prolonged fasts may not be restricted to the denning period. During the summer through autumn "ice-free" period in western Hudson Bay (Chapter 2), polar bears have little or no access to food and are thus obliged to fast for up to 4 months (Ramsay and Hobson 1991; Derocher, Andriashek and Stirling 1993b). Although most polar bears, except pregnant females, do not occupy dens regularly during this ice-free fast, biochemical data on urea:creatinine ratios suggest that many individuals are nevertheless able to adopt an efficient state of protein conservation similar to that of denning bears during the winter (Nelson 1987; Ramsay, Nelson and Stirling 1991). Furthermore, such a fasting response may also function in polar bears at other times of the year, for instance during the mating season in spring when adult males may forego feeding in order to compete for access to females (Ramsay et al. 1991).

To date, most evidence of protein sparing in bears has been inferential and data have yet to be presented that quantify actual changes in the body composition of free-ranging bears during a fast. As part of my investigation into the nutritional ecology of polar bears in western Hudson Bay, therefore, I measured body composition changes in free-ranging, reproductively inactive, adult and sub-adult males during their summer to autumn ice-free fast. The overall objective of this study was to determine the magnitude of both fat and lean tissue losses during fasting in order to establish the relative importance of lipid and protein fuels in meeting energy requirements. In addition, I examined the pattern of variation in body composition changes among individuals and compared our results with those derived from other studies on bears.

6.2 Methods.

6.2.1 Capture, handling and body composition changes.

Data were collected at the study site near Churchill during the ice-free season of 1993. Although little food was available during this study period, all bears had ready access to free water from the numerous ponds in the region or as snow later on in the season. Between late July and early August, adult and sub-adult male polar bears were captured, using standard immobilization techniques (Stirling, Spencer and Andriashek 1989), shortly after they had come ashore. While immobilised, bears were lip tattooed, weighed and their body composition determined by isotopic dilution as previously described (Chapter 2). When necessary a tooth was extracted for the purpose of aging. Males less than eight years of age were considered sub-adults.

In order to facilitate relocation, two VHF ear-tag radio-transmitters (Holohil Systems, Woodlawn, Ontario, Canada) were attached to each animal. The same bears were then recaptured during October, approximately 2-2.5 months after initial capture, and before they had returned to the newly formed sea-ice to feed. Upon recapture, bears were reweighed, their body composition determined and the radio-transmitters removed. Changes in the body composition of individual bears during the study period were calculated from capture and recapture body composition data. In addition, data for male bears were compared with the results of a previous study on body composition changes that occurred in pregnant female polar bears over a 6-8 month fast that encompassed both the ice-free season and an over-winter maternity denning period (Atkinson and Ramsay 1995).

6.2.2 Blood Parameters.

At both capture and recapture, two additional blood samples (10ml) were taken from each bear prior to injection of the isotopic water. Upon returning to our field camp, one sample was carefully agitated and sub-sampled for micro-hematocrit determination (Brown 1988). The remaining blood from this sample was centrifuged and plasma collected. Plasma samples were frozen in cryogenic vials and later used to measure plasma water content at capture and recapture. This was done by drying a known amount of plasma in an oven at 70°C until a constant mass was achieved. Serum obtained from the second of the two samples was assayed for the concentrations of urea and creatinine by staff at the Department of Veterinary Pathology, University of Saskatchewan. Serum urea nitrogen was determined by spectrophotometry with a urease reagent kit (Abbott Diagnostics, Dallas, TX.). Urea nitrogen values were then divided by 0.466 to obtain serum urea concentrations. Serum creatinine was determined as outlined by Nelson, Beck and Steiger (1984). The data for each bear were then expressed as the ratio of serum urea to creatinine (U/C).

6.3 Results.

6.3.1 Body Composition.

Ten male polar bears, including five adults and five sub-adults between 2 and 22 years of age, were captured and recaptured during the ice-free period. These bears came ashore in widely varying body condition, ranging in relative fatness from 0.12 to 0.58 kg of fat per kg of LBM at initial capture (Table 6.1). The individual that was visibly

Table 6.1. Changes in the body composition of five adult (>7 years of age) and five sub-adult male polar bears during the ice-free period (July - October) in western Hudson Bay.

Age	Initial body mass (kg)	Initial relative fatness (Fat/LBM)	Capture interval (days)	Mass loss (kg)	LBM loss (kg)	Fat loss (kg)
Adults:						
15	259.5	0.12	74	71.7	47.2	24.5
22	469.5	0.33	76	76.7	47.3	29.4
19	477.2	0.41	88	101.6	56.8	44.8
17	574.2	0.47	76	115.6	43.5	72.1
14	586.5	0.44	86	121.1	77.6	43.5
Sub-adults:						
2	197.8	0.32	80	41.8	30.3	11.5
3	228.6	0.58	66	47.6	3.8	43.8
2	298.5	0.45	82	64.0	41.5	22.4
6	392.4	0.55	73	79.4	33.2	46.2
4	342.0	0.54	85	79.8	28.3	51.5

Note: Within each age class, bears are listed in order of quantity of mass lost during fasting.

in the poorest condition (initial relative fatness of 0.12) appeared to have a dislocated or broken fore-limb which had likely reduced its success at catching seals, the prey of polar bears (Stirling and Archibald 1977). Subsequently, over an interval that ranged from 66 to 88 days, these male bears lost between 42 and 121 kg of body mass (Table 6.1). Of this loss, 12 to 72 kg was fat, while 4 to 78 kg was LBM. All bears thus lost some LBM and six of the ten lost more LBM than fat on a kilogram basis.

Assuming that the hydration of lean tissue remained constant over the sampling period, protein was taken to compose 22.3% of LBM (Farley and Robbins 1994). Using constants of 39.3 and 23.6 MJ/kg for the energy contents of fat and protein respectively (Blaxter 1989), body composition changes were converted into units of energy. On the basis of these data, bears lost 285.9 kJ of body energy/kg of body mass$^{0.75}$/day (± 30.3) with no significant difference between adults (265 ±31) and sub-adults (307 ±52) (Student's *t*-test, $t_8 = 0.72$, $P > 0.4$). Between 74 and 99% of this loss in body energy was attributable to loss of body fat (mean = 85.8 ±2.4). Although wide, variation in the proportional contributions of fat and protein to energy losses was in part explained by the relative fatness of bears when they were initially captured. Bears that were relatively fat in the summer subsequently lost a higher percentage of body energy in the form of fat than did leaner bears (Fig. 6.1; $r_{\mathrm{spearman}} = 0.85$, $P < 0.005$).

6.3.2 Blood Parameters.

Between initial capture and recapture, hematocrit values (%) decreased significantly from 46.8% (±0.5) to 43.7% (±0.9) (Wilcoxon signed ranks test, $n = 9$, $T^+ = 41.5$, $P < 0.03$). Plasma water contents (% by mass) did not change significantly (90.2 ±0.3 to 90.3 ±0.2%, $n = 10$, $T^+ = 36$, $P > 0.4$) and were very similar among all individuals. Serum urea to creatinine ratios (U/C) varied both within and among

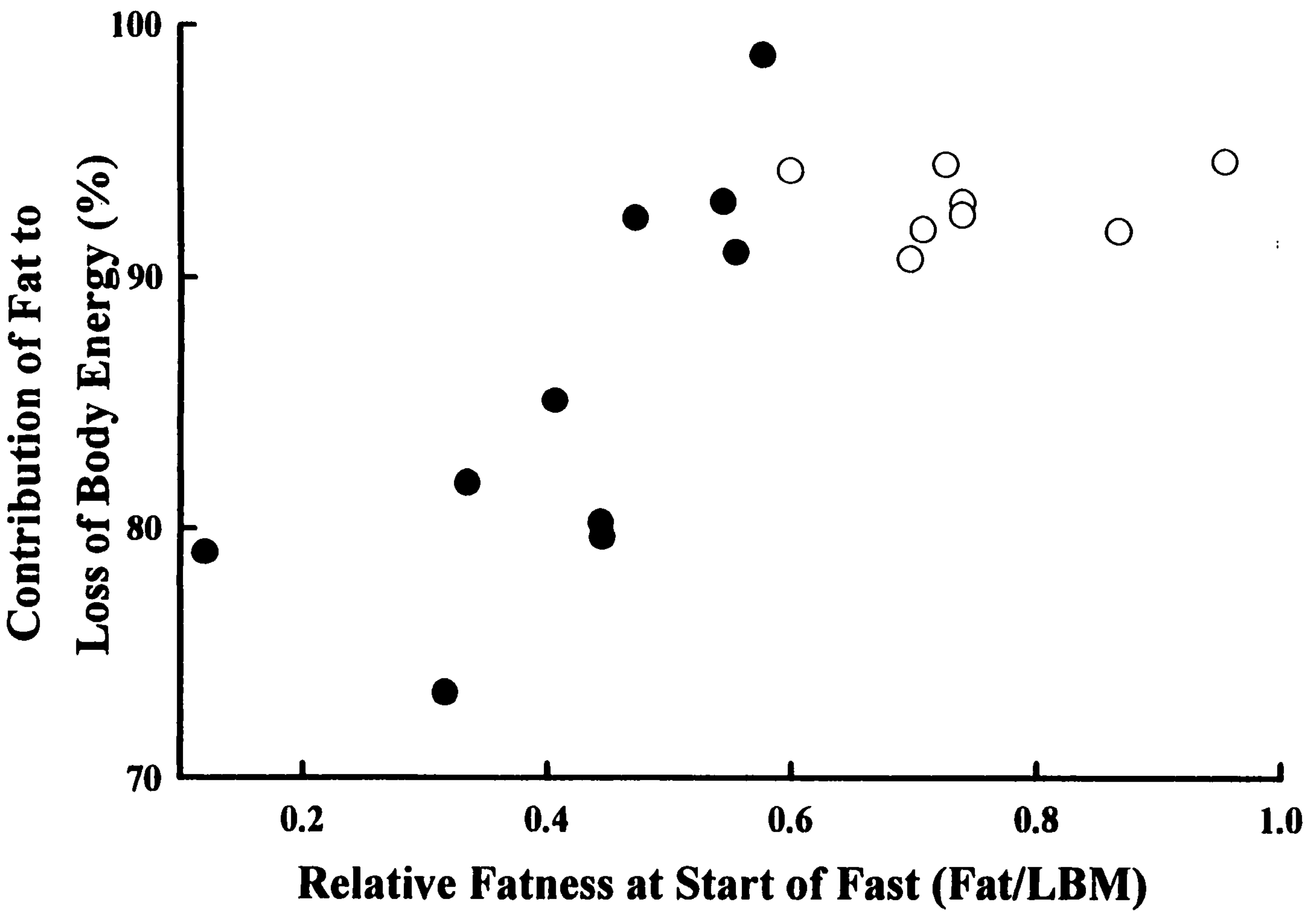

Figure 6.1. The effect of initial body composition on the relative contribution of body fat to subsequent losses of body energy in fasting adult/sub-adult male (filled circles), and adult female polar bears (open circles). Energy losses occurred over 79 (±2) and 192 (±9) days for males and females respectively. Note that adult females transferred some protein to cubs over the study period. The proportional contribution of fat to maternal maintenance energy requirements may thus be underestimated by the data.

individuals. Although the correlation was weak ($r_{\text{spearman}} = 0.44$, $P_{\text{(one-tailed)}} < 0.11$), bears that derived a lower percentage of their energy needs from fat, hence a higher percentage from protein, tended to exhibit higher mean U/C ratios (see Fig. 6.2, where mean U/C was calculated for each bear as the mean of urea at initial and recapture divided by the mean of creatinine at initial and recapture).

6.4 Discussion.

6.4.1 Effect of Relative Fatness on Body Protein Conservation.

During the summer-autumn ice-free season in western Hudson Bay, fasting male polar bears do lose significant amounts of lean tissue in addition to body fat (Table 6.1). In all cases but one the observed extent of LBM loss was well beyond any error or variation that might be expected from repeated measures of TBW on the same individual (Farley and Robbins 1994). Consistent with previous studies of bears and other animals (Nelson et al. 1975; Lundberg et al. 1976; Pfeiffer, Reinking and Hamilton 1979; Ahlquist et al. 1984; Castellini, Castellini and Kretzmann 1990; Reilly 1991), the absence of an increase in hematocrit and the constancy of plasma water content in bears during the present study suggests that fasting did not result in hemoconcentration through circulatory dehydration. In addition to the fact that polar bears had ready access to water, these blood parameters support strongly the view that estimated losses of LBM were not simply the result of dehydration, but involved losses of both protein and water. Contrary, therefore, to previous proposals that polar bears are highly adapted for avoiding the net catabolism of body protein while fasting (Nelson 1987; Ramsay et al. 1991), our data indicate that some males may catabolise significant portions of their body protein during the ice-free season.

Controlled laboratory studies have shown that initial obesity at the on-set of a fast

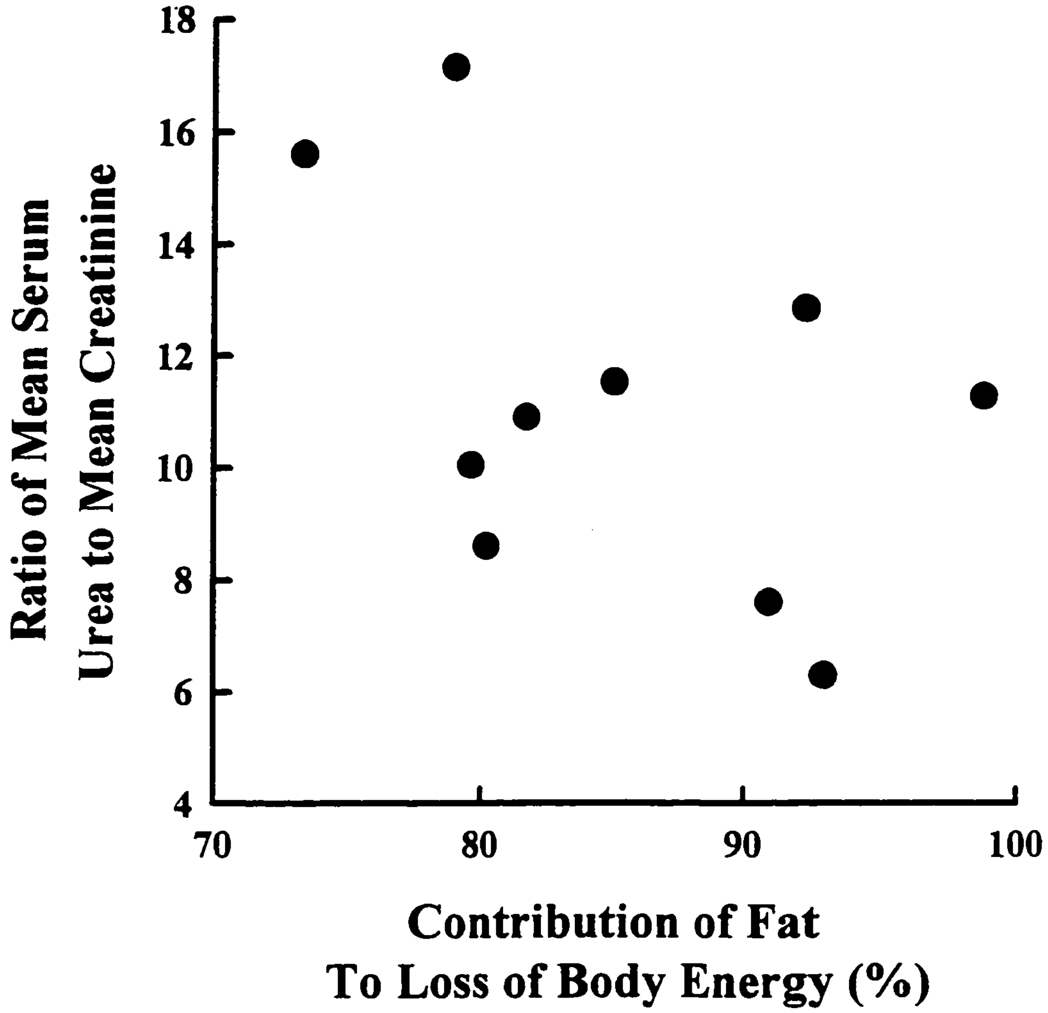

Figure 6.2. The relationship between the relative contribution of fat to losses of body energy in fasting male polar bears, and mean urea/mean creatinine ratio over the same period of energy loss.

may subsequently determine the relative rates of body fat and protein catabolism in a fasting animal. Relatively fat individuals are able to achieve and maintain a lower rate of protein catabolism than leaner subjects. Such an effect, whereby the relative rather than absolute size of fat and protein pools at the on-set of a fast determines their pattern of depletion, has been demonstrated both intra- and inter-specifically (Goodman et al. 1984; Robin et al. 1988; Belkhou et al. 1990; Cherel et al. 1992; Cherel et al. 1993). Similarly, in the case of male polar bears, the relative use of fat and protein fuels appears to be dependent upon the relative fatness or obesity of individuals when they come on-shore in the summer (Fig. 6.1). Individuals that are relatively lean when they arrive on-shore at the start of their fast subsequently derive a larger proportion of their energy requirements from body protein.

Data from a previous study (Atkinson and Ramsay 1995) provide additional support for the proposed hypothesis that relative fatness affects protein loss in fasting polar bears. At the start of an ice-free season, solitary adult females are typically the most obese of all polar bears; some having accumulated up to 1.0 kg of fat per kg of LBM. Individuals in this reproductive class are usually pregnant and will go without food for up to eight-months, from late summer to spring, including a 5-6 month maternity denning period (Watts and Hansen 1987; Ramsay and Stirling 1988). Although not directly comparable because of a large discrepancy in the duration of fasting between the two studies, the data available suggest that these obese adult females generally derive a higher proportion of their energy needs from fat stores than the relatively lean males (Fig. 6.1). It should also be noted, that over part of their "reproductive fast", adult females transfer some protein to cubs during gestation and lactation. Consequently, calculated changes in maternal body composition during this period will understimate the proportional contribution of body fat to maternal maintenance energy requirements.

6.4.2 Urea:Creatinine as an Indicator of Net Protein Catabolism.

It has been suggested that a decrease in the ratio of serum urea to creatinine (U/C), to a value of around 10 or less, indicates the attainment of an efficient protein-sparing state in a fasting bear (Nelson et al. 1984; Ramsay et al. 1991). While only statistically weak, the limited data available in the present study are suggestive that variation in U/C ratios may reflect differences among polar bears in the proportional use of fat and protein fuels during the summer-autumn fast in western Hudson Bay (Fig. 6.2). Furthermore, cross-sectional data for a larger sample of bears (Ramsay et al. 1991) demonstrate that the U/C ratios of some individuals are well above 10 even in the later stages of the ice-free season. A significant proportion of polar bears may therefore come ashore in late summer with fat stores that are insufficient to achieve or maintain a particularly effective state of protein conservation while fasting.

6.4.3 Significance of The Results to Other Species.

Unlike denning bears in winter, black bears that are deprived experimentally of access to food and water during the summer become uraemic and exhibit relatively high U/C ratios thus indicating that a significant amount of protein is being catabolized (Nelson et al. 1975). In contrast, a majority of polar bears that experience a natural summer to autumn fast appear to maintain relatively low U/C ratios (Ramsay et al. 1991). From these observations, it has been suggested (Nelson 1987; Ramsay et al. 1991) that while the ability to adopt an efficient protein-sparing state is restricted to the denning period in black bears, such a fasting response may occur in polar bears during any period of food shortage. Inter-specific comparison of data obtained from naturally fasting bears with that from animals kept under experimental conditions may, however, result in misleading conclusions.

On the basis of my results from polar bears, I propose that among ursids in general the ability to avoid the net catabolism of protein during a fast is largely dependent upon relative fatness at the start of the fast. Relative fatness, in turn, will follow an annual cycle, reflecting seasonal changes in food abundance, which may differ significantly between polar bears and their largely omnivorous congeners. For example, among polar bears, such as those in western Hudson Bay, the peak period of hyperphagia and fattening occurs in spring before the summer fast (Ramsay and Stirling 1988; Messier, Taylor and Ramsay 1992). Most individuals may thus arrive on shore in summer with relatively large fat stores. In comparison, food availability for wild black bears does not usually reach a peak until the summer or autumn (Rogers 1987). Consequently, black bears that are experimentally starved during summer may be unable to avoid an extensive loss of protein simply because their fat stores are insufficient at this time of the year. As the body condition of black and grizzly bears reaches a peak shortly before denning, the relative fatness of individuals at this time is undoubtedly a significant factor contributing to their ability to maintain a remarkably constant LBM during the denning period (Lundberg et al. 1976). In one experiment for which data are available (Lunberg et al. 1976), the captive black bears were in better condition prior to denning (0.78 kg of fat/kg of LBM, [±0.05]) than were any of the male polar bears captured during late summer in our study (Table 6.1).

In conclusion, I suggest that polar bears are no more proficient at minimizing the net catabolism of protein during a fast than are other ursid species. Seasonal differences among holarctic ursid species in the ability to conserve LBM during fasts likely reflects inter-specific variation in annual cycles of feeding and body condition. Furthermore, the previously reported efficiency of protein conservation in bears relative to many other species, (Castellini and Rea 1992) may be, at least in part, a consequence of the obese proportions that individuals can attain prior to fasting (Pond and Ramsay 1992).

7. GENERAL DISCUSSION.

Polar bears occupy a niche of the Arctic marine ecosystem in which they have evolved to exploit a food resource that varies in availability both temporally and spatially. From ecological and physiological perspectives, I have examined the effects of this variable food supply on the body composition, body size and reproductive patterns of polar bears. In so doing, I have illustrated some of the adaptations and strategies which enable this Holarctic ursid to avoid or alleviate the adverse effects of nutritional stress (King and Murphy 1985) on survival and reproduction.

7.1 The significance of obesity in polar bears.

Fat, an energy rich nutrient, plays a particularly significant role in the lives of polar bears. My studies have shown that, during any period when polar bears do not have access to prey, lipids released from adipose deposits meet a majority of metabolic energy requirements for survival (Chapter 6). For adult females, stored body fat is also the most important nutrient affecting reproductive performance during a fast. Prior to the long denning period, pregnant bears reach extremely obese proportions, some individuals possessing as much as 1 kg of fat per kg of lean body mass (Chapter 3). Despite variation in the timing of capture and sampling intervals, the size of these maternal fat stores was shown to exert a particularly strong influence on the weight (and probably condition) of young cubs when they emerged from dens in spring (Chapter 3). Furthermore, at a later stage of the lactation cycle, the fat content (hence energetic value) of polar bear milk was found to be sensitive to maternal body fat content (Chapter 4).

Mothers in relatively poor condition producing milk of lower nutritional value. This close dependency upon fat, for survival and reproduction, undoubtedly accounts for the observation that during spring, when is food abundant, polar bears sometimes consume only the adipose tissue of their prey (Stirling and McEwan 1975; pers. obs.).

7.2 Protein reserves.

Although the accumulation, storage and utilization of fat is very much the main theme in the nutritional ecology of polar bears, other nutrients still play an important role. Young bears will obviously need to consume and assimilate significant quantities of protein in-order to grow, and adult females must undoubtedly possess some labile protein reserves to sustain gestation and lactation while fasting. Among polar bears in general, my studies suggested that protein is an essential component of the diet for reasons other than growth or reproduction. A heightened ability to minimize the catabolism of protein is thought to be a principle adaptation enabling polar bears to endure prolonged fasts. In an effort to test this proposal, however, I found that some bears do in fact catabolize significant quantities of protein to meet maintenance energy requirements while fasting (Chapter 6). Furthermore, my studies demonstrated that the efficiency of protein sparing is not fixed but varies according to the relative size of body fat and protein pools.

Protein reserves depleted while fasting must be replenished at other times, suggesting that lean body mass follows a seasonal cycle some what similar to that of fat. Indeed, during periods of hyperphagia such as the spring, deposition of extensive fat stores seems to be accompanied by an accumulation of lean tissue (Chapter 3). Whilst providing a protein reserve, this increase in lean mass may serve another functional purpose, reflecting a build-up of muscle tissue that results from transporting large fat deposits over the long distances polar bears are known to move. As fat stores are depleted during fasting, maintenance of lean tissue that was accumulated during weight gain may become a significant metabolic burden. Protein from this 'excess' lean tissue may thus be the first or only protein catabolized.

7.3 The significance of age.

Polar bears develop a certain proficiency at hunting whilst with their mothers (Stirling and Latour 1978). The finding that body condition (in particular fat content) increases with age among pregnant bears, however, strongly suggested that foraging success may continue to improve long after weaning (Chapter 3). Among adult females, the effects of hunting experience on body condition are most likely to be seen in pregnant bears because these individuals are unencumbered by the nutritional demands of offspring. Nevertheless, conclusive proof of the effects of experience will require data on changes in the body condition of individual bears as they age. Rather than (or in addition to) the effects of experience, bears that are poor hunters may die at an earlier age thus accounting for the association between age and condition among bears.

The importance of age as parameter in the reproductive life-histories of polar bears was clearly emphasised by the results of my research. Whether due to experience or differential mortality, age-specific patterns of body condition that were observed among pregnant females will have a pronounced effect on reproductive performance during the denning period (Chapter 3): Older, fatter mothers tending to produce heavier cubs that are subsequently more likely to survive. In addition, a study of lactation during the ice-free season suggested that, underlying the effects of age on body condition and reproduction, there may be adaptive changes in maternal reproductive strategies with age (Chapter 4). Evidence, that milk production in the later stages of fasting was less dependent of body condition and more dependent upon age, provided strong support for the idea that reproductive effort increases with age. As pointed out by several authors (Clutton-Brock 1984; Part et al. 1992), many studies have equated reproductive effort with the energetic costs of reproduction. In its strictest sense, however, an increase in reproductive effort is associated with increased costs to survival and future reproductive potential. The unique aspect of my study (Chapter 4) is that, although I was unable to document such costs of reproduction, any expenditure that is independent of resource availability (in this case body condition) is likely to have some detrimental effects, even if not immediately apparent.

Clearly, age-specific reproductive strategies are a subject that warrant further investigation in polar bears. One aspect I find particularly intriguing is a situation in males that is some what analogous to the trade-offs between body condition and reproduction made by adult females while fasting. Males do not make any post-partum investment in offspring but their pre-partum investment may be substantial. Even though the mating season coincides with the period when food availability is highest (Ramsay and Stirling 1986), preliminary data show that males may lose considerable amounts of body mass while pursuing and competing for oestrous females (Ramsay unpublished data). For males to lose body condition by engaging in mating activities, at a time when other bears are accumulating nutrient stores that are probably essential for survival later in the year, may represent a significant cost. It is therefore conceivable that the energy males allocate to mating activities changes with age in a manner similar to that apparent in lactating females (Chapter 4); Older males tending to make trade-offs between foraging and reproduction that result in greater reproductive effort.

Very little is known about the juvenile years after bears become independent of their mothers. Nutritionally, this stage of life may be one of the most restricting. Bears must rely on their own hunting abilities (that may still be developing) in order to survive, whilst also allocating a proportion of their food intake to growth. For males, in which growth continues well beyond the period of maternal care, conditions experienced as a juvenile may have a particularly significant impact on survival, development and ultimately reproductive success. Long-term studies of polar bears in western Hudson Bay provided a rare opportunity to examine changes in the body size of individual bears during their juvenile years. I demonstrated that differences in relative body size established at an early age tend not to persist to adulthood in males (Chapter 5). This effect was attributed to the influence of environmental variation on juvenile growth. Furthermore, I speculated that the weak link between early growth and adult body size would limit the potential for the presence of male-biased maternal investment in polar bears. Whether maternal investment is biased in favour of males is a question that I am just starting to address in analyses not presented in this thesis.

7.4 Some concluding remarks.

At the start of my research, I made a decision to sacrifice sample sizes in exchange for the time and money required to collect data on body composition in free-ranging polar bears. This approach proved to be valuable for at least two reasons. First, most previous studies of the nutritional and reproductive ecology of bears have relied upon data on total body mass, or estimates of total body mass, to draw conclusions about subjects such as seasonal cycles in body condition and the effects of condition on reproduction (eg. Tietje and Ruff 1980; Kolenosky 1990; Stringham 1990; Derocher, Stirling and Andriashek 1992; Derocher and Stirling 1994; Samson and Huot 1995). While many of these studies have provided real and valuable insights, significant effects and features may have been over looked due to a lack of sensitivity in the type of data collected (ie total body mass). By going to go a level of organization beyond most earlier studies, chapter 4 of my thesis, which looks at factors affecting variation in lactational performance, illustrates quite well the short comings of using even accurate measures of total body mass as indices of condition.

Second, current understanding of the ability of bears to endure prolonged fasts stems largely from research on captive bears (Lundberg et al. 1976; Nelson 1980). Extrapolating from the results of these experimental studies in-order to make inferences about bears in the wild, however, presents the potential for misleading conclusions. For example, based on results obtained from studies of captive bears, the ability to conserve body protein while fasting was thought to differ between polar bears and their congeners (Nelson et al. 1975; Nelson, Beck and Steiger 1984; Nelson 1987; Ramsay, Nelson and Stirling 1991). By examining body composition changes in free-ranging bears, and placing the results in context with inter-specific differences in seasonal cycles of food intake, I was able to present evidence suggesting that this hypothesis is incorrect (Chapter 6).

To conclude, although my studies focused on one of the most southerly populations of polar bears, I feel that the results are applicable to the species in general. At higher latitudes bears may experience seasonal periods of fasting or nutritional restriction which are shorter than those typical of western Hudson Bay. Nevertheless, there is no reason to assume that similar adaptations to fasting (Chapter 6), characteristics of growth (Chapter 5), and interactions between maternal body condition, age and reproductive performance (Chapter 3 and 4), are absent among bears in more northerly locations. Research conducted on any species at the edges of its geographical range is simply more likely to expose the limits of that species' adaptability to short- or long- term changes within its environment. Of course, with respect to my research on polar bears, the ambient temperatures were also generally more pleasant to work in!

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