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THE UNIVERSITY OF ALBERTA

ASPECTS OF PHYSICAL CONDITION IN BLACK BEARS AND POLAR BEARS

by

MARC CATTET

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1988

ISBN 0-315-45548-9

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: MARC CATTET

TITLE OF THESIS: ASPECTS OF PHYSICAL CONDITION IN BLACK BEARS AND POLAR BEARS

DEGREE FOR WHICH THESIS WAS PRESENTED: MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED: FALL 1988

(SIGNED) Marc Cattet

PERMANENT ADDRESS:

....

....

DATED 4 AUG 1988

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

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Date: 2 August, 1988.

Abstract

Thirty-eight black bears (*Ursus americanus*) and forty-three polar bears (*U. maritimus*) were dissected to determine the most statistically reliable equations for predicting total body weight (TBW) and non-fat body weight (NFBW). Physical condition was evaluated by calculating a fat-to-non-fat ratio, equalling (TBW - NFBW)/NFBW. This ratio was independent of body size, and thus comparable between sex and age classes.

Measurements of marrow and intramuscular lipid content, and morphometric measurements that can be obtained in the field, were evaluated as indicators of physical condition. TBW and NFBW were predicted by multiple regression equations using various combinations of measured variables. The neutral lipid content of marrow or muscle was not a reliable indicator of physical condition.

The fat-to-non-fat ratio is best applied in intraspecific comparisons of groups of black or polar bears. Comparisons among individual bears require the development of more accurate techniques.

Anatomical and chemical investigations were conducted, on five black bears and six polar bears, to determine: (1) distribution of neutral lipid by tissue; (2) relationships between physical condition indices and whole body lipid content; and (3) relationships between lipid and energy content on a tissue and whole body basis.

Adipose tissue was the major lipid storage tissue for both species. However, the lipid content of most tissues was significantly related to whole body lipid content. Polar bears accumulated adipose tissue lipid in a positive allometric pattern while black bears did so isometrically. This may reflect greater emphasis on long-term lipid storage in polar bears relative to black bears.

Among physical condition indices, the fat-to-non-fat ratio was the best

indicator of percentage whole body lipid content; percentage lipid in marrow or muscle did not show significant relationships with percentage whole body lipid content.

Lipid and energy content were significantly related in all tissues and the whole body in both species, although the relationship was strongest in adipose tissue. Approximately 60% of the whole body gross energy of black and polar bears could be accounted for by the energy content of all neutral lipids in the body; lipid in adipose tissue contained most of this energy.

Acknowledgements

There are many people and numerous agencies that have provided support and encouragement for my research in its progression from an idea to a realization. To the following, I should like to offer my appreciation and gratitude.

John Lee, Dr. Ray Schweinsburg and Gord Stenhouse provided much advice and encouragement at the inception of my research project. Gord Stenhouse arranged much of the logistical support for the polar bear portion of my research and was instrumental in making the project a reality.

I should like to thank Drs. Ian Stirling and Jan Murie, my research co-supervisors, for committing themselves to my aspirations. Ian provided me with many opportunities to share knowledge and information with researchers outside of the university setting; this I very much appreciated. To me, Jan exemplified scientific research as part of, but not the reason for, being. In a competitive and demanding world, the tendency to become obsessed with one's career is all too prevalent. I would also like to extend my gratitude to my other supervisory committee members, Drs. Sue Hannon and Mick Price, who gave valuable criticism of my ideas.

I thank Kidlapik Alogut, Cory Booth, Mark Bradley, Heather and Monique Cattet, Dan Clouthier, Nick Lunn, Bob McClymont, Robert Mulders, Tomassie Nakoolak, Claire Stirling, David Schwartz, and Bruce Treichel for their assistance during the collection and dissection of bears. I should also thank Raymond Bourget and Ben Kovic for their assistance and cooperation in Coral Harbour and Eskimo Point, Northwest Territories. In Edmonton, valuable assistance during the homogenization and chemical analysis of carcasses was provided by Jacquie Beaudry, Inez Gordon, and Orst Palyniak.

The Fish and Wildlife Division of Alberta Forestry, Lands, and Wildlife

kindly provided black bears killed in the defense of life or property and allowed me to use their facilities to conduct dissections. The Hunters and Trappers Associations of Coral Harbour, Eskimo Point, and Resolute Bay kindly provided polar bears killed during their annual hunts. Polar bears killed in the defense of life or property were also provided by the Manitoba Department of Natural Resources, Churchill.

Support for my research project was received from the Boreal Institute for Northern Studies, the Canadian Wildlife Service, the National Sciences and Engineering Council of Canada, the Northwest Territories Department of Renewable Resources, and the Polar Continental Shelf Project.

I should especially like to thank those people who, with their knowledge and experience, saved me much time and trouble throughout my research; they are Dennis Andriashek, Wendy Calvert, Willma Cook, Gavin Godby, Mike Jourdan, Michael Kingsley, and Cheryl Walker. Finally, I should like to give a special thanks to Dr. Malcolm Ramsay; his friendship and support were an integral part of my research.

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TABLE 3.2. Constants for regression of tissue lipid (Y) on whole body lipid (X) in black bears and polar bears

Tissue	Species effect[a]	Species	a	b±SE	Sign. of slope (H_0:b=0)	R^2	N
Adipose	*/P	Black	-0.336	1.003±0.055	**	0.994	4
		Polar	-1.171	1.191±0.017	***	0.999	5
Skin	---	Black	-2.124	0.875±0.343	n.s.	0.765	4
Bone	*/P	Black	-2.681	1.199±0.211	*	0.942	4
		Polar	-0.661	0.628±0.053	**	0.979	5
Muscle	*/C	Black	-2.105	0.635±0.272	n.s.	0.731	4
		Polar	-2.002	0.859±0.162	*	0.904	5
Viscera	n.s.	Pooled	-3.429	0.918±0.113	***	0.904	9

[a] Regression lines compared between species by a partial F-test for parallelism (P). If lines were parallel, then the regression lines were compared between species by a partial F-test for coincidence (C). Results of comparison tests are denoted as 'level of significance/P or C'. If tests for parallelism and coincidence were both non-significant, then results are denoted as 'n.s.', and regression was performed on data pooled from both species.

TABLE 3.3. Constants for regression of three physical condition indices (Y) on percent whole body lipid[a] (X) for black bears and polar bears.

Index (Y)	Species effect	Species	a	b±SE	Sign. Slope (H_0:b=0)	R^2	N
<u>Fat-to-non-fat ratio</u>							
	n.s.	Pooled	-0.067	1.685±0.204	***	0.883	11
<u>Percentage lipid in marrow</u>							
Femur	n.s.	Pooled	1.090	0.000±0.000	n.s.	0.000	9
Humerus	n.s.	Pooled	1.079	-0.377±0.392	n.s.	0.116	9
Tibia-fibula	n.s.	Pooled	1.064	-0.639±0.637	n.s.	0.125	9
Radius	*/P	Black	0.877	0.895±0.418	n.s.	0.696	4
		Polar	1.147	-1.252±0.478	n.s.	0.696	5
Ulna	n.s.	Pooled	1.115	-0.611±0.753	n.s.	0.086	9
<u>Percentage lipid in muscle</u>							
Biceps brachii	n.s.	Pooled	0.034	0.015±0.059	n.s.	0.008	10
Biceps femoris	n.s.	Pooled	0.021	0.173±0.086	n.s.	0.337	10

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[a] Percent whole body lipid refers to the percent lipid content of the whole body on a wet weight basis.

TABLE 3.4. Constants for regression of energy[a] content (Y) on lipid content[b] (X) of the whole body and tissues of black bears and polar bears

Tissue	Species effect	Species	a	b±SE	(H_0:b=0)	R^2	N
Whole body	n.s.	Pooled	9.935	0.887±0.033	***	0.988	11
Adipose	n.s.	Pooled	9.217	0.988±0.024	***	0.996	9
Skin	---	Black	9.891	1.422±0.162	*	0.975	4
Bone	n.s.	Pooled	9.780	0.929±0.079	***	0.951	9
Muscle	n.s.	Pooled	10.757	0.837±0.205	**	0.704	9
Viscera	n.s.	Pooled	9.997	0.832±0.150	***	0.815	9

[a] Energy content of whole body and tissues measured in kilocalories.

[b] Lipid content of whole body and tissues measured in kilograms.

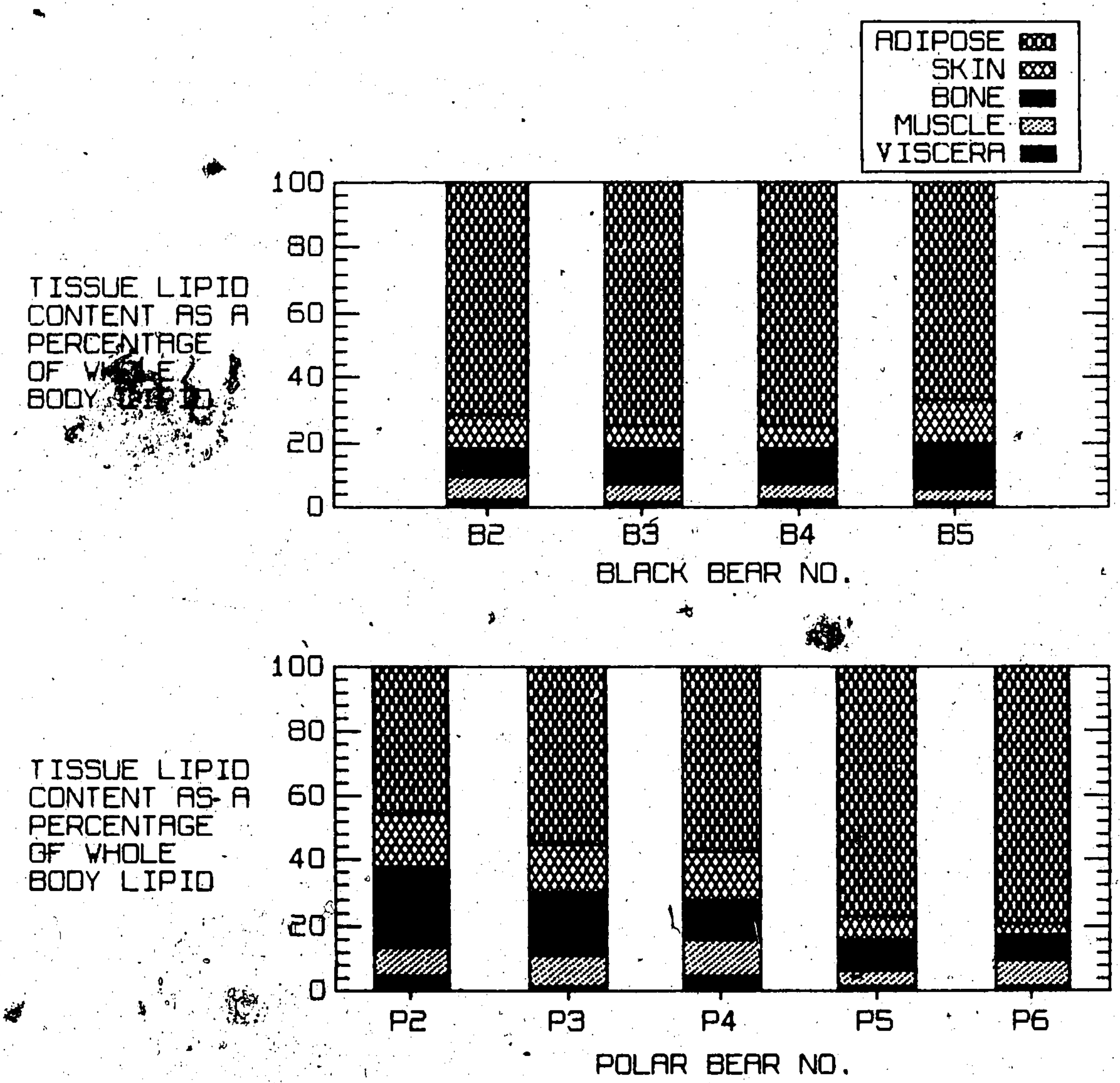
TABLE 3.5. Estimated percentage[a] of whole body gross energy accounted for by neutral lipid and distribution (%) of neutral lipid energy by tissue in black bears and polar bears

Tissue	Black			Polar			F_{max}-test[b] (sign.)	t-test[c] (sign.)	Pooled mean
	mean	SD	n	mean	SD	n			
Whole body	60.3	19.4	5	62.7	15.5	6	n.s.	n.s.	61.6
Adipose	72.0	3.5	4	62.9	14.4	5	*	n.s.	66.9
Skin	9.0	2.9	4	16.0	----	1	----	----	----
Muscle	5.0	1.6	4	8.5	2.7	5	n.s.	n.s.	7.0
Viscera	2.3	0.5	4	2.9	1.2	5	n.s.	n.s.	2.6
Bone	11.6	2.6	4	14.7	6.9	5	n.s.	n.s.	13.3

[a] Estimated percentage of body gross energy in neutral lipid calculated as total lipid content (g) of whole body multiplied by 9.3 kcal/g, and then divided by the gross energy content (kcal) of the whole body. The average metabolizable energy of lipid is 9.3 kcal/g (Hochachka and Somero 1973).

[b] F_{max}-test used to test for homogeneity of variances between black and polar bears.

[c] t-test used to test for significant differences between mean values of black and polar bears.



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4. CONCLUDING DISCUSSION

The aspects of physical condition in black and polar bears are briefly reviewed here to provide a suitable framework for discussing the contributions, implications, and shortcomings of this research to our current knowledge of black and polar bears.

The first aspect explored was the determination of methods for evaluating physical condition of black and polar bears from morphological measurements. Previously, body weight was considered [illegible] be the best predictor of physical condition in bears. However, an increasing understanding of the ecology of these species has made desireable a more sensitive approach (Folk *et al.* 1970; Ramsay 1986). As an indicator of physical condition, the fat-to-non-fat ratio is an improvement upon total body weight and reflects the quantity of stored fat maintained by a bear. This contrasts with the few advocated physical condition indices for bears in which the relationship between index and total body fat is not known (Schroeder 1986; Franzmann and Schwartz 1988).

To be useful, the estimation of fat-to-non-fat ratios requires morphological measurements that are easy, rapid, and inexpensive to collect. Most of these measurements are routinely collected so that evaluation of physical condition in captured or killed bears is often possible from previous years. This may benefit long-term population studies of black or polar bears by contributing valuable information to the relationships between survival, reproductive success, the effect of environmental disturbance, and physical condition (Kirkpatrick 1980; Robbins 1983).

The possible shortcomings of estimating fat-to-non-fat ratios also need to be emphasized. The ratio depends upon the measurements (or predictions) of total body weight and the prediction of non-fat body weight. In situations where total body weight cannot be directly measured, the fat-to-non-fat ratio may lose much accuracy through the introduction of an additional error source. It is also important to realize gut content weight and, to a lesser extent, blood weight may sometimes severely bias ratio estimation.

The errors and biases associated with estimating the fat-to-non-fat ratio limits use of the ratio to intraspecific comparisons of groups of black or polar bears or comparisons of individual bears differing substantially in physical condition. Comparisons among individual bears in similar physical condition require the calibration and application of more accurate techniques, e.g. isotopic techniques, nuclear magnetic resonance, bioelectrical impedance.

The validity of quantifying the physical condition of black and polar bears, based on the quantity of measureable body fat, since the availability of stored neutral lipid most directly reflects the physical condition of a mammal. The chemical composition of fat is variable and neutral lipid is not restricted in distribution to adipose tissue suggesting that the relationship between measurable body fat and physical condition may not be as simple as is often assumed. Unfortunately some field studies have used physical condition indices without attempting to determine whether an index chosen has even the slightest biological validity (Robbins 1983).

Adipose tissue is the major tissue for lipid storage in black and polar bears. However, in both species the lipid content of most tissues was significantly related to the lipid content of the whole body. This suggests further attention should be directed towards the sampling and measuring of lipid content in non-adipose tissues as an indicator of physical condition in bears. The major difficulty with this potential technique is the heterogeneous distribution of lipid in the body tissues (Schemmel 1976; Pond and Mattacks 1985; Aguilar 1985).

There were differences between black and polar bears in the pattern of lipid deposition in some of the tissues of the body. That was especially true for adipose tissue. Assuming adipose tissue functions predominately as an energy storage organ, polar bears may be better adapted to long-term lipid storage than black bears. The possibility that the adipose tissue of black and polar bears may have other functional roles, in addition to energetics, should also be considered. However, additional information regarding the distribution and dynamics of adipose tissue are required to determine the functional significance of this tissue in bears.

The fat-to-non-fat ratio provided a fairly accurate prediction of whole body lipid content, and is therefore of some biological validity if one assumes that neutral lipid is the major source of energy for black and polar bears. That assumption is strongly supported by the findings of other researchers (Nelson *et al.* 1983; Ramsay 1986; Watts and Hansen 1987). The lipid contents of marrow and muscle were not significantly related to whole body lipid content and, therefore, were not valid as indicators of physical condition in black and polar bears. This raises concern about the many studies that have advocated such techniques for other mammals, few of which have determined any relationship between whole body and marrow or muscle lipid content, e.g. elk (Carbyn 1983), caribou (Eide and Ballard 1982), moose (Franzmann and Arneson 1976), white-tailed deer (Kie *et al.* 1983), and possum (Cowan 1985).

The relationship between neutral lipid and energy in black and polar bears was also explored. Changes in neutral lipid content were strongly related to changes in the gross energy content of the various body tissues in both species. However, lipid/energy relationships differed considerably among tissues. This emphasizes the importance, in energetic models of black or polar bears, of establishing the effect of weight gain or loss on each tissue.

Approximately 60% of the whole body gross energy of black and polar bears could be accounted for by the energy content of all neutral lipids in the body. Much of this potential energy existed in the neutral lipid stored in adipose tissue. This gives further support for use of the fat-to-non-fat ratio as a reliable indicator of physical condition in black and polar bears.

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1. INTRODUCTION

Few organisms have a food supply so regular and sufficient that no energy storage is necessary (Pond 1981). That is especially true of black (*Ursus americanus*) and polar bears (*U. maritimus*), two species that experience one of the most pronounced 'boom-and-bust' annual feeding cycles of any large terrestrial mammals. Annually, members of both species undergo prolonged fasts lasting from four to eight months in duration (Stirling *et al.* 1977; Lunn and Stirling 1985; Ramsay and Dunbrack 1986; Rogers 1987). The length of time spent fasting varies with species and location, but it is generally longer for more northerly populations (Johnson and Pelton 1980).

Although mammals can cope with food scarcity by several mechanisms, black and polar bears rely largely on storing energy in the form of fat, and it is not uncommon for members of both species to attain body fat contents ranging from 30-45% of total body weight (Hock 1960; Lono 1970; Watts and Hansen 1987). The ability to obtain and store food energy is of paramount importance to these species, and is a primary constraint on the survival and reproductive success of individuals (Rogers 1987; Ramsay and Stirling 1988).

The consequence of body fat stores to survival and reproductive success is not unique to black or polar bears, and is of vital significance to many mammals (McNab 1980; Eisenberg 1981; Lindstedt and Boyce 1985). Thus, physical condition is assumed to relate directly to quantity of stored fat, and many indices of physical condition use measurements of the various fat stores of an animal (Kistner *et al.* 1980; Lindstrom 1983; Austin 1984; Pitcher 1986; Gales and Burton 1987).

Indices of physical condition have not been developed for polar bears, and only recently, have been developed for black bears (Schroeder 1986; Franzmann and Schwartz 1988). However, the utility of those indices are questionable as relationships between indices and quantity of stored fat were were not determined in either study.

In Chapter 2, I have presented techniques and multiple regression equations for predicting physical condition in black and polar bears. Physical condition was quantified by a ratio that represents the ratio of the amount of fat to the amount of non-fat tissue in the body of a bear. I also explored the applicability of the neutral lipid content of marrow and muscle as indicators of physical condition in bears. Such indices have been applied with varying success to other animals (Neiland 1970; Hutchinson 1984; Cowan 1985).

The simple linking of physical condition with body fat quantity does not take into account either the variable composition of adipose tissue or the distribution of neutral lipid in non-adipose tissue. The chemical composition of fat can vary (Schemmel 1976) and, thus, weight of fat may not be wholly indicative of lipid content. As well, neutral lipids are not only restricted to adipose tissue and may be distributed among other tissues (Berg and Butterfield 1976).

In Chapter 3, I have determined the distribution of neutral lipid by body tissue and show how the lipid content of non-adipose tissues relate to the whole body lipid content of bears. As well, I have tested the usefulness of the physical condition indices, from Chapter 2, as indicators of whole body lipid content. It is, after all, the amount of stored lipid that is important to the survival and reproductive success of a bear, and not the weight of its fat.

Finally, in Chapter 3, I have explored some of the relationships between the lipid and energy content of bears. In few mammals has the association between lipid and energy been so closely demonstrated as in black and polar bears (Nelson *et al.* 1983; Ramsay 1986; Watts and Hansen 1987). Knowledge of the some of the relationships between lipid and energy may further contribute to understanding the relative importance of lipids to the survival of individuals of these species.

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2. EVALUATION OF PHYSICAL CONDITION IN BLACK BEARS AND POLAR BEARS BASED ON MORPHOLOGICAL INDICES[1]

2.1 Introduction

The body composition of most adult mammals shows seasonal changes in the mass of existing muscle, bone, and fat. These changes reflect the storage or loss of nutrients and energy reserves associated with growth and metabolic responses to environmental stressors. Physical condition is an aspect of body composition concerned primarily with the amount of adipose tissue and stored lipids (collectively termed 'fat') maintained by a mammal. The ability to accumulate, store, and use lipids as a source of energy is important to free-living mammals when faced with uncertain food availability and environmental stress (Young 1976).

Determination of the physical condition of mammals within populations can provide valuable information concerning the survival, reproductive success, and 'well-being' of populations in relation to human-caused and natural environmental disturbances (Kirkpatrick 1980; Robbins 1983).

Physical condition was quantified by Murray (1919) as the ratio of the amount of fat to the amount of non-fat tissue in the body of an animals. Total dissection of mammals for the measurement of physical condition is unsuitable as a routine method, both because of the expense and labour involved and the practical problems of field conditions (Ringberg *et al.* 1981). A large amount of research, however, has been directed towards predicting the physical condition of mammals from easily measurable indicators such as derivatives of body weight and measures of indicator bone, muscle, and fat tissues (Berg and

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[1] A version of this chapter has been submitted for publication: M. Cattet. 1988. Canadian Journal of Zoology.

Butterfield 1976).

The objective of this study was to determine the statistically best equations for the prediction of physical condition in black bears (*Ursus americanus*) and polar bears (*U. maritimus* Phipps); two species for which knowledge of physical condition is limited. Both species are of interest because of their marked seasonal body weight fluctuations between periods of hyperphagia and extended fasting during winter dormancy (Folk *et al.* 1970).

Total body weight (TBW) and non-fat body weight (NFBW) can be combined, (TBW - NFBW)/NFBW, to calculate a fat-to-non-fat ratio. Ideally, total body weight is determined by weigh scales. However, the large body weight of some adult bears make direct measurement of body weight difficult in the field and, in such cases, an indirect measure is unavoidable.

In this study, predictions of total body weight and non-fat body weight were determined by using combinations of muscle and bone weights, and morphometric measurements that can be obtained in the field. In addition, the marrow and intramuscular lipid contents of some tissues were assessed as indicators of physical condition.

2.2 Materials and Methods

2.2.1 Collections

Thirty-eight black bears and 43 polar bears were collected from September, 1984, to November, 1986. Collections were made at various times of the year to obtain animals representative of a wide range of physical conditions. Black bears were collected between April and November; winter denning precluded collections between December and March. Polar bears were collected during most seasons, although the greatest number was obtained between September and December.

Collected animals were from three sources; 41 polar bears were collected from Inuit hunters in Coral Harbour, Eskimo Point, and Resolute Bay, Northwest Territories, 2 polar bears were collected as 'bears killed in defense of human life or property' in Churchill, Manitoba by the Manitoba Department of Natural Resources, and black bears were collected as 'bears killed in defense of human life or property' throughout Alberta by the Fish and Wildlife Division of Alberta Forestry, Lands and Wildlife. Bears killed from Churchill and throughout Alberta were not atypical of most bears in their feeding habits and should not be confused with bears that rely heavily on food scavenged from refuse dumps.

Prior to dissection, morphometric measurements were made of each bear; these were straight-line body length, axillary girth, and foreleg circumference. Since foreleg circumference is not a standard measurement, further description is warranted. With a bear in a dorsally recumbent position, the foreleg was extended away from the body and a measuring tape was placed around the circumference of the foreleg, at the area of articulation between the humerus and the radius and ulna (elbow). The foreleg was then bent at the elbow until the upper and lower foreleg were at a right angle. At this point, the foreleg circumference was recorded, making sure the measuring tape was across the olecranon (point of the elbow).

A vestigial premolar tooth was extracted from all bears. Extracted teeth were thin-sectioned following methods outlined by Thomas and Bandy (1973) and Stirling *et al.* (1977a) and the age determined from counts of cementum annulation rings.

Total body weights of collected animals were determined by dissecting and weighing all tissues, and subtracting the contents of the gastro-intestinal tract. Because the animals were shot, blood loss was unavoidable and presented a bias to the measurement of total body weight. Blood accounts for approximately 8% of body mass, regardless of animal size (Calder 1984). However, residual blood still remained in the tissues of dissected bears and, in cattle, may represent up to 50% of the total blood volume (Pearson *et al.* 1979). Thus, correction for blood loss was not made because weight of blood loss, relative to total body weight or non-fat body weight, is small and a correction for blood loss would have little effect on the fat-to-non-fat ratio.

Prediction equations for total body weight in polar bears are based on data collected by the Canadian Wildlife Service (CWS) in the areas of western Hudson Bay and the Canadian Beaufort Sea, between 1969 and 1987. From the CWS data, information was extracted for bears from which scale weights were available. The use of the CWS data was necessary as most polar bears collected in this study had been previously skinned by Inuit hunters, thus preventing the measurement of axillary girth.

2.2.2 Dissections

All bears were kept frozen at -15^{o}C for up to six months after death before dissections were conducted. During freezing, previously-skinned bears were wrapped in plastic, and bears with the skin intact were left uncovered. By repeated weighing of some carcasses over a six month period, water loss was determined to be small (< 1%).

During dissection, a bear was skinned such that minimal subcutaneous fat adhered to the skin. The skin and fur were then weighed to 0.5 kg. This 'hide' weight included the fore-and hind-feet which were severed at the radius-ulna-carpal and tibia-fibula-tarsal articulations.

Only the right halves (along the median plane) of skinned carcasses were dissected, unless tissue damage limited dissection to the left half. Dissections of the left half-carcass were necessary for two black bears only. Each carcass side was separated into bone, muscle, and fat. The viscera and adhering adipose tissue could not be measured in halves. Rather, these tissues were separated and weighed to the nearest 0.1 kg in their entirety.

Total muscle weight was recorded to 0.5 kg, after being separated from intermuscular fat. Total muscle weight included all muscular tissue, tendons, and ligaments, doubled from measures of the half-carcass. The biceps brachii and b. femoris were collected for lipid extractions (described below). These muscles were selected as potential indicators of physical condition because they are easily identified and dissected.

Total bone weight was recorded to 0.5 kg, and included all bones, cartilage, and the brain and spinal chord contained within the cranium and spinal column. The weights of all bones, except the skull and spinal column, were doubled from half carcasses to estimate total bone weight. The skull and spinal column were weighed in their entirety. The humerus, radius, ulna, femur, and tibia-fibula were collected for lipid extractions of marrow. These bones were selected as potential indicators of physical condition because of their large size and ease of dissection.

Dissectable adipose tissue was divided into five separate depots (subcutaneous, intermuscular, thoracic, abdominal, and mesenteric). A description of the anatomical differentiation of these depots is provided in Appendix 1. Only the subcutaneous and intermuscular depots were dissected from half carcasses and doubled in weight; other depots were dissected and weighed in their entirety. The combined weight of these depots was recorded as the total dissectable fat weight. This value was measured to the nearest 0.1 kg.

After dissections, non-fat body weights were estimated to 0.1 kg as combined weights of the hide, viscera, total muscle, and total bone. A fat-to-non-fat ratio could then be determined for each bear as the total dissectable fat weight divided by the non-fat body weight.

2.2.3 Lipid extractions

Bone marrow samples (10 - 20 g) were collected from the radius, ulna, humerus, femur, and tibia-fibula, and muscle samples (20 - 50 g) were collected from the biceps brachii and b. femoris of all bears. All samples were analyzed for their neutral lipid content. These data were used to measure the association between marrow lipid content and fat-to-non-fat ratios, and intramuscular lipid content and fat-to-non-fat ratios.

Tissue samples were wrapped in air-tight plastic bags and stored at $-15^{o}C$ until lipids were extracted. Two weeks prior to lipid extractions, tissues were homogenized and dried to constant weight in a convection oven at $40^{o}C$. Neutral lipids were extracted from samples in a Soxhlet apparatus using petroleum ether as a solvent following the methods outlined in AOAC (1980). A blank and standard were included during some sets of extractions to monitor variation in the quality of the extracting solvent and the efficiency of the extraction technique. Two or three replicate subsamples were run from each sample to monitor variation within samples (Mean range between lowest and highest estimate ± standard error equals 3.46 ± 0.57, $n = 43$). By subjecting subsamples of muscle and bone to reflux periods of 2, 4, 6, 8, and 10 hours, it was determined that greater than 95% of neutral lipids were extracted within a four-hour reflux period. Thus, all subsequent extractions were refluxed for a period of four hours.

2.2.4 Statistical methods

Data were analyzed using Statgraphics (STSC Inc. 1986) and SAS (SAS Institute Inc. 1985). Forward stepwise multiple regression was used to predict total body weight and non-fat body weight (Y) from the measured variables (X_1, X_2, ..., X_i). Non-fat body weight prediction equations were developed to be applicable under two conditions; the first or 'restricted' condition involves a bear that is live-captured and physical condition evaluation is limited to external morphological measurements, and the second or 'unrestricted' condition involves a bear that has been killed and physical condition evaluation can include internal morphological measurements.

Correlation analysis was used to assess the significance of associations between percentage bone marrow lipid content and observed fat-to-non-fat ratios, and percentage intramuscular lipid content and observed fat-to-non-fat ratios.

To satisfy the assumptions of least squares regression and correlation analysis, it was necessary that statistical analyses be carried out on transformed data. Transformations, using the natural log, were carried out on all data except those presented as percentages or ratios, for which arc-sine transformations were applied (Sokal and Rohlf 1981).

Final predictive equations are presented in their curvilinear form, ($Y = e^{b0}X_1^{b1}X_2^{b2}...X_i^{bi}$), to facilitate the use of arithmetic values for independent variables. Transformation bias has been corrected by multiplying predictive equations by $e^{s^2/2}$, where s^2 is the residual sum of squares for the regression line (Beauchamp and Olson 1973; Miller 1984).

The effects of sex, age class (subadults: 0 - 4 years; adults: 5 years and greater), and species were evaluated by a dummy-variable regression model and partial F-tests (Kleinbaum and Kupper 1978). Initially, the F_{max}-test for homogeneous variances was performed on the transformed data. If homogeneity of variances existed, a partial F-test was used to test for parallelism. If parallelism existed, another partial F-test was used to test for coincidence. Finally, if coincidence existed, the data from both species were pooled and regression analysis was conducted on the pooled data. If the conditions of homogeneous variances, parallel slopes, or coincidence were not met; then, regression models were computed for each species.

Descriptive statistics for all variables used in this study are presented in Appendices 2 and 3.

2.3 Results

2.3.1 Predicting total body weight

In Table 2.1, stepwise regressions were calculated with axillary girth (cm), straight-line length (cm), and age in years as potential independent variables. The range of weights described by the black bear regression line represents the typical weight range of this species, from 5-172 kilograms. The polar bear weight range, however, is biased towards subadult animals with only 16 bears in the weight range from 250-410 kg.

Comparison of species-specific equations showed no significant effect of sex in black bears (partial F-test, $p > 0.05$), but a significant effect of sex did occur in polar bears (partial F-test, $p < 0.01$). This necessitated the calculation of sex-specific equations for polar bears.

Significant effects of age class were not detected in black bears (partial F-test, $p > 0.05$). Age class effects were also not detected in polar bears (partial F-test, $p > 0.05$), but the assumption of homogeneous variances was not met for this species (F_{max}-test, $p < 0.001$). Species effects, also, were not tested due to heterogeneous variances between species (F_{max}-test, $p < 0.001$).

2.3.2 Predicting non-fat body weight

Restricted stepwise regressions were calculated using the following independent variables: foreleg circumference (cm), straight-line length (cm), and age in years (Table 2.2). Unrestricted regressions also were calculated using these independent variables, as well as the weights of five bones (radius, ulna, humerus, femur, and tibia-fibula) and two muscles (biceps brachii and b. femoris). The polar bear data used to predict non-fat body weight was collected during this study and is exclusive of the CWS polar bear data.

The calculated equations accounted for 95 to 99% of the variance in non-fat body weight using either two or three independent variables. In both species, a greater coefficient of determination and smaller standard error of the estimate occurred under conditions where the types of measurements were not restricted.

Two prediction equations are presented for polar bears under restricted conditions. The second equation, although not as strong a predictor as the first, is included to enable researchers to predict non-fat body weight from 'historical' polar bear data. The predictor variables of this equation, age and straight-line body length, are standard measurements recorded in many mammal studies. Foreleg circumference, however, is a measurement not commonly made.

The calculation of species-specific equations was necessary as the effect of species was significant for conditions where the types of measurements were both restricted (partial *F*-test, $p < 0.05$) and unrestricted (partial *F*-test, $p < 0.01$).

For the species-specific equations, the effect of sex under both restricted and unrestricted conditions was non-significant in black and polar bears (partial *F*-tests, $p > 0.05$). As well, age class did not show significant effects for either species under either condition (partial *F*-tests, $p > 0.05$).

2.3.3 Neutral lipid content of bone marrow and muscle

The strongest correlation, between the fat-to-non-fat ratio and percent lipid in the marrow of five indicator bones, occurred with the radius of black bears and explained only 28% of the variance in the fat-to-non-fat ratio (Table 2.3). Significant correlations occurred with the ulna and femur in polar bears. These correlations, however, were negative in contrast to the significant positive correlations for the radius, ulna, and femur of black bears.

In black bears, the association between the fat-to-non-fat ratio and the percent lipid in the radius marrow was significantly affected by sex (partial *F*-test, $p < 0.01$), but not age class (partial *F*-test, $p > 0.05$). However, grouping the data by sex did not improve the association and, at most, only 45% of the variation was explained when analyzed within sex.

The strongest correlation, between the fat-to-non-fat ratio and percent intramuscular lipid of two muscles, occurred with the biceps brachii of black bears (Table 2.4). However, only 25% of the variance in fat-to-non-fat ratio was explained by this association.

As with percent lipid in radius marrow, the association between the fat-to-non-fat ratio and the percent lipid in the biceps brachii of black bears was affected by sex (partial *F*-test, $p < 0.05$), but not age class (partial *F*-test, $p > 0.05$). However, grouping the data by sex did not improve the association and, at most, only 32% of the variation was explained when analyzed by each sex.

2.4 Discussion

2.4.1 Predicting total body weight

Several studies have reported correlations between total body weight and axillary girth in black (Payne 1976, Swenson *et al.* 1986) and polar bears (Stirling *et al.* 1977b; Ramsay 1986; Kolenosky *et al.* 1988). In a study of interpopulation applicability of equations predicting total body weight in black bears, Swenson *et al.* (1986) concluded that regressions using axillary girth appear to be relatively accurate in predicting the total body weight of black bears; however, interpopulation and sexual variations in body measurement-weight relationships make it impossible to derive a single equation for the species. Presumably, the same may be true for the applicability of prediction equations for polar bears.

Swenson *et al.* (1986) also concluded that regressions using both axillary girth and total length are limited in applicability for the same reasons as equations using axillary girth alone. However, this conclusion is misleading as the applicability of prediction equations using axillary girth and total length as independent variables was not tested. Rather, what was tested was a single-variable prediction equation using a body size index (total length times axillary girth squared) as the independent variable. The combining of length and girth into a body size index assumes that each measure has an equal effect on total body weight. Thus, for example, the change in the total body weight of a bear increasing in length by 9 cm would be equivalent to the change in body weight of a bear (of the same initial length) increasing in girth by 3 cm.

Multiple regression equations enable a better prediction of the dependent variable than would be possible by any single independent variable (Sokal and Rohlf 1981). Such equations allow for the independent contributions of two or more independent variables towards explaining the variance observed in the dependent variable. The contribution of numerous independent variables make multiple-variable equations more sensitive to interpopulation and sexual variations in body measurement-weight relationships, thus increasing the possibility of deriving a single equation for a species.

The predictions of the multiple-variable equations calculated in this study were not affected by sex (in either species) or age class (heterogeneous variances prevented testing in polar bears). Interpopulation effects were not measured. However, axillary girth and total body length quantify the three spatial dimensions of an animal; that is, length, width, and depth. Thus, it seems likely that these equations can be used to make intraspecific comparisons among populations of either species.

There is one caution to note with regard to the prediction equation for total body weight of polar bears, and its application in estimating fat-to-non-fat ratios. Total body weights of polar bears were determined as the live body weight (from CWS data) which includes the contents of the gastro-intestinal tract. As well, live body weight is not biased by blood loss. Because non-fat body weight prediction equations for polar bears were based on empty guts and some blood loss, the fat weight (TBW - NFBW) estimated from predicted total body and non-fat body weights are inflated.

A standard correction factor for this problem is not appropriate as gut content weight and blood loss weight can be highly variable between bears. Assuming blood volume accounts for approximately 8% of an animal's body weight (Calder 1984) and residual blood in tissues can account for up to 50% of total blood weight (Pearson *et al.* 1979), a 50% blood loss will increase the estimated fat weight (TBW - NFBW) by four percent.

For polar bears, the gut content weight can approach 15-20% of the ingesta-free body weight (Best 1976). Thus, depending on gut content weight, the estimated fat weight may be in error from 4% (empty gut, 50% blood loss) to 24% (full gut, 50% blood loss). The potential magnitude of this error could severely limit the accuracy of the estimated fat-to-non-fat ratio. Thus, in some situations, a correction for gut content may be necessary. For a bear with a full gut, the predicted total body weight may be crudely corrected by reducing its value by 19-24 percent. In the case of a polar bear with an empty gut, a correction of approximately 4% may be applied.

Finally, it is important to realize for both species, in situations where total body weight must be estimated, an additional error factor is introduced to the fat-to-non-fat ratio. This error may be compounded by defining body fat as TBW - NFBW.

2.4.2 Predicting non-fat body weight

The prediction equations for non-fat body weight in black and polar bears show stronger predictive ability for conditions where measurements were unrestricted. These equations rely on direct measures of muscle and bone, whereas restricted conditions rely only on external morphological measurements and age. External morphological measurements are less sensitive to changes in tissue composition, so two animals having identical external morphological measurements may show significant differences in tissue composition (Berg and Butterfield 1976).

Age in years was selected as a predictor variable for all non-fat body weight equations, except the 'unrestricted' equation for polar bears. Age has been shown to correlate well with body composition in some species, including domestic rabbits (de Blas *et al.* 1977) and sheep (Donnelly and Freer 1974), but poorly in others, including white-tailed deer (Odocoileus virginianus*) (Robbins* et al. *1974) and mule deer (*O. hemionus*) (Anderson* et al. *1974). Age did appear* to correlate well with the body composition of black and polar bears in this study.

The morphological measurements necessary for prediction of non-fat body weight in live black and polar bears are easy, rapid, and inexpensive to collect. The estimation of age of polar bears by sectioning of teeth is more difficult and time-consuming, but accurate techniques have been developed (Thomas and Bandy 1973; Stirling *et al.* 1977a).

Prediction of non-fat body weight in black and polar bears that are found dead requires identification and dissection of the biceps brachii (and femur, if applied to black bears), in addition to measurement of straight-line body length and age. The identification of the biceps brachii and femur is relatively easy and minimal effort would be required to train field-workers or hunters to collect these tissues.

2.4.3 Neutral lipid content of bone marrow and muscle

Neutral lipid content of marrow has been extensively used to indicate physical condition in ungulates (Cheatum 1949; Neiland 1970; Davis *et al.* 1987). However, the applicability of this test is limited, in that it is only a one-way test of condition (Mech and Delgiudice 1985). If the lipid content of marrow is low, the animal probably is in poor condition. However, if the lipid content is high, one cannot conclude that the animal is in good condition. The marrow lipid depot, relative to other lipid depots, is the only one which can become 'full'. When full, marrow lipid content becomes insensitive to increases in body fatness.

To a lesser extent, percentage lipid in marrow has been used as an indicator of physical condition in other groups of animals, including waterfowl (Hutchinson 1984) and marsupials (Cowan 1985). The data from this study suggest that the technique cannot be effectively applied as a two-way test of physical condition of black and polar bears.

In polar bears, percent lipid in the ulna and femur showed a weak significant correlation with the fat-to-non-fat ratio. In contrast to black bears, however, these correlations were negative suggesting low marrow lipid content was associated with a high fat-to-non-fat ratio. Perhaps, in polar bears the dynamics of marrow lipid stores differ from the pattern observed in ungulates or black bears. The marrow lipids of ungulates are depleted later than other depot lipids as nutritional condition deteriorates (Dauphine 1971).

Percent intramuscular lipid has been correlated to physical condition in caribou (Ringberg *et al.* 1981; Hout and Goudreault 1984). Ringberg *et al.* (1981) found the chemically extractable lipid of muscles to correlate well with total body lipid for animals across a wide range of conditions. In contrast, Huot and Goudreault (1984) found intramuscular lipid to correlate well with total body lipid only when caribou were lean. Intramuscular lipid content showed weak significant correlations with the fat-to-non-fat ratio in black and polar bears, and it was ineffective for evaluating physical condition in these species.

2.4.4 Applications and limitations of predicting physical condition

The physical condition of a mammal is generally equated with the quantity of its fat reserves. This association relies on the assumption that fatness provides some measure of performance of a wild animal and of its chance of survival or potential for reproduction (Huot and Goudreault 1984).

In this study, 'fatness' was expressed as the ratio of the weight of body fat to the non-fat body weight. This ratio has the effect of adjusting the total body fat weight for variation in body size. It is advisable, however, to distinguish between a fairly fat but stunted specimen and an obese, large-framed animal in equating fat stores with reproductive potential (Verme and Ozoga 1980). The fat-to-non-fat ratio for black and polar bears should only be used as an indicator of their probability of surviving through periods of uncertain food availability or environmental stress. Indication of reproductive potential in bears requires equating the fat-to-non-fat ratio with some measure of absolute body size, e.g. non-fat body weight.

As stated above, ratios are used to remove the confounding effects of body size. It is critical, however, that the calculated ratio is independent of body size (Packard and Boardman 1988). If that is not so, the use of ratios may lead investigators to draw incorrect conclusions. Measurement of the association between the fat-to-non-fat ratio and non-fat body weight showed non-significant associations for black bears ($r = 0.11$, $p = 0.99$, $N = 33$) and polar bears ($r = 0.12$, $p = 0.99$, $N = 31$). Thus, this index of condition is size-independent and may be used to compare between bears of different sex and age classes.

Comparison of the applicability of the fat-to-non-fat ratio with indices of physical condition from other studies is limited, as few studies of physical condition in bears have been completed. Schroeder (1986) concluded that the ratio of total body weight to straight-line body length permits objective physical condition comparisons between sex and age classes of black bears. However, the ratio of total body weight to straight-line body length is size-dependent and, when applied to my data, shows strong positive associations with non-fat body weight in both black bears ($r = 0.94$, $p < 0.001$, $N = 33$) and polar bears ($r = 0.93$, $p < 0.001$, $N = 31$). This strong association severely limits the application of the 'weight/length' ratio as an index of physical condition.

Physical condition of black bears has also been assessed through analysis of various blood parameters including total protein, albumin, triglyceride, glucose, and cholesterol (Erickson and Youatt 1961; Matula *et al.* 1977; Franzmann and

Schwartz 1988). However, the full potential uses of blood analyses as indicators of metabolic status have not been reached and before interpretations about physical condition can be made, the effects of age, sex, season, reproductive condition, and methods of handling must be considered (LeResche *et, al.* 1974), as well as, relationships between blood parameters and total body fat.

Evaluation of physical condition in polar bears has received only limited attention. Watts (1983) concluded that backfat depth, as an index of total body fat, did not have good predictive value, possibly, because of a highly curvilinear relationship with total body fat. An index must have a linear or only a slightly curvilinear relation to the dependent variable to be suitable for predictive purposes (Robbins 1983).

The use of dissectable adipose tissue weight, as an index of physical condition, does not take into account the amount of lipid contained within the adipose tissue. Lipid content of adipose tissue in rats was found to vary from 56-90% (Schemmel 1976); similar variability was observed to occur in the bears of this study. Low lipid content results from depleted storage lipids coupled with retention of the structural elements of adipose tissue (Grande 1968). The implications that variable lipid content may have for the fat-to-non-fat ratio of black bears and polar bears are discussed in the following chapter.

Variation between the predicted and observed fat-to-non-fat ratios (Fig. 2.1), for bears of this study, suggest that predictions can best be used in intraspecific comparisons of groups of bears Comparisons among individual bears require the development of more accurate techniques. To illustrate this point, the predicted values used in Figure 2.1 are the best possible predictions from the data of this study, and are based on the observed total body weights and the predicted non-fat body weights for both species under conditions where measurements were not restricted. For both species, there is considerable scatter about the line of expected values, scatter which only increases when predicted total body weights are used to calculate fat-to-non-fat ratios. Thus, it is important to emphasize that fat-to-non-fat ratios based on predicted, as opposed to observed, total body weights are less accurate predictors of physical condition and, whenever possible, effort should be made to measure directly the weights of bears.

TABLE 2.1. Multiple-variable equations for predicting total body weight of black bears and polar bears

Species	n	Equation[a]	r^2	SE(est.)
Black[b]	34	$Y = e^{-8.16}X_1^{1.39}X_2^{1.21}X_3^{0.08}$	0.98	0.123
Polar[c]				
Male	179	$Y = e^{-8.87}X_1^{1.22}X_2^{1.55}$	0.99	0.124
Female	184	$Y = e^{-9.77}X_1^{1.30}X_2^{1.66}X_3^{-0.06}$	0.99	0.120

[a] Y is the predicted total body weight (kg), X_1 is the axillary girth (cm), X_2 is the straight-line body length (cm), and X_3 is the age in years.

[b] Effect of sex was non-significant for black bears.

[c] Canadian Wildlife Service (CWS) polar bear data.

TABLE 2.2. Predictive equations for non-fat body weight in black and polar bears under conditions where (A) measurements are externally restricted or (B) measurements are unrestricted

Species	n	Equation[a]	r^2	SE(est.)
<u>Condition A</u>				
Black bears	33	$Y = e^{-8.69}X_1^{2.52}X_2^{0.17}$	0.98	0.124
Polar bears[b]				
(i)	28	$Y = e^{-7.88}X_1^{1.61}X_2^{0.15}X_3^{1.03}$	0.97	0.095
(ii)	28	$Y = e^{-9.07}X_1^{2.63}X_2^{0.12}$	0.95	0.123
<u>Condition B</u>				
Black bears	31	$Y = e^{-1.62}X_4^{0.29}X_5^{0.68}X_2^{0.10}$	0.996	0.053
Polar bears	22	$Y = e^{-3.60}X_4^{\text{[illegible]}.69}X_1^{0.85}$	0.99	0.065

[a] Y is the predicted lean body weight (kg), X_1 is the straight-line body length (cm), X_2 is age in years, X_3 is the foreleg circumference (cm), X_4 is the biceps brachii weight (g), and X_5 is the femur weight (g).

[b] Two equations are provided for polar bears under Condition A. Equation (i) is the statistically best equation for predicting non-fat body weight. Equation (ii) is included to enable researchers to predict non-fat body weight from 'historical' polar bear data. The polar bear data used to calculate prediction equations were from this study.

TABLE 2.3. Associations between bone marrow lipid percentage[a] and fat-to-non-fat ratio in black bears and polar bears

Bone	Correlation (r)[b]	n	Significance[c]
Black bears			
Radius	0.526	28	***
Ulna	0.420	28	***
Humerus	0.073	28	n.s.
Femur	0.440	28	***
Tibia-fibula	0.152	28	n.s.
Polar bears			
Radius	-0.215	24	n.s.
Ulna	-0.293	24	*
Humerus	-0.107	24	n.s.
Femur	-0.322	24	*
Tibia-fibula	-0.113	24	n.s.

[a] Percent lipid based on dry tissue weight.

[b] Correlation analysis completed on arcsine-transformed data.

[c] n.s. - non significant ($p > 0.05$)
* - $p < 0.05$
** - $p < 0.01$
*** - $p < 0.001$

TABLE 2.4. Associations between intramuscular lipid percentage and fat-to-non-fat ratio in black bears and polar bears

Muscle	Correlation (r)	n	Significance
Black bears			
Biceps brachii	0.495	34	***
Biceps femoris	0.119	34	n.s.
Polar bears			
Biceps brachii	0.127	28	n.s.
Biceps femoris	0.469	28	***

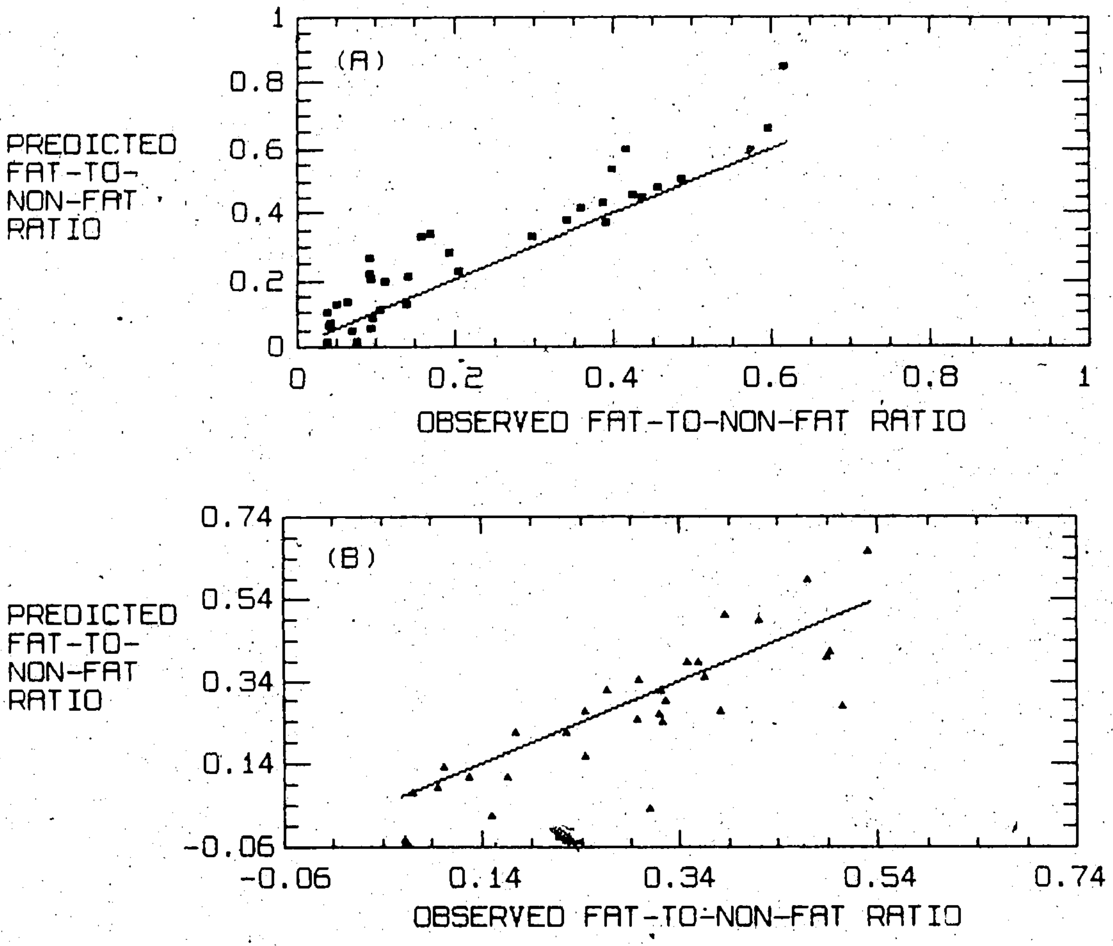

FIGURE 2.1. The predicted versus observed fat-to-non-fat ratios of black and polar bears used in this study. Predicted fat-to-non-fat ratios were calculated using observed total body weights. (A) black bears, (B) polar bears

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3. RELATIONSHIPS BETWEEN LIPID, PHYSICAL CONDITION INDICES, AND ENERGY IN BLACK BEARS AND POLAR BEARS[2]

3.1 Introduction

Lipids are an important group of organic compounds that show much diversity of function in living animals (Schemmel 1976; Hadley 1985). One class of lipids, the neutral lipids, is the major form of stored energy in mammals. Its high energy yield and anhydrous nature, relative to protein or carbohydrate, suggest why neutral lipids are functional in an energetic role (Young 1976; Pond 1978).

The association between neutral lipids and energy has provided the basis for the development of many indices of physical condition. Wildlife ecologists and managers have attempted to develop physical condition indices to relate ultimately to survival and reproductive success (Robbins 1983) and to provide information concerning the 'well-being' of mammal populations in relation to human-caused and natural environmental disturbances (Kirkpatrick 1980). However, many researchers have not tested the relationship between an index of physical condition and the total neutral lipid content of an animal (Kistner *et al.* 1980; Lindstrom 1983; Austin 1984; Pitcher 1986; Schroeder 1986; Gales and Burton 1987; Franzmann and Schwartz 1988).

In the previous chapter, techniques were presented for predicting physical condition in black (*Ursus americanus*) and polar bears (*U. maritimus*); physical condition was indicated by the ratio of the total weight of dissectable fat over the non-fat body weight. Since the chemical composition of fat can vary (Schemmel 1976), weight of adipose tissue and stored lipids (collectively

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[2] A version of this chapter has been submitted for publication: M. Cattet. 1988. Canadian Journal of Zoology

termed 'fat') may not be wholly indicative of lipid content (Berg and Butterfield 1976). As well, neutral lipids are not restricted only to adipose tissue and may be distributed among other tissues (Berg and Butterfield 1976).

The implications these observations have for physical condition indices of black and polar bears are of primary concern. If the lipid content of adipose tissue is variable and neutral lipids also occur in non-adipose tissues, relationships between indices of physical condition and total body fat may not be adequate for assessing the physical condition of bears. The objectives of this study were to determine (1) the distribution of neutral lipid by body tissue; and (2) the relationships of indices of physical condition to whole body lipid content. Another area investigated was the relationship between lipid and energy content of specific tissues and the whole body. The energy content of an animal is affected by its chemical composition, especially the relative quantities of protein, carbohydrate, and lipid. Perhaps in few mammals has the direct association between lipid stores and energy been so closely linked as in the bears (Ursidae) (Nelson *et al.* 1983; Ramsay 1986; Watts and Hansen 1987).

Black bears are unusual among mammals in their ability to endure months, during winter, with no food and water and to meet energy requirements by lipid catabolism only, while conserving their lean body weight (Nelson 1973). Similar metabolic adaptations are thought to occur in polar bears (Ramsay *et al.* 1985). Knowledge of the lipid/energy relationships of black and polar bears can contribute to further understanding the relative importance of lipids to the survival of individuals.

3.2 Materials and Methods

3.2.1 Collections

The collection techniques and associated measurements of physical condition were described in the previous chapter. From thirty-eight black bears and forty-three polar bears collected between September, 1984, and November, 1986, five black bears and six polar bears were chosen for determination of lipid and energy content.

The bears were chosen to represent a broad range in weight and fat-to-non-fat ratio (Table 3.1). The broad weight range ensured variation in the absolute lipid and energy content of bears from both species, while a broad range in fat-to-non-fat ratios was necessary to measure the relationship between varying proportions of dissectable adipose tissue and lipid content, independent of body size .

Of the three physical condition indices considered, the fat-to-non-fat ratio, calculated as the weight of dissectable adipose tissue divided by the non-fat body weight, is the only index that reflects the proportion of dissectable adipose tissue in a bear. The other two physical condition indices, percentage lipid in marrow and muscle, showed only weak associations with dissectable adipose tissue and were deemed unsuitable as indices of physical condition (see Chapter 2).

The left halves (along the median plane) of skinned carcasses were dissected into three tissue composites: adipose, muscle, and bone. Adipose tissue included all dissectable adipose tissue comprising the subcutaneous, intermuscular, thoracic, abdominal, and mesenteric depots (described in Appendix b). The muscle composite included all muscular tissue, tendons, and ligament. The bone composite included all bones, cartilage, and the brain and spinal cord contained within the cranium and spinal column. A fourth tissue composite, the 'skin', included the skin, fur, and fore-and hind-feet, severed at the radius-ulna-carpal and tibia-fibula-tarsal articulations. The skin was prepared such that minimal subcutaneous fat adhered. Skins were available for all black bear carcasses used in chemical composition determinations, but for polar bears, a skin could only be obtained from one animal, P2. The viscera, stripped of their associated adipose tissue and gastro-intestinal contents, were categorized as a fifth tissue composite. A sixth tissue composite was the whole body, the sum of the five other tissues. The lipid and energy content of the whole body composite was calculated from the chemical composition results of the other five tissues and the proportional weight, relative to the total body weight, that each tissue contributed to the intact carcass.

The total body weights of black and polar bears were determined as the bled body weight less the contents of the gastro-intestinal tract. Thus, the determination of lipid and energy content of tissues only took into account residual blood contained within the tissues. In white-tailed deer (*Odocoileus virginianus borealis*), the contribution of blood to the whole body lipid and energy content is small (<5%) (McCullough and Ullrey 1983). The same was assumed for black and polar bears and no attempt was made to correct for blood loss.

3.2.2 Lipid and energy determinations

All tissues were wrapped in plastic and kept frozen at -15°C until further processing and chemical analysis. Processing involved mincing the tissue composites of each bear separately in a commercial meat grinder. The small size of bears P1 and B1 required that they be minced in their entirety, rather than as separate tissues, because some tissue loss was accrued during each grinding, and such loss could significantly bias tissue composites weighing less than 1 kg. All tissues were minced two or three times and thoroughly mixed. A 500 g sample was collected from each tissue homogenate and retained for chemical analyses.

Each sample was subsampled and analyzed for lipid and energy content. Prior to lipid extractions, approximately 10 g of each subsample was dried to constant weight in a convection oven at 40°C. Neutral lipid content was determined by extraction, from approximately 3 g samples. Extraction occurred in a Soxhlet apparatus using petroleum ether as a solvent, following the methods outlined in AOAC (1980). Lipid content was calculated as percentage lipid in tissue on a wet weight basis, and then multiplied by tissue or whole body weight, in order to estimate absolute lipid content.

The caloric values of tissue homogenates were determined with 1-2 g samples using an adiabatic bomb calorimeter. Energy content was calculated as kilocalories per gram (kcal/g) of wet tissue, and then multiplied by tissue or whole body weight, in order to estimate absolute energy content.

Each analysis from each sample was done in duplicate or triplicate, in order to monitor variation in the analyses. A statistical investigation of the results (e.g. 2-3 subsamples per tissue homogenate per bear where $N = 43$) showed the following mean ranges between lowest and highest estimates (mean ± standard error): lipid 3.46% ± 0.57 and energy 0.29 kcal/g ± 0.05.

Determination of whole body lipid and energy content of polar bears, for which hides were not available, was done by extrapolating the skin lipid and energy content of the five black bears and P2 to the other four polar bears. Extrapolation was based on calculating simple linear regression lines to predict percentage lipid and energy content of skin based on the independent variable, age. Correlation analysis showed age to have a strong negative association with percentage lipid in skin ($r = -0.86$, $p < 0.01$) and energy content of skin ($r = -0.97$, $p < 0.0001$). These prediction equations were as follows:

[1] % Lipid (dry weight) $=$ -1.005(Age) + 21.29 ($R^2 = 0.804$, $N = 6$)

[2] Energy (kcal/g) $=$ -0.091(Age) + 3.50 ($R^2 = 0.941$, $N = 6$)

The use of these predictive equations is based on the assumption that there are no significant species differences in the relationships between age and skin lipid content, and between age and skin energy content, on a per weight basis. The fact that few differences seem to exist between black and polar bears with respect to lipid and energy composition (see Results) and that black and polar bears mature at relatively similar rates (Sauer 1975; Kingsley 1979; Rogers 1987) suggests this assumption is not unreasonable.

3.2.3 Statistical methods

Data were analyzed using Statgraphics (STSC Inc. 1986) and SAS (SAS Institute Inc. 1985). Simple linear regression was used to describe the relationships between lipid content, energy content, and physical condition indices. It should be emphasized that the regression constants were estimated from extremely small samples and are of use only for descriptive purposes. The estimation of predictive equations requires considerably larger samples and is outside the scope of this study.

Prior to regression analysis, a dummy-variable regression model and partial F-tests were used to test for significant effects of species (Kleinbaum and Kupper 1978). Initially, an F_{max}-test was used to test for homogeneity of variance between the independent variables of both species. If homogeneity of variance occurred, a partial F-test was used to test for parallelism. If parallelism existed, another partial F-test was used to test for coincidence. Finally, if coincidence existed, the data from both species were pooled and regression analysis was then conducted on the pooled data. If the conditions of homogeneous variances, parallel slopes, or coincident lines were not met; then, regression lines were computed for each species.

Tests of isometry were performed, on the relationships between tissue and whole body lipid content, using the null hypothesis, H_0: b (slope) = 1. A t-statistic was calculated, $t = (b - 1)/\mathrm{SE}_{\mathrm{slope}}$, and compared with the critical values of the Student's t-distribution (Sokal and Rohlf 1981).

Comparisons of variances and means were made between species for the estimated percentage of gross body energy represented by neutral lipid and the distribution of neutral lipid energy by tissue. Variances were tested for homogeneity using the F_{max}-test and means were compared for significant differences using a two-sample t-test.

To satisfy the assumptions of the above parametric statistical tests, it was necessary that analyses were carried out on transformed data. Transformations, using the natural log, were carried out on all data except those presented as percentages or ratios. For those data, arc-sine transformations were applied.

Descriptive statistics for all variables measured in this study are presented in Appendices 2 and 3.

3.3 Results

3.3.1 Distribution of lipid by body tissue

Although, considerable variation exists between bears, there is an obvious pattern in the distribution of lipid among tissues (Figures 3.1A and 3.1B). Adipose tissue lipid accounts for approximately 40-80% of whole body lipid content and itself contains more lipid than the other tissues combined. The remaining tissues, in order of decreasing lipid content as a percentage of whole body lipid content, are bone, skin, muscle, and viscera.

Significant relationships, between whole body lipid content and the lipid content of individual tissues, occurred with all tissues except the skin and muscle of black bears (Table 3.2). Regression constants were not calculated for polar bear skin because the data were extrapolated. Of the other four tissues, viscera was the only tissue for which species differences were non-significant.

The adipose, bone, and viscera lipid of black bears showed relationships which were isometric (*t*-test, $p > 0.05$) with whole body lipid content. Thus, the lipid content of these tissues changed in constant proportions with changes in whole body lipid content. Only the viscera and muscle lipid of polar bears showed an isometric relationship (*t*-test, $p > 0.05$). In contrast, polar bear adipose and bone lipid showed allometric relationships in which adipose lipid had a slope significantly greater than 1 (*t*-test, $p < 0.001$) and bone lipid had a slope significantly less than 1 (*t*-test, $p < 0.01$). Therefore, the proportion of adipose lipid content of polar bears increased while the proportion of bone lipid content decreased in relation to increases in whole body lipid content.

3.3.2 Relationships of condition indices to percentage lipid in whole body

For percentage lipid in marrow and muscle, specific tissues were used from each species to evaluate physical condition. Percentage lipid in marrow was based on lipid analysis of the femur, humerus, tibia-fibula, radius, and ulna marrow of black and polar bears. Percentage lipid in muscle was based on lipid analysis of the biceps brachii and the biceps femoris of both species.

In the analysis of relationships between percentage lipid in the whole body and the three condition indices in black and polar bears, significant species differences occurred only in the relationship with percentage lipid in the radius marrow (Table 3.3). However, the slopes of the species-specific relationships were non-significant.

Of the nine relationships analyzed, only that between the fat-to-non-fat ratio and percentage lipid in the whole body was statistically significant. However, only 88% of the variance in the fat-to-non-fat ratio was explained by the relationship.

3.3.3 Relationship between lipid and energy content

Significant species differences in the relationships between lipid and energy content were not detected for the whole body or any of the tissues (Table 3.4). Extrapolated data precluded the calculation of a relationship for polar bear skin.

Significant lipid/energy relationships occurred in all tissues and the whole body. From these regressions, it was possible to estimate the net energy change associated with a one gram change in tissue or whole body lipid content. Thus, for a one gram change in lipid content, the changes in the net energy content of the tissues and whole body were as follows: adipose -10.9 kcal, skin - 1.1 kcal, bone - 28.9 kcal, muscle -144.8 kcal, viscera - 70.1 kcal, and whole body - 45.1 kcal.

Assuming the average metabolizable energy of lipid is 9.3 kcal/g (Hochachka and Somero 1973), it was possible to estimate the percentage of gross energy (as determined by calorimetry) which could be accounted for by neutral lipid for each bear. The calculation involved multiplying the total lipid content (g) for a tissue, or the whole body, by 9.3 kcal/g, dividing this value by the tissue or whole body energy content (kcal), and multiplying by 100 to determine the percentage of gross energy available from neutral lipid.

Table 3.5 presents the species-specific means and standard deviations for the estimated percentage of gross energy available from neutral lipid, as well as the percentage distribution of neutral lipid energy by tissue. Pooled means were calculated where non-significant differences of means occurred between species.

The percentage of gross energy available from neutral lipid did not significantly differ between species, nor did the percentage distribution of neutral lipid energy in the muscle, viscera, and bone tissues. Polar bears did, however, vary significantly more than black bears in the percentage distribution of neutral lipid energy occurring in adipose tissue. Percentage distribution of neutral lipid energy in skin was not compared between species because the sample size (*n* = 1) for polar bears was too small to permit statistical analyses. However, the percentage lipid content of the polar bear skin did fall within the range of black bear values.

3.4 Discussion

3.4.1 Distribution of lipid by body tissue

Consideration of tissue lipid content as a percentage of whole body lipid content provided an indication of the relative importance of the tissues as reserves of stored energy. Not surprisingly, in black and polar bears, adipose tissue was the major storage tissue for lipid and contained 43-79% of the total body lipid. For most mammals, the main function of adipose tissue is as an energy reserve (Emery 1969; Pond 1981), which is especially important in allowing animals to survive food shortages, gestation and lactation, and stresses associated with competition for mates (Young 1976).

Other tissues store neutral lipids where they serve as a local fuel reserve and, at the same time, perform a variety of functions of adaptive significance to the animal, e.g. heat production and lubrication (Hadley 1985). However, the lipid content of these tissues is considerably less than that of adipose tissue.

The adipose tissue lipid content of black and polar bears showed a highly significant relationship with whole body lipid content suggesting that adipose tissue lipid content is a potentially good indicator of physical condition in these species. The problem arises, however, as to how to measure adipose lipid content without dissecting and homogenizing the full mass of dissectable adipose tissue composing a bear. Unfortunately, adipose tissue offers serious sampling problems, as its composition is neither homogeneous nor its density constant (Aguilar 1985; Lockyer *et al.* 1985).

The lipid content of black bear skin was highly variable and did not significantly relate to whole body lipid content. Thus, there was little potential for the use of skin lipid content as an indicator of physical condition in this species.

There is some evidence to suggest that skin lipid content may have a close relationship to new hair growth (Dolnick 1969). As hairs grow, small adipose cells surrounding the hair follicle have been observed to accumulate lipid and eventually fill the dermis from the base of the hair follicle to the lower limits of the dermal boundary.

In black and polar bears, much of the variability in bone lipid content was explained by its significant relationship to whole body lipid. The principal lipid depot of bone is in the marrow and it is generally believed that the quantity varies with the state of nutrition of the animal (Zobrisky 1969). The results of this study, however, did not indicate that bone marrow lipid content has potential as an indicator of physical condition. More discussion concerning the applicability of marrow lipid content as an index of physical condition is provided below.

The lipid content of muscle in black and polar bears showed little variability and ranged from 4-11% of the whole body lipid content. Approximately 90% of the variability in the muscle lipid content of polar bears was explained by its significant relationship with whole body lipid content. However, the relationship between muscle lipid content and whole body lipid content, in black bears, was non-significant. This contrasts with observations in other mammals where there is a strong relationship between the lipid content of muscle and the lipid content of the whole body; such mammals include steers (Seebeck and Tulloh 1968), caribou (Ringberg *et al.* 1981), and fin (*Balaenoptera physalus*) and sei whales (*B. borealis*) (Lockyer 1987). The significance of this observation in black bears is not known. There is the possibility that the lack of significance is a result of the small sample size (a Type II error); but that is also true for the results of most tests performed in this study.

In both species, the lipid content of viscera accounted for the smallest percentage of whole body lipid content, relative to other tissues. The lipid content of this tissue showed a significant relationship with whole body lipid content, but the heterogeneous lipid composition of viscera presents difficulties in sampling for indication of physical condition. In general, the heterogeneous lipid composition of all tissues preclude the possibility of randomly sampling a tissue and analyzing its lipid content as an index of physical condition. Rather, it is necessary to sample a tissue at a specific anatomical location and determine whether or not the lipid content of the sample yields any significant relationship with whole body lipid content.

Some significant differences did occur between black and polar bears in their relationships between tissue lipid content and whole body lipid content. In general, it appears that as black bears accumulated lipid, they did so by allocating lipid to adipose, bone, and viscera in relatively constant proportions as whole body lipid content increased. In polar bears, the lipid content of viscera and muscle also showed an isometric relationship with whole body lipid content. In contrast, polar bear adipose tissue and bone showed allometric relationships with whole body lipid content such that adipose lipid accumulated in increasing proportions, while bone lipid accumulated in decreasing proportions, as whole body lipid content increased.

The percentage of total body energy explained by the neutral lipid content of bone is relatively small, approximately 13% (from Table 3.5), and a difference between species in bone lipid dynamics is expected to be of little energetic significance. Aside from energetics, the functional significance of lipid in bone tissue remains to be explored (Pond 1978).

The principal function of adipose tissue is as an energy reserve (Young 1976; Pond 1978) and a difference between species in adipose lipid dynamics is of importance in energetic considerations of black and polar bears. If the differences between species in their pattern of lipid deposition in adipose tissue is of biological significance, it may be suggested that polar bears place greater importance on long-term lipid storage than do black bears. This would enable polar bears to face the stress of food shortage and endure longer periods of food scarcity than black bears. Both species are known to face unpredictable food shortages and have been observed to be affected in similar ways. Reproductive rate and cub survivorship can decline by more than 50% for populations of black and polar bears during periods of food scarcity (Stirling *et al.* 1976; Rogers 1987). There is, however, no information available comparing the relative tolerance of black and polar bears to periods of food scarcity.

Other functions of adipose tissue, other than as an energy reserve, may also influence the neutral lipid dynamics in polar bear adipose tissue. Thermal or mechanical protection of organs, buoyancy, locomotory mechanics, and modification of body contours for social or sexual signalling have also been shown to influence the distribution and dynamics of adipose tissue in numerous wild vertebrates (Pond 1978). If adipose tissue in polar bears is important in functions other than energetics, it is necessary that the distribution and dynamics of the tissue are compatible with suggested functions.

3.4.2 Relationships of condition indices to percentage lipid in whole body

In this study, three physical condition indices were evaluated as predictors of whole body lipid content in black and polar bears. Only the fat-to-non-fat ratio showed a significant relationship to percentage lipid in the whole body. However, approximately 12% of the variance in the fat-to-non-fat ratio was not explained by this relationship.

A possible factor contributing to the unexplained variance is the chemical composition of adipose tissue and the effect it may have on the weight of dissectable adipose tissue used in the calculation of the fat-to-non-fat ratio. The chemical composition of adipose tissue can vary and weighing of this tissue may not accurately indicate its lipid content (Berg and Butterfield 1976). Furthermore, the fat-to-non-fat ratio only reflects the lipid content of the dissectable adipose tissue and not the lipid content of other tissues. In fact, the lipid content of the non-adipose tissues contributes to the measure of non-fat body weight, the denominator of the fat-to-non-fat ratio.

Regardless of the unexplained source(s) of variation, the strength of the relationship between the fat-to-non-fat ratio and percent whole body lipid suggests that the fat-to-non-fat ratio is best used in intraspecific comparisons of groups of black or polar bears. Comparisons among individual bears require the development of more accurate techniques.

Percentage lipid in bone marrow did not show a significant relationship with percentage lipid in the whole body, and hence, was not a suitable indicator of physical condition for black or polar bears. This contrasts with numerous studies that have advocated this technique to evaluate physical condition in mammals, including elk (*Cervus elaphus*) (Carbyn 1983), caribou (Eide and Ballard 1982), moose (*Alces alces*) (Franzmann and Arneson 1976), white-tailed deer (Kie *et al.* 1983) and possum (*Trichosurus vulpecula*) (Cowan 1985). However, the data of these studies is not based on equivalent data and in no case were relationships shown to exist between marrow lipid depots and the lipid content of the whole body.

There is also some support for using marrow lipid content as a one-way test of physical condition in which low marrow lipid content is indicative of poor physical condition, but high marrow lipid content does not necessarily indicate good physical condition (Mech and Delgiudice 1985). As a one-way test of physical condition, percentage lipid in the marrow of some bones may indicate poor physical condition in black bears, but not in polar bears (see Table 2.3 in Chapter 2).

For percentage lipid in marrow to provide a two-way indication of physical condition, it is necessary [illegible] a significant relationship exist between the lipid contained within a specific bone and the lipid contained within the whole body. In this study, no such relationships were found, although the lipid content of the total bone in the body showed significant relationships with whole body lipid content in both species. Perhaps, instead of considering only marrow lipid content, analysis of the lipid content of the entire bone may yield a significant relationship with whole body lipid content. Although the principal lipid depot of bone is in the marrow, significant quantities of lipid may also exist elsewhere in the bone, especially in the articular ends (Zobrisky 1969; Binford 1973).

Percentage lipid in muscle also failed to show a significant relationship with the percentage lipid in the whole body of black or polar bears. Intramuscular lipid content has been suggested as an index of physical condition in caribou (Ringberg *et al.* 1981; Hout and Goudreault 1984). In this study, the sampling technique used for the intramuscular lipid analysis may have masked any possible relationships. Muscle samples (20-50 g wet weight) were collected from similar locations on the biceps brachii and biceps femoris of each species. Significant relationships might have been established had the entire muscles been sampled, thus eliminating the effects of heterogeneous lipid distribution within muscles.

Similar sampling difficulties [illegible] have occurred for marrow lipid analysis, but inadequate sampling technique may not necessarily provide any explanation as to why significant relationships did not exist between percentage lipid in marrow or muscle, and whole body lipid content. Several studies of caribou have relied on similar techniques and found significant relationships (Ringberg *et al.* 1981; Hout and Goudreault 1984). This suggests that marrow and intramuscular lipid content of black and polar bears might be influenced by other factors, aside from physical condition.

3.4.3 Relationship between lipid and energy content

Calorimetric determinations show that the energy derived from the oxidation of lipid is more than twice as high as from the oxidation of carbohydrate or protein (Hadley 1985). The high energy yield of lipid, relative to carbohydrate and protein, and the mean lipid content of the various tissues of black and polar bears, ranging from 15.8% in muscle to 84.6% in adipose explains the significant lipid/energy relationships observed in the tissues and whole body of both species.

Of prime importance to the formulation of energetics models is the estimation of the energy content and composition of weight gain and loss during an animal's life (Robbins 1983; Price and White 1985). From this study, it is possible to estimate the energy content of weight change provided information is available regarding changes in the lipid content of the various tissues of black and polar bears. Conversely, it is possible to estimate the lipid content of weight change provided information is available regarding changes in the energy content of the various tissues.

Changes in energy content affected by a one gram change in lipid content showed the energy content of adipose to change by 10.9 kilocalories. This value is close to the value of 9.3 kcal, the average metabolizable energy of one gram of lipid (Hochachka and Somero 1973). The difference of 1.6 kcal may be partly explained by changes in the protein and phospholipid content of adipose tissue, associated with changes in lipid content.

Tissues varied greatly with respect to energy content changes resulting from changes in lipid content. That is best explained by differences between tissues in their composition of weight change. Thus, muscle showed a change in energy content of 144.8 kcal when the lipid content changed by one gram. Since 1 g of lipid, on average, accounts for only 9.3 kcal, it must be assumed 135.5 kcal of the energy change must be a result of changes in the content of other components such as protein and carbohydrate.

The measure of energy content change effected by lipid content change permits ranking tissues by decreasing strength of association between lipid and energy. Adipose tissue showed the strongest association between lipid and energy because changes in lipid content accounted for 85.3% (equals 9.3 kcal/g divided by 10.6 kcal/g) of the change in energy content. Bone, viscera, and muscle were the next tissues in order of rank; the association between lipid and energy in muscle being weakest because changes in lipid content accounted for only 6.4% of the change in energy content.

The energy content change effected by lipid content change in skin appears anomalous in that the change in energy content, 1.1 kcal/g of lipid, was considerably less than the average metabolizable energy of lipid (9.3 kcal/g). This may be explained by evidence that suggests skin lipid content is closely related to the onset of new hair growth (Dolnick 1969). In black bears, new hair growth is associated with the shedding of old fur during late spring and summer. Thus, although lipid may accumulate around new hair follicles and change skin energy content in a positive direction, the shedding of old fur would result in loss of protein and affect skin energy content in a negative direction; the net energy gain of 1.1 kcal/g of lipid being the result of these two opposing energy fluxes. This idea is supported by the observation of a negative association between skin lipid and skin protein content ($r = -0.83$, $p < 0.05$, $N = 4$) for black bears in this study

The change in whole body energy content associated with a change in lipid content (45.1 kcal/g of lipid) indicates 35.8 kcal is accounted for by components other than lipid. However, that assumes the change in lipid content occurs in all tissues in equal proportions, which is not always the case. Changes in the lipid content of one tissue are not necessarily associated with changes in other tissues, and the rate of deposition and utilization of lipid can vary between and within tissues (Berg and Butterfield 1976; Pond 1984; Pond and Mattacks 1985).

Differences among tissues in their relationship between lipid and energy content emphasizes the importance, in energetic models, of establishing the effect of weight gain or loss on each tissue. Differences in effect will be largely dependent on the age and physical condition of an animal. For example, weight changes in an adult animal with abundant adipose lipid stores will largely affect the adipose tissue. However, weight change in a young growing animal, with minimal adipose lipid, will largely affect muscle and, to a lesser extent, bone.

Another way of viewing the relationship between lipid and energy is to convert the weight of lipid into units of energy, and then determine what percentage of the gross energy of the whole body can be accounted for by the energy in neutral lipid. A mean of 61.6% of the whole body gross energy was explained by the whole body neutral lipid content of black and polar bears (Table 3.5). The range of values for this mean was between 35.5 and 80.4 percent. McCullough and Ullrey (1983) reported a mean of 52.7%, for relatively fat white-tailed deer, with a minimum and maximum of 43.1% and 61.4%, respectively. The mean pooled value for black and polar bears did not differ significantly (*t*-test, $p > 0.05$) from those of white-tailed deer. However, McCullough and Ullrey (1983) note that their study animals were taken in the fall and winter of a high acorn crop year and were in excellent physical condition.

In this study, black and polar bears ranged from poor to good physical condition, but are known to be able to attain better physical condition under natural conditions. Watts (1983) completed carcass analyses on five female polar bears with lipid contents ranging from 20-45% of the whole body, wet weight, which is a higher range of values compared with the lipid content range of 6-32% of animals used in this study. This may be explained by the fact that the bears used in Watts' study were captured at an earlier stage of the fasting period of the annual feed/fast cycle.

In comparisons of white-tailed deer and black or polar bears of similar physical condition, bears would have a larger mean percentage of their total energy contained within lipid. The greater potential energy storage of bears may, in part, be explained as an adaptation towards extended fasting; greater potential energy storage allows longer survival without food. However, consideration must also be given to differences in body size between genera. Pitts and Bullard (1968) showed fatness (total extractable lipid) to be directly related to fat-free body weight.

Adipose tissue contained approximately 65% of the whole body gross energy accounted for by neutral lipid. This result was expected given the major function of adipose as an energy storage organ (Young 1976; Pond 1978). The adipose tissue of polar bears varied significantly more than that of black bears in its percentage neutral lipid energy content. This difference may reflect the positive allometric pattern of lipid deposition observed in the adipose tissue of polar bears. As whole body lipid content increased, polar bears deposited an increasing proportion of lipid in adipose tissue. Thus, in polar bears, the percentage neutral lipid energy content should also become proportionately greater with increasing whole body lipid. In contrast, the isometric pattern of adipose tissue lipid deposition observed in black bears suggests the percentage neutral lipid energy in this tissue should remain relatively constant, regardless of whole body lipid content. This explanation is supported by the relative strengths of association, between whole body lipid content and percentage neutral lipid energy in adipose tissue, in black bears ($r = 0.20$, $p > 0.05$) and polar bears ($r = 0.92$, $p < 0.01$).

Comparison of the percentage distribution of neutral lipid energy by tissue between black or polar bears and white-tailed deer (McCullough and Ullrey 1983) shows the distribution of neutral lipid energy to be greater in the skin and bone, and less in the muscle and viscera, of bears. This may relect differences between genera in their pattern of lipid deposition and mobilization between tissues. Unfortunately, little research has focussed on this aspect of lipid metabolism.

TABLE 3.1. General information on black bears and polar bears analyzed for lipid and energy content

No.	Age (years)	Sex	Weight (kg)	Date of death	Fat-to-non-fat ratio	Total[a] lipid (kg)	Total[b] energy (kcal)
Black bears							
B1	0.5	F	5.0	July '86	0.05	0.37	9200
B2	1.3	M	24.0	May '86	0.45	7.18	88806
B3	1.4	M	26.4	June '86	0.44	8.34	97483
B4	14.6	M	156.0	August '86	0.36	28.15	407793
B5	6.4	M	157.8	June '86	0.16	15.64	348007
Polar bears							
P1	0.2	M	4.0	March '83	0.002	0.25	6613
P2	0.3	M	38.6	May '86	0.23	8.59	119821
P3	5.3	M	114.6	May '86	0.17	17.88	292813
P4	6.3	F	157.1	May '86	0.17	28.68	433227
P5	6.8	M	335.6	November '86	0.39	87.52	1108359
P6	14.8	M	512.0	November '86	0.47	164.37	1948856

[a] Total lipid content of body estimated from lipid extraction results.

[b] Total energy content of body estimated from bomb calorimetry results.

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Appendix 1. Description of adipose tissue depots defined in black and polar bears

Depot	Location
Subcutaneous	- included all adipose tissue located between skin and surficial muscles of body
Intermuscular	- included all adipose tissue located between the individual muscles of the body
Thoracic	- included all adipose tissue located within the thoracic cavity. - largely associated with pericardium and heart
Mesenteric	- included all adipose tissue attached to the gastro-intestinal tract, liver and spleen
Abdominal	- included all adipose tissue located within the abdominal cavity and pelvic channel, excluding the mesenteric depot

Appendix 2. Descriptive statistics for all black bear variables presented in Chapters 2 and 3

Variable	Mean	Standard deviation	Sample size
Age (years)	5.1	6.0	38
male	5.9	6.7	23
female	3.8	3.5	15
Foreleg circumference (cm)	34.3	10.0	33
male	38.0	9.5	21
female	27.8	7.5	12
Axillary girth (cm)	82.3	26.0	34
male	91.8	23.3	22
female	64.9	21.8	12
Straight-line body length (cm)	131.7	35.1	36
male	140.7	32.3	23
female	115.8	35.6	13
[illegible]n-fat body weight (kg)	53.9	34.8	35
[illegible]	64.7	37.9	20
female	38.6	23.5	15
Total body weight (kg)	66.5	44.0	38
male	78.6	46.8	23
female	47.1	31.5	15
Fat-to-non-fat ratio	0.23	0.17	35
male	0.27	0.18	20
female	0.16	0.16	15
Biceps brachii weight (g)	160.4	109.5	37
male	187.9	119.6	22
female	120.0	80.2	15
% lipid, dry weight	3.04	1.92	36
Biceps femoris weight (kg)	0.6	0.4	36
male	0.7	0.4	21
female	0.5	0.3	15
% lipid, dry weight	5.59	4.73	35
Radius weight (g)	96.8	57.0	36
male	114.1	60.2	22
female	69.7	40.1	14
% lipid, dry weight	83.6	8.5	29

Appendix 2. continued

Ulna weight (g)	138.1	80.9	36
male	163.4	84.5	22
female	98.5	57.6	14
% lipid, dry weight	81.4	13.1	29
Humerus weight (g)	303.9	172.5	34
male	366.4	176.6	20
female	214.6	123.7	14
% lipid, dry weight	78.4	12.5	29
Femur weight (g)	317.2	181.1	36
male	371.8	189.8	22
female	231.4	130.8	14
% lipid, dry weight	81.5	12.6	29
Tibia-fibula weight (g)	226.8	122.8	36
male	262.5	126.4	22
female	170.6	96.0	14
% lipid, dry weight	76.8	14.8	29
Tissue lipid content (%, dry weight)			
adipose	82.5	8.5	4
muscle	13.0	8.9	4
bone	30.7	10.7	4
skin	31.1	12.2	4
viscera	25.3	10.4	4
whole body	42.3	17.5	5
Tissue lipid content (kg)			
adipose	10.7	7.3	4
muscle	0.7	0.4	4
bone	1.8	1.2	4
skin	1.3	0.7	4
viscera	0.4	0.3	4
whole body	11.9	10.6	5
Tissue energy content (kcal/g, dry weight)			
adipose	8.14	0.04	4
muscle	5.73	0.39	4
bone	5.26	0.82	4
skin	6.06	0.65	4
viscera	5.98	0.43	4
whole body	6.52	0.69	5
Tissue energy content (kcal)			
adipose	107430	71022	4
muscle	52594	47067	4
bone	34859	25928	4
skin	30201	22792	4
viscera	10441	8199	4
whole body	190260	175897	5

Appendix 3. Descriptive statistics for all polar bear variables presented in Chapters 2 and 3

Variable	Mean	Standard deviation	Sample size
Age (years)	6.2	5.7	41
male	6.7	6.4	25
female	5.4	4.7	16
Foreleg circumference (cm)	54.4	9.4	29
male	57.9	9.3	17
female	49.5	7.3	12
Axillary girth (cm)	138.3	42.3	4
male	138.3	42.3	4
female	-----	----	0
Straight-line body leng[illegible] (cm)	186.1	45.0	34
male	196.5	52.2	21
female	169.3	23.0	13
Non-fat body weight (kg)	141.8	74.1	31
male	169.2	83.5	18
female	103.9	34.5	13
Total body weight (kg)	180.5	102.9	35
male	203.6	121.5	21
female	146.0	53.3	14
Fat-to-non-fat ratio	0.29	0.14	31
male	0.26	0.13	18
female	0.32	0.15	13
Biceps brachii weight (g)	404.4	220.0	42
male	468.7	246.0	26
female	299.9	112.7	16
% lipid, dry weight	4.86	1.99	30
Biceps femoris weight (kg)	1.6	1.0	40
male	1.9	1.1	24
female	1.3	0.5	16
% lipid, dry weight	7.82	4.11	29
Radius weight (g)	288.9	132.1	38
male	332.1	143.7	24
female	214.9	61.3	14
% lipid, dry weight	78.6	9.2	26

Appendix 3. continued

Ulna weight (g)	477.4	233.8	40
male	557.8	256.1	25
female	343.4	94.8	15
% lipid, dry weight	72.0	15.1	28
Humerus weight (g)	1038.9	523.4	41
male	1233.8	573.0	25
female	734.3	207.3	16
% lipid, dry weight	84.8	8.0	29
Femur weight (g)	1051.1	483.4	40
male	1205.9	519.2	26
female	763.8	213.8	14
% lipid, dry weight	86.0	10.2	30
Tibia-fibula weight (g)	768.9	354.8	40
male	888.9	378.0	26
female	546.1	143.6	14
% lipid, dry weight	81.0	10.3	28
Tissue lipid content (%, dry weight)			
adipose	86.3	6.5	5
muscle	18.1	6.0	5
bone	34.7	7.0	5
skin	38.7	---	1
viscera	28.2	9.3	5
whole body	45.6	15.0	6
Tissue lipid content (kg)			
adipose	45.6	53.7	5
muscle	4.7	5.3	5
bone	6.2	4.7	5
skin	1.4	---	1
viscera	1.4	1.2	5
whole body	51.2	63.5	6
Tissue energy content (kcal/g, dry weight)			
adipose	8.38	0.39	5
muscle	6.08	0.18	5
bone	5.14	0.54	5
skin	6.50	----	1
viscera	6.06	0.40	5
whole body	6.40	0.64	6
Tissue energy content (kcal)			
adipose	433178	512892	5
muscle	153087	131899	5
bone	89383	58759	5
skin	23226	-----	1
viscera	27130	19364	5
whole body	651615	743870	6