

A body composition model to estimate mammalian energy stores and metabolic rates from body mass and body length, with application to polar bears

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SUMMARY

Many species experience large fluctuations in food availability and depend on energy from fat and protein stores for survival, reproduction and growth. Body condition and, more specifically, energy stores thus constitute key variables in the life history of many species. Several indices exist to quantify body condition but none can provide the amount of stored energy. To estimate energy stores in mammals, we propose a body composition model that differentiates between structure and storage of an animal. We develop and parameterize the model specifically for polar bears (*Ursus maritimus* Phipps) but all concepts are general and the model could be easily adapted to other mammals. The model provides predictive equations to estimate structural mass, storage mass and storage energy from an appropriately chosen measure of body length and total body mass. The model also provides a means to estimate basal metabolic rates from body length and consecutive measurements of total body mass. Model estimates of body composition, structural mass, storage mass and energy density of 970 polar bears from Hudson Bay were consistent with the life history and physiology of polar bears. Metabolic rate estimates of fasting adult males derived from the body composition model corresponded closely to theoretically expected and experimentally measured metabolic rates. Our method is simple, non-invasive and provides considerably more information on the energetic status of individuals than currently available methods.

Key words: structure, storage, dynamic energy budgets, energy reserve, body fat, lean body mass, isotopic water dilution, bioelectrical impedance analysis, body condition index, nutritional status, *Ursus maritimus*.

INTRODUCTION

Individuals of many species experience fluctuations in body condition as a result of fluctuations in energy intake and expenditure (e.g. Boswell et al., 1994; Fietz and Ganzhorn, 1999; Parker et al., 2009; Ryg et al., 1990; Watts and Hansen, 1987). When energy intake exceeds expenditure, individuals allocate the surplus to storage, which can then be used during periods of food scarcity to fuel physical processes such as maintenance, growth or reproduction. Each of these processes may be compromised at low storage energy, making body condition a potential driving variable for population dynamics (Nisbet et al., 2000; Parker et al., 2009; Stevenson and Woods, 2006). Many factors may affect energy intake and expenditure, and thus body condition, including resource availability, ecological interactions and anthropogenic influences, such as habitat destruction, habitat restoration or climate change (Stevenson and Woods, 2006). Body condition has therefore been identified as a variable for monitoring by ecologists and population managers alike but the best measure for body condition remains debated (Green, 2001; Krebs and Singleton, 1993; Stevenson and Woods, 2006).

Several indices are routinely used to qualify mammalian body condition, ranging from categorical indices that classify individuals on a fatness scale (e.g. Lyver and Gunn, 2004; Stirling et al., 2008; Vervaecke et al., 2005) to a variety of continuous indices usually based on body mass and some measure of length (e.g. Blackwell, 2002; Krebs and Singleton, 1993; Stevenson and Woods, 2006).

Such indices may sometimes correlate with more direct measures of body condition, such as the percentage lipid content of adipose tissue (e.g. Stirling et al., 2008) or the combined mass of fat and skeletal muscle (e.g. Cattet et al., 2002), but they cannot provide information on the amount of stored energy. Knowledge of individual energy stores, however, can provide mechanistic and quantitative insight into processes ranging from individual reproduction and survival to population and ecosystem dynamics (Brown et al., 2004; Kleiber, 1975; Kooijman, 2000; Nisbet et al., 2000).

Body composition, and thus the amount of energy stored in body fat, may be quantified by experimental methods, such as isotopic water dilution or bioelectrical impedance analysis (Speakman, 2001). Water dilution is expensive, requires prolonged immobilization of the study animal and is impractical for large-scale field studies. Impedance analysis is less time-consuming but has many error sources and requires extensive training to obtain accurate measurements (Farley and Robbins, 1994; Parker, 2003). Neither of these methods can be used to re-interpret historic (mostly length and mass) data.

In the present study we develop a simple non-invasive method to estimate energy stores in live-caught animals from mass and length data. Our approach is based on dynamic energy budget theory, and relies on the concept that all tissue may be characterized as either structure or storage (Kooijman, 2000). Storage encompasses all materials that can be used as an energy source for growth,

maintenance and reproduction (e.g. non-structural lipids and proteins), plus body water and ash associated with these materials. Structure consists of any remaining tissue, body water and ash, and cannot be utilized for energy even under extreme starvation (e.g. bones, brain, lungs, etc.). Some tissue belongs partially to structure and partially to storage: muscle mass, for example, may be accumulated when feeding and catabolized when fasting (Atkinson et al., 1996a; Ryg et al., 1990), but some muscle is retained even when starving. We fully develop the method using polar bears (*Ursus maritimus* Phipps) as an example, but all concepts are general and the method is applicable to other species.

Polar bears provide a good case study, because they experience large seasonal fluctuations in food supply and body condition, and depend on stored energy for many aspects of their life history (Derocher et al., 2004; Ramsay and Stirling, 1988; Stirling and Øritsland, 1995). Pregnant females, for example, can fast up to eight months during gestation and early lactation (Atkinson and Ramsay, 1995). During this time all energy for survival, gestation and lactation must be drawn from fat and nutrient stores, and insufficient energy stores can negatively affect reproductive success (Derocher et al., 2004). Furthermore, in the southern portions of the geographical range of this species, bears are forced ashore in summer when the sea ice melts. Little or no food is available on land and all bears rely on stored energy for survival during a 4–5 month fasting period (Derocher et al., 1993; Ramsay and Hobson, 1991). Body condition and, more specifically, energy stores thus become key variables in polar bear population dynamics.

We first develop and parameterize a body composition model to estimate structural mass, storage mass, storage composition and storage energy of individual polar bears. Structural mass is estimated from straight-line body length, a morphometric measurement easily obtained in the field and readily available for previously handled individuals. Storage mass and storage energy are estimated from straight-line body length and total body mass. Furthermore, we apply the body composition model to estimate the metabolic rates of fasting adult polar bears from consecutive measurements of straight-line body length and total body mass only.

MATERIALS AND METHODS

To describe body composition, we differentiate between structure and storage and assume constant chemical composition of both compartments, i.e. strong homeostasis [see p. 30 in Kooijman (Kooijman, 2000)]. We further assume isomorphic growth, i.e. the conservation of structural shape throughout the lifetime of an

individual (Kooijman, 2000). The definitions of structure and storage together with strong homeostasis imply that structural mass only changes with growth and otherwise remains constant, whereas storage mass fluctuates with food intake and energy expenditure.

We first show how to estimate structural mass from an appropriately chosen measure of length. In polar bears, straight-line body length (defined as the dorsal straight-line distance from the tip of the nose to the end of the last tail vertebra when the bear is lying in a sternally recumbent position) is a natural choice for a measure of structural size, because this measure of length is minimally affected by nutritional status and, furthermore, strongly correlates with skeletal mass, which is a major part of structure (Cattet et al., 2002). We then estimate storage mass as the difference between total body mass and structural mass, and obtain storage energy from storage mass by accounting for storage composition. State variables used in the model are summarized in Table 1.

Model development

Total body mass, M , is by definition the sum of structural mass, M_{STR} , and storage mass, M_{STO} (units: kg):

$$M = M_{STR} + M_{STO}. \quad (1)$$

Structural mass is the product of structural volume, V_{STR} (units: m^3), and structural density, ρ_{STR} (units: $kg\ m^{-3}$). Due to the assumption of isomorphic growth, V_{STR} is proportional to cubed straight-line body length (Kooijman, 2000). The relationship between structural mass and straight-line body length (L) is therefore:

$$M_{STR} = \rho_{STR} V_{STR} = \rho_{STR} k L^3, \quad (2)$$

where k is a dimensionless parameter, accounting for the irregular shape of the animal.

To relate storage mass to storage energy, we need to account for storage composition. Ignoring glycogen, a short-term energy source, we assume that storage consists of fat (M_{STO-F}), protein (M_{STO-P}), ash (M_{STO-A}) and water (M_{STO-W}) (Farley and Robbins, 1994). Storage mass then equals the sum of the masses of each storage constituent:

$$M_{STO} = M_{STO-F} + M_{STO-P} + M_{STO-A} + M_{STO-W}. \quad (3)$$

Of these, only fat and protein are energy sources, but all four storage components are accumulated by polar bears when feeding and depleted when fasting, consistent with the strong homeostasis assumption (Arnould and Ramsay, 1994; Atkinson and Ramsay, 1995; Atkinson et al., 1996a; Cattet et al., 2002).

Table 1. State variables used in the body composition model

State variable	Definition	Units
Measurable state variables		
L	Straight-line body length	m
M	Total body mass	kg
Derived state variables		
M_{STR}	Mass of structure	kg
M_{STO}	Mass of storage	kg
M_{STO-F}	Mass of body fat in storage	kg
M_{STO-P}	Mass of protein in storage	kg
M_{STO-A}	Mass of ash in storage	kg
M_{STO-W}	Mass of body water in storage	kg
M_{STO-L}	Mass of non-structural lean (i.e. fat-free) tissue ($= M_{STO-P} + M_{STO-A} + M_{STO-W}$)	kg
V_{STR}	Volume of structure	m^3
E	Total energy content of storage	MJ
E_F	Energy in storage fat	MJ
E_P	Energy in storage protein	MJ

Summarizing protein, ash and water in storage as non-structural lean (i.e. fat-free) tissue, we write:

$$M_{\text{STO}} = M_{\text{STO-F}} + M_{\text{STO-L}}, \quad (4)$$

where $M_{\text{STO-L}}$ represents the mass of non-structural lean tissue, which by definition equals the sum of $M_{\text{STO-P}}$, $M_{\text{STO-A}}$ and $M_{\text{STO-W}}$. The relationships between $M_{\text{STO-L}}$ and $M_{\text{STO-P}}$, $M_{\text{STO-A}}$ and $M_{\text{STO-W}}$ are:

$$M_{\text{STO-P}} = M_{\text{STO-L}} (1 - \eta_{\text{W}}) \eta_{\text{P}}, \quad (5A)$$

$$M_{\text{STO-A}} = M_{\text{STO-L}} (1 - \eta_{\text{W}}) (1 - \eta_{\text{P}}), \quad (5B)$$

$$M_{\text{STO-W}} = M_{\text{STO-L}} \eta_{\text{W}}, \quad (5C)$$

where η_{W} represents the proportion of lean body mass that is water, and η_{P} is the proportion of dry lean body mass that is protein.

Because we aim to convert storage mass into energetic content, and only protein provides an energy source from non-structural lean tissue, we use Eqn 5A to rewrite Eqn 4 as:

$$M_{\text{STO}} = M_{\text{STO-F}} + \frac{M_{\text{STO-P}}}{(1 - \eta_{\text{W}}) \eta_{\text{P}}}. \quad (6)$$

Substituting the energy densities of fat, ϵ_{F} , and protein, ϵ_{P} (units: MJ kg^{-1}), we rewrite Eqn 6 as:

$$M_{\text{STO}} = \frac{E_{\text{F}}}{\epsilon_{\text{F}}} + \frac{E_{\text{P}}}{(1 - \eta_{\text{W}}) \eta_{\text{P}} \epsilon_{\text{P}}}, \quad (7)$$

where E_{F} and E_{P} are the respective amounts of energy (units: MJ) in the fat and protein stores of an animal.

The total energy content of storage, E , equals the sum of energy in the fat and protein stores (i.e. $E = E_{\text{F}} + E_{\text{P}}$). We define γ as the proportion of total storage energy that is stored in body fat and write:

$$E_{\text{F}} = \gamma E, \quad (8A)$$

$$E_{\text{P}} = (1 - \gamma) E. \quad (8B)$$

Combining Eqn 7 and Eqn 8, we obtain the relationship between storage mass and storage energy:

$$M_{\text{STO}} = E \left(\frac{\gamma}{\epsilon_{\text{F}}} + \frac{1 - \gamma}{(1 - \eta_{\text{W}}) \eta_{\text{P}} \epsilon_{\text{P}}} \right). \quad (9)$$

Inserting Eqn 2 and Eqn 9 into Eqn 1 yields the relationship between total body mass, straight-line body length and storage energy:

$$M = \rho_{\text{STR}} k L^3 + E \left(\frac{\gamma}{\epsilon_{\text{F}}} + \frac{1 - \gamma}{(1 - \eta_{\text{W}}) \eta_{\text{P}} \epsilon_{\text{P}}} \right). \quad (10)$$

Solving Eqn 10 for E gives storage energy as a function of total body mass and straight-line body length:

$$E = \alpha (M - \rho_{\text{STR}} k L^3), \quad (11)$$

where:

$$\alpha = \left(\frac{\gamma}{\epsilon_{\text{F}}} + \frac{1 - \gamma}{(1 - \eta_{\text{W}}) \eta_{\text{P}} \epsilon_{\text{P}}} \right)^{-1}, \quad (12)$$

represents the energy density of storage (units: MJ kg^{-1}).

Moreover, storage composition is also specified by the body composition model, and the respective proportions of storage mass

that are fat, protein, ash and water can be estimated from the following equations (see Appendix for derivation):

$$\frac{M_{\text{STO-F}}}{M_{\text{STO}}} = \alpha \frac{\gamma}{\epsilon_{\text{F}}}, \quad (13A)$$

$$\frac{M_{\text{STO-P}}}{M_{\text{STO}}} = \alpha \frac{1 - \gamma}{\epsilon_{\text{P}}}, \quad (13B)$$

$$\frac{M_{\text{STO-A}}}{M_{\text{STO}}} = \alpha \frac{(1 - \eta_{\text{P}}) (1 - \gamma)}{\eta_{\text{P}} \epsilon_{\text{P}}}, \quad (13C)$$

$$\frac{M_{\text{STO-W}}}{M_{\text{STO}}} = \alpha \frac{\eta_{\text{W}} (1 - \gamma)}{(1 - \eta_{\text{W}}) \eta_{\text{P}} \epsilon_{\text{P}}}. \quad (13D)$$

Model parameterization

The model contains seven parameters (Table 2), two of which (ρ_{STR} and k) relate straight-line body length to structural mass. The remaining five convert storage mass into energetic content. We used data from starved polar bears as well as literature data on bear body composition for model parameterization, and introduce these data more specifically when used. All bears were handled under the approval of research permits that followed guidelines of the Canadian Council on Animal Care. Data on two starving bears were collected by government agencies as part of animal control actions for public safety. Statistical analyses were performed in SYSTAT 10 (Systat Software, Chicago, IL, USA). Results were considered significant at $P \leq 0.05$. Means are presented \pm s.e.m.

The parameters ρ_{STR} and k need not be estimated separately, because only their product, $\rho_{\text{STR}} k$, determines the relationship between straight-line body length and structural mass (cf. Eqn 2). To estimate $\rho_{\text{STR}} k$, we used the body masses and straight-line body lengths of two starving adult polar bears: a female (total body mass: 89.8 kg; straight-line body length: 1.81 m; age ≤ 10 years) and a male (total body mass: 163.3 kg; straight-line body length: 2.23 m; age: 7 years). Both bears were in extremely poor condition, with empty stomachs, empty intestinal tracts and no subcutaneous body fat. They were described as lethargic and the male was hardly able to stand. We assumed that these bears had no (or only negligible amounts of) storage energy left and set $E = 0$. Body mass then equals structural mass and Eqn 10 can be written as:

$$\rho_{\text{STR}} k = \frac{M}{L^3}. \quad (14)$$

Inserting straight-line body lengths and total body masses into Eqn 14 yields $\rho_{\text{STR}} k = 15.14 \text{ kg m}^{-3}$ for the female, $\rho_{\text{STR}} k = 14.73 \text{ kg m}^{-3}$ for the male, and a mean estimate of $\rho_{\text{STR}} k = 14.94 \text{ kg m}^{-3}$, which is used in all further calculations (the low sample size used to estimate $\rho_{\text{STR}} k$ does not present a major concern, cf. the Sensitivity analysis, Model validation and Discussion sections below).

The body composition parameters η_{W} and η_{P} have been estimated for black and brown bears as $\eta_{\text{W}} = 0.734$ and $\eta_{\text{P}} = 0.835$ (Farley and Robbins, 1994). No estimates exist for polar bears, so we adopted these estimates for model parameterization in accordance with previous polar bear body composition studies (Atkinson and Ramsay, 1995; Atkinson et al., 1996a). For modelling purposes, the energy densities of fat and protein were assumed to be $\epsilon_{\text{F}} = 39.3 \text{ MJ kg}^{-1}$ and $\epsilon_{\text{P}} = 18.0 \text{ MJ kg}^{-1}$ (Schmidt-Nielsen, 1997).

To estimate the remaining parameter, γ , we rearranged Eqn 10 as:

$$\gamma = \frac{M_{\text{STO-F}} \epsilon_{\text{F}}}{(M - \rho_{\text{STR}} k L^3 - M_{\text{STO-F}}) [(1 - \eta_{\text{W}}) \eta_{\text{P}} \epsilon_{\text{P}}] + M_{\text{STO-F}} \epsilon_{\text{F}}}. \quad (15)$$

Table 2. Parameter estimates for the polar bear body composition model

Parameter	Definition	Estimate (mean \pm s.e.m.)	Units	Source
ρ_{STR}	Density of structure	–	kg m^{-3}	Present study (only the product $\rho_{STR}k$ is estimated)
k	Shape parameter relating structural volume to straight-line body length	–	–	
$\rho_{STR}k$	–	14.94	kg m^{-3}	Present study – using data from Arnould and Ramsay (1994) and Atkinson et al. (1996a)
γ	Proportion of total storage energy that is stored in body fat	0.899 \pm 0.011 ^a	–	
		0.941 \pm 0.006 ^b		
		0.943 \pm 0.014 ^c		
		0.935 \pm 0.004 ^d		
		0.885 \pm 0.007 ^e		
ϵ_F	Energy density of fat	39.3	MJ kg^{-1}	(Schmidt-Nielsen, 1997)
ϵ_P	Energy density of protein	18.0	MJ kg^{-1}	(Schmidt-Nielsen, 1997)
η_W	Proportion of lean body mass that is water	0.734	–	(Farley and Robbins, 1994)
η_P	Proportion of dry lean body mass that is protein	0.835 \pm 0.016	–	(Farley and Robbins, 1994)

^aCubs-of-the-year, ^byearlings, ^cadult females, ^dsubadult males, ^eadult males.

We parameterized Eqn 15 using data from tables 1 and 2 in Arnould and Ramsay (Arnould and Ramsay, 1994) and table 1 in Atkinson et al. (Atkinson et al., 1996a), who measured straight-line body length, total body mass and total fat mass of adult females ($N=9$), cubs-of-the-year ($N=7$), yearlings ($N=7$), subadult males ($N=5$) and adult males ($N=5$). Both studies determined body masses (± 0.5 kg) by weighing immobilized bears with an electronic load cell and estimated total body fat using isotopic water dilution. Each bear was sampled twice, between 17 and 88 days apart. One cub-of-the-year and one adult male were in exceptionally poor condition, with body fat constituting only 1.4% and 1.7% of their respective body mass. We excluded both bears from analyses because patterns of fat and protein utilization probably change under extreme starvation, with potentially large effects on storage composition and, consequently, γ . Straight-line body lengths and adult female body fat were unreported in the respective tables so we obtained these data from the authors (Arnould, 1990).

In polar bears, only a small fraction of body fat is structural [i.e. only in cell membranes, the brain, and small depots in the eye sockets and foot pads (Pond et al., 1992)]. We therefore simplified body composition in all further calculations by assuming that all body fat belongs to storage. Fat measurements in Arnould and Ramsay (Arnould and Ramsay, 1994) and Atkinson et al. (Atkinson et al., 1996a) thus provided estimates of storage fat masses. Two measurements of storage fat mass, total body mass and straight-line body length were available for each bear because each individual was sampled twice. By inserting these estimates into Eqn 15 we obtained two estimates of γ for each bear. No systematic differences in γ were observed within individuals, in accordance with the strong homeostasis assumption. We therefore averaged both estimates to obtain a single estimate of γ for each individual.

Sex- and age-class had a significant effect on storage composition (Kruskal–Wallis, $H=14.61$, $P=0.006$), with mean γ highest in adult females ($\gamma=0.943\pm 0.014$), followed by yearlings ($\gamma=0.941\pm 0.006$), subadult males ($\gamma=0.935\pm 0.004$), cubs-of-the-year ($\gamma=0.899\pm 0.011$) and adult males ($\gamma=0.885\pm 0.007$) (Fig. 1). Differences in storage composition may reflect sex- and age-related differences in morphology (Derocher et al., 2005; Stirling et al., 2008; Thiemann et al., 2006) and energy utilization (Atkinson et al., 1996a; Atkinson et al., 1996b), and significantly affect storage energy predictions (cf. sensitivity analysis below). We therefore parameterized the body composition model separately for all five sex- and age-classes, using the respective mean estimates of γ .

A statistical comparison between observed fat masses (Arnould and Ramsay, 1994; Atkinson et al., 1996a) and model predictions

for storage fat masses (Eqn 13A) supported the use of sex- and age-class specific estimates of γ : regressing observations against predictions and simultaneously testing for unit slope and zero intercept (Mayer et al., 1994) yielded a significant difference between observed and predicted fat masses when using the across sex- and age-class mean of γ , $\bar{\gamma}=0.925$ ($F_{2,60}=11.81$, $P<0.001$). No such difference was found when using sex- and age-class specific means ($F_{2,60}=0.65$, $P=0.524$).

RESULTS

Body composition model

The parameterized body composition model provides predictive equations for structural mass, storage mass and storage energy of a polar bear from its straight-line body length and total body mass:

Structural mass can be estimated from straight-line body length (cf. Eqn 2):

$$M_{STR} = 14.94L^3. \quad (16)$$

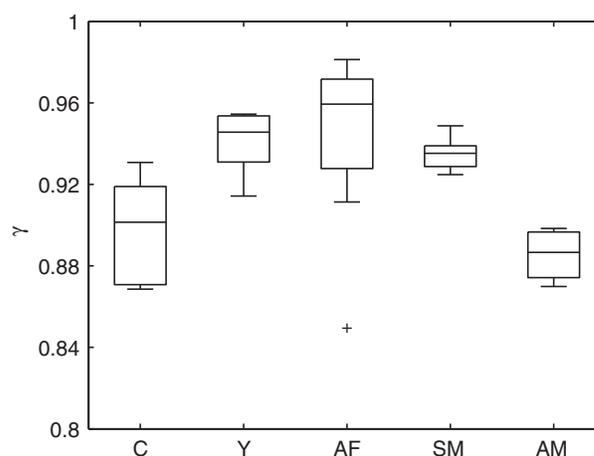


Fig. 1. Estimates of the proportion of storage energy that is stored in body fat (γ) for six cub-of-the-year (C), seven yearling (Y), nine adult female (AF), five subadult male (SM) and four adult male (AM) polar bears from Arnould and Ramsay (Arnould and Ramsay, 1994) and Atkinson et al. (Atkinson et al., 1996a). Each box plot shows the median, the upper and lower quartiles, and whiskers that extend to include data no more than 1.5 times the interquartile range away from the quartiles. Data beyond the whiskers are marked by crosses.

Table 3. Estimated storage composition of polar bears

	Estimated percentage of storage mass that is:			
	Fat	Protein	Ash	Water
Cubs-of-the-year	47.5	11.7	2.3	38.5
Yearlings	61.9	8.5	1.7	28.0
Adult females	62.7	8.3	1.6	27.4
Subadult males	59.4	9.0	1.8	29.8
Adult males	43.9	12.5	2.5	41.2

Storage mass is the difference between total body mass and structural mass (cf. Eqn 1):

$$M_{\text{STO}} = M - 14.94L^3. \quad (17)$$

Storage composition was estimated from Eqn13 and differed between sex- and age-classes (Table3). Relative fat content of storage was highest in adult females, followed by yearlings, subadult males, cubs-of-the-year and adult males. The pattern was reversed for protein, ash and water.

Storage energy can be estimated from total body mass and straight-line body length (cf. Eqn11). Predictive equations for storage energy are presented separately for cubs-of-the-year (C), yearlings (Y), adult females (AF), subadult males (SM) and adult males (AM):

$$E_C = 20.77M - 310.30L^3, \quad (18A)$$

$$E_Y = 25.84M - 386.05L^3, \quad (18B)$$

$$E_{\text{AF}} = 26.14M - 390.53L^3, \quad (18C)$$

$$E_{\text{SM}} = 24.97M - 373.05L^3, \quad (18D)$$

$$E_{\text{AM}} = 19.50M - 291.33L^3. \quad (18E)$$

Although Eqn 18A–E are structurally the same, their coefficients differ due to sex- and age-class specific differences in storage composition. For example, comparing an adult female with an adult male of equal body mass and length, we predict ~1.34 times more storage energy for the female (Eqn 18C,E) (Fig.2C,D) due to the higher relative fat content of storage. By contrast, the relationship between storage energy, total body mass and straight-line body length differs little between yearlings, adult females and subadult males (Eqn 18B–D), or between cubs-of-the-year and adult males (Eqn 18A,E), reflecting similarities in storage composition.

Fig.2 shows model predictions of storage energy from straight-line body length and total body mass. The zero-isoclines ($E=0$) represent starved bears, where energy stores are exhausted and all tissue belongs to structure (i.e. $M=14.94L^3$). We limit illustrations to the usual range of straight-line body lengths for each sex- and age-class, and to bears with total body mass at most 4 times structural mass (i.e. $M \leq 59.76L^3$), an approximate upper bound to total body mass. At this limit, body fat is estimated as 47.0% and 32.9% of total body mass for adult females and adult males, respectively (from Eqn 1 and Eqn 13A), which is close to the maximal relative body fat contents observed [females: 49% (Atkinson and Ramsay, 1995); males: 32% (Atkinson et al., 1996a)]. However, all limits were chosen for illustrative purposes only and Eqn 18A–E could be used beyond the depicted ranges.

Model application: estimating metabolic rates

Here we show how the body composition model can be applied to estimate the metabolic rate of fasting, resting, non-growing and non-

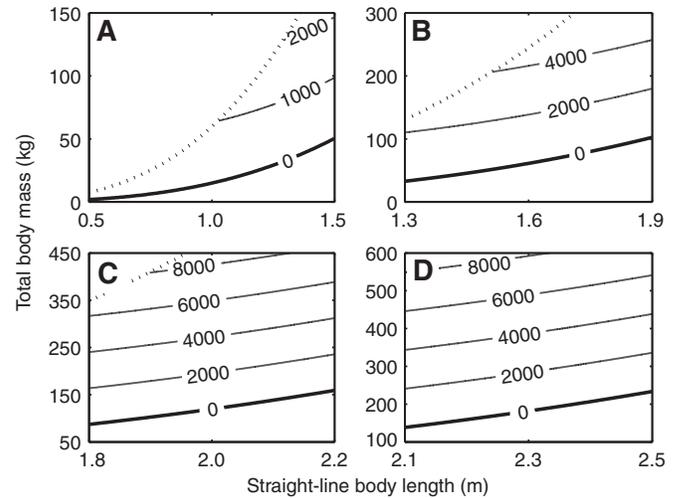


Fig.2. Contour lines showing model predictions (Eqn 18A–E) for polar bear storage energy, E (units: MJ), from straight-line body length and total body mass for (A) cubs-of-the-year, (B) yearlings, (C) adult females and (D) adult males. Thick solid lines correspond to starved bears, dotted lines to bears whose total body mass is four times structural mass.

reproducing polar bears in a thermoneutral state, using straight-line body lengths and consecutive measurements of total body mass only. Such bears expend storage energy only for somatic maintenance, and storage energy decreases with a rate of change proportional to the mass of tissue that requires maintenance (Kooijman, 2000). In dynamic energy budget theory, these maintenance requirements are usually assumed to be limited to structural mass (Kooijman, 2000; Nisbet et al., 2000) whereas classical metabolic work relates changes in storage energy to total body mass (Kleiber, 1975). Both assumptions can be accommodated within the framework presented here. However, for polar bears, we assume that both structural and non-structural lean tissue requires maintenance, and that maintenance requirements of body fat are negligible relative to those of lean tissue (Aarseth et al., 1999; Atkinson and Ramsay, 1995; Boyd, 2002; Segal et al., 1989). The rate of change in storage energy is therefore given by the following differential equation:

$$\frac{dE}{dt} = -m(M - M_{\text{STO-F}}), \quad (19)$$

where metabolic rate, m , is the energy required per unit time to maintain a unit mass of lean tissue.

Using Eqn 1, Eqn 2, Eqn 11 and Eqn 13A to convert storage energy and storage fat mass into functions of total body mass and straight-line body length, and solving the resulting differential equation, gives total body mass as a function of time t (see Appendix for details):

$$M(t) = C \exp\left(-\frac{m(1-\phi)}{\alpha} t\right) - \frac{\phi}{1-\phi} \rho_{\text{STR}} k L^3, \quad (20)$$

where $\phi=(\alpha\gamma)/\epsilon_F$ represents the proportion of storage mass that is fat (cf. Eqn 13A), α is a composite parameter given by Eqn 12, and C is the integration constant.

Given two measurements of body mass T time units apart, $M(0)=M_0$ and $M(T)=M_1$, Eqn 20 can be solved to obtain the integration constant:

$$C = M_0 + \frac{\phi}{1-\phi} \rho_{\text{STR}} k L^3 \quad (21)$$

and an estimate for metabolic rate:

$$m = -\frac{\alpha}{(1-\phi)T} \ln \left(\frac{(1-\phi)M_1 + \phi\rho_{\text{STR}}kL^3}{(1-\phi)M_0 + \phi\rho_{\text{STR}}kL^3} \right). \quad (22)$$

If more than two measurements of body mass are available, a non-linear regression of body mass against time using Eqn 20 will yield estimates of both C and m .

Sensitivity analysis

Small sample sizes for model parameterization may have resulted in low accuracy in determining the parameters $\rho_{\text{STR}}k$ and γ . To understand how deviations in these parameters may affect storage energy predictions, we varied them one at a time, while holding the other constant at either $\rho_{\text{STR}}k=14.94 \text{ kg m}^{-3}$ or at $\bar{\gamma}=0.925$ (the across sex- and age-class mean of γ). We then calculated $(E-\bar{E})/\bar{E}$, the resultant proportional change in storage energy E relative to \bar{E} , the storage energy of an individual of equal body mass and length, whose structural mass and storage composition are specified by $\rho_{\text{STR}}k=14.94 \text{ kg m}^{-3}$ and $\bar{\gamma}=0.925$, respectively.

The proportional change in storage energy $(E-\bar{E})/\bar{E}$ between two individuals of equal body length, body mass and structural mass (specified by $\rho_{\text{STR}}k$) but differing storage composition (specified by γ and $\bar{\gamma}$, respectively) is given by:

$$\frac{E-\bar{E}}{\bar{E}} = \left(\frac{\gamma}{\epsilon_f} + \frac{1-\gamma}{(1-\eta_w)\eta_p\epsilon_p} \right)^{-1} \left(\frac{\bar{\gamma}}{\epsilon_f} + \frac{1-\bar{\gamma}}{(1-\eta_w)\eta_p\epsilon_p} \right) - 1, \quad (23)$$

whereas for equal storage composition (specified by $\bar{\gamma}$), but differing structural mass (specified by $\rho_{\text{STR}}k$ and $\bar{\rho}_{\text{STR}}k$, respectively), we obtain:

$$\frac{E-\bar{E}}{\bar{E}} = -p \left(\frac{M}{\rho_{\text{STR}}kL^3} - 1 \right), \quad (24)$$

where $p=(\rho_{\text{STR}}k-\bar{\rho}_{\text{STR}}k)/\bar{\rho}_{\text{STR}}k$ represents the proportional increase or decrease in $\rho_{\text{STR}}k$ relative to $\bar{\rho}_{\text{STR}}k$.

Storage energy is sensitive to storage composition and increases monotonically with γ (Fig. 3A). For instance, an average adult male ($\gamma=0.885$) has 17.5% less storage energy than an individual of equal body mass, length and structure but with $\gamma=\bar{\gamma}$. An average adult female ($\gamma=0.943$) of equal mass, length and structure has 10.6% more storage energy than the reference individual with $\gamma=\bar{\gamma}$. The sensitivity of storage energy to γ , and thus storage composition, reflects the differing energy densities of body fat and lean tissue, emphasizing the importance of body fat for energy storage and the need to specify γ as accurately as possible.

Model predictions of storage energy are generally less sensitive to $\rho_{\text{STR}}k$ (Fig. 3B). However, unlike in γ , sensitivity depends on the ratio between total body mass (M) and structural mass as specified by $\bar{\rho}_{\text{STR}}k$ and L (Eqn 24). Sensitivity of storage energy to $\rho_{\text{STR}}k$ is low for obese bears, increases with decreasing storage mass and is greatest for starving bears. For instance, a 15% increase in $\rho_{\text{STR}}k$ results in a 15% decrease of storage energy for a bear whose total body mass is twice its structural mass, but only a 5% decrease in bears with total body mass four times their structural mass. It is unlikely that we underestimated $\rho_{\text{STR}}k$ by more than 15%, because lean bears with non-zero storage energy ($E \neq 0$) have been observed where M/L^3 equals ~ 1.15 times the current estimate of $\rho_{\text{STR}}k$ [A.E.D., unpublished data; cf. also the leanest adult male in Atkinson et al. (Atkinson et al., 1996a), where $M/L^3=17.16 \text{ kg m}^{-3}$]. These bears probably provide an approximate upper bound for $\rho_{\text{STR}}k$ (cf.

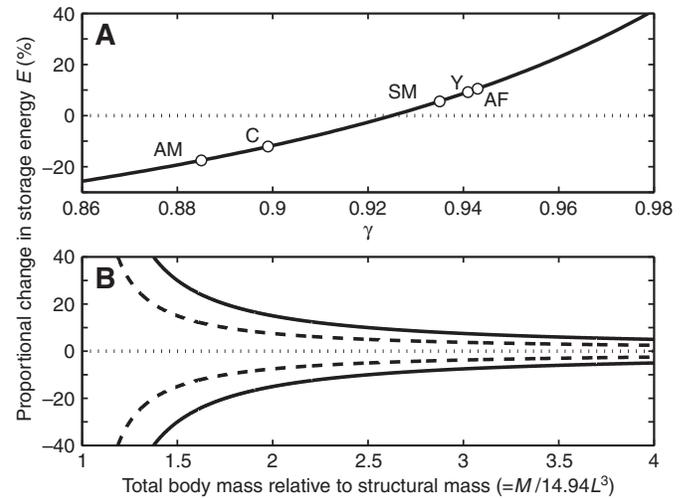


Fig. 3. Proportional change in storage energy (E) relative to \bar{E} , the storage energy of an individual of equal body mass and length with $\rho_{\text{STR}}k=14.94 \text{ kg m}^{-3}$ and $\bar{\gamma}=0.925$, (A) when varying γ but holding $\rho_{\text{STR}}k=\bar{\rho}_{\text{STR}}k$ constant, and (B) as a function of total body mass relative to structural mass for a 7.5% decrease or increase (upper and lower broken lines, respectively) and a 15% decrease or increase (upper and lower solid lines, respectively) in $\rho_{\text{STR}}k$ (holding $\gamma=\bar{\gamma}$ constant). Open circles in A represent sex- and age-class specific means of γ for cub-of-the-year (C), yearling (Y), adult female (AF), subadult male (SM) and adult male (AM) polar bears. ρ_{STR} , density of structure; k , shape parameter relating structural volume to straight-line body length; γ , proportion of total storage energy that is stored in body fat.

Eqn 14), so we limited sensitivity analyses to perturbations of $\rho_{\text{STR}}k$ not exceeding 15%.

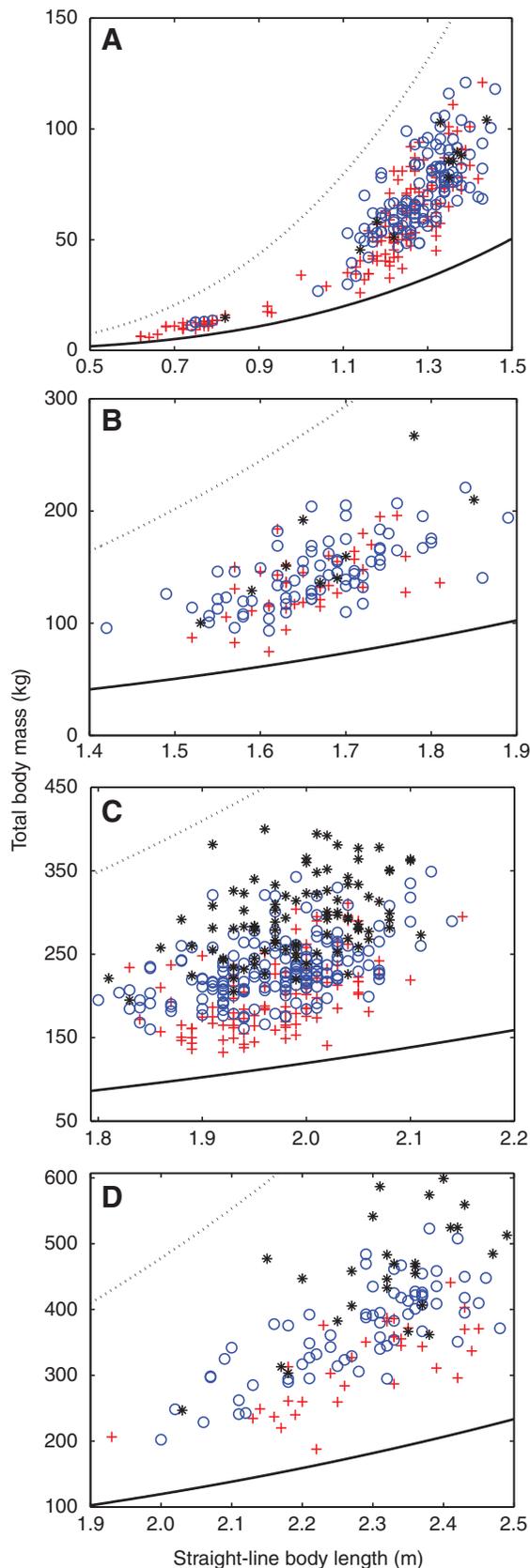
Model validation

Full model validation is not possible because insufficient independent body composition data exist to test model predictions. However, some tests of model consistency for derived variables are possible using straight-line body lengths and total body masses only. For this purpose, we obtained straight-line body lengths and total body masses of 970 polar bears from western Hudson Bay (all sex- and age-classes; $N=505$) and southern Hudson Bay (cubs-of-the-year, yearlings, subadult and adult females; $N=465$). For a description of the study populations, see Stirling et al. (Stirling et al., 1999) and Obbard et al. (Obbard et al., 2006). Data were collected in 1989–1996 in western Hudson Bay and in 1984–1986 and 2000–2005 in southern Hudson Bay. Total body masses were determined by spring scale for cubs-of-the-year in spring ($\pm 0.25 \text{ kg}$) and with a spring-loaded scale or an electronic load cell otherwise ($\pm 0.5 \text{ kg}$). Females ≥ 4 and males ≥ 7 years old were considered adults because polar bears in western Hudson Bay complete structural growth at about 4 (females) and 6.5 (males) years of age, respectively (Derocher and Stirling, 1998). Females 2–3 years old and males 2–6 years old were considered subadults. All capture and handling procedures were approved annually by the Animal Care Committees of the Canadian Wildlife Service and Ontario Ministry of Natural Resources.

We performed the following tests for model consistency. First, no bear should be lighter than its predicted structural mass. Second, estimated body compositions were compared against published body composition data. Third, estimates for storage mass and energy density were examined relative to qualitative expectations from polar bear physiology and life history. Fourth, metabolic rates were estimated for fasting adult males and compared with expected metabolic rates.

Structural mass and body composition

One implication of differentiating between structure and storage is that no bear should be lighter than its structural mass. Our model



fulfilled this requirement for all bears regardless of sex, age or population (Fig. 4): total body mass of subadult and adult females ranged from 114% to 366% of their structural mass, with a similar range for cubs-of-the-year (117–339%), yearlings (120–317%) and subadult and adult males (115–321%). These ranges correspond to bears with body fat constituting 7.7–45.6% of their total body mass (adult females), 6.9–33.4% (cubs-of-the-year), 10.3–42.4% (yearlings) and 5.7–30.2% (adult males), respectively (as estimated from Eqn 1 and Eqn 13A). The variability in observed body masses and estimated body fat corresponds to documented variability in these state variables (Atkinson and Ramsay, 1995; Pond et al., 1992; Watts and Hansen, 1987), largely due to seasonal changes in food availability. Upper estimates of relative body fat content corresponded closely to previously observed maximal values for both adult females [49% (Atkinson and Ramsay, 1995)] and adult males [32% (Atkinson et al., 1996a)], and accordingly all bears were lighter than 4 times their structural mass, which we considered an approximate upper bound to total body mass.

Storage mass and energy density

Mean storage mass was smallest in cubs-of-the-year and increased proportionally with structural mass (Fig. 5A,B), in accordance with patterns to be expected from size-dependent energy acquisition and utilization (Kooijman, 2000). Males cease growth later than females, and their asymptotic length exceeds that of females (Derocher and Stirling, 1998). Mean structural mass is therefore largest in adult males, and so was mean storage mass (Fig. 5A).

Energy density is defined as the energetic content of storage relative to the mass of tissue that requires energy for somatic maintenance. Using our previous assumption of negligible maintenance requirements for body fat, we estimated energy density as the ratio between storage energy and lean body mass, $E/(M - M_{\text{STO-F}})$. Despite lower mean storage mass, mean energy density of adult females exceeded that of adult males (Fig. 5A,C) due to a proportionally higher fat content of storage (Table 3). Differences in body composition as specified here are supported by previous findings that female adipose tissue generally contains a higher percentage of lipids than male adipose tissue (Thiemann et al., 2006; Stirling et al., 2008).

Variability in storage mass and energy density was large for all sex- and age-classes, reflecting large seasonal fluctuations in food supply and consequently body condition (Stirling and Øritsland, 1995; Watts and Hansen, 1987), as well as within-class differences in age and reproductive status. Storage mass, for instance, was most variable in adult males (Fig. 5A), probably because males continue to accumulate body mass until ~13 years old (Derocher and Wiig, 2002), while structural growth is completed by ~6.5 years of age. By contrast, variability in energy density was largest in adult females (Fig. 5C), where the accumulation of body fat before pregnancy, an extended reproductive fast and subsequent lactation demands result in large fluctuations in body condition during a three-year

Fig. 4. Straight-line body lengths and total body masses of polar bears in western and southern Hudson Bay. (A) Cubs-of-the-year, (B) yearlings, (C) subadult and adult females, (D) subadult and adult males. Red crosses are bears classified as '1' or '2' on a subjective fatness scale (Stirling et al., 2008), open blue circles are bears classified as '3', black asterisks are bears classified as '4' or '5'. Solid lines show predicted structural mass as a function of straight-line body length, dotted lines show an approximate upper bound to total body mass, taken as 4 times the structural mass.

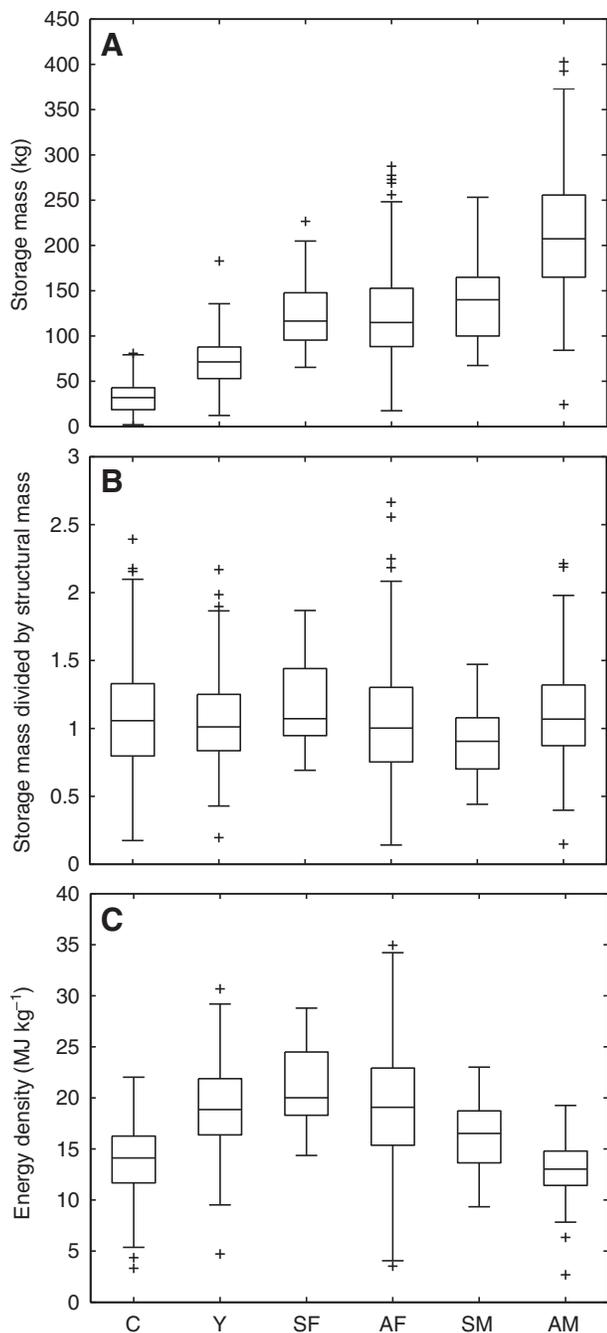


Fig. 5. Estimated (A) storage mass, (B) storage mass relative to structural mass and (C) energy density of cub-of-the-year (C), yearling (Y), subadult female (SF), adult female (AF), subadult male (SM) and adult male (AM) polar bears from western and southern Hudson Bay. Each box plot shows the median, the upper and lower quartiles, and whiskers which extend to include data no more than 1.5 times the interquartile range away from the quartiles. Data beyond the whiskers are marked by crosses.

reproductive cycle (Arnould and Ramsay, 1994; Atkinson and Ramsay, 1995; Ramsay and Stirling, 1988).

Metabolic rates

Adult males ($N=13$, ages ≥ 8 years) were measured and weighed twice during the fasting season in western Hudson Bay. Measurements for each bear were between 14 and 91 days apart

and were obtained between late-July and early-November. Fasting adult males in western Hudson Bay move little (Derocher and Stirling, 1990), are in a thermoneutral state due to mild temperatures (Best, 1982) and have completed structural growth (Derocher and Stirling, 1998). We therefore assume that energy is solely expended for somatic maintenance, and use Eqn 22 to estimate metabolic rates (m) from straight-line body lengths and changes in total body mass. Metabolic rate estimates ranged from 0.050 to 0.175 MJ per kg lean body mass per day (mean: 0.089 ± 0.011 MJ kg $^{-1}$ d $^{-1}$).

Metabolic rates of these bears should by definition correspond closely to their basal metabolic rates (Bligh and Johnson, 1973). However, a direct comparison between our metabolic rate estimates and those predicted by Kleiber (Kleiber, 1975) is difficult. We estimate the rate of energy expenditure relative to a unit mass lean tissue, whereas Kleiber's law predicts the rate of energy expenditure relative to a unit body mass, regardless of body composition. To compare our results with Kleiber's predictions, we rescaled metabolic rate estimates for each bear by multiplying m with the proportion of total body mass that is lean tissue, $(M - M_{\text{STO-F}})/M$, to obtain the rate of energy expenditure relative to a unit body mass, m^* .

Estimates for m^* ranged from 58% to 212% of the values predicted by Kleiber's equation (mean: $107 \pm 9.0\%$), with m^* lower than predicted in 8 out of 13 males (range: 58–98%, mean: $76 \pm 3.1\%$). These results compare favourably with previous measurements of polar bear resting metabolic rates, which were reported as $73 \pm 8.5\%$ relative to Kleiber's predictions for three adult females under simulated denning conditions (Watts et al., 1987), as 107% for two subadult males under similar conditions (Watts et al., 1991), and as $107 \pm 5.0\%$ for pregnant and lactating females in maternity dens (Atkinson and Ramsay, 1995). The higher metabolic rates found in the latter two studies indicate increased energy expenditure towards growth and reproduction, respectively, and thus basal metabolic rates consistent with those found here for the majority of adult males, and those documented by Watts et al. for adult females (Watts et al., 1987). Metabolic rates ranging from 141% to 212% of Kleiber's predictions (4 out of 13 males in the present study) suggest increased energy expenditure due to movement, but these values still fall within predicted values for field metabolic rates (Nagy et al., 1999).

DISCUSSION

Using concepts of dynamic energy budget theory, we developed a mechanistic model to evaluate body condition in mammals from simple measurements commonly recorded in the field. Specifically, we have shown how to estimate structural mass, storage mass and storage energy in polar bears from their total body mass and straight-line body length. The model was presented and parameterized specifically for polar bears but the concepts of structure and storage are universal, and the model could be adapted to any species for which the assumptions of strong homeostasis, isomorphic growth, and storage consisting of fat, protein, ash and water are valid. Hereby, an appropriate species-specific measure of length must be determined that can serve as a predictor variable for structural mass. Furthermore, re-parameterization of the model would be necessary, and care must be taken with regard to two assumptions made for polar bears. First, we assumed that starved animals have no storage energy left. In general, it is not true that starvation occurs when all storage energy has been depleted. Rather, starvation can occur in many species when ample energy stores remain, but the energy flow from storage is insufficient to cover the costs of somatic maintenance (e.g. Zonneveld and Kooijman, 1989). Second, we assumed that in

polar bears all body fat belongs to storage. In some species (e.g. seals, whales) a significant portion of lipids is structural, so that in these cases some method must be developed to estimate the proportion of body fat that is structural (e.g. Klanjscek et al., 2007). If the assumptions of strong homeostasis or isomorphic growth are violated, more complex body composition models could be considered, also within the framework of dynamic energy budget theory (Kooijman, 2000).

The body composition model proposed in the present study provides considerably more information on the energetic status of individuals than currently available methods. Polar bears, for example, are routinely classified on a subjective fatness scale from 1 to 5 as a measure of their body condition (Stirling et al., 2008). This method is simple but suffers from low resolution and potential misclassifications and inconsistencies from intra- and inter-observer variability. For instance, assuming equal body composition, two bears of equal mass and length should always receive the same fatness rating, a condition that was frequently violated in our study populations for all sex- and age-classes, and particularly for cubs-of-the-year and yearlings (Fig. 4). Alternatively, an objective and continuous body condition index based on standardized residuals from regressing body mass against straight-line body length is available for polar bears (Cattet et al., 2002). However, unlike our method, neither the subjective fatness index nor the body condition index proposed by Cattet and colleagues can provide estimates of structural mass, storage mass or storage energy.

Experimental methods, like isotopic water dilution and bioelectrical impedance analysis, can estimate the energetic content of body fat but will underestimate storage energy because body fat constitutes only part of storage. The energetic content of non-structural lean tissue cannot be estimated by these two techniques without supplemental use of a body composition model, because they cannot differentiate between structural and non-structural lean tissue. Furthermore, our method provides several practical advantages over isotopic water dilution and bioelectrical impedance analysis. Unlike impedance analysis it does not require extensive training to collect the necessary data and is not affected by error sources like depth of anaesthesia, limb and electrode positioning, or previous injuries of the bear (Farley and Robbins, 1994). Unlike water dilution our method is quick, inexpensive, non-invasive and does not require laboratory analyses. However, the parameterization of our model relied heavily on body composition data obtained by isotopic water dilution, and new data would help to validate and refine the model. We therefore recommend our method as a supplement to these techniques.

In fact, the accuracy of the presented polar bear model is currently limited by the low sample size of bears that was available for model parameterization. Although the model performed well for a variety of life history and physiological traits, model analysis revealed high sensitivity of storage energy predictions to the storage composition parameter γ . This sensitivity is not a model artefact but reflects the differing energy densities of body fat and lean tissue, emphasizing the necessity to estimate γ as accurately as possible. Many factors could affect storage composition, including season, age, or reproductive status of females, but we had insufficient data to determine covariates for γ other than the proposed sex- and age-classes. Model refinements should therefore be attempted as more data become available.

The sample size of two starved bears to estimate the structural mass coefficient ρ_{STRk} does not present a major concern for storage energy predictions. The coefficient ρ_{STRk} usually varies little within species (Kooijman, 2000) (cf. also the individual estimates

for the two starving bears used to parameterize ρ_{STRk}), and sensitivity of storage energy to ρ_{STRk} is generally low (Fig. 3). Furthermore, model predictions of structural mass using the current estimate of ρ_{STRk} proved robust for 970 polar bears of all sex- and age-classes from two populations (Fig. 4). The sensitivity of storage energy to ρ_{STRk} for very lean bears does not affect the usefulness of our model because few bears reach such poor body condition (e.g. 94.7% of sampled polar bears were heavier than 1.5 times estimated structural mass).

In some ways, model parameterization, validation and refinement may be easier in small mammals. However, in general, our approach is applicable across taxa and could provide the unifying approach Stevenson and Woods called for in their recent review on body condition indices (Stevenson and Woods, 2006). For instance, they note the diversity of measures used across species, difficulties to interpret units in many currently used indices and the lack of an underlying framework to model changes in body condition. Our method provides a mechanistic approach towards body condition, yields easily interpretable state variables, allows considering mammals within a dynamic energy budget modelling framework (Kooijman, 2000; Nisbet et al., 2000) and thus a mechanistic understanding of changes in body condition. In polar bears, for example, the body composition model together with a dynamic energy budget model could allow a mechanistic understanding of documented declines in body condition, reproduction and survival, thought to result from climate change associated reductions in sea ice and feeding opportunities (Obbard et al., 2006; Regehr et al., 2007; Stirling et al., 1999). Energy density may hereby provide a natural measure of body condition, because it relates available storage energy to the mass of tissue that requires energy for somatic maintenance (Ross and Nisbet, 1990).

The outlined modelling approach improves our understanding of individual bioenergetics, and could be used to link energy flow in the environment to individual body condition, survival, growth and reproduction, not just in polar bears but in many species that rely on stored energy for aspects of their life history. As the method utilizes commonly measured length and mass data, it could also be used to distinguish trends in long-term historic datasets, such as those caused by climate change and other anthropogenic influences.

APPENDIX

Derivation of Equations 13A–D (storage composition)

1. Equations 13A and 13B

To estimate the respective proportions of storage mass that are fat and protein, we rewrite the masses of storage fat (M_{STO-F}) and storage protein (M_{STO-P}) using the energetic content of each compartment (E_F and E_P) and the energy densities of fat and protein (ϵ_F and ϵ_P):

$$M_{STO-F} = \frac{E_F}{\epsilon_F}, \quad (A1A)$$

$$M_{STO-P} = \frac{E_P}{\epsilon_P}. \quad (A1B)$$

Using Eqn 8A,B, we rewrite Eqn A1 as:

$$M_{STO-F} = \frac{\gamma E}{\epsilon_F}, \quad (A2A)$$

$$M_{STO-P} = \frac{(1-\gamma)E}{\epsilon_P}. \quad (A2B)$$

The respective proportions of storage mass that are fat and protein are therefore given by:

$$\frac{M_{\text{STO-F}}}{M_{\text{STO}}} = \frac{\gamma E}{\epsilon_F M_{\text{STO}}}, \quad (\text{A3A})$$

$$\frac{M_{\text{STO-P}}}{M_{\text{STO}}} = \frac{(1-\gamma)E}{\epsilon_P M_{\text{STO}}}. \quad (\text{A3B})$$

Substituting $\alpha^{-1}E$ for M_{STO} (Eqn 9) in Eqn A3 yields Eqn 13A and Eqn 13B.

2. Equations 13C and 13D

By combining Eqn 5A with Eqn 5B and Eqn 5C, respectively, we rewrite the masses of storage ash ($M_{\text{STO-A}}$) and storage water ($M_{\text{STO-W}}$) as:

$$M_{\text{STO-A}} = \frac{1-\eta_P}{\eta_P} M_{\text{STO-P}}, \quad (\text{A4A})$$

$$M_{\text{STO-W}} = \frac{\eta_W}{(1-\eta_W)\eta_P} M_{\text{STO-P}}. \quad (\text{A4B})$$

The respective proportions of storage mass that are ash and water are therefore given by:

$$\frac{M_{\text{STO-A}}}{M_{\text{STO}}} = \frac{1-\eta_P}{\eta_P} \frac{M_{\text{STO-P}}}{M_{\text{STO}}}, \quad (\text{A5A})$$

$$\frac{M_{\text{STO-W}}}{M_{\text{STO}}} = \frac{\eta_W}{(1-\eta_W)\eta_P} \frac{M_{\text{STO-P}}}{M_{\text{STO}}}. \quad (\text{A5B})$$

Combining Eqn A5A and Eqn A5B with Eqn 13B yields Eqn 13C and Eqn 13D.

Derivation of Equation 20 (decline in body mass over time)

Here we provide the derivation of Eqn 20, which describes total body mass (M) as a function of time (t) for fasting, resting, non-growing and non-reproducing polar bears in a thermoneutral state.

For such bears, the rate of change in storage energy (E) was given by the differential equation:

$$\frac{dE}{dt} = -m(M - M_{\text{STO-F}}). \quad (\text{A6})$$

Using Eqn 11 to convert storage energy into a function of total body mass and straight-line body length, we obtain:

$$\frac{d(\alpha M - \alpha \rho_{\text{STR}} k L^3)}{dt} = -m(M - M_{\text{STO-F}}), \quad (\text{A7})$$

which can also be written as:

$$\alpha \frac{dM}{dt} - \alpha \rho_{\text{STR}} k \frac{dL^3}{dt} = -m(M - M_{\text{STO-F}}). \quad (\text{A8})$$

In non-growing bears straight-line body length is constant, so that the derivative dL^3/dt is zero, and Eqn A8 simplifies to:

$$\frac{dM}{dt} = -\frac{m(M - M_{\text{STO-F}})}{\alpha}. \quad (\text{A9})$$

Storage fat mass ($M_{\text{STO-F}}$) can also be written as a function of total body mass and straight-line body length (from Eqn 1, Eqn 2 and Eqn 13A):

$$M_{\text{STO-F}} = \alpha \frac{\gamma}{\epsilon_F} (M - \rho_{\text{STR}} k L^3). \quad (\text{A10})$$

Inserting Eqn A10 into Eqn A9, we obtain the following differential equation describing the rate of change in total body mass:

$$\frac{dM}{dt} = -\frac{m(1-\phi)}{\alpha} M - \frac{m\phi\rho_{\text{STR}}kL^3}{\alpha}, \quad (\text{A11})$$

where, for brevity, we wrote $\phi = (\alpha\gamma)/\epsilon_F$, representing the proportion of storage mass that is fat (cf. Eqn 13A).

Solving Eqn A11 (a first-order, non-homogeneous linear differential equation) gives total body mass M as a function of time t as described by Eqn 20.

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