

## Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis

M.A. Ramsay<sup>1</sup>, \* and K.A. Hobson<sup>2</sup>

<sup>1</sup> Freshwater Institute, Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada

<sup>2</sup> Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

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**Summary.** The mean stable-carbon isotope ratios ( $\delta^{13}\text{C}$ ) for polar bear (*Ursus maritimus*) tissues (bone collagen  $-15.7\%$ , muscle  $-17.7\%$ , fat  $-24.7\%$ ) were close to those of the same tissues from ringed seals (*Phoca hispida*) ( $-16.2\%$ ,  $-18.1\%$ , and  $-26.1\%$ , respectively), which feed exclusively from the marine food chain. The  $\delta^{13}\text{C}$  values for 4 species of fruits to which polar bears have access when on land in summer ranged from  $-27.8$  to  $-26.2\%$ , typical of terrestrial plants in the Arctic. An animal's  $\delta^{13}\text{C}$  signature reflects closely the  $\delta^{13}\text{C}$  signature of its food. Accordingly, the amount of food that polar bears consume from terrestrial food webs appears negligible, even though some bears spend 1/3 or more of each year on land during the seasons of greatest primary productivity.

**Key words:** Polar bears –  $\delta^{13}\text{C}$  – Fasting – Arctic food web – *Ursus maritimus*

Bunnell and Tait (1981) have proposed that the observed inverse relationship between natality rate and latitude among polar bear (*Ursus maritimus*) populations is due to increased access to terrestrial food webs with decreasing latitude. Although polar bears are the most carnivorous of the bears, preying primarily on ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) of the arctic sea ice, they effectively have no access to seals each summer in portions of their range where they are forced onto land by the complete or partial melting of the sea ice (Lønø 1970; Schweinsburg 1979; Ramsay and Stirling 1988). Polar bears have an opportunity to adopt an herbivorous diet then, similar to that of their terrestrial congenics, since the time spent on land coin-

cides with the annual season of greatest primary productivity. Although anecdotal accounts show that some polar bears eat limited amounts of sedges (*Carex* spp.) and berries while on land (Russell 1975; Knudsen 1978; Lunn and Stirling 1985), the importance of terrestrial foods in their annual diet is not known.

A test to determine whether an animal has been feeding on a terrestrial or marine food web is to measure the stable-carbon isotopic composition of its tissues. The basis for this method is that the isotopic signature of carbon incorporated by photosynthetic pathways differs characteristically between terrestrial (C-3) and marine ecosystems and this difference is maintained through successive trophic levels in both food webs (Chisholm et al. 1982). Animal tissues such as bone collagen, muscle, and fat turn over carbon at different rates because of differences in their metabolic activity. Isotopic signatures in these tissues may thus vary in such a way as to allow long-term or recent-past dietary information (Tieszen et al. 1983). Stable-carbon isotope signatures are expressed as parts per mil (‰) relative to the Pee Dee Belemnite standard (PDB) as follows (Craig 1957):

$$\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

Where R is the ratio  $^{13}\text{C}/^{12}\text{C}$ .

The seal species that polar bears prey on feed entirely within a marine food web. If polar bears feed exclusively on seals, therefore, their tissues will have a marine  $\delta^{13}\text{C}$  signature. In terrestrial food webs, plants using a C-3 photosynthetic pathway typically have  $\delta^{13}\text{C}$  values in the range of  $-27$  to  $-22\%$  while plants with C-4 photosynthetic pathways are in the range of  $-14$  to  $-9\%$  (Smith et al. 1976). The Arctic is predominantly a C-3 biome (Tieszen and Boutton 1989). If bears obtain a significant amount of their yearly food intake when they are on land in a terrestrial C-3 biome, then the  $\delta^{13}\text{C}$  values of their body tissues should reflect the proportion of their diet that is from C-3 terrestrial plants, fitting on

\* Present address and address for offprint requests: Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, Canada

**Table 1.** Values of  $\delta^{13}\text{C}$  (‰) for selected tissues of ringed seals and polar bears expressed relative to the Pee Dee Belemnite standard

	Bone Collagen	Muscle	Fat
Ringed seal			
Mean $\pm$ S.D.	-16.2 $\pm$ 0.3	-18.1 $\pm$ 0.2	-26.1 $\pm$ 0.2
<i>n</i>	10	27	17
Range	-17.2 to -14.5	-20.6 to -16.6	-27.5 to -24.5
Polar bear			
Mean $\pm$ S.D.	-15.7 $\pm$ 0.1	-17.7 $\pm$ 0.2	-24.7 $\pm$ 0.1
<i>n</i>	12	12	12
Range	-16.1 to -15.3	-18.3 to -16.6	-25.0 to -24.0

a linear scale between the extremes for marine top trophic-level consumers and terrestrial C-3 herbivores (Chisholm et al. 1982).

We determined  $\delta^{13}\text{C}$  values for three tissue types from both polar bears and ringed seals collected in western Hudson Bay, Canada. To test our assumption that bears on land had access to C-3 plants, we measured also the isotopic signature of fruits from representative plant species found in the study area. The polar bears were sampled at the end of their annual period on land in a region which is near the southern limit of their range. We chose this sampling site because all polar bears there are forced on shore each summer by the complete melting of the sea ice and, thus, experience the longest tenure on land each year of any polar bear population. They also have the highest recorded natality rate, and shortest inter-birth interval for any polar bear population (Ramsay and Stirling 1988). We reasoned that if feeding on terrestrial foods is responsible for the observed inverse correlation of natality rate with latitude in polar bears, as proposed by Bunnell and Tait (1981), then tissues from the bears we sampled should have  $\delta^{13}\text{C}$  values that are clearly skewed away from marine values and toward those of a terrestrial environment.

## Material and methods

Polar bear tissue samples were obtained from 4 female and 8 male animals killed legally during November, 1986 by native hunters from Eskimo Point, Northwest Territories (61°10' N, 94°15' W). Bone (femur), muscle (biceps brachii), and adipose (subcutaneous) tissues were collected. Ringed seal tissues were obtained from 27 animals killed legally during April and June, 1986 by native hunters in Eskimo Point, Rankin Inlet (62°52' N, 92°00' W), and Coral Harbour (64°10' N, 83°15' W), Northwest Territories. The tissues collected were bone (humerus), muscle (biceps brachii), and adipose (subcutaneous). Not every tissue type was available from every seal collected.

In August 1990, fruits of strawberry (*Fragaria virginiana*), cloudberry (*Rubus chamaemorus*), bog bilberry (*Vaccinium uliginosum*), and low bush cranberry (*Viburnum edule*) were collected for carbon isotope analysis from a region in NE Manitoba (58°40', 93°09' W) frequented in summer by polar bears from the sampled population (Ramsay and Stirling 1988).

Bones were scraped of attached muscle and marrow, then ground to 20 mesh in a Wiley mill. Collagen was extracted as a gelatin using the method of Chisholm et al. (1983). Lipids were removed from freeze-dried collagen using a soxhlet apparatus with chloroform solvent. Muscle tissues were freeze dried and lipids removed. For adipose tissue, the lipid component was used for

stable isotope analysis. For each species of plant examined, at least 10 fruits collected from 2 or more plants were freeze dried, ground to a fine powder, and pooled. Approximately 10 mg of the dried collagen, muscle, lipid or fruit from each sample was loaded into Vycor tubes with CuO wire, the tubes sealed under vacuum, and the contents combusted at 850° C for 6 hours. The resultant CO<sub>2</sub> was analysed for its carbon isotopic composition using a Micromass 602E mass spectrometer. Measurement precision, based on replicates of a graphite standard, was estimated as 0.1‰ (SD).

## Results

A summary of  $\delta^{13}\text{C}$  values for the animal tissues sampled is given in Table 1. The mean  $\delta^{13}\text{C}$  value of polar bear tissues tended to be higher than the respective tissue from ringed seals although these differences were not significant for bone collagen ( $t_{20} = 1.8$ ,  $P > 0.1$ ) or muscle ( $t_{37} = 1.5$ ,  $P > 0.1$ ). For adipose tissue, however, the mean  $\delta^{13}\text{C}$  value for polar bears was significantly higher than that for ringed seals ( $t_{27} = 6.5$ ,  $P < 0.001$ ). Ringed seals showed no significant differences among collection sites in mean  $\delta^{13}\text{C}$  values for any tissue (for all ANOVA, maximum  $F < 1.4$ ,  $P > 0.3$ ). The  $\delta^{13}\text{C}$  value for the pooled fruits of strawberry was -26.2‰, of cloudberry -26.3‰, of bog bilberry -27.78‰ and of low bush cranberry -27.3‰. The mean  $\delta^{13}\text{C}$  value for all 4 species of fruits combined was  $-26.9 \pm 0.2$ ‰ SD.

## Discussion

Polar bears forced on land in summer by the disappearance of sea ice are virtually without access to their normal prey. The period on land can exceed 4 months for all members of the sampled population and 8 months for pregnant females. While on land in summer and autumn, adult polar bears in the study population lose approximately 1.0 to 1.5 kg · day<sup>-1</sup> of body mass (Ramsay and Stirling 1988). Therefore, polar bears forced on land in summer might be expected to forage while there.

The extent to which stable isotopic fractionation occurs between trophic levels depends upon the tissue type analysed (Tieszen and Boutton 1989). We found that adipose tissue in polar bears and ringed seals was depleted in <sup>13</sup>C greater than that of the other tissues analysed. A similar pattern and magnitude of <sup>13</sup>C fractionation in adipose tissue relative to other tissues was found by Vogel (1978) and Tieszen et al. (1983) in

herbivores. This is as expected since lipid synthesis discriminates against  $^{13}\text{C}$  (DeNiro and Epstein 1977).

Herbivores living in the Arctic show collagen and muscle  $\delta^{13}\text{C}$  values close to  $-21.0$  and  $-26.0\%$ , respectively (unpub. data, Nelson et al. 1986; Schell and Ziemann 1989). Fruits in the study area that polar bears could feed on show a clear C-3 carbon isotope signature, typical of the arctic biome (Tieszen and Boutton 1989). Polar bears, however, do not show a negative shift in their tissues toward C-3 herbivore endpoints but, instead, have  $\delta^{13}\text{C}$  values consistently more enriched than those of their marine prey. Our isotopic results suggest, therefore, that polar bears feed little or not at all on terrestrial food webs.

Terrestrial species of bears have secondarily adopted a largely herbivorous diet. Their gut is not modified for the digestion of cellulose and, consequently, they are limited to feeding on plant parts that have relatively high concentrations of proteins, lipids, or non-cellulose carbohydrates (Dierenfeld et al. 1982). Polar bears, while retaining the unspecialized gut of bears, have tertiarily reverted to carnivory and have molariform teeth less well adapted to mechanically processing plant foods than other bear species (Hylander 1978). In consequence, polar bears probably achieve little net energy gain by foraging during their forced tenure on land (Lunn and Stirling 1985). The inverse relationship between natality rate and latitude that Bunnell and Tait (1981) noted for polar bears would seem, therefore, not to be due to increased access to terrestrial foods in the more southerly limits of their range.

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## Apologia

The Editors of *Oecologia* apologize to Dr. Dolph Schluter for the publication of his comments on a paper by Roberts and Stone (1990 *Oecologia* 83:567). These comments were extracted from a confidential letter review. They were never intended for publication and were published without Dr. Schluter's knowledge, approval,

or review. The Editors of *Oecologia* regret this breach of trust. This unfortunate incident occurred during a period of transition from one set of Editors-in-Chief to another. While the confusion that may have existed during the period is no excuse, it does suggest that it was unique and we pledge that it will not recur.