Nutrition and growth of suckling black bears (*Ursus americanus*) during their mothers' winter fast

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In black bears the last 6–8 weeks of gestation and the first 10–12 weeks of lactation occur in winter while the mother is in a dormant state, and reportedly does not eat, drink, urinate or defaecate. Measurements were made of the body composition and organ weights of cubs, of the composition of milk, and of milk intake (by dilution of ^2H_2O), in the first 3 months after birth. Additional milk samples were collected until 10 months postpartum. Bear cubs were small at birth, only 3·7 g/kg maternal weight, and chemically immature, as indicated by the high concentration of water (840 g/kg) in their bodies. Organ weights at birth were similar to those of puppies. In the first month after birth cubs gained 22 g/d or 0·23 g/g milk consumed; the milk was high in fat (220 g/kg) and low in water (670 g/kg). About 30 % of the ingested energy and 51 % of the ingested N were retained in the body. Over the entire 12-week period bear cubs required about 11 kg milk, containing (kg) water 7, fat 2·5, protein 0·8 and total sugar 0·25, to achieve a 2·5 kg weight gain. The birth of immature young and the production of high-fat, low-carbohydrate milk seem to be maternal adaptations to limit the utilization of glucogenic substrates during a long fast. Isotope recycling indicates that mothers may also recover most of the water (and perhaps much of the N) exported in milk by ingesting the excreta of the cubs. Lactation represents another aspect of the profound metabolic economy of the fasting bear in its winter den.

Neonatal nutrition: Milk intake: Body composition: Black bears

The small size of the newborn bear in relation to the size of the mother (about 0·3–0·4 %) has long been regarded as remarkable. Even more remarkable is the fact that fetal development, delivery and milk secretion take place during the mother's winter dormancy, while she normally does not eat or drink, urinate or defaecate (Nelson, 1980). While the metabolism of adult male black bears (*Ursus americanus*) has been studied by Nelson and his colleagues (e.g. Nelson, 1978, 1980), little attention has been paid to the additional physiological adaptations that the pregnant and lactating female must make (Ramsay & Dunbrack, 1986), and still less to the nutrition and development of the suckling cubs. The opportunity to make such an investigation provided the impetus for the study reported in the present paper.

The dormant black bear has evolved a variety of means of conserving protein and water and, hence, lean tissue during the long period of fasting and thirsting. Lipids laid down in the adipose tissue during the summer and autumn provide the main substrates for oxidative metabolism, and are a source of fatty acids for the synthesis of milk triacylglycerols (Iverson & Oftedal, 1992). Although some urine is formed, there is evidence that both water and urea are reabsorbed through the bladder wall (Nelson *et al.* 1975). By injecting [¹⁴C]urea into male black bears Nelson *et al.* (1975) demonstrated that urea is produced at

a rate only one-tenth that in summer. The N in the urea seems to be re-utilized, the tracer appearing in a number of amino acids and in plasma proteins (Lundberg *et al.* 1976; Wolfe *et al.* 1982).

Black bears mate primarily in June and July (Alt, 1989), but implantation does not occur until late November or early December (Wimsatt 1963; Kordek & Lindzey 1980), at about the time that bears 'den up' for the winter. They remain in their dens throughout the 4–5 month period of winter dormancy. Fetal development proceeds rapidly in the 6–8 weeks after implantation and the young are born in January (Alt 1983, 1989), in the coldest part of the winter when the outside temperature is usually well below freezing. Although dormant, the mother maintains sufficient awareness to feed and care for her cubs. Her temperature falls only a few degrees (Maxwell *et al.* 1988; Hellgren *et al.* 1990) and the warmth from her large body provides a source of heat for the cubs. They are suckled in the den for 10–12 weeks, until late March or early April (Alt, 1982), when mother and cubs emerge and have their first opportunity to find water and food.

The object of the present study was to obtain quantitative information on the growth of black bear cubs, on the composition and amount of milk consumed by cubs during the mother's dormant period, and on the incorporation of nutrients into their bodies during early development.

MATERIALS AND METHODS
Location and capture of animals

Black bears in the Poconos Mountains of eastern Pennsylvania, USA were studied in 1984. The present study was initiated as part of a long-term research project on black bear biology by the Pennsylvania Game Commission (e.g. Alt, 1989). Pregnant and lactating bears in the present study were 4–9 years of age. Collar-mounted radio-transmitters had previously been attached to the bears so their locations could be determined by aerial survey (Alt *et al.* 1976). The sites of occupied dens were verified by ground searches.

Seven pregnant bears were located in natural dens in late December and early January, immobilized with ketamine hydrochloride and xylazine, and transferred to an unheated barn near Moscow, Pennsylvania where they were housed in artificial dens constructed from wood or metal culvert pipe. Each den was provided with substantial amounts of straw to serve as bedding. All bears adjusted to the artificial dens without complication. As the bears were in a state of winter dormancy, water and food were not provided. These dens were monitored daily for the vocalizations of cubs, and the first day on which such vocalizations were heard was considered the date of birth (day 0). Initial maternal care appeared to be normal for six of the seven bears; one female apparently ignored her young at birth, and they perished of exposure to cold.

The delivery dates of eighteen additional radio-collared pregnant bears were determined in the field from cub vocalizations, as described by Alt (1983). Milk was collected from these bears, and those in a subset were used in studies of milk intake in the third month postpartum.

Milk collection

Lactating bears in the field and in the artificial dens were immobilized with about 440 mg ketamine hydrochloride and 220 mg xylazine hydrochloride per 100 kg body weight. Newborn and young cubs were immediately removed to a warm area and the female was weighed with a hanging spring scale. Oxytocin (30–40 IU) was administered intra-muscularly, the nipples were cleaned of adhering material and milk was expressed manually. An effort was made to empty the glands as completely as possible, although not all nipples were milked. The milk samples were stored frozen at $-20°$ in air-tight tubes. The

female was returned to her den and the cubs replaced. In the field the entrance to the den was blocked with rocks, logs and other heavy debris in an attempt to prevent females with young cubs from deserting the den during the recovery phase.

After females had emerged from their dens in April they were immobilized for milk collection with drugs injected by darts fired from a CO_2 rifle. The same drugs, dosages and procedures were used as indicated previously. In November, additional milk samples were obtained from bears that had been legally shot by hunters. These samples were collected by manual expression within 12 h of death.

Total body water and water turnover

Isotopically-labelled water (D_2O) was used to determine body water and water turnover in cubs during three periods: 1, 0–4 weeks; 2, 4–6 weeks; 3, 8–12 weeks.

Period 1. Captive bears with litters of two to four cubs were chemically immobilized at 0–2 d postpartum. The cubs were weighed to the nearest 0·1 g. One to three cubs in each of five litters were administered preweighed doses of D_2O by intragastric intubation. A large dose (mean dose 23 g/kg) was given in anticipation that cubs would next be handled several weeks or 1 month later. The syringe and tube were flushed with small quantities of water and air to ensure complete isotope delivery. The cubs did not appear to experience gastric discomfort and did not vomit. One cub in each litter was not given isotope and served as a control to account for isotope recycling. The cubs were kept warm during the equilibration period. Blood samples of 1–2 ml were obtained from each cub by jugular puncture at 1 and 1·5 h after isotope administration. After being returned to their mothers, one cub each in three litters died, apparently due to maternal neglect and exposure to cold. The mothers were immobilized one to two times between 14 and 31 d postpartum to permit the weighing and bleeding of the cubs.

Period 2. The same procedures were followed as in the first period. After an initial bleed, cubs in three of the litters in captivity were administered D_2O (mean dose 19 g/kg), bled after 1·5 and 2 h, and returned to their mothers. One of the female bears escaped from her artificial den 3 d later (February 14) and her cubs died. Thus, isotope turnover could be measured in only three cubs in two litters. The females were immobilized at 36–48 d postpartum and their cubs weighed and bled. At the termination of the study period the females and cubs were transported to the wild for release.

Period 3. Three radio-collared wild bears with litters 53–65 d of age were chemically immobilized in their dens on March 18–21. The cubs were weighed to the nearest 1 g. All but one cub in each litter were administered D_2O by gastric intubation (mean dose 13 g/kg), bled after 1·5 and 2 h, and returned to their mothers. These mothers emerged from their dens with their cubs in late March and early April. The adult females were relocated by radiotelemetry and ground searches on April 17–18, and the cubs caught on the ground or retrieved from trees they had climbed. The cubs were weighed and bled, but due to logistical constraints it was not possible to re-administer isotopes. The cubs were then released and rejoined their mothers who were not captured but remained in the vicinity.

Dissections and chemical analysis of the bodies of cubs

Newborn and young cubs that died in captivity and a litter of three cubs abandoned shortly after birth in the wild were used for compositional studies. Since ambient temperatures were below freezing and cubs succumbed quickly, it was assumed that cubs had not mobilized more than small amounts of nutrients from body stores. Cubs that died did not appear to be smaller or otherwise distinct from cubs that survived. We chose not to disturb dens containing live cubs for some days after the death of sibling cubs; the bodies, when

retrieved, were intact, often frozen, and mostly in good condition, although some autolysis occurred in some cases (see below). Since cubs had been handled shortly before they died their weights on the dates of death were known and could be used to calculate postmortem weight losses which were assumed to be water. The bodies were stored in sealed plastic bags at $-20°$.

The bodies were thawed before dissections and adhering dirt or bedding was removed. Crown-rump length was measured from the front of the crown of the head to the base of the tail, and chest girth was measured in the axillary region. The bodies were weighed and opened by mid-line abdominal incision. The internal organs of nine of the fifteen bodies were in excellent condition, but six showed some evidence of autolysis. The latter were refrozen without further dissection. In the remaining bodies the gastrointestinal tract was tied off at the oesophagus and rectum, weighed, and divided into stomach and intestines. No distinction was made between small and large intestines because the junction was difficult to discern. The intestines were separated from the omentum and connective tissue and laid out without stretching for measurement of length. The stomach and intestines were emptied of contents and weighed. The weight of gastrointestinal contents was subtracted from total body weight to calculate empty body weight. Kidneys, spleen, pancreas and thymus were removed and weighed. After extraction of blood clots the liver, heart and lungs were also weighed.

All parts of the body, as well as all collectable fluids, were returned to the original plastic bag and the total was reweighed to determine losses during dissection. In calculations of body composition it was assumed that these losses were due to evaporation of water. The bag with contents was refrozen, but part of the liver was sampled for other studies and the remainder was stored separately. The frozen material (other than the liver) for each animal was ground three times in a small meat grinder fitted with a die with 0·25 inch (6 mm) holes, spread in shallow pans and dried to constant weight in a forced-convection oven at 100°. After reweighing to determine water by difference, the material was ground through a Wiley food mill with a 1 mm mesh screen, mixed and subsampled for chemical analysis. The livers were individually blended 1:1 (w/v) with water before drying to constant weight at 100°.

All analyses were made on duplicate subsamples. Fat was determined as extractable neutral lipid when the dried material was exposed to light petroleum (b.p. 38–56°) in Soxhlet extractors for 18 h. N was determined by the macro-Kjeldahl method with $CuSO_4$ as catalyst. N recovery by this method was 99%. Protein was calculated as $N \times 6·25$. Ash was weighed after incineration of a weighed sample at 600° in a muffle furnace for 18 h. Gross energy was determined by combustion in an adiabatic bomb calorimeter.

Three full-term, stillborn Welsh corgi puppies (mean weight 272 g) from a 10·4 kg bitch were dissected, processed and analysed along with the bear cubs, using identical methods. These findings, although limited, will be used for comparative purposes in the Discussion.

Milk analysis

Sample vials were immersed in warm water to thaw the frozen milk and were then gently shaken. Samples from several nipples of an individual bear were pooled to increase sample volume. All analyses were made on duplicate subsamples. Dry matter was determined by drying at 100° in a forced-convection oven for 5 h. Fat was extracted by the Roese-Gottlieb method (Association of Official Analytical Chemists, 1990), using sequential additions of ethanol, diethyl ether and light petroleum (b.p. 38–56°). N was determined by the macro-Kjeldahl method, using $CuSO_4$ as catalyst. N was converted to protein using the accepted conversion factor for milks, 6·38. Total sugar was measured by the phenol–H_2SO_4 method (Dubois et al. 1956; Marier & Boulet, 1959), using lactose monohydrate for preparation of

standards. In a small number of samples lactose was measured by an enzymic procedure using lactase (*EC* 3.2.1.108; Lactose kit; Boeringer Mannheim). Gross energy was calculated according to an equation adapted from Perrin (1958) as previously described (Oftedal 1984*a*, *b*):

Energy (kcal/g) = (fat × 9·11 + protein × 5·86 + sugar × 3·95)/100, where fat, protein and sugar are in units of g/100 g. Values were subsequently converted to kJ.

Isotope analysis and calculation of milk intake

Water was isolated from blood samples by distillation on a hot plate until the residues were dry in order to avoid errors due to fractionation effects. Water samples were analysed for ^{2}H concentration by infra red spectrophotometry, using matched BaF_2 cells in a Perkin Elmer 599B double-beam grating infra-red spectrophotometer. The method of isotope analysis, details of calculations, and the assumptions and potential errors have been discussed in detail elsewhere (Oftedal & Iverson, 1987; Oftedal *et al.* 1987).

Pool size of body water was determined from isotope concentration at the end of the equilibration period. Isotope turnover rates of cubs were calculated from the decline over time in the logarithm of isotope concentration. As in studies on the dog (Oftedal 1984*b*), it was necessary to leave one young in each litter as an uninjected control. Concentrations of isotope in the control in each litter were subtracted from concentrations in isotope-labelled cubs of the same litter to correct for the recycling of isotope. Isotope concentration at a given time was also corrected for changes in pool size by the equation:

$$c_t^* = c_t \times P_t/P_o,$$

where c_t^* is corrected concentration at time t, c_t is measured concentration at time t, P_t is pool size at time t, and P_o is initial pool size (see Oftedal, 1984*b*; Oftedal & Iverson, 1987). In period 1 pool sizes were measured by isotope dilution at the beginning and end, and pool sizes at intermediate bleeds were interpolated. However, in periods 2 and 3 pool sizes were measured only at the beginning. Pool sizes at the end of period 2 were estimated from the average percentage of water in the body at the beginning of period 3. Unfortunately, no pool size measurements could be made at the end of period 3. The water pool size:body weight ratio remains relatively constant in puppies at mid-lactation (Oftedal 1984*b*), and it was assumed that the same is true of bear cubs in period 3. The error introduced by this assumption is probably minor because the increase in body weight over this period was only a modest 18%. We expect that the change in pool size was similarly modest compared with the larger changes in younger cubs.

Fractional turnover rate (k), daily water loss ($L = k \times (P_t + P_0)/2$), daily water gain ($G = (P_t - P_0)/t$) and total daily water intake (TWI = $G + L$) were calculated from isotope dilution data as previously described (Oftedal, 1984*b*; Oftedal *et al.* 1987). Milk intake (MI; g/d) of cubs was calculated from total water intake (g/d) according to the equation developed by Oftedal *et al.* (1987) to account for metabolic water production:

$$\mathrm{MI} = 100 \times \frac{(\mathrm{TWI} + 1{\cdot}07 F_D + 0{\cdot}42 Pr_D)}{(\% W_M + 1{\cdot}07 \% F_M + 0{\cdot}42 \% Pr_M + 0{\cdot}58 \% S_M)},$$

in which F_D and Pr_D are fat and protein deposition (g/d) and $\% W_M$, $\% F_M$, $\% Pr_M$ and $\% S_M$ are percentages of water, fat, protein and total sugar in the ingested milk respectively. For these calculations milk composition data were averaged for each time-period. Rates of fat and protein deposition were measured directly in period 1, but were estimated in periods 2 and 3 from changes in percentage water and the composition of the fat-free mass of cubs at 1 month after birth.

RESULTS

Body and organ weights

Table 1 shows that mean cub weight in eight litters ranged from 325 to 432 g at 0–2 d postpartum, equivalent to only 3·0–5·0 g/kg maternal weight. The entire litter averaged 12 g/kg maternal weight.

Mean body weight of cubs increased by 500 g or about 1300 g/kg birth weight in the first month after birth; cubs also increased in length and girth (Table 2). The proportional increase in mass of some organs (pancreas, heart, lungs, spleen, kidneys) was similar (870–1320 g/kg initial weight) to that of the total body, but this was not true of all organs (Table 2). The liver and intestines increased only by 300–370 g/kg initial weight, while the stomach and thymus increased by 2270 and 3120 g/kg initial weight respectively. The small increase in liver and intestinal weights was particularly surprising, but may be due in part to the fact that measurements of the 'newborn' cubs were made after they had suckled (see p. 71).

Changes in body composition

By carcass analysis, newborn cubs contained 837 g water/kg empty body weight (defined as live weight minus gastrointestinal contents), or 845 g water/kg fat-free empty body (Table 3). Newborn cubs also contained (g/kg empty body wt) fat 9·2, protein 120 and ash 25. After 1 month, body water had decreased to 728 g/kg empty body weight, while fat increased to 109 g/kg empty body weight. Weight gain comprised (g/kg) water 642, fat 181, protein 144, ash 19 and 12·7 kJ (3·03 kcal).

The livers were assayed separately from the rest of the body as they had been sampled for other studies. The livers contained (g/kg) water 783 (SE 6·3), fat 11 (SE 1·7) and protein 158 (SE 3·3) in newborn cubs and water 769 (SE 6·5), fat 51 (SE 15·6) and protein 144 (SE 8·6) in cubs 1 month after birth.

Separate estimates of body water were obtained by isotope dilution. The results were reasonably similar to those from direct analyses of carcasses of both newborn and 1-month-old cubs (Table 3). Isotope dilution overestimated total body water (including water in the gastrointestinal tract) by 30–40 g/kg body weight, as would be expected (see pp. 73–74).

Composition of milk

Black bear milk had a relatively low concentration of water and total sugar, but high concentrations of dry matter, fat and energy; its composition varied with stage of lactation (Figs. 1 and 2). Water decreased from 740 g/kg at 0–2 d to 530 g/kg at 9 months postpartum, while fat rose from about 90 to 300 g/kg over this period. The concentration of protein declined after birth, from 126 g/kg in colostrum to 59 g/kg in transitional milk (1–2 d postpartum). For the remainder of winter dormancy it remained fairly constant at about 70–80 g/kg, but after emergence from the den increased somewhat, reaching 115 g/kg at 9 months (Fig. 1). The concentration of total sugar increased from 9 to 30 g/kg during winter dormancy, but then declined to 13 g/kg at 5–6 months and 6 g/kg at 9 months. Although the identity of the sugars in the milk was not determined, lactose was only a minor constituent. An enzymic lactase assay indicated that black bear milk contained only 1·7 (SE 0·26) g lactose/kg (n 5; 48–63 d postpartum) even though the total sugar of these samples was 28·6 (SE 1·49) g/kg, as measured by the phenol–H_2SO_4 method.

The gross energy value of black bear milk increased from 6·57 kJ/g (1·57 kcal/g) in colostrum to 11·7 kJ/g (2·80 kcal/g) at the end of winter dormancy, and to 14·2 kJ/g (3·39 kcal/g) in late lactation (Fig. 2(a)). Despite the large variation in milk composition with stage of lactation, the relative proportions of energy provided by fat and protein

Table 1. *Weights of black bear* (Ursus americanus) *cubs at or soon after birth**

Maternal identification no.	Time since birth (d)	Maternal wt (MW; kg)	Litter size	Mean wt of cubs (CW; g)	Litter wt (LW; g)	Relative cub wt (CW/MW; g/kg)	Relative litter wt (LW/MW; g/kg)
3411	0	95·2	4	356	1424	3·7	15·0
3523	0	110·7	2	333	666	3·0	6·0
3407	1	103·4	3	364	1092	3·5	10·6
4018	1	82·1	3	378	1134	4·6	13·8
6627	1	99·8	3	326	978	3·3	9·8
929	2	87·1	3	432	1296	5·0	14·9
5463	2	103·4	4	324	1296	3·1	12·5
Mean	—	97·4	3·1	359	1127	3·7	11·8
SEM	—	3·78	0·26	14·4	95·3	0·28	1·23

* For details of procedures, see p. 60.

Table 2. *Measurements of bodies and organs of black bear* (Ursus americanus) *cubs**

(Mean values with their standard errors)

	Newborn cubs (1–2 d; *n* 5)		Cubs at 1 month (28–31 d; *n* 5)		Difference	
	Mean	SE	Mean	SE	Absolute	% initial value
Empty body wt (g)	394	14·4	894	52·2	500	127
Crown–rump length (mm)	199	3·7	268	6·0	69	35
Girth of chest (mm)	160	5·8	203	6·0	43	27
Organ wts (g)						
Liver	17·5	1·53	23·9	2·88	6·4	37
Pancreas	0·94	0·014	1·76	0·21	0·82	87
Heart	2·29	0·189	5·32	0·558	3·03	132
Lungs	10·2	0·93	20·8	3·53	10·6	104
Spleen	1·60	0·227	3·07	0·390	1·47	92
Kidneys	4·06	0·386	7·83	0·510	3·77	93
Thymus	0·41	0·079	1·69	0·221	1·28	312
Stomach	1·44	0·271	4·71	0·462	3·27	227
Intestines	13·8	0·39	17·9	0·64	4·1	30
Intestine length (mm)	1680	75	1870	60	190	11

* For details of procedures, see pp. 61–62.

remained fairly constant at about 76–83 and 14–20 % respectively, from 1–2 d to 9 months postpartum (Fig. 2(*b*)). Sugars accounted for a small percentage of milk energy (1·7–4·2 %) up until 6 months, and even less (0·6 %) at 9 months.

Water kinetics and milk intake

In the first month five cubs were bled on three separate dates. A linear regression model of the decline of the logarithm of isotope concentration with time fitted these data tightly (mean r^2 0·997), indicating that use of two-point estimates of isotope decline in other cubs did not introduce a large error.

Table 3. *Body composition of black bear* (Ursus americanus) *cubs estimated by isotope dilution and carcass analysis**

Age of cubs (d)…	0–2		28–31		53–65	
	Mean	SE	Mean	SE	Mean	SE
Isotope dilution studies						
n	11		5		8	
Total body wt (g)	351	12·0	1016	101·2	2084	130·1
Body water (g/kg)	882	5·5	760	3·8	723	11·7
Body composition studies						
n	10		5		—	
Total body wt (g)	386	14·8	909	53·9	—	
Body water (g/kg)	838	5·9	730	10·6	—	
Composition of empty body						
Empty body wt (g)	375	14·5	894	52·2	—	
Water (g/kg)	837	6·1	728	10·8	—	
Fat (g/kg)	9·2	2·77	109	6·5	—	
Protein (g/kg)	118	3·4	133	6·2	—	
Ash (g/kg)	24·7	1·07	21·4	0·40	—	
Energy (kJ/g)	3·79	0·245	9·03	0·389	—	
Composition of fat-free empty body						
Water (g/kg)	845	4·5	816	6·7	—	
Protein (g/kg)	119	3·5	150	7·8	—	
Ash (g/kg)	24·9	1·1	24·0	0·4	—	

* For details of procedures, see pp. 61–62.
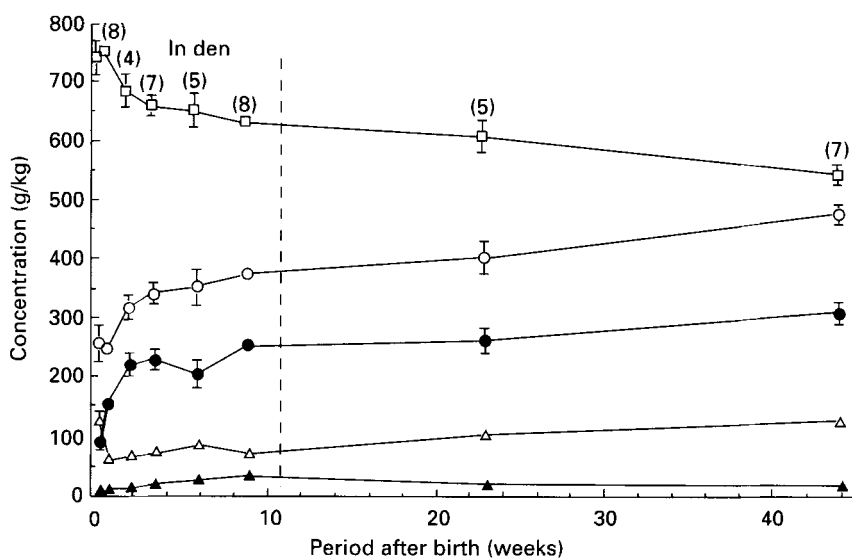
Fig. 1. The concentrations of water (□), dry matter (○), fat (●), crude protein (nitrogen × 6·25; △) and total sugar (▲) in the milk of the black bear (*Ursus americanus*) over the course of 10 months of lactation. (– – –), Approximate time-interval since birth that mother and cubs emerge from their winter den. Values are means with their standard errors represented by vertical bars; numbers of samples analysed are shown in parentheses. Two samples of colostrum were analysed. For details of procedures, see pp. 62–63.
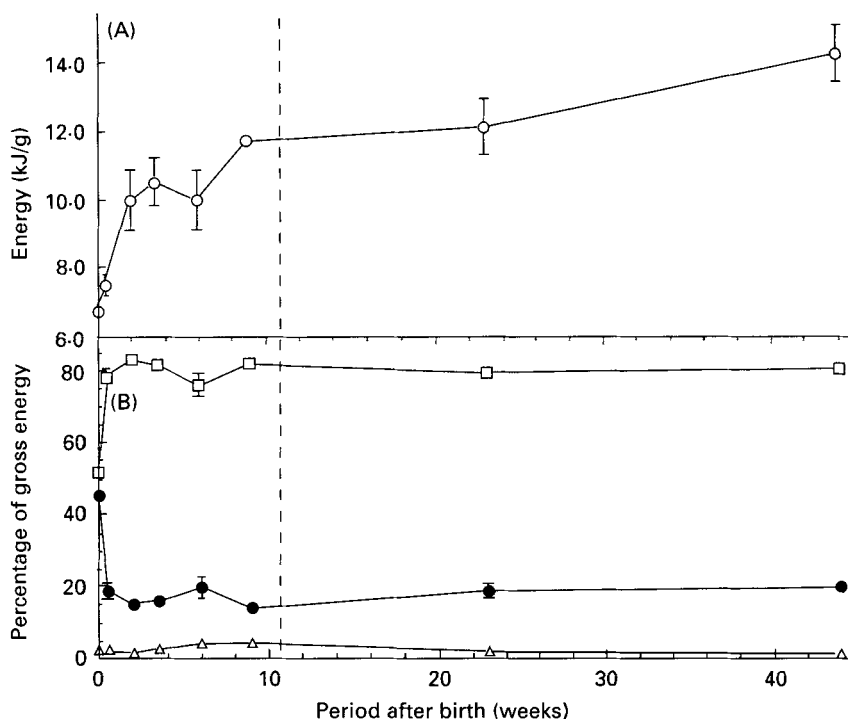
Fig. 2. The concentration of gross energy in milk of the black bear (*Ursus americanus*). (A) Energy concentration on a fresh weight basis (kJ/g) and (B) percentage contribution of fat (□), crude protein (●) and total sugar (△) to the gross energy in milk. Values are means with their standard errors represented by vertical bars. (– – –), Approximate time-interval since birth that mother and cubs emerge from their winter den.

Table 4. *Calculations of milk intakes of suckling black bears* (Ursus americanus)*

Period of study...	1		2		3	
Lactation stage (weeks)...	0–4		4–6		8–12	
No. of young...	8		3		8	
No. of litters...	5		2		3	
	Mean	SE	Mean	SE	Mean	SE
D_2O administered (g)	7·99	0·11	19·7	2·07	27·6	1·85
Initial wt (g)	347	14·3	1104	216·2	2091	130·6
Wt gain (g/d)	21·9	1·58	34·4	11·30	13·8	3·02
Body water (g/kg)	880	5·9	759	8·9	721	11·4
Turnover rate (/d)	0·131	0·0063	0·086	0·0070	0·089	0·0059
Mean pool size (g)	503	22·3	953	208·8	1660	84·8
Water loss (g/d)	66·2	4·41	82·5	21·00	144·4	4·37
Water gain (g/d)	14·5	1·13	19·7	8·19	8·9	2·21
Water intake (g/d)†	80·7	5·20	102·3	29·17	153·3	4·14
Milk intake (g/d)	91·0	5·87	120·2	34·30	166·8	4·51

* For details of procedures, see p. 63.
† Includes metabolic water production, see p. 68 of proof.

The turnover rate of body water of cubs was consistently low, especially in the second (mean k 0·086) and third (mean k 0·086) periods (Table 4). Calculated daily rates of water loss, water gain and water intake are presented in Table 4. Daily milk intake of cubs

Table 5. *Nutrient intakes of suckling black bear* (Ursus americanus) *cubs**

Month of lactation...	First	Second	Third
Milk intake (g/d)	91·0	120·2	166·8
Milk composition (g/kg)			
No. of samples assayed	10	8	6
Water†	672	644	624
Dry matter	328	356	376
Fat	223	220	251
Protein	67	77	70
Sugar	14	24	30
Energy (kJ/g)	10·3	10·6	11·7
Daily intake (g/d)			
Water†	61·2	77·4	104·1
Dry matter	29·9	42·8	62·6
Fat	20·3	26·4	41·9
Protein	6·1	9·2	11·7
Sugar	1·2	2·9	5·0
Energy (kJ/d)	937	1270	1960
Intake relative to wt (g/kg)			
Mean wt (g)	653·6	1620	2298
Water†	94	48	45
Dry matter	46	26	27
Fat	31	16	18
Protein	9·4	5·7	5·1
Sugar	1·9	1·8	2·2
Gross energy: kJ/kg	144	78·7	84·9
kJ/kg BW$^{0·75}$	1260	887	1050
kJ/kg BW$^{0·83}$	1300	854	979
Intake relative to wt gain (g/g)			
Growth rate (g/d)	21·9	34·4	13·8
Water†	2·79	2·25	7·54
Dry matter	1·36	1·24	4·54
Fat	0·93	0·77	3·04
Protein	0·28	0·27	0·85
Sugar	0·06	0·09	0·36
Energy (kJ/g)	42·7	37·2	142

BW, body weight.
* For details of procedures, see pp. 62–63.
† Preformed water in milk.

averaged 92, 120 and 167 g in the first, second and third experimental periods respectively. No relationship was found between milk intake of individual cubs and litter size, but this may be due to the small number of litters studied.

The milk yield of the mother was calculated from the milk intakes of cubs, assuming that milk intake per unit body weight of control cubs was the same as that of isotope-labelled littermates. In the first period (0–4 weeks) the five females produced a mean of 228 (SE 33·7) g milk/d. These bears initially weighed 98·2 (SE 4·76) kg, but lost 408 (SE 29·5) g body weight/d. They lost 1·9 (SE 0·18) g body weight/g milk produced. Relative to maternal body weight at the mid-point of the period, milk production was very low, 2·5 g/kg. Litter size averaged 2·6 cubs.

In the second (4–6 weeks) and third (8–12 weeks) periods, initial maternal weight (kg) averaged 92·2 (*n* 2) and 92·8 (*n* 3) but weight loss was not measured. In period 2, two females, each with two cubs, produced 120 and 287 g milk/d; the cubs in the first litter were uncommonly small (average body weight over the study period 714 g). In period 3, milk
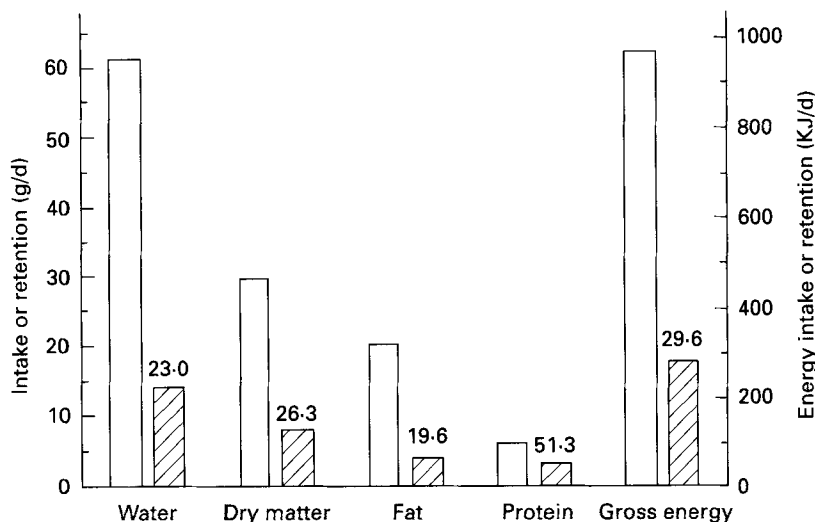
Fig. 3. The intake (□) and retention (▨) of water (water intake includes metabolic water), dry matter, fat, and crude protein (nitrogen × 6·25) by black bear (*Ursus americanus*) cubs in the first month after birth. The figures above each retention bar indicate the percentage of intake that was retained.

yield averaged 575 (SE 47·4) g/d in three bears rearing three to four cubs (mean litter size 3·7).

Intake and deposition of nutrients

The nutrient intakes of cubs in the first, second and third months postpartum were calculated on the basis of average values for milk composition and milk intake (Table 5). Data on colostrum and transitional milk (1–2 d postpartum) were not included in the averages for the first month. The amounts of preformed water and dry matter consumed (g/kg body weight per d) were estimated as 94 and 46 in the first month, 48 and 26 in the second month, and 45 and 27 in the third month respectively. Fat and protein intakes were about 0·9 and 0·3 g/g body weight gain in the first 2 months, but increased markedly thereafter when growth rate declined. The gross energy intakes (MJ (kcal)/kg body weight$^{0.83}$ per d) of cubs were equivalent to 1·30 (311), 0·85 (204) and 0·98 (234) respectively.

The retention of nutrients by cubs during the first month after birth is illustrated in Fig. 3. Cubs incorporated 20% of ingested fat, 51% of ingested protein and 30% of gross energy into new tissues. About 14 g water/d was retained in the body, which is about 18% of the combined intake of preformed water in milk (61 g/d) and metabolic water (20 g/d) produced by catabolism of ingested fat, protein and total sugar.

DISCUSSION

The small size of the newborn bear

Black bears are very small at birth, each representing only 3–5 g/kg maternal weight (Table 1) compared with 10–50 g/kg in most carnivores (Oftedal & Gittleman, 1989). The small size can be explained by the short period of 6–8 weeks from implantation of the blastocyst until birth (Wimsatt, 1963). After implantation the bear fetus grows at about the expected rate from the pattern of fetal growth in sheep and other domestic species (Joubert, 1956; McCance & Widdowson, 1978). Newborn black bear cubs are only slightly heavier than beagle puppies born after 9 weeks gestation (Anderson, 1970). Generally speaking, large species of placental mammals have longer gestation periods than small ones, and it is this

that allows the fetus to grow to a large size. There is nothing remarkable about the rate of growth of the fetal bear; what is surprising is such a short period of 'true gestation' in a large mammal.

Mammalian fetuses have an obligatory requirement for glucose as the primary metabolic fuel (Battaglia & Meschia, 1978). It seems likely that the lack of a dietary source of glucose and the reduction in gluconeogenesis that occurs in prolonged fasting (Cahill, 1976, 1982; Hochachka & Somero, 1984) hinder the ability of the pregnant fasting bear to supply glucose to the conceptus. She is able to meet her own metabolic requirements mainly from the breakdown of triacylglycerols in adipose tissue, but would be unable to produce large amounts of glucose without catabolizing too much protein in her body. It is doubtful whether a dormant bear which does not drink or urinate could cope with a large increase in nitrogenous wastes. The physiological constraints on the pregnant bear have been reviewed by Ramsay & Dunbrack (1986) who came to the conclusion, as we had done, that it is the requirement for glucose that limits the size to which the fetal bear can grow and, hence, the time it spends in the uterus before it is delivered.

The relatively short gestation period is reflected by the chemical composition of the cubs. In mammals development is accompanied by a progressive decline in the percentage of water in the lean body as the cellular mass increases (Spray & Widdowson, 1950). Because newborn bears had so little fat, water concentration was about 840 g/kg whether expressed on an empty body or on a fat-free empty-body basis (Table 3). Three stillborn puppies were analysed by identical methods, and were found to contain (g/kg) water 804 (SE 2·5), fat 9 (SE 0·5), protein 145 (SE 1·7) and ash 26 (SE 0·9). These values are similar to results obtained by Thomas (1911). On a fat-free basis newborn bears contain more water than newborn puppies (810 g/kg), kittens (820 g/kg; Spray & Widdowson, 1950) or mink kits (830 g/kg; Oftedal, 1981), suggesting that they are a little less mature chemically. The newborn bear is similar to a 2 kg human fetus, at least in water and protein concentrations (Widdowson & Spray, 1951).

Survival after birth

The extent of neonatal mortality in the winter den has not been quantified in undisturbed populations of black bears. In colonies of domestic dogs 15–30% of puppies may die between birth and weaning, with the highest mortality immediately after birth (Anderson, 1957; McCay, 1963). Even higher preweaning mortality has been reported in colonies of non-domestic carnivores, such as 60% in the striped skunk, *Mephitis mephitis* (Wade-Smith & Richmond, 1975). In the present study seven captive bears gave birth to twenty-four cubs; of these 50% died during our studies, seven within a few days of birth and five at about 1 month of age.

Some of this mortality appeared to be associated with confinement or our research procedures. One captive bear apparently ignored her newborn cubs (n 4) which then died. A wild bear with 2-d-old cubs (n 5) abandoned her den and cubs while recovering from chemical immobilization, but two other wild bears with 0–2-d-old cubs (n 8) did not. Six captive bears that were immobilized at 0–1 d continued to rear cubs, although one cub in each of three litters died shortly after being returned to their mothers. Hypothermia was the most likely cause of death of newborn bears, although suffocation cannot be ruled out given the great disparity in size between mother and cubs. The small size, sparsity of hair and low body fat of newborn cubs results in rapid chilling in the cold ambient temperatures found in bear dens (Blix & Lentfer, 1979). Our decision to minimize disturbance of mothers and cubs prevented us from locating or removing chilled or weakened cubs before death. There was no evidence that any of the cubs had been attacked or eaten by the mother or siblings, as occurs in some species of carnivores (e.g. Wade-Smith & Richmond, 1975).

The mortality at 1 month postpartum occurred during a brief bout of spring-like

weather, at which time many of the mothers became aroused and agitated, and one managed to escape. These cubs may have died from hypothermia, suffocation or trampling. In zoos, wild-caught bears are more easily agitated and less likely to rear cubs successfully than are captive-born or hand-reared bears (Crandall, 1964). Mortality of black bear cubs in the wild can also occur in association with the collapse or flooding of dens (Alt, 1982). In Pennsylvania cub mortality in free-ranging black bears was 28 % during the time period between emergence from the den and independence of the cubs from the mother (Alt, 1982).

The rapid chilling and death of cubs that become separated from their mothers highlights the importance of behavioural mechanisms to maintain contact. We observed that young cubs emitted loud scream-like vocalizations when exposed to cold air during handling, but would quiet down when placed in a warm location. In the den this behaviour presumably serves to arouse the dormant mother so that she may retrieve displaced cubs.

Growth of the body and changes in its constituents in the first month after birth

Relative growth rate can be measured in a number of ways, one of which is the time required for a newborn animal to double its birth weight (t_d; d). Since t_d is size-dependent (Oftedal, 1986), comparisons among species should be restricted to newborn animals of similar size. At an average growth rate of 21·9 g/d in the first month, bears double their birth weight in 16 d. By comparison newborn cats (100 g) and dogs (225 g) double their birth weights in about 7 and 8 d respectively (Widdowson, 1965). Bear cubs grow relatively slowly, at least by comparison with other carnivores.

During the first 30 d the bear cub nearly tripled in weight, but all constituents did not increase equally. While the amount of protein in the body increased only 2·6 times (from 44 to 119 g), fat rose from 3 to 97 g, or more than 30-fold. Fat accounted for 181 g/kg weight gain. This proportion of fat in the tissue deposited is similar to that in other species, for example rabbits, kittens and pigs, while they are increasing their birth weights by two to three times (Spray & Widdowson, 1950; Manners & McCrea, 1963). Thus, although the rate of growth of newborn bears is slow, the rate of fattening is not.

At birth the organs of bear cubs are similar in relative size to those of newborn, unfed puppies that were dissected by the same methods (Table 6), and fall within the range that has been observed in other newborn animals (Oftedal *et al.* 1989). Newborn bears resemble puppies in having relatively heavy digestive organs (liver, pancreas, intestines), lungs and spleen.

One might suspect that the large digestive organs have to do with the composition of the milk. But even though the pancreas of bear cubs and puppies is two to three times larger (relative to body weight) than that of other newborn mammals (Table 6), this is not simply an adaptation to a high-fat diet. In many suckling mammals, including puppies, digestion of the lipids in milk fat globules occurs by the action of preduodenal rather than pancreatic lipases (Hamosh, 1979; Iverson *et al.* 1991). In addition, seals consume even greater amounts of fat but have a pancreas of average relative size (Oftedal *et al.* 1989). The large weight of the intestines of the bears is probably explained by the fact that the cubs were 1–2 d of age and had probably already suckled when they died. Rapid growth of the intestines occurs in response to milk intake in the first few days after birth in dogs, pigs and some other species (Widdowson *et al.* 1976; Hall & Widdowson, 1979; Berseth *et al.* 1983; Heird *et al.* 1984). The intestines of suckling bears were generally short and simple in structure, without any sign of the vestigial caecum present in puppies. The large spleen in newborn bears may be responsible for the synthesis of erythrocytes and granulocytes, as it is after birth in puppies (McCance & Widdowson, 1955).

During the first month after birth the organs that were relatively large at birth tended to gain proportionately less weight than the body as a whole. For example, the weight of the

Table 6. *Comparison of the organ weights of black bear* (Ursus americanus) *cubs* and puppies at or soon after birth*

Species...	Black bear	Dog	Other mammals†
No. examined	5	3	
Age (d)	1–2	0	0
Empty body wt (BW; g)	394	272	6–23200
Crown-rump length (L; mm)	199	171	
Organ weights (g/kg BW)			
Liver	44	62	24–52
Pancreas	2·4	3·1	0·8–1·5
Heart	5·8	7·1	5·6–10·9
Lungs	26	30	14–33
Spleen	4·1	3·7	0·2–5·3
Kidneys	10·3	19·8	5·7–11·7
Thymus	1·0	3·4	—
Stomach	3·7	1·7	2·3–15·1
Intestines	35·0	27·7	16·6–31·5
Intestine length (as multiple of L)	10·5	6·1	—

* For details of procedures, see pp. 61–62.

† The range of values as tabulated by Oftedal *et al.* (1989) for the following species: rat, rabbit, pig, human, sheep, harp seal (*Phoca groenlandica*), hooded seal (*Cystophora cristata*).

intestines was only 30 % heavier at 1 month than at birth, even though the entire body increased by 127 % (Table 2). Only the heart, stomach and thymus had proportional weight gains that were similar to, or in excess of, that of the entire body.

The milk of the black bear

Milk composition is known to change with stage of lactation in several species of carnivore (Oftedal, 1984*a*; Gittleman & Oftedal, 1987). Large changes occurred in the concentrations of all constituents of black bear milk, both during the period of winter dormancy and after the bears emerged from the den (Fig. 1). The concentrations of fat and energy doubled from early to late lactation, while total sugar initially increased during the period of winter dormancy and then declined to very low levels.

The transition to extrauterine life involved a switch from glucose to fatty acids as the primary metabolic substrate. Lipids accounted for about 80 % of the gross energy in black bear milk at all stages after the first day (Fig. 2). Lipid digestion in suckling black bears is presumably facilitated both by bile-salt-stimulated lipase, which has been measured in milk of the black bear (Freed *et al.* 1986), and by preduodenal lipases which have been demonstrated in puppies (Iverson *et al.* 1991).

As noted previously, the sparing of glucose and, hence, tissue proteins may be critical to the economy of the fasting, dormant black bear. The glucose demand for lactation is probably quite low since the milk of black bears contains only 10–30 g carbohydrate/kg, equivalent to less than 5 % of gross energy. The mammary glands of black bears also use little if any glucose for lipogenesis; the predominant fatty acids of the milk appear to originate from stored lipids rather than *de novo* synthesis (Iverson & Oftedal, 1992).

The colostrum of the black bear contained nearly 130 g protein/kg, compared with 60–80 g/kg in milk produced during the rest of the dormant period. The high concentration of protein in the immediate postpartum period may indicate the presence of immuno-

globulins; passive transfer of immunity from colostrum is known to occur in dogs and cats (Brambell, 1970). The rather small percentage (14–20) of milk energy contributed by protein during the remainder of winter dormancy may be an evolutionary adaptation that helps preserve tissue proteins (and, hence, lean body mass) of the mother. In comparison, protein supplies 28–35 % of gross energy in the milks of dogs, foxes, mink, cats and other species of carnivore that feed on protein-rich prey during the lactation period (Oftedal, 1984 a). It has been suggested that the protein intakes of at least some suckling carnivores exceed their requirements (Oftedal, 1981), but this does not seem likely in bears.

In most mammals the total sugar concentration in milk tends to fall when fat and protein rise (Oftedal, 1984 a). The pattern seen in black bears is, however, more similar to that in marsupials (Green, 1984). For example, the concentration of total sugar in milk of the tammar wallaby (*Macropus eugenii*) increases from 60 g/kg to 130 g/kg while the young are in the pouch, and then declines to about 10 g/kg after the young leave the pouch (Messer & Green, 1979). Black bear milk exhibited similar trends, but at lower absolute levels (Fig. 1). It is not known if the postnatal rise in total sugar concentration relates to changes in substrate requirements of the young during development. The fact that both marsupials and bears are small and immature at birth and, hence, both undergo development after birth that occurs in the uterus in most large placental mammals (Tyndale-Biscoe, 1973; Ramsay & Dunbrack, 1986), is intriguing.

In marsupials the increase in total sugar concentration at mid-lactation is due to the secretion of complex oligosaccharides, but these disappear in late lactation (Messer & Green, 1979). The fact that there was little lactose (1·7 g/kg) in the milk of black bears when the concentration of total sugar was maximal suggests that this species may also produce unusual milk carbohydrates. Jenness *et al.* (1972) found a sugar in brown bear (*Ursus arctos*) milk with low relative mobility in paper chromatography, and that on acid-hydrolysis yielded a value of 2:1 for galactose:glucose. This sugar was tentatively identified as a trisaccharide but further investigation is needed. The oligosaccharides of marsupial milks are also high in galactose (Messer & Green, 1979).

Previous studies on black bear milk have been limited to a single sample analysed by Hock & Larson (1966), and five samples analysed by Jenness *et al.* (1972). The samples in the latter study were obtained in late summer and, accordingly, were quite high in fat (245 g/kg) and protein (145 g/kg) but low in sugar (4 g/kg). In comparing these values with values from brown bears, polar bears (*Thalarctos maritimus*) and a Malayan sun bear (*Helarctos malayanus*), Jenness *et al.* (1972) concluded that the milk produced by bears in zoos was higher in carbohydrate than that produced by wild bears. Unfortunately this comparison was confounded by differences in the stage of lactation of captive (2–3 months postpartum) and wild (5–18 months postpartum) bears. The difference in sugar concentration between the zoo bears (19–32 g/kg) and the wild bears (2–7 g/kg) parallels the changes observed in black bears from 2–3 months to 9 months postpartum. It is unlikely that diet or other facets of captivity have an influence on the sugar concentration of the milk of bears or other carnivores.

Measurement of milk intake by isotope dilution

Although the use of H isotopes of water to measure milk intake of young animals has been validated for several species, including human babies (Holleman *et al.* 1975; Dove & Freer, 1979; Robbins *et al.* 1981; Coward *et al.* 1979; Fjeld *et al.* 1988), a number of potential errors must be taken into account. Although most investigators have found that isotope procedures overestimate body water by only a few percentage points, Sheng & Huggins (1971 a, 1979, 1986) concluded, from a set of data on growing beagle puppies, that isotope dilution may seriously overestimate the amount of water in young, growing animals. This

was not the case with either newborn or 1-month-old bear cubs, since the difference between estimates obtained by isotope dilution and direct analysis were only 44 and 30 g/kg body weight respectively (Table 3). The average body water measured by carcass analysis of newborn puppies in the present study (804 g/kg) and in the study of Thomas (1911) (801 g/kg) are considerably higher than the average (749 g/kg) reported by Sheng & Huggins (1971 a, b). In addition, isotope measurements of body water of suckling puppies presented by Oftedal (1984 b) are lower than the isotope estimates of Sheng & Huggins (1971 a). It is not clear why Sheng & Huggins (1971 a) found such discrepancies between the two methods (Culebras et al. 1977).

A second potential error arises from isotope recycling. If isotope re-enters the body water pool of suckling young after it has been excreted in urine, faeces, respiratory water or insensible water loss, the turnover rate of body water (and, hence, milk intake) will be underestimated (Baverstock & Green, 1975). We corrected for this error by measuring accumulation of isotope in control littermates that had not been dosed at the start of each experimental period. Significant concentrations of isotope were found in all controls, indicating that this correction is essential in bears, as it is in dogs (Oftedal, 1984 b). For example, in the first period failure to correct for recycling would have led to a milk intake estimate of 77·8 (3·75 SE) g/d, or an underestimate of 13·7 (2·44 SE)%.

The predominant route of recycling is probably through the free water in maternal milk, assuming that female bears ingest the urine and faeces of their cubs. We have incidental data which supports this assumption. Single blood samples were taken from four of the mothers in period 1, 13–27 d after isotope administration to their cubs. These four samples contained 0·23 (0·012 SE) g D_2O/kg water. For purposes of comparison we developed predictions of isotope levels in maternal body water, assuming that: (1) all water and isotope excreted by cubs is ingested by their mothers, (2) mothers contain 550 g/kg water at delivery, (3) the amount of water that mothers lose to the environment (excluding water in milk) is equivalent to the amount of metabolic water produced (about 0·46 kg/d, assuming that oxidation of fat yields 17 MJ/d; Nelson, 1980), (4) the increase in body water content of cubs is matched by a decrease in maternal body water (i.e. total water content of mother and cubs remains constant). At the dose rates employed and water turnover rates observed, maternal isotope levels were predicted to increase to 0·20 g/kg by 14 d, peak at 0·23 g/kg at 28 d, and gradually decline to 0·19 g/kg at 60 d. The measured isotope concentrations were close to these predicted values. In addition, a blood sample from a female bear taken 54 d after her cubs were administered isotope contained 0·19 g isotope/kg. Thus, it appears that most if not all the isotope-enriched water excreted by the cubs is ingested by the mother, and that her water losses (other than to milk) must be minimal. This is consistent with the observation that dormant bears do not urinate or defaecate and, hence, their primary route of water loss will be respiration.

Several other sources of error in isotope measurements could not be measured. For example, if cubs consumed any water from any source other than milk, milk intake may be overestimated. Although this is unlikely when cubs are in the den, bear cubs have been observed licking at the mouth of their mother and could ingest some saliva (G. L. Alt, personal communication). Once outside the den cubs could drink water, but the fact that turnover rate remained so low (0·089) suggests otherwise. Isotope fractionation can occur at evaporative surfaces (especially in the lungs) due to the heavier mass of D atoms compared with H atoms. Fractionation causes water turnover and, hence, milk intake to be underestimated, with the magnitude of the error dependent on the proportion of the water loss that is subject to fractionation (Fjeld et al. 1988). By contrast, water absorbed from inspired air causes an error of overestimation (Nagy & Costa, 1980), counteracting the effect of fractionation. In the winter den, water influx due to respiration is probably a

minor component since low air temperatures imply that the absolute humidity of inspired air is low, whereas losses of fractionated water may be increased by the presumed disparity in absolute humidity between cold inspired air and warm expired air. Although the quantitative importance of these errors is difficult to assess, it is fortunate that many of the potential errors of isotope methods of milk intake appear to cancel each other out.

In relation to body weight the daily milk intakes of bear cubs were quite low (139, 89 and 67 g/kg body weight at about 14, 35 and 70 d postpartum). By contrast, puppies, striped skunk pups and mink kits have higher intakes (150–270 g/kg body weight), at least at peak lactation (Oftedal, 1981, 1984a). The relatively low milk intake of bear cubs is related to the high fat and energy concentrations of the milk and its low percentage of water.

Energy intakes are best compared among species on a metabolic size basis. Oftedal (1984a) found that suckling young of a broad array of species consumed about 0.84–1.09 MJ (200–260 kcal/d per kg body weight$^{0.83}$) at peak lactation. Although we do not know when peak lactation occurs in the black bear, the highest milk intake measured (166.8 g/d) was at 10 weeks. At this age the energy intake of cubs (0.98 MJ (235 kcal/d per kg body weight$^{0.83}$)) was similar to the values for other mammalian species, including puppies, mink kits and skunk pups, measured at peak lactation.

The incorporation and catabolism of nutrients in the milk

About 30% of the energy intake of cubs was retained as fat and protein, and the remaining amount was presumably used to cover the energetic costs of growth and maintenance. The energetic cost of maintenance must be relatively high in small bear cubs with their large surface area and limited insulation at a cold ambient temperature (e.g. Blix & Lentfer, 1979). Their only source of heat is the body of the mother which, although large, has a deep body temperature that may be no warmer than about 31–36° (Maxwell et al. 1988) and a skin temperature undoubtedly lower. We estimate that catabolism of milk nutrients provided bear cubs with 0.70 MJ (167 kcal)/d during the first 4 weeks after birth, or about 0.96 MJ (230 kcal)/d per kg bodyweight$^{0.75}$.

An adequate supply of water is an essential requirement for a newborn animal. During the first 4 weeks after birth milk provided a cub with 61 g preformed water/d (Table 5), and additional water was obtained from the catabolism of milk constituents. From the difference between nutrient intakes and nutrient deposition (Fig. 3), and assuming that faecal losses are insignificant, it is estimated that a bear cub catabolized about 16 g fat, 3 g protein and 1 g carbohydrate per day, yielding 19 g metabolic water. Since metabolic water production exceeded the amount of water retained in new tissues (14 g/d), the amount of water (66 g/d) lost by the cub (as urine, faeces, respiratory water, etc.) actually exceeded the amount of free water obtained in milk. This presents an opportunity to the fasting mother to recover the water lost in milk.

Ingestion of the urine and faeces of cubs appears to play a central role in the water economy of the mother and is not just a means of keeping the nest clean, as has been suggested for other carnivores (Ewer, 1973). Over the first 4 weeks after birth each cub obtained about 1.7 kg preformed water in milk, so the mother rearing a litter of three exported about 5.1 kg water. However, over this same period the litter of three lost about 5.6 kg to excretion and evaporation. If the mother consumes the urine and faeces of the young, and if the excreta represent most of the water loss of the cubs, the mother will import about as much water by consuming their excreta as she exports in milk.

Maternal consumption of urine and faeces may also be important to her N economy. In the first 4 weeks the bear cub retained about 51% of the intake of N, which is a little higher than estimates of 35% N incorporation by suckling puppies and 46% by suckling mink kits (Oftedal, 1981), but considerably less than 72% reported for young rabbits (Davies et al.

1964). The 49 % of N intake that is not retained is excreted primarily in urine, presumably as urea, and as faecal N of endogenous origin (Cunningham & Brisson, 1957; Jagusch & Mitchell, 1971; Walker, 1979). The mother recovers this N along with urinary and faecal water and, thus, potentially recovers half the amount of N secreted in the milk.

There is evidence that urea produced endogenously in dormant bears may be recycled to amino acids and then to plasma and other proteins (Lundberg *et al.* 1976; Wolfe *et al.* 1982). This presumably involves passive diffusion of urea into the lumen of the hindgut, ammonia production via bacterial ureolysis, re-absorption of the N as NH_3, and transport to the liver where incorporation into amino acids occurs (Mason, 1984; Egan *et al.* 1986; Stevens, 1988). In the lactating bear urea from the cubs is also presented to the digestive tract but, since the route of entry differs, the primary site of bacterial ureolysis in the digestive tract may not be the same. The consumption of exogenous urea may, thus, result in higher circulating levels and/or higher turnover of urea than in dormant bears that are not lactating, but this remains to be tested. If the lactating bear is able to re-utilize completely the N in the excreta of cubs, the net loss of N during lactation could be as little as half the amount secreted in milk.

The cost of milk production to the mother

During the first 12 weeks following delivery a lactating black bear with a litter of three produced about 32 kg milk, equivalent to 33 % of initial body weight, without feeding or drinking (other than the excreta of the young). Although about 21 kg water and 2·3 kg protein were included in the secreted milk, virtually all the water and much of the N may have been re-utilized. Recycling appears to be essential to the conservation of the lean body mass of the mother during her prolonged fast. The primary cost of lactation is the need to hydrolyse triacylglycerols in adipose tissue, providing fatty acids and glucose (from glycerol) for secretion of milk fat. About 7·5 kg lipids were secreted in the first 12 weeks.

The importance of recycling is illustrated by a simple calculation of the amount of mass that a 100 kg black bear with three young would lose without it. Over 12 weeks the mother would lose at least the mass of milk (about 32 kg) plus the mass loss experienced by dormant non-reproductive females (about 23 kg; Hellgren *et al.* 1990). Thus, in the absence of recycling, mass loss would be about 55% of initial mass, which may be more than a female could withstand.

In conclusion, lactation provides another example of the profound metabolic economy of bears during their period of winter dormancy. It would be interesting to examine milk production and nutrient deposition after the female bear and her cubs emerge from the winter den. We found that cubs gained little weight between mid-March and mid-April, which is the time they first emerge from the den. However, little if any food is available to the mother at this time and milk production remains relatively low, about 0·5 kg/d or 7 g/kg maternal weight. It is unlikely that this represents peak production because in other large (> 10 kg) mammals peak yields are typically 15–80 g/kg maternal weight (Oftedal, 1984*a*). Perhaps peak production occurs later in the lactation period, which may last for 10 months or more. One possibility is that milk production of the black bear increases during late spring and summer months when food becomes plentiful.

REFERENCES

Alt, G. L. (1982). Reproductive biology of Pennsylvania's black bear. *Pennsylvania Game News* **53**, 9–15.

Alt, G. L. (1983). Timing of parturition of black bears (*Ursus americanus*) in northeastern Pennsylvania. *Journal of Mammalogy* **64**, 305–307.

Alt, G. L. (1989). Reproductive biology of female black bears and early growth and development of cubs in northeastern Pennsylvania. PhD Thesis, West Virginia University.

Alt, G. L., Alt, F. W. & Lindzey, J. S. (1976). Home range and activity patterns of black bears in northeastern Pennsylvania. *Proceedings of the Northeast Section of the Wildlife Society* **33**, 45–56.

Anderson, A. C. (1957). Puppy production to the weaning age. *Journal of the American Veterinary Medical Association* **130**, 151–158.

Anderson, A. C. (1970). Reproduction. In *The Beagle as an Experimental Dog*, pp. 31–39 [A. C. Anderson, editor]. Ames, Iowa: Iowa State University Press.

Association of Official Analytical Chemists (1990). *Official Methods of Analyses of the Association of Official Analytical Chemists*, 15th ed. [K. Helrich, editor]. Arlington, Virginia: Association of Official Analytical Chemists Inc.

Battaglia, F. C. & Meschia, G. (1978). Principal substrates of fetal metabolism. *Physiological Reviews* **58**, 499–527.

Baverstock, P. & Green, B. (1975). Water recycling in lactation. *Science* **187**, 657–658.

Berseth, C. L., Lichtenberger, L. M. & Morriss, F. H. (1983). Comparison of the gastrointestinal growth-promoting effects of rat colostrum and mature milk in newborn rats in vivo. *American Journal of Clinical Nutrition* **37**, 52–60.

Blix, A. S. & Lentfer, J. W. (1979). Modes of thermal protection in polar bear cubs – at birth and on emergence from the den. *American Journal of Physiology* **5**, R67–R74.

Brambell, F. W. (1970). *The Transmission of Passive Immunity From Mother to Young*. New York: American Elsevier.

Cahill, G. F. (1976). Starvation in man. *Clinics in Endocrinology and Metabolism* **5**, 397–415.

Cahill, G. F. (1982). Starvation. *Transactions, American Clinical and Climatological Association* **94**, 1–21.

Coward, W. A., Sawyer, M. B., Whitehead, R. G., Prentice, A. M. & Evans, J. (1979). New method for measuring milk intakes in breast-fed babies. *Lancet* **i**, 13–14.

Crandall, L. S. (1964). *Management of Wild Mammals in Captivity*. Chicago: University of Chicago Press.

Culebras, J. M., Fitzpatrick, G. F., Brennan, M. F., Boyden, C. M. & Moore, F. D. (1977). Total body water and the exchangeable hydrogen. II. A review of comparative data from animals based on isotope dilution and desiccation, with a report of new data from the rat. *American Journal of Physiology* **232**, R60–R65.

Cunningham, H. M. & Brisson, G. J. (1957). The endogenous urinary and metabolic fecal nitrogen excretion of newborn dairy calves. *Canadian Journal of Animal Science* **37**, 152–156.

Davies, J. S., Widdowson, E. M. & McCance, R. A. (1964). The intake of milk and the retention of its constituents while the newborn rabbit doubles its weight. *British Journal of Nutrition* **18**, 385–392.

Dove, H. & Freer, M. (1979). The accuracy of tritiated water turnover rate as an estimate of milk intake in lambs. *Australian Journal of Agricultural Research* **30**, 725–739.

Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A. & Smith, F. (1956). Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* **28**, 350–356.

Egan, A. R., Boda, K. & Varady, J. (1986). Regulation of nitrogen metabolism and recycling. In *Control of Digestion and Metabolism in Ruminants*, pp. 386–402 [L. P. Milligan, W. L. Grovum and A. Dobson, editors]. Englewood Cliffs, NJ: Prentice-Hall.

Ewer, R. F. (1973). *The Carnivores*. Ithaca, New York: Cornell University Press.

Fjeld, C. R., Brown, K. H. & Schoeller, D. A. (1988). Validation of the deuterium oxide method for measuring average daily milk intake in infants. *American Journal of Clinical Nutrition* **48**, 671–679.

Freed, L. M., York, C. M., Hamosh, M., Sturman, J. T., Oftedal, O. T. & Hamosh, P. (1986). Bile salt stimulated lipase: the enzyme is present in nonprimate milk. In *Human Lactation*, vol. 2, *Maternal and Environmental Factors*, pp. 595–601 [M. Hamosh and A. S. Goldman, editors]. New York: Plenum Press.

Gittleman, J. L. & Oftedal, O. T. (1987). Comparative growth and lactation energetics in carnivores. *Symposia of the Zoological Society of London* **57**, 41–77.

Green, B. (1984). Composition of milk and energetics of growth in marsupials. *Symposia of the Zoological Society of London* **51**, 369–387.

Hall, R. A. & Widdowson, E. M. (1979). Response of the organs of rabbits to feeding during the first days after birth. *Biology of the Neonate* **35**, 131–139.

Hamosh, M. (1979). A review. Fat digestion in the newborn: Role of lingual lipase and preduodenal digestion. *Pediatric Research* **13**, 615–622.

Heird, W. C., Schwartz, S. M. & Hansen, I. H. (1984). Colostrum-induced enteric mucosal growth in beagle puppies. *Pediatric Research* **18**, 512–515.

Hellgren, E. C., Vaughan, M. R., Kirkpatrick, R. L. & Scanlon, P. F. (1990). Serial changes in metabolic correlates of hibernation in female black bears. *Journal of Mammalogy* **71**, 291–300.

Hochachka, P. W. & Somero, G. N. (1984). *Biochemical Adaptation*. Princeton, New Jersey: Princeton University Press.

Hock, R. J. & Larson, A. M. (1966). Composition of black bear milk. *Journal of Mammalogy* **47**, 539–540.

Holleman, D. F., White, R. G. & Luick, J. R. (1975). New isotope methods for estimating milk intake and yield. *Journal of Dairy Science* **58**, 1814–1821.

Iverson, S. J., Kirk, C. L., Hamosh, M. & Newsome, J. (1991). Milk lipid digestion in the neonatal dog: the combined action of gastric and bile salt stimulated lipases. *Biochimica et Biophysica Acta* **1083**, 109–119.

Iverson, S. J. & Oftedal, O. T. (1992). Fatty acid composition of black bear (*Ursus americanus*) milk during and after the period of winter dormancy. *Lipids* **27**, 940–943.

Jagusch, K. T. & Mitchell, R. M. (1971). Utilization of the metabolizable energy of ewe's milk by the lamb. *New Zealand Journal of Agricultural Research* **14**, 434–441.

Jenness, R., Erickson, A. W. & Craighead, J. J. (1972). Some comparative aspects of milk from four species of bears. *Journal of Mammalogy* **53**, 34–47.

Joubert, D. M. (1956). A study of pre-natal growth and development in the sheep. *Journal of Agricultural Science, Cambridge* **47**, 382–428.

Kordek, W. S. & Lindzey, J. S. (1980). Preliminary analyses of female reproductive tracts from Pennsylvania black bears. *International Conference on Bear Research and Management* **4**, 159–161.

Lundberg, D. A., Nelson, R. A., Wahner, H. W. & Jones, J. D. (1976). Protein metabolism in the black bear before and during hibernation. *Mayo Clinic Proceedings* **51**, 716–722.

McCance, R. A. & Widdowson, E. M. (1955). The size and function of the spleen in young puppies. *Journal of Physiology* **129**, 636–638.

McCance, R. A. & Widdowson, E. M. (1978). Glimpses of comparative growth and development. In *Human Growth*, vol. 1, pp. 145–166 [F. Falkner and J. M. Tanner, editors]. New York: Plenum Publishing.

McCay, C. M. (1963). Kennel management and efficient production of pups. *Journal of the American Veterinary Medical Association* **142**, 1015–1018.

Manners, M. J. & McCrea, M. R. (1963). Changes in the chemical composition of piglets during the 1st month of life. *British Journal of Nutrition* **17**, 495–513.

Marier, J. R. & Boulet, M. (1959). Direct analysis of lactose in milk and serum. *Journal of Dairy Science* **42**, 1390–1391.

Mason, V. C. (1984). Metabolism of nitrogenous compounds in the large gut. *Proceedings of the Nutrition Society* **43**, 45–53.

Maxwell, R. K., Thorkelson, J., Rogers, L. L. & Brander, R. B. (1988). The field energetics of winter-dormant black bear (*Ursus americanus*) in northeastern Minnesota. *Canadian Journal of Zoology* **66**, 2095–2103.

Messer, M. & Green, B. (1979). Milk carbohydrates of marsupials. II. Quantitative and qualitative changes in milk carbohydrates during lactation in the Tammar wallaby (*Macropus eugenii*). *Australian Journal of Biological Sciences* **32**, 519–531.

Nagy, K. A. & Costa, D. P. (1980). Water flux in animals: Analysis of potential errors in the tritiated water method. *American Journal of Physiology* **238**, R454–R465.

Nelson, R. A. (1978). Urea metabolism in the hibernating black bear. *Kidney International* **13**, S177–S179.

Nelson, R. A. (1980). Protein and fat metabolism in hibernating bears. *Federation Proceedings* **39**, 2955–2958.

Nelson, R. A., Jones, J. D., Wahner, H. W., McGill, D. B. & Code, C. F. (1975). Nitrogen metabolism in bears: Urea metabolism in summer starvation and in winter sleep and role of urinary bladder in water and nitrogen conservation. *Mayo Clinic Proceedings* **50**, 141–146.

Oftedal, O. T. (1981). Milk, protein and energy intakes of suckling mammalian young: a comparative study. PhD Thesis, Cornell University.

Oftedal, O. T. (1984*a*). Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symposia of the Zoological Society of London* **51**, 33–85.

Oftedal, O. T. (1984*b*). Lactation in the dog: Milk composition and intake by puppies. *Journal of Nutrition* **114**, 803–812.

Oftedal, O. T. (1986). Growth rate and milk composition: a critical appraisal. *Report of the 91st Ross Conference on Pediatric Research*, pp. 50–58. Ohio: Ross Laboratories.

Oftedal, O. T., Bowen, W. D., Widdowson, E. M. & Boness, D. J. (1989). Effects of suckling and the postsuckling fast on weights of the body and internal organs of harp and hooded seal pups. *Biology of the Neonate* **56**, 283–300.

Oftedal, O. T. & Gittleman, J. L. (1989). Patterns of energy output during reproduction in carnivores. In *Carnivore Behavior, Ecology and Evolution*, pp. 355–378 [J. L. Gittleman, editor]. Ithaca, New York: Cornell University Press.

Oftedal, O. T. & Iverson, S. J. (1987). Hydrogen isotope methodology for the measurement of milk intake and the energetics of growth in suckling young. In *Approaches to Marine Mammal Energetics. Society for Marine Mammalogy Special Publication* no. 1, pp. 67–96 [A. C. Huntley, D. P. Costa, G. A. J. Worthy and M. A. Castellini, editors]. Kansas: Allen Press.

Oftedal, O. T., Iverson, S. J. & Boness, D. J. (1987). Milk and energy intakes of suckling california sea lion

Zalophus californianus pups in relation to sex, growth, and predicted maintenance requirements. *Physiological Zoology* **60**, 560–575.

Perrin, D. R. (1958). The calorific value of milk of different species. *Journal of Dairy Research* **25**, 215–220.

Ramsay, M. A. & Dunbrack, R. L. (1986). Physiological constraints on life history phenomena: the example of small bear cubs at birth. *American Naturalist* **127**, 735–743.

Robbins, C. T., Podbielancik, N., Roberta, S., Wilson, D. L. & Mould, E. D. (1981). Growth and nutrient consumption of elk calves compared to other ungulate species. *Journal of Wildlife Management* **45**, 172–186.

Sheng, H. & Huggins, R. A. (1971a). Direct and indirect measurement of total body water in the growing beagle. *Proceedings of the Society for Experimental Biology and Medicine* **137**, 1093–1099.

Sheng, H. & Huggins, R. A. (1971b). Growth of the beagle: Changes in chemical composition. *Growth* **35**, 369–376.

Sheng, H. & Huggins, R. A. (1979). A review of body composition studies with emphasis on total body water and fat. *American Journal of Clinical Nutrition* **32**, 630–647.

Sheng, H. & Huggins, R. A. (1986). Total body water measurements by tritiated water in growing animals. *Growth* **50**, 447–455.

Spray, C. M. & Widdowson, E. M. (1950). The effect of growth and development on the composition of mammals. *British Journal of Nutrition* **4**, 332–353.

Stevens, C. E. (1988). *Comparative Physiology of the Vertebrate Digestive Tract.* Cambridge: Cambridge University Press.

Thomas, K. (1911). Über die Zusammensetzung von Hund und Katze während der ersten Verdoppelungsperioden des Geburtgewuchtes. *Archiv für Anatomie und Physiologie, Physiologischer Abteilung* **1**, 9–38.

Tyndale-Biscoe, H. (1973). *The Life of Marsupials.* New York: Elsevier Press.

Wade-Smith, J. & Richmond, M. E. (1975). Care, management, and biology of captive striped skunks (*Mephitis mephitis*). *Laboratory Animal Science* **25**, 575–584.

Walker, D. M. (1979). Nutrition of preruminants. In *Digestive Physiology and Nutrition of Ruminants*, pp. 258–280 [D. C. Church, editor]. Corvallis, Oregon: O & B Books.

Widdowson, E. M. (1965). Food, growth and development in the suckling period. In *Canine and Feline Nutritional Requirements*, pp. 9–17 [O. Graham-Jones, editor]. London: Pergamon Press.

Widdowson, E. M., Colombo, V. E. & Artavanis, C. A. (1976). Changes in the organs of pigs in response to feeding for the first 24 h after birth. II. The digestive tract. *Biology of the Neonate* **28**, 272–281.

Widdowson, E. M. & Spray, C. M. (1951). Chemical development *in utero*. *Archives of Disease in Childhood* **26**, 205–214.

Wimsatt, W. A. (1963). Delayed implantation in the Ursidae, with special reference to the black bear (*Ursus americanus* Pallas). In *Delayed Implantation*, pp. 49–74 [A. C. Enders, editor]. Chicago: University of Chicago Press.

Wolfe, R. R., Nelson, R. A., Wolfe, M. H. & Rogers, L. (1982). Nitrogen cycling in hibernating bears. *Proceedings of the Society for Mass Spectrometry* **30**, 426.