Radioprotection, Suppl. 1, vol. **40** (2005) S351-S357

DOI: 10.1051/radiopro:2005s1-052

^{14}C and tritium dynamics in wild mammals: A metabolic model

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Abstract. The protection of biota from ionising radiations needs reliable predictions of radionuclide dynamics in wild animals. Data specific for many wild animal – radionuclide combinations is lacking and a number of approaches including allometry have been proposed to address this. However, for ^{14}C and ^{3}H, which are integral components of animal tissues and their diets, a different approach is needed. Here we propose a metabolically based model which can be parameterised predominantly on the basis of published metabolic data. We begin with a metabolic definition of the ^{14}C and OBT loss rate (assumed to be the same) from the whole body and specific organs. The mammalian body is conceptually partitioned into compartments (body water, viscera, adipose, muscle, blood and remainder) and a simple model defined using net maintenance and growth needs of mammals. The model is tested with data from studies using rats and sheep. It provides a reliable prediction for whole body and muscle activity concentrations without the requirement for any calibration specific to ^{3}H and ^{14}C. Predictions from the model for representative wild mammals) are presented. Potential developments of a metabolic model for birds and the application of our work to human foodchain modelling are also discussed.

1. INTRODUCTION

The protection of biota from ionising radiation needs reliable predictions of radionuclide dynamics in wild animals. Data for many wild animals – radionuclide combinations is lacking and a number of approaches including allometry have been proposed to address this [1,2].

Tritium is present in, and emitted by, some nuclear installations at comparatively high levels (e.g. heavy water reactors, fuel reprocessing plants, military factories or future fusion reactors). Due to these high potential releases the environmental impacts need to be assessed, even though tritium has a low radiotoxicity. Carbon-14 is among the radionuclides of concern in waste management. Recently we have presented an approach to assess the equilibrium transfer of routine emissions on biota, distinguishing between tritiated water (HTO) and organically bound tritium (OBT) intakes and considering the metabolic regulation of tritium and radiocarbon [3]. We further expanded this metabolic approach to provide dynamic predictions and successfully tested this using data for laboratory and housed farm animals [4]. Here we present an overview of our metabolic model and apply it to example wild animals taking into consideration the variability of basal and daily metabolism, and the influences of diet and environment.

2. MODEL DESCRIPTION

As there is no difference between the tritium and hydrogen metabolism (disregarding isotopic discrimination), exchangeable organic tritium (hydrogen) is assumed to be in full equilibrium with body water and included in the body water compartment, increasing the amount by about 5 %. The non-exchangeable organic tritium (hydrogen) and organic carbon in the body are modelled as additional compartments: blood plasma, red blood cells, adipose tissue, muscle, viscera and 'remainder'. Viscera includes liver, kidney, heart and portal drained organs (pancreas, spleen, stomach and intestine), combining in a single compartment all organs with high metabolic rate (with the exception of brain). Ingested HTO is assumed to be immediately mixed in the body water compartment. The metabolisable fraction of dietary intakes of organic tritium and carbon are transferred to systemic body compartments; the remainder being excreted. In the case of dietary tritium, the exchangeable fraction is transferred to directly body water and only the non-exchangeable fraction enters blood plasma. The transfer rates from blood plasma to model compartments are assessed using the mass balance of the stable analogues (organic carbon or non-exchangeable organically bound hydrogen). Excretion rates of organic compounds in urine or milk are also established from stable analogue data (e.g. composition and daily production of urine and the amount of stable analogue in blood plasma). Transfers include the net flux after the digestion and transformation of dietary compounds in protein, lipids or carbohydrates for storage or maintenance. All material that is catabolized is expired (carbon) or excreted as body water (tritium). The respiration rate is also assessed using the mass balance of stable analogues. It is well known that a fraction (20-40 %) of non-exchangeable bound hydrogen in the body is derived from free hydrogen in body water, and we therefore have a transfer from the body water to blood plasma OBT. For more details and a structural model diagram see [4].

The key point in our model is the assessment of loss rate from compartments to the blood plasma organic pool. Based on a published review of cellular energy utilisation and molecular origin of standard metabolic rate in mammals [5] we advanced the working hypothesis that the energy turnover rate can be used as a surrogate for organic carbon/tritium transfer rates from organs in our model. We consider a mammal with a daily energy expenditure (DEE) required as the net energy to sustain basal metabolism, thermo-regulation and activity. We define the energy turnover rate as the ratio between DEE and the energy content in the body (enthalpy of combustion). We assess the whole body turnover rate of organic matter for our model assuming that it is given by the energy turnover rate. This definition can be expanded at organ level if we know the fraction of DEE used by the organ. The specific metabolic rate (SMR) is the metabolic rate for a unit of fresh tissue mass of whole body or any organ. For basal metabolism (basal metabolic rate, BMR) we utilise experimental data for major organs in some mammals. For active mammals, muscle has a definite increased SMR [6], heart and skin have moderate increase of SMR, while other organs have only slight changes. As the enthalpy of combustion is dependent of organ composition (fraction of lipids, protein and carbohydrates) we can define our loss rate for any organs, or group of organs, if we know their composition and SMR. In the case of laboratory and housed farm animals, the model-input parameters can be assessed using available experimental data.

3. DATABASE FOR WILD ANIMALS

In contrast to laboratory of housed farm animals, wild mammals and birds are subjected to large environmental and dietary variability to which they must adapt. There are many studies demonstrating allometric (mass dependent) relations for basal metabolic rate, daily energy expenditure and organ mass [7]. These relationships have some limitations as body mass (BM) is the independent variable without consideration of factors such as with diet and activity [8]. For example, visceral mass fraction is predicted to decrease with the body mass while experimental data on a series of mammals shows large fluctuations (Figure 1), being influenced by diet quality and availability.

For DEE there is considerable evidence of taxon specific allometric relationships [9,10,11], but, dietary habits can still have a large influence as can be seen in Figure 2 for rodents with herbivorous, omnivorous or granivorous diets. DEE also depends on environmental temperature [10], for instance small mammals in the Arctic have a 2 fold higher DEE for the same body mass compared with

animals in Mediterranean climates. Where available we use classified (by e.g. family, environment or diet) allometric relationships rather than more generic (e.g. mammal) allometric relationships. Organ composition is considered the same across all mammals, extrapolating the few measured values.

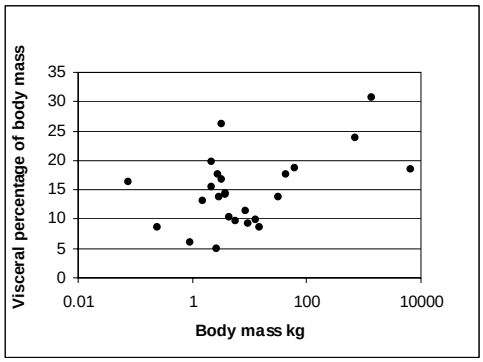

Figure 1. Variation with body mass in the mass of visceral organs expressed as a percentage of whole body mass.

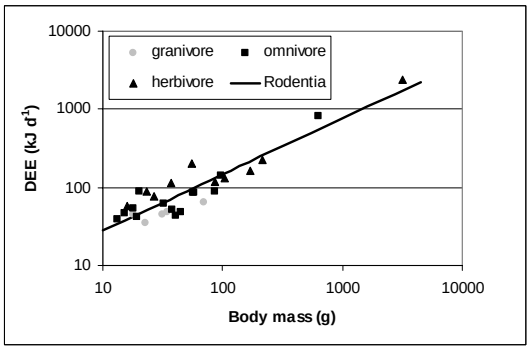

Figure 2. DEE (kJ d^{-1}) for granivorous, carnivorous, and herbivorous diets, compared with an allometric relationship for rodents.

A gap in the database for wild animals is the assessment of SMR for organs, in basal and active states. There are some measured values for laboratory and farm animals and humans, in basal or resting metabolism. We have derived allometric relationships on the basis of the available data for application to wild animals (Table 1).

Table 1. Allometric relationship constants derived for organ SMR=a*BMb; BM (kg fw); SMR (MJ d^{-1} kg^{-1} fw).

Tissue	a	B
Adipose	0.06	-0.21
Muscle	0.23	-0.28
Liver	3.16	-0.21
Kidney	2.6	-0.09
Heart	4.4	-0.11
GIT	0.8	-0.22
Brain	2.0	-0.14
Skin	0.11	-0.28
Skeleton	0.04	-0.28

Due to paucity of the available database we could expect some potential errors when using the values in Table 1. We have assessed this by predicting the basal metabolic rate of humans, rats and a generic mammal. For humans and rats, organ masses have been taken from the literature, for the generic mammal, allometric relationships were used to estimate organ masses [7]. The predicted BMRs for the adult human and rat are within 20% of measured values. For the generic mammal BMR is close to that which can be estimated from published relationships [14]. For the few examples of wild animals where we have organ mass and BMR our predicted BMR values are in good agreement with measured values (Table 2).

Some data for wild mammal BMRs are available [12] and these have been used to derive ‘local’ allometric relationships in order to obtain an estimate for mammals of interest if measured values are not measured.

Table 2. Reconstruction of BMR for sample wild mammals.

Species*scient.* Species	Mass (kg fw)	Measured BMR (MJ d^{-1})	Estimated BMR (MJ d^{-1})
Hare *(Lepus carpensis)*	2.9	0.78	0.79
Jackal *(Canis mesomelas)*	2.8	0.7	1.05
Racoon *(Procyon lotor)*	2.2	0.5	0.76
Puma *(Felis capensis)*	9.6	1.9	1.5
Wild cat *(Felis ocreata)*	2.7	0.5	0.52
Chipmunk *(Tamias striatus)*	0.0075	0.045	0.07

4. MODEL APPLICATION

To demonstrate model application we selected mammals representative of reference organism suggested for use within some of the proposed environmental impact assessment frameworks [2]. For protection of biota we are interested in the whole body dynamics of radionuclides and integrated retention function values; for food chain modelling dynamics in muscle, as the main edible part of animals, are also useful. The whole body dynamics of ^{3}H and ^{14}C are largely determined by the value of DEE and body composition but muscle dynamics are influenced by energy partitioning between organs. The increase in energy expenditure between basal and an active state is mostly due to muscular activity [6], and the ratio between DEE and BMR is important in assessing model parameters. The ratio between DEE and BMR depends on diet quality and taxa and appropriate values were selected from those published [10] if measurements were not available. Organ mass fraction was assessed from closest mammal measured in the same family-diet group. Diet characteristics (gross and metabolisable energy, C and organic hydrogen concentration) were taken from literature [9,11].

Our mammal list includes a large herbivore (reindeer), a carnivore (red fox), a small herbivore (rabbit or hare), and two rodents (chipmunk and a lemming). These are mostly in the list of representative mammals in current proposed assessment frameworks. The lemming is modelled as being in the Arctic with enhanced energy needs [10]. Input model parameters are collected in Table 3. For each mammal consider a unique intake of 1 Bq of ^{14}C or ^{3}H in the diet is modelled. The integrated whole body and muscle activity concentrations are given in Table 4.

Table 3. Model input data.

Mammal	Mass kg	BMR kJ d^{-1}	DEE kJ d^{-1}	Viscera mass fraction	Muscle mass fraction	DEE of Viscera fraction	DEE of muscle fraction
Reindeer	150	16	43	0.15	0.4	0.25	0.55
Red fox	6	1.4	5.6	0.13	0.45	0.2	0.7
Rabbit	1.8	0.55	1.3	0.13	0.45	0.28	0.62
Chipmunk	0.096	0.06	0.143	0.22	0.43	0.35	0.55
Lemming	0.06	0.075	0.19	0.15	0.43	0.25	0.55

Table 4. Model results for different representative mammals assuming a unique dietary intake of 1 Bq ^{14}C and 1 Bq ^{3}H.

Mammal	C intake in diet kg C d^{-1}	Integrated ^{14}C activity whole body (Bq d)	Integrated ^{14}C activity muscle (Bq d)	Normalised integrated ^{14}C activity	Integrated activity body water (Bq d)	Integrated activity body OBT (Bq d)	Integrated total ^{3}H activity (Bq d)	Normalised integrated ^{3}H activity
Reindeer	1.6	22	5	0.24	6	14	20	0.035
Red fox	0.17	8	2	0.23	8	7	15	0.054
Rabbit	0.05	8	2	0.23	3	6	9	0.036
Chipmunk	0.0051	3	1	0.17	2	2	5	0.034
Lemming	0.0068	2	0.5	0.26	1	2	3	0.041

To compare the risks from exposure to ^{14}C and ^{3}H, across mammals of various mass and diets, we have normalised the integrated whole body activity to body mass of each species and an activity concentration of 1 Bq kg^{-1} (dw) of each of the two radionuclides in the diet (Table 4). This is equivalent to the concentration ratio under equilibrium conditions. We observe a low variability of the normalised values, reflecting the metabolic regulation in the transfer of these radionuclides a result compatible with our earlier work on farm animals [13]. The values in the Table 4 are however subject to inherent uncertainties. The assessment of DEE, in absence of direct measurements will at best be based on data for a similar mammal-diet combination; we estimate (from [9,10]) that this may be 50% in error. Changing the DEE value in this range we will induce change of a similar order in the integrated activity (see Figure 3 for estimated ^{14}C variation in red fox). In the case of dietary tritium intake, we need to consider the variability of water flux in mammals, which is influenced by diet quality and quantity, and ambient temperature. For the same species, the water flux can vary by a factor of *circa* 2 around the mean (see Figure 4 for example of rabbits) and because the water fraction in the body is quite constant, the water halftime will differ (by *circa* 2-fold). Consequently, the integrated HTO activity in the body will be affected; doubling the water intake, the total integrated tritium activity decrease by 20 %. All other model parameters have less influence on whole body integrated activity although mass and energy partition in organs can influence the muscle-integrated activity (by a factor less than 2). Consequently we can conclude that the values presented in Table 4 are likely to vary by less than an order of magnitude.

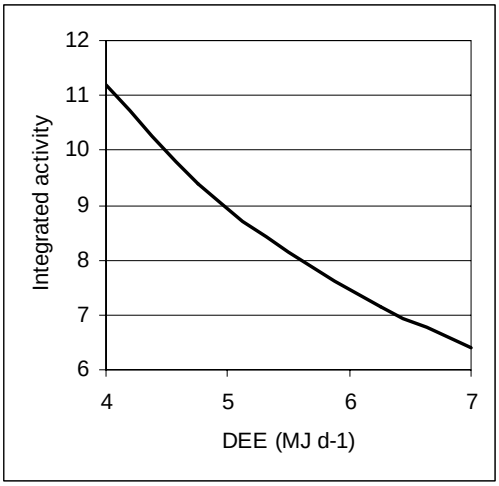

Figure 3. Uncertainty of integrated activity due to DEE for red fox.

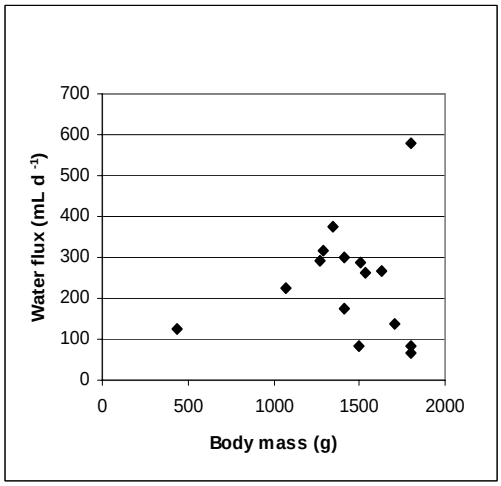

Figure 4. Variability of water flux in rabbits.

5. DISCUSSION

Wild mammals generally have a lower fat content than domestic animals and must adapt to variable environmental conditions. Body mass remains the major factor in describing the radionuclide transfer and small mammals have a fast dynamics, as seen in Figure 5 for the ^{14}C retention functions of our example animals. Environmental temperature, taxon and diet must be also considered. Interpreting the model results in the frame of classical transfer function (see Table 5 for ^{14}C) raises some interesting observations. We distinguish a fast and a slow component with the long halftime 6-14 times larger than the short one, reflecting the various balances between internal and peripheral organs. Neither the short half-time nor the effective half-time are determined simply by mass (compare fox and rabbit).

This is the result of the effects of taxon and diet. Based on these results allometric relationships have been derived (Table 5). It is interesting that the effective halftime for carbon is about 4 times longer than for Cs, a radionuclide uniformly spread in the body and the turnover of which has previously been suggested as being linked to protein turnover rate [15]. The allometric relationship over predicts the transfer coefficient for reindeer; a consequence of considering only mass as the driving parameter.

When considering biota we must also include birds in the list of reference animals. For non-passerine birds, the basal metabolic rate is similar to mammals of comparable mass [11], however, passerine species have 50 % higher BMRs. It is not clear if it is due to increased visceral mass only or if the specific metabolic rate is increased. Birds have a daily energy expenditure [9] *circa* two times higher than mammals of same mass. There are significant differences between taxon and diets but sufficient experimental data are available. Birds have also higher body temperature than mammals. To be able to expand the model for birds we must first clarify the origin of enhanced basal metabolism of passerines and to test if our SMR estimations can be used for birds. The results presented here are preliminary, if required, the model could be adapted to incorporate birds, seasonal effects and growth.

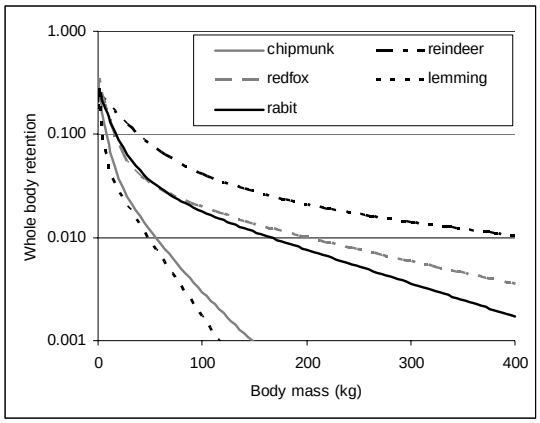

Figure 5. Retention dynamics of ^{14}C in representative mammals.

Table 5. Parameters of ^{14}C transfer in test mammals; the allometric relationships are fits to these parameters.

Species	Mass (kg)	T2 (d)	T1 (d)	F (d kg^{-1})	Tef (d)
Lemming	0.06	18.4	2.0	38.0	5.2
Chipmunk	0.096	23.7	4.0	33.0	7.4
Rabbit	1.8	72.0	8.4	4.5	19.6
Red fox	6	95.5	6.6	1.5	17.1
Reindeer	150	153.5	19.6	0.1	47.2
Allometry		$56M^{0.21}$	$5.5M^{0.24}$	$7.9M^{-0.58}$	$13.1M^{0.25}$

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