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Predicting animal $\delta^{18}O$: Accounting for diet and physiological adaptation

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Abstract—Theoretical predictions and measured isotope variations indicate that diet and physiological adaptation have a significant impact on animals $\delta^{18}O$ and cannot be ignored. A generalized model is therefore developed for the prediction of animal body water and phosphate $\delta^{18}O$ to incorporate these factors quantitatively. Application of the model reproduces most published compositions and compositional trends for mammals and birds. A moderate dependence of animal $\delta^{18}O$ on humidity is predicted for drought-tolerant animals, and the correlation between humidity and North American deer bone composition as corrected for local meteoric water is predicted within the scatter of the data. In contrast to an observed strong correlation between kangaroo $\delta^{18}O$ and humidity ($\Delta\delta^{18}O/\Delta h \sim 2.5 \pm 0.4‰/10\%$ r.h.), the predicted humidity dependence is only $1.3 - 1.7‰/10\%$ r.h., and it is inferred that drinking water in hot dry areas of Australia is enriched in ^{18}O over rainwater. Differences in physiology and water turnover readily explain the observed differences in $\delta^{18}O$ for several herbivore genera in East Africa, excepting antelopes. Antelope models are more sensitive to biological fractionations, and adjustments to the flux of transcutaneous water vapor within experimentally measured ranges allows their $\delta^{18}O$ values to be matched. Models of the seasonal changes of forage composition for two regions with dissimilar climates show that significant seasonal variations in animal isotope composition are expected, and that animals with different physiologies and diets track climate differently. Analysis of different genera with disparate sensitivities to surface water and humidity will allow the most accurate quantification of past climate changes.

1. INTRODUCTION

An important goal in stable isotope geology is to use the compositions of preserved ancient biological materials to infer climate and animal physiology in the past. This goal relies on the separation of the compositional effects of climatic factors like temperature and humidity from physiological factors like metabolism, water turnover, and diet. Unfortunately, recent oxygen isotope studies of modern biogenic phosphates have resulted in somewhat mixed interpretations regarding the importance of climate vs. physiology. Some studies show that even under similar climatic settings, different genera can have radically different compositions (Koch et al., 1990; Kohn et al., 1996a), other data show little if any variability (e.g., Longinelli, 1984; Luz et al., 1984; D'Angela and Longinelli, 1990), and still others ascribe an important control to local climate (Ayliffe and Chivas, 1990; Luz et al., 1990; Huertas et al., 1995). In making sense of the published data, it is critical to recognize the fundamental links between an animal's isotope composition, its isotope mass balance, and physiology. If sufficiently detailed information is available about diet, metabolism, water turnover, heat loss mechanisms, etc., then quantitative interpretations of the physiological effects on isotope compositions can be made, and if desired, such biologic factors can be subtracted out for paleoclimate interpretations.

The purpose of this paper is to refine predictive models of animal oxygen isotope compositions, and to see whether the refined model explains the disparate isotope trends that have been observed empirically. Several predictive models of the oxygen isotope composition of animals have been proposed (Luz and Kolodny, 1985; Schoeller et al., 1986; Speakman and Racey, 1987; Tatner, 1988; Ayliffe and Chivas, 1990; Luz et al., 1990; Bryant and Froelich, 1995), and it is worthwhile justifying a new treatment. As discussed below, an important consideration for modeling compositions are physiological and dietary differences among genera, which can affect oxygen isotope compositions by 5 to 10‰. Despite the obvious advances made by previous models, they are typically either too general and do not incorporate specific physiological information about each animal, or they are so specific as to be applicable only to a single species. These limitations further propagate into errors in accounting for or interpreting climatic factors using isotope data. Physiological adaptation imparts differing sensitivities to water composition, temperature, and humidity, and accurate interpretation of climate thus requires addressing the isotope effects of each animal's specific adaptations.

Any quantitative predictive model must address five general observations concerning oxygen isotope compositions of biogenic phosphates: (1) Phosphate oxygen isotope composition is strongly correlated with local meteoric water compositions (Longinelli, 1984; Luz et al., 1984, 1990; D'Angela and Longinelli, 1990). (2) There is a correlation between herbivore composition and local average humidity (Ayliffe and Chivas, 1990; Luz et al., 1990). (3) There is a dependence of tooth isotope composition on diet (e.g., Koch et al., 1990; Kohn et al., 1996a). (4) Different animal genera from the same location can have quite different isotope compositions (e.g., Koch et al., 1990; Kohn et al., 1996a). (5) There may be systematic changes of composition with time in an individual (Bryant et al., 1996; Fricke and O'Neil, 1996; Kohn et al., 1996b). The generalized

model described below is used not only to see whether these observations can be independently predicted, but also to provide insights into how the empirical trends reflect various climatic and physiological factors.

2. THE MODEL

There are three types of models that have been proposed for predicting oxygen isotope compositions. General models (Luz and Kolodny, 1985; Ayliffe and Chivas, 1990; Luz et al., 1990) identify the amounts and compositions of the most important isotope inputs and outputs of an animal, and the interrelationships among climate, food source, and animal $\delta^{18}O$, without specific quantitative application to free-living animals. Specific models (Schoeller et al., 1986; Tatner, 1988) assign values for input and output parameters to solve for a specific genus, without specifying how the model can be generalized to different animals. Hybrid models (Speakman and Racey, 1987; Bryant and Froelich, 1995) identify general input and output amounts and compositions, with application to specific animals; commonly oxygen amounts are ratioed and representative fractionations are used. The model developed here is a hybrid model, but uses a more complete genus-specific approach in assigning oxygen fluxes and isotope fractionations. New factors considered are differences in animal diet, respiratory H_2O vapor gain and loss, heat regulation and waste loss mechanisms, and body temperature (for cold-blooded animals), as well as oxygen isotope fractionations in plants (food source). Predicted and measured compositional differences arising from differing animal physiologies and diets reinforce the philosophy that accurate modeling requires a detailed understanding of animal and plant physiology as well as a knowledge of genus-specific oxygen fluxes and fractionations.

Because Bryant and Froelich (1995) used many of the same sources of data as the present study, it is especially important to distinguish the two approaches. Most importantly, Bryant and Froelich (1995) rely on average scaling equations, representative proportions of oxygen fluxes, and representative fractionations. This approach has the advantage that the mass balance equations are relatively simple, but at the disadvantage that the modeled compositions of animals whose physiology deviates from their assumptions may be inaccurate. Based on their theoretical calculations, Speakman and Racey (1987) argued that compositional differences of up to 30‰ could result from differences in physiology and diet. Systematic differences in isotope compositions of several permil are found at the tribe-level for animals from the same area (e.g., Kohn et al., 1996a), probably reflecting differing physiologies (total water turnover, proportions of oxygen fluxes, etc.), and significant physiological and dietary differences occur at the genus-level. Consequently, the approach adopted below is to use specific physiological information to develop genus-specific models. This approach has the advantage of reproducing more observed trends and allowing specific predictions for a wider range of animals, but at the disadvantage that only physiologically investigated genera can be modeled.

A detailed derivation of input and output amounts is presented in Appendix A, and the results are summarized below, followed by a discussion of input and output compositions. Oxygen fluxes and isotope fractionations are described in more detail for mammals because their compositions are strongly dependent on specific physiologal adaptations and diet, and because more isotope data are available. A less detailed discussion of aquatic animals is presented subsequently. The basic quantities that must be characterized prior to modeling are air temperature, relative humidity, diet and digestive characteristics, fraction of oxygen taken up in the lungs per breath, water content and temperature of exhaled air, free water content of food, total daily water turnover, free water content of feces, fraction of water lost as urine, skin permeability to water vapor loss, and the ratio of sweating to panting. Most terms are not strongly variant among species and diets, but some are highly genus-specific. Typical values are discussed below and in the appendices, but these should be cross-checked against specific physiological data for the animal in question.

3. OXYGEN INPUT AND OUTPUT AMOUNTS FOR TERRESTRIAL ANIMALS

3.1. Inputs

Inputs of oxygen considered are air oxygen, air water vapor, chemically bound oxygen in food, free water in food, and drinking water. All components except air water vapor have an important effect on predicted isotope compositions. The quantities of these inputs are related to four factors: metabolic requirements, diet, the extraction efficiency of oxygen from air, and water economy (the ratio of daily water turnover to energy expenditure).

Like Bryant and Froelich (1995), it is assumed for simplicity that energy expenditure can be scaled according to body mass (e.g., Nagy and Peterson, 1988), but because all other parameters excepting transcutaneous water vapor loss are ultimately scaled to energy use based on specific physiological data, exact energy values are not critical. Once a metabolic requirement is assigned, dietary parameters determine the mass of food ingested and the amount of air oxygen required. Based on assigned oxygen uptake, the amount of air fluxed through the lungs can then be determined, which for a specified air temperature and relative humidity also gives the input contribution of air H_2O. The product of the water content of the ingested food and the mass of food ingested gives the amount of food-associated free water taken in. Metabolic water comprises two oxygen components: chemically bound oxygen in the (dry) food matter itself, and air oxygen. The amounts of both these components are derivable from the mass of food digested and its proportions of protein, carbohydrate, and fat. That is, for an assigned metabolic requirement, the amounts of all oxygen input components except drinking water simply reflect oxygen uptake and diet.

The amount of drinking water is based on total water turnover rates, but it is quite important that assignment of total water fluxes is controversial, that the approach adopted here is different from previous approaches, and that some detailed discussion is therefore required. One useful measure of water use is the water economy index (WEI), which is the ratio of daily water turnover to energy expenditure (Nagy and Peterson, 1988). Although WEI is broadly constant (~0.2 mL/KJ) when all investigations of wild animals are considered, there are large variations among genera in excess of measurement errors. For example, typical values for desert-adapted animals are $\leq$0.15 and for humans are $\geq$0.3, whereas errors are at most $\pm$0.05. Furthermore, as noted by Bryant and Froelich (1995), there is a severe paucity of data for free-living animals with large body masses, whereas most isotope data have been collected from large herbivores.

One approach advocated by Bryant and Froelich (1995) is to base WEI on the larger data set for captive animals (summarized by Nagy

and Peterson, 1988); these data suggest that WEI scales with body mass, and increases with increasing mass. A significant implication is that larger animals derive proportionately more of their oxygen from drinking water, and will therefore track surface water compositions more closely than do smaller animals. For several reasons, the present model does not use a scaling relationship between mass and WEI. Firstly, according to Nagy and Peterson (1988), "[w]ater flux scales differently in the field than it does in captive animals, suggesting that quantitative ecological conclusions based on studies of water flux rates of captive animals may be misleading" (p. 17), and field studies do not resolve a correlation between body-size and WEI (Nagy and Peterson, 1988). Secondly, juvenile WEI is higher than for adults (e.g., data in Macfarlane and Howard, 1972; data in Schoeller, 1988; Williams et al., 1993), the reverse of the body-size trends indicated by studies of adult captive animals. Most importantly, however, experimental and observational studies of animals in arid or semi-arid settings clearly demonstrate that desert adaptation (low WEI) is physiologically and behaviorally controlled at the genus level, and is not simply related to body mass (e.g., Macfarlane, 1964; Taylor, 1968, 1975; Macfarlane and Howard, 1972; Maloiy, 1973; Dawson et al., 1975; King et al., 1978). At the most fundamental observational level, some animals drink water every day (e.g., reedbuck, ~30 kg), whereas others do not and even refuse to drink water when offered (e.g., oryx, ~170 kg), indicating radically different mass-independent WEIs (Spinage, 1986).

To account for widely variable physiological adaptations, the present model WEIs are based on specific physiological and observational data, rather than a scaling relationship. This restricts applicability of the models because despite extensive physiological data, not every animal is well studied. Nonetheless, even for physiologically unstudied animals, accurate estimates of water turnover can sometimes be derived from known behavior. For example, many animals do not drink, and their water turnover must equal the intake from air water vapor, metabolic water, and free water in food. Alternative rough estimates for animals that do drink include the scaling equations of Nagy and Peterson (1988) or of Bryant and Froelich (1995). Within the context of the present model, the latter equations simply require that WEI increases systematically with body mass, from ~0.10 at 1 kg to ~0.27 at 200 kg.

Once a WEI is established, total water turnover can be assigned based on daily metabolic requirements, and the amount of drinking water can then be determined simply by subtracting the contributions of air H_2O, metabolic water, and food-associated free water from the total water turnover.

3.2. Outputs

Outputs of oxygen considered are CO_2, urea or uric acid, fecal water, urine, respiratory and transcutaneous H_2O vapor, and sweat, of which all but urea and uric acid are important for modeling. Metabolism and diet determine CO_2 output, urea or uric acid loss, and fecal water. The amounts of oxygen excreted as urea or uric acid and as fecal water simply reflect the protein content of ingested food, food digestibility, and fecal water contents. The CO_2 output is equal to the air O_2 input corrected for urea or uric acid production and for air O_2 used for metabolic water. Urinary water loss is assigned according to genus, and is ordinarily 15–25% of total water turnover, but can be considerably lower (≤10%) or higher (30–50%) depending on salt concentrating capabilities and degree of water stress.

The difference between total water turnover and the sum of urea or uric acid loss, urine, and fecal water must be apportioned among oral respiration, nasal respiration, transcutaneous water vapor loss, and sweat. These proportions are rarely fully quantified for large animals, and as detailed in the Appendix, some simplifying assumptions were made (ordinarily the application of measurements on one genus to a different genus). No correction was made for the oxygen content or composition of dry feces. Fecal matter has a similar energy content as food, and a substantial portion of feces is in fact undigested food which can therefore contribute no oxygen or hydrogen to the overall O_2 and H_2O balances.

4. OXYGEN ISOTOPE INPUT AND OUTPUT COMPOSITIONS FOR TERRESTRIAL ANIMALS

4.1. Inputs

Compositions of input oxygen (air oxygen, drinking water, air water vapor, free water in food, and chemically bound oxygen in food) are related either to air oxygen or to surface water.

Air oxygen has a nearly constant composition worldwide of ~23.5‰ (Kroopnick and Craig, 1972), but lungs preferentially take up ^{16}O (Epstein and Zeiri, 1988; Zanconato et al., 1992). The composition of O_2 utilized in the lungs is determined by the fraction of O_2 used (oxygen utilization fraction) and a measurable z-factor:

$$z(‰) = [\delta^{18}O(\text{exhaled } O_2) - 23.5]/[\text{oxygen utilization fraction}] \quad (1)$$

The composition of intake oxygen is then

$$\delta^{18}O(O_2 \text{ utilized}) \sim 23.5‰ - z\cdot(1 - \text{oxygen utilization fraction}). \quad (2)$$

Z-factors are 9–12‰ for humans, and oxygen utilization fractions are ordinarily 15–25% for terrestrial animals (e.g., Stahl, 1967; Altman and Dittmer, 1971; Beaver et al., 1981; Schroter et al., 1987), leading to a typical $\delta^{18}O$ of O_2 (taken up) of ~15‰. Bryant and Froelich (1995) derived a value of 17.2‰ by ratioing respiratory equations of Stahl (1967) with a basal metabolic rate equation of McNab (1988) that they scaled by a factor of 2.5 to account for increased energy use during activity. Their resulting estimate of the oxygen utilization fraction is 30–35%, nearly 2 times higher than indicated by studies of terrestrial animals. For example, the scaling equations of Stahl (1967) imply typical mass-independent oxygen utilization fractions of ~15%. Use of the 17.2‰ value would systematically bias predicted phosphate compositions by ~0.5‰.

The z-values in humans increase (i.e., $\delta^{18}O$ decreases) as blood hemoglobin content increases (Epstein and Zeiri, 1988; Zanconato et al., 1992). Blood hemoglobin contents are not strongly variable (ISIS, 1992), implying that for a similar metabolic rate and oxygen utilization fraction, different animals should not fractionate intake oxygen differently. Human z-values also decrease ($\delta^{18}O$ increases) as metabolism increases (Zanconato et al., 1992). The metabolism-dependence of isotope fractionations is unstudied in nonhumans, but smaller animals with higher metabolisms tend to pant to cool themselves, which lowers the oxygen utilization fraction. Thus, the isotope effect of a higher metabolism (increased $\delta^{18}O$) should be offset by a decreased utilization fraction (decreased $\delta^{18}O$) because of panting. In the absence of data for nonhumans, isotope fractionation parameters for intake oxygen are assumed to be the same as for humans.

Surface (= drinking) water is assumed to be either known, or predictable from a general relationship between mean annual temperature and meteoric water composition (Dansgaard, 1964):

$$\delta^{18}O(\text{surface water}) \sim 0.69\cdot T(°C) - 13.6. \quad (3)$$

Water vapor in the air is assumed to be in equilibrium with surface water at the average air temperature (T in kelvins; Bottinga and Craig, 1969):

$$\delta^{18}O(\text{water vapor in air}) \sim \delta^{18}O(\text{surface water}) - 2.644 + 3206/T - 1.534 \times 10^6/T^2. \quad (4)$$

Food compositions depend on the type of food eaten. Free water in plant stems is essentially the same as surface water (e.g., Yakir, 1992) and so

$$\delta^{18}O(\text{stem water}) \sim \delta^{18}O(\text{surface water}). \quad (5)$$

In contrast, the average composition of free water in plant leaves is enriched in ^{18}O over surface water because of preferential evaporation of $H_2{}^{16}O$, and is ordinarily modeled using the simple Craig-

Gordon equation (Craig and Gordon, 1965; Sternberg et al., 1989; Flanagan et al., 1991):

$$\delta^{18}O(\text{leaf water}) \sim \delta^{18}O(\text{surface water}) + (1 - h)\cdot[\delta^{18}O(\text{surface water}) - \delta^{18}O(\text{water vapor in air}) + 16‰]. \quad (6)$$

This equation predicts that the degree of enrichment depends on ambient humidity. For example, at 75% r.h., average leaf water is enriched over surface water by ~6.5‰.

The oxygen isotope compositions of proteins and fats in plants have not been measured, and for simplicity were assumed to be the same as cellulose oxygen. Most data for leaf cellulose suggest that its composition is simply ~27‰ higher than leaf water (e.g., Sternberg et al., 1989):

$$\delta^{18}O(\text{leaf cellulose}) \sim \delta^{18}O(\text{leaf water}) + 27‰. \quad (7)$$

The compositional variability of nonleaf cellulose within plants is less clear, but the preponderance of data (e.g., Burk and Stuiver, 1981; Edwards et al., 1985; Yakir, 1992) supports a zero fractionation between stem and leaf cellulose:

$$\delta^{18}O(\text{stem cellulose}) \sim \delta^{18}O(\text{leaf water}) + 27‰ \quad (8)$$

probably because constituent sugars of stem cellulose are manufactured in leaves (conversely see discussion of Sternberg, 1989).

The apparently simple dependence of cellulose composition on surface water and humidity is additionally complicated by differences among plants in their photosynthetic capabilities. At high temperature and low humidity, photosynthesis in C3 plants (trees, shrubs, and cold climate grasses) slows or stops, whereas C4 plants (warm climate grasses) are less affected. This leads to higher $\delta^{18}O$ values in C4 plants than in C3 plants. The C3–C4 $\delta^{18}O$ offset is small in cool and humid environments (e.g., $\leq$1‰ in Wisconsin: Epstein et al., 1977), but attains 10‰ in hot semiarid settings (Sternberg et al., 1984). The approach adopted for modeling is to first assign an average leaf-water and cellulose $\delta^{18}O$ according to average relative humidity (i.e., the Craig-Gordon equation), and a C3–C4 isotope offset according to the climatic environment (10‰ in arid and semi-arid settings, 0‰ in cool and humid settings). The C3–C4 isotope offset is then split evenly about the average compositions, enriching C4 leaf water (and hence cellulose) and depleting C3 leaf water (and cellulose) in ^{18}O by the same amounts.

Allowing an explicit dependence of plant composition on humidity and surface water differs from previous models, in which the relative difference between food and surface water compositions was fixed. Use of a fixed fractionation leads to systematic animal $\delta^{18}O$ overestimates in humid settings and underestimates in dry settings. For example, the 21‰ fractionation assigned by Bryant and Froelich (1995) to leaf water vs. surface water implies an average relative humidity of ~20% (e.g., Dongmann et al., 1974; Flanagan et al., 1991). Most areas of the world inhabited by herbivores are much more humid (60–80% r.h.) and the assigned 21‰ value is ordinarily at least 10‰ too large. Depending on diet, this can lead to systematic errors in predicted isotope compositions of as much as 5‰.

For carnivorous or insectivorous animals, the composition of free water associated with food was assumed to be equal to the calculated body water composition of an average herbivore in the same climatic setting. The fractionation between animal proteins or fats and water is not well known, but one hydroxyl group on a protein is enriched in ^{18}O over water by ~7‰ (Tredget et al., 1993), and for lack of better data, this fractionation was assumed to apply to all bound oxygen in animal fats and proteins.

4.2. Outputs

Compositions of output oxygen (CO_2, urea or uric acid, fecal water, urine, respiratory and transcutaneous H_2O vapor, and sweat) are all related to body water composition. The fractionations of all these components except urea and uric acid have strong effects on modeled isotope compositions.

The fractionation of CO_2 and water is approximately (Pflug et al., 1979)

$$\delta^{18}O(CO_2) \sim \delta^{18}O\text{ (body water)} + 17604/T(K) - 17.93 \quad (9)$$

or at typical mammal body temperatures

$$\delta^{18}O(CO_2) \sim \delta^{18}O\text{ (body water)} + 38‰. \quad (10)$$

There are three different components to water vapor loss from animals. Water vapor lost through the mouth is in equilibrium with body water at body temperature (Schoeller et al., 1986a; Wong et al., 1988), with a fractionation described by Eqn. 4 above (Bottinga and Craig, 1969). At mammal body temperatures

$$\delta^{18}O(H_2O\text{ vapor, respiratory, mouth}) \sim \delta^{18}O\text{ (body water)} - 8‰. \quad (11)$$

Air expired through the nose is saturated with water at a temperature approximately half-way between the body and ambient temperatures (e.g., Langman et al., 1979), and an equilibrium fractionation corresponding to this lower temperature was assumed. For most animals and climates, this implies a fractionation of nasally lost H_2O of −15 to −18‰ relative to body water. The composition of water vapor lost directly through the skin is less well constrained, and reported fractionations range from −8‰ to −21‰ (Schoeller et al., 1986a; Coward, 1988; Haggarty et al., 1988). An intermediate value was used between the average of the data reported by Schoeller et al. (1986; −20‰) and the values commonly used to evaluate water turnover in human physiological studies (~ −15‰):

$$\delta^{18}O(H_2O\text{, vapor, skin}) \sim \delta^{18}O\text{ (body water)} - 18‰. \quad (12)$$

Clearly this preliminary value deserves additional investigation. Following arguments in Schoeller et al. (1986), Bryant and Froelich (1995) assumed a larger depletion for transcutaneous water vapor (−24‰), implying a nonbiologically mediated kinetic process (Dansgaard, 1964).

Sweat and urine have an isotope composition equal to body water (Schoeller et al., 1986; Wong et al., 1988), and fecal water was also assumed to be unfractionated relative to body water. The fractionation between urea or uric acid and water is not known, and was assumed to be zero. Because the oxygen flux associated with nitrogenous waste products is so small, this fractionation is not very important.

5. AQUATIC ANIMALS

A model for cetaceans was based on the measured water turnover and oxygen source data of Hui (1981), Andersen and Nielsen (1983), and Sokolov et al. (1994). Extremely rapid exchange of seawater and body water through the skin occurs (Hui, 1981; Andersen and Nielsen, 1983), implying extraordinarily high amounts of seawater input and body-water output for cetaceans. This rapid transcutaneous water exchange should virtually overwhelm all other sources of oxygen input or output. For example, assuming typical compositions and water contents of marine food consumed by dolphins (Hui, 1981; Sokolov et al., 1994), the water balance data of Hui (1981) and Andersen and Nielsen (1983) indicate roughly 98% of oxygen input is from seawater (with 0.3% and 1.2% inhaled as water vapor and oxygen respectively), whereas 98% of output is body water (with 0.6% and 1.1% exhaled as water vapor and CO_2 respectively). Predicted body water isotope compositions are expected to track ambient water composition almost perfectly, with only a small offset (−0.2‰) due to food and air oxygen compositions, CO_2 output, and water vapor differences between inhaled and exhaled air. Therefore, no special balancing of oxygen amounts or compositions is required.

Water exchange also occurs extremely rapidly in fish through gills, and on a per kilogram basis, water turnover rates are ~100–1000 times greater than for terrestrial mammals (Nagy and Peterson,

1988). Because with few exceptions fish spend all their time in water, it was assumed that their body water compositions and temperatures are essentially identical to the water in which they live (e.g., Kolodny et al., 1983), and as for cetaceans no special mass balancing of oxygen fluxes or of oxygen compositions is required.

Modeling of amphibians is less straightforward, because some spend little time in water and because of behavioral adaptations. Rapid transcutaneous water exchange is common, and tracers introduced into surrounding water appear inside frogs within a few minutes by exchange through their skin (Wentzell et al., 1993). Consequently, following rehydration all amphibians will likely have body water compositions similar to surface waters. Between rehydrations, oxygen fluxes are virtually all associated with water loss. Frogs and salamanders lose water by excreting a liquid onto their skins, from which it evaporates (Alvarado, 1979). If little exchange occurs between the isotopically enriched skin residues and body water, then body water composition will not change. For toads, water is lost as vapor and isotopic enrichment of residual body water is inevitable. The maximum water loss from toads is ~25% (Jørgensen, 1994), and assuming a 18‰ fractionation between water vapor and body water and a Rayleigh distillation process, the $\delta^{18}O$ of body water could be increased by as much as 6‰ over surface water. Such a strong enrichment is probably uncommon, because toads with access to free water or moist soil may rehydrate every 1–2 days, which implies a water loss of only 3–6% (Jørgensen, 1994). The maximum likely enrichment is then only 0.5–1.0‰, or 0.25–0.5‰ on average. That is, there is little reason to expect amphibians to have body water compositions significantly different from surface water compositions.

6. GENERAL CONSIDERATIONS

Once amounts and compositions of oxygen bearing materials are calculated specific to the animal's physiology and diet, the input and output oxygen isotope masses can be equated:

$$\sum M_{in,\alpha} \cdot \delta^{18}O_{\alpha} = \sum M_{out,\beta} \cdot \delta^{18}O_{\beta}. \quad (13)$$

where $M_{in,\alpha}$ and $M_{out,\beta}$ are the moles of oxygen associated with each input component (α) and each output component (β), $\delta^{18}O_{\alpha}$ and $\delta^{18}O_{\beta}$ are the compositions of the input and output components, and the sums are over all input and output components. This standard mass-balance equation is analogous to Eqn. 2 of Luz et al. (1984), Eqn. 3 of Ayliffe and Chivas (1990), and Eqn. 31 of Bryant and Froelich (1995), but distinguishes more oxygen fluxes and incorporates different fractionations. Because the compositions of all input and output components except air oxygen are expressed in terms of fractionations relative to surface water and body water, it is useful to recast Eqn. 13 accordingly:

$$\delta^{18}O_{BW} = \frac{M_{in,air\,O_2} \cdot \delta^{18}O_{air\,O_2} + \Sigma M_{in,\gamma} \times \Delta^{18}O_{\gamma\text{-}SW} - \Sigma M_{out,\beta} \cdot \Delta^{18}O_{\beta\text{-}BW}}{\Sigma M_{out,\beta}} + \frac{\Sigma M_{in,\gamma} \cdot \delta^{18}O_{SW}}{\Sigma M_{out,\beta}}, \quad (14)$$

where $M_{in,\gamma}$ refers to the input components other than air oxygen, $\delta^{18}O_{SW}$ and $\delta^{18}O_{BW}$ are the compositions of surface and body water, respectively, $\delta^{18}O_{\gamma\text{-}SW}$ is the fractionation between the input component γ and surface water, the summation over γ includes all input sources other than air, and $\Delta^{18}O_{\beta\text{-}BW}$ is the fractionation between the output component β and body water. The summations in Eqn. 14 are dependent on physiology and climate (especially humidity), but otherwise involve only specified fractionations, molar proportions, and the isotope composition of surface water. Therefore, as noted by Luz and Kolodny (1985), for a specified animal in a specified environment, Eqn. 14 can be simplified to a linear relationship:

$$\delta^{18}O_{BW} = A + B \cdot \delta^{18}O_{SW}, \quad (15)$$

where the first and second terms in both equations are the same. Specific examples of amounts and compositions of oxygen associated with different input and output components are listed in Appendix C for "typical" herbivores (ungulates), carnivores (eutherian), omnivorous rodents, insectivorous reptiles, and herbivorous birds. Simplified values of oxygen input and output amounts and compositions are listed in Table 1. These values are principally based on dietary data from Robbins (1983), water turnover data from Nagy and Peterson (1988), general reviews of reptile, amphibian, avian, rodent, and marsupial physiologies (e.g., Alvarado, 1979; Bentley, 1979; Fyhn, 1979; Minnich, 1979; Willoughby and Peaker, 1979), and specific physiological and dietary studies of East African animals (references included in Appendix C notes).

Several features of Eqn. 14 and the terms in Table 1 deserve special comment. (1) Of all the input compositions, only air oxygen is independent of surface water, and all the output compositions are related to body water composition. Therefore, body water composition should never track surface water composition perfectly. The slope will always be one minus the fraction of air O_2 in total input oxygen (second terms in Eqns. 14 and 15). The actual composition will then additionally reflect offsets associated with local climatic and physiological fractionations (first terms in Eqns. 14 and 15). Because for terrestrial mammals, O_2 ordinarily constitutes approximately 25–30% of the total input oxygen, body water composition should be related to surface water composition by a factor of 0.7–0.75. A qualitatively similar but quantitatively different conclusion was reached by Bryant and Froelich (1995). In contrast, the ratio of air O_2 to total oxygen input is quite small for cetaceans, and they should very nearly track water composition. (2) The dependence of body water composition on surface water does not depend that strongly on whether an animal drinks surface water. Most animals derive the bulk of their water from metabolism of food and from free water associated with food (Table 1 and Appendix C). The correlation between animal and surface water compositions occurs primarily because food composition tracks surface water, and not because of direct drinking water input. (3) Most animals will inevitably lose a significant portion of their body water as vapor simply because they must breathe. Because water vapor is substantially depleted in ^{18}O compared with liquid water, this effect tends to keep body water $\delta^{18}O$ fairly high. (4) Animals use a large amount of water in dissipating heat (cutaneous water loss and panting = ~30–35%). Because of differences in the isotope compositions of liquid water vs. vapor, whether an animal sweats or pants to lose heat should affect body compositions.

The sensitivity of the calculations to perturbations in the

Table 1. Simplified Summary of Oxygen Fluxes and Isotope Compositions

Source	Herbivore	Carnivore	Herbivorous Bird	Omnivorous Rodent	Reptile	Turkana Gazelle	Turkana Dikdik	Turkana Goat	Turkana Zebra	Turkana Oryx
Amounts(%)										
Air O_2	24	26	30	36	24	32	36	28	24	32
Air H_2O	3	4	4	5	4	7	8	6	5	7
Bound O_2 in food	8	1	9	6	1	11	11	9	8	11
Free H_2O in food	48	27	44	45	34	50	46	43	55	50
Drinking H_2O	17	42	13	7	36	0	0	13	7	0
Fecal H_2O	12	2	22	5	3	8	4	7	28	12
Urea	0	1	1	0	1	0	1	0	0	0
Urine	19	19	0	14	12	10	10	18	19	10
Nasal H_2O	5	5	12	7	5	7	7	6	5	7
Skin Vapor H_2O	7	4	26	21	47	9	12	9	6	9
Oral H_2O	22	43	13	20	12	30	31	22	12	18
Sweat	12	4	0	0	0	4	2	11	7	13
CO_2	23	21	27	32	20	31	34	27	23	31
Compositions (‰)										
$\delta^{18}O_{Air}$	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1
$\Delta_{Air\ H_2O\ -\ SW}$	-10.0	-10.0	-10.0	-10.0	-10.0	-8.8	-8.8	-8.8	-8.8	-8.8
$\Delta_{Food\ O_2\ -\ SW}$	33.5	10.4	33.5	22.0	10.4	40.2	35.2	44.2	45.2	45.2
$\Delta_{Food\ H_2O\ -\ SW}$	3.2	3.4	3.2	3.3	3.4	10.0	7.4	8.6	9.1	9.1
$\delta^{18}O_{SW}$	-3.2	-3.2	-3.2	-3.2	-3.2	6.0	6.0	6.0	6.0	6.0
Δ(i-BW)										
Fecal H_2O	0	0	0	0	0	0	0	0	0	0
Urine	0	0	0	0	0	0	0	0	0	0
Nasal H_2O	-17.0	-17.0	-17.0	-17.0	-18.3	-16.3	-16.3	-16.3	-16.3	-16.3
Skin H_2O	-18.0	-18.0	-18.0	-18.0	-18.0	-18.0	-18.0	-18.0	-18.0	-18.0
Oral H_2O	-8.2	-8.2	-8.2	-8.2	-10.0	-8.2	-8.2	-8.2	-8.2	-8.2
Sweat	0	0	0	0	0	0	0	0	0	0
CO_2	38.6	38.6	38.6	38.6	43.2	38.6	38.6	38.6	38.6	38.6
A:	2.64	1.47	5.83	2.22	6.39	6.84	4.71	5.52	6.04	5.85
B:	0.76	0.74	0.71	0.64	0.76	0.68	0.64	0.72	0.76	0.68
$\delta^{18}O$ (Phosphate)	17.7	16.6	20.5	17.7	26.4	28.4	26.1	27.3	28.1	27.4

Note: Turkana animals were modeled at T=29°C and r.h. = 47%. Other animals were modeled at T=15°C and r.h. = 75%. A detailed listing of input parameters and sources of data is given in Appendix C. Final A and B terms are for the relationship between animal body water and meteoric (drinking) water compositions: BW(‰) = A(‰)+B*SW(‰).

physiological parameters and assumed fractionations is listed in Table 2. For most animals in temperate settings, uncertainties in body compositions are moderately, but not inordinately dependent on physiological uncertainties. The most important factors are cutaneous water vapor fluxes and fractionations, the composition of food, and the amount of CO_2 exhaled, which contribute 80–90% to the estimated uncertainty. For example, a 2‰ change in food composition can change body compositions of some animals by as much as 1‰, and variations in the amounts and compositions of H_2O that are output as vapor can readily shift body compositions by 0.5–2‰. Fortunately, many components for which oxygen isotope fractionations are difficult to measure (protein, fat, urea, and uric acid) ordinarily contribute least to the oxygen mass balance (<2% each), and results are insensitive to these assumed fractionations. An overall estimate of the uncertainty in average animal composition is probably ±1–2‰, but clearly genera-dependent physiological and dietary differences can cause substantial deviations from "average" compositions.

Figure 1 illustrates the importance of incorporating specific dietary and physiological factors in accurately modeling isotope compositions of herbivores. The predictions were standardized at 15°C and 75% r.h., and are based on a model for goats (Appendix C, Table 1), because goats have intermediate dietary and physiological properties. For example, they are not especially water dependent or independent, they consume both C4 and C3 vegetation, they are not selective feeders, they use both panting and sweating for heat regulation, and there are both domestic and wild varieties. Figure 1a-b show that animals that pant for heat regulation, consume C4 plants, and select leaves should have a systematically higher $\delta^{18}O$ than animals that sweat, consume C3 plants, and are less selective or prefer stems. Domestic animals tend to consume dryer food and drink more than wild animals, because herding practices prevent animals from feeding late at night and early in the morning when it is most humid and plants have their highest water content. Low water content in plants causes a decrease in herbivore $\delta^{18}O$ (Fig. 1c), because more low $\delta^{18}O$ surface water must be drunk to maintain water balance. Differences in WEI have a weak effect on predicted $\delta^{18}O$ (Fig. 1d). Although animals with low WEI obtain proportionately more of their oxygen from high $\delta^{18}O$ plants, there is less oxygen taken in overall to counterbalance the amount of high $\delta^{18}O$ CO_2 exhaled (e.g., dikdik vs. average herbivore, Table 1). Water loss through the skin has a strong effect on predicted $\delta^{18}O$ (Fig. 1e-f), a point that has significant implications for interpreting measured compositions, as explored in detail below. Animals that pant exclusively or have low skin resistance to cutaneous water vapor loss are predicted to have a higher $\delta^{18}O$ than animals that sweat or that have high skin resistance. This occurs

Table 2. Sensitivity of Models to Input Parameters

Animal	Herbivore	Carnivore	Herb. Bird	Rodent	Ins. Reptile
Baseline Composition	17.66	16.57	20.51	17.66	26.35
Differences					
H_2O Air vapor (mo)/2	0.18	0.19	0.21	0.26	0.18
Food ingested *1.05	0.22	0.14	0.28	0.22	0.15
Food O_2 content*1.05	-0.03	-0.02	-0.05	-0.06	-0.03
Food H_2 content*1.05	0.19	0.10	0.25	0.20	0.11
Free H_2O in food*1.05	0.25	0.14	0.23	0.23	0.19
Water Turnover*1.10	-0.02	0.23	0.20	0.20	0.45
Uncertainty	±0.43	±0.37	±0.53	±0.50	±0.55
Fraction Fecal H_2O+0.05	-0.11	-0.04	0.00	-0.11	-0.06
Nasal H_2O*1.10	0.07	0.05	0.05	0.06	0.04
Skin H_2O/2	-0.50	-0.22	-1.25	-1.02	-1.88
Oral H_2O*1.10	0.18	0.38	0.04	0.16	0.07
Urine H_2O*1.10	-0.07	-0.14	---	-0.11	-0.11
Sweat/(Sw+Pant) + 0.1	-0.19	-0.29	---	---	---
CO_2*1.05	-0.43	-0.40	-0.68	-0.71	-0.47
Uncertainty	±0.73	±0.68	±1.42	±1.26	±1.94
O_2 uptake factor + 0.05	0.00	0.09	0.13	0.16	0.12
Z (‰) + 1.0	-0.19	-0.21	-0.24	-0.29	-0.19
$\delta^{18}O$ (food) + 2‰	0.98	0.56	0.89	1.01	0.72
leaf/(leaf+stem)+0.1	0.32	---	0.29	0.14	---
Uncertainty	±1.05	±0.60	±0.98	±1.07	±0.75
$\Delta^{18}O$ (CO_2)+1‰	-0.22	-0.21	-0.27	-0.32	-0.20
$\Delta^{18}O$ (skin vapor)+4‰	-0.28	-0.16	-1.08	-0.83	-1.87
$\Delta^{18}O$ (Urea/U.A.)+5‰	-0.01	-0.05	-0.02	-0.05	-0.07
Uncertainty	±0.36	±0.27	±1.11	±0.89	±1.88
Total Uncertainty Range	±1.39	±1.02	±2.12	±1.94	±2.86

Note: Each uncertainty was derived numerically by perturbing the parameter by the specified amount, determining the change to the predicted $\delta^{18}O$, and subtracting from the baseline $\delta^{18}O$. This approach assumes no correlation, which is a good approximation for the components that contribute most to the overall uncertainty (e.g., cutaneous water vapor fluxes and fractionations, the composition of food, and the amount of CO_2 exhaled). Cumulative uncertainties are obtained from root mean square of the constituent uncertainties. "---" indicates that the assigned perturbation is inapplicable to this organism.

because water vapor has a much lower $\delta^{18}O$ than liquid water, and the preferential loss of low $\delta^{18}O$ vapor enriches residual body water in ^{18}O. The magnitude of this effect depends in part on the actual fractionation between cutaneous water vapor and body water, which is not well known (Appendix B).

7. COMPARISON OF MODEL RESULTS TO DATA

7.1. Dependence of $\delta^{18}O$ on Meteoric Water

Figure 2 shows a comparison of the model predictions with most of the published data for warm-blooded animals. Models were computed for warm-blooded animals by first calculating a composition at 15°C and 75% relative humidity (an estimated average for the entire data set), and then simply varying meteoric water composition. Curves for cold-blooded animals were constructed assuming that ambient temperature is related to the $\delta^{18}O$ of surface water according to the equation of Dansgaard (1964). The temperatures assigned this way are meant to be illustrative only, rather than realistic estimates of the ranges of temperature and surface water $\delta^{18}O$ over which cold-blooded animals ordinarily live: the range of water compositions in Fig. 2 (−25‰ to +10‰) implies a temperature range of −16.5°C to +34.2°C. Herbivorous and omnivorous species were assumed to consume equal proportions of C3 and C4 plants. Compositions of Australian kangaroos and wallabies, and of North American deer are not included because they show a clear correlation with local humidity. As discussed in detail below, lower humidity causes an increase in plant $\delta^{18}O$, and hence an increase in the $\delta^{18}O$ of plant consumers.

Virtually all reported data are for large herbivores and for modern humans, although substantial data have also been collected for whales, dolphins, and mice. No attempt was made to model the human data, because humans modify local environments and do not necessarily obtain foods locally. For example, some interpreters of water turnover rates in humans reduce the rate of transcutaneous water vapor loss by 50% to account for clothing (e.g., Schoeller et al., 1986b). The large amount of scatter exhibited by the data in Fig. 2 nearly precludes critical evaluation of the models, but the models and data show reasonable correspondence. Some explanations for the large amount of scatter as well as any misfit between models and data include differences in humidity between investigated areas (Ayliffe and Chivas, 1990; Luz et al., 1990), differences in drinking water vs. rainwater compositions (Ayliffe et al., 1992), and higher $\delta^{18}O$ values of local water during seasonal bone growth (Luz et al., 1990). For example, most of the areas with high $\delta^{18}O$ meteoric water values are also dryer, whereas the model

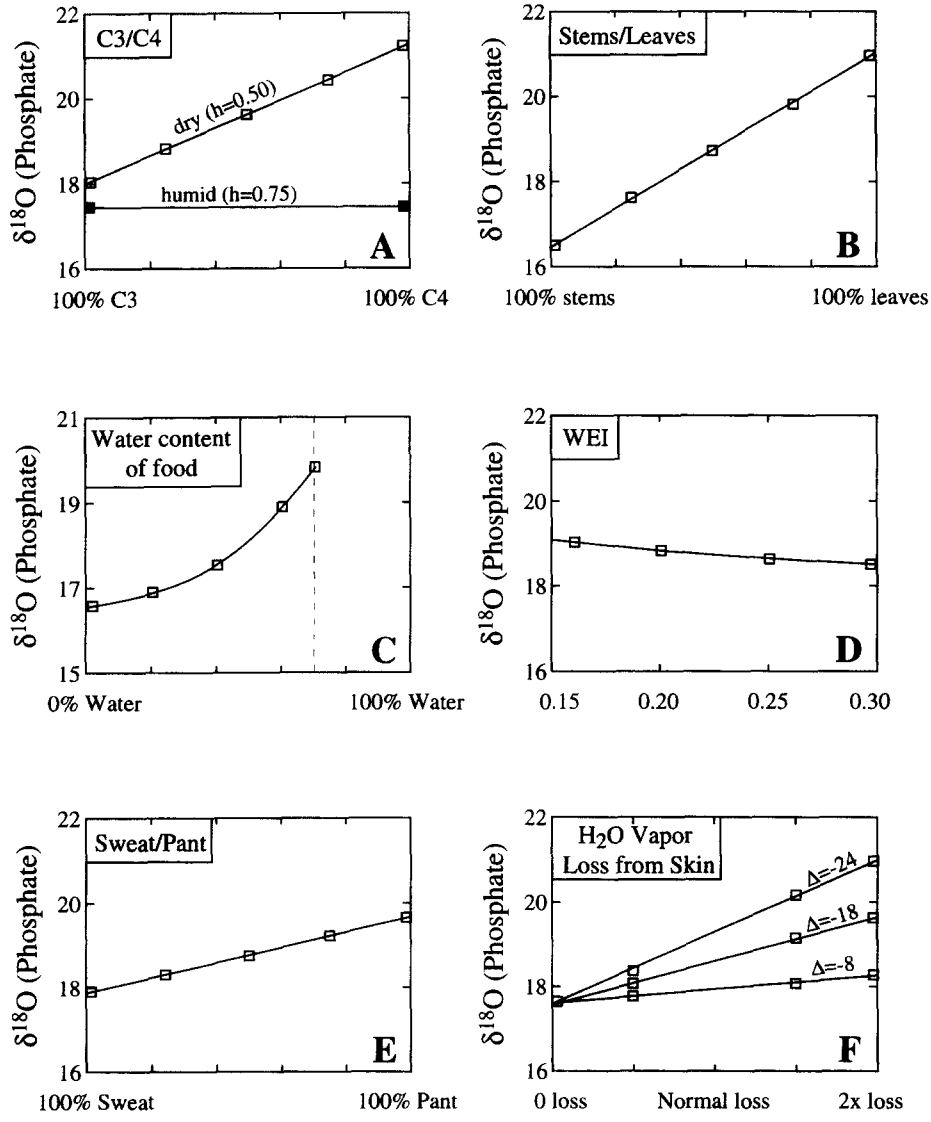

FIG. 1. Effects of dietary and physiological differences on predicted biogenic phosphate $\delta^{18}O$, using the physiology of goats as a baseline. (a) Under dry conditions (open squares; relative humidity = 50%), consumption of C4 plants (warm climate grasses) increases animal $\delta^{18}O$ compared to consumption of C3 plants (cool climate trees and shrubs), because of the enrichment of C4 $\delta^{18}O$ over C3 (e.g., Sternberg et al., 1984). In cool, humid settings (solid squares; h = 75%), the effect is much smaller or eliminated (e.g., data in Epstein et al., 1977). (b) Preferential consumption of leaves increases animal $\delta^{18}O$ because leaf water is enriched in $\delta^{18}O$ over stem water (e.g., Yakir, 1992). (c) Consumption of dry food (e.g., because of domestication) causes a decrease in $\delta^{18}O$ because more low $\delta^{18}O$ surface water must be drunk to maintain water balance. Models were not constructed at food water contents greater than 70% (dashed line), because water flux is then so high that major modifications to the proportions of oxygen loss avenues would be required. (d) The water economy index (ratio of water turnover to energy expenditure) has only a small effect on $\delta^{18}O$. An increase in the $\delta^{18}O$ of oxygen influxes is offset by a higher proportion of high $\delta^{18}O$ CO_2 exhaled (Table 1). (e) Because liquid water (sweat) has a higher $\delta^{18}O$ compared to water vapor, animals that pant should have a higher $\delta^{18}O$ than animals that sweat. (f) The sensitivity of skin to diffusional loss of water vapor has a moderate effect on predicted $\delta^{18}O$ when permeabilities are high. Different curves show the effect of different fractionations between body water and water vapor lost through the skin.

curves were calculated with a fixed humidity. If humidity were systematically decreased with increasing meteoric water $\delta^{18}O$, predicted animal $\delta^{18}O$ would be higher.

The locations and slopes of the model curves for reptiles and fish + amphibians require additional explanation. The oxygen isotope fractionation between phosphate and water is temperature-sensitive, increasing with decreasing temperature (Kolodny et al., 1983):

$$\delta^{18}O(\text{Phosphate}) \sim \delta^{18}O(\text{Water}) + 25.9 - T(°C)/4.38. \quad (16)$$

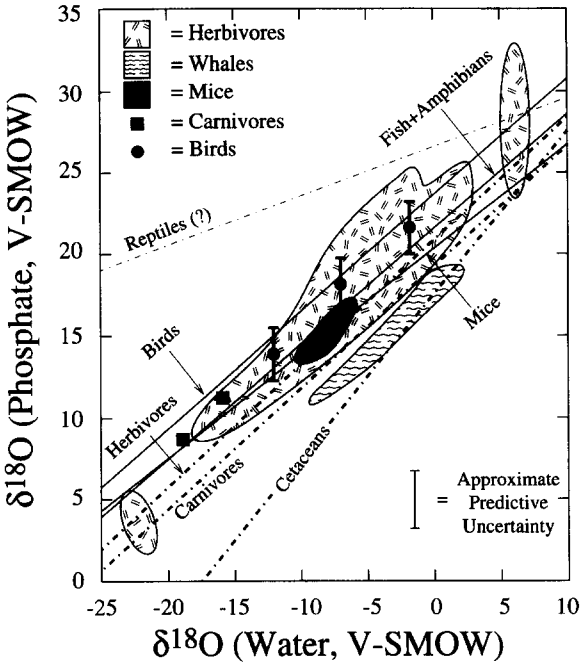

FIG. 2. Comparison of model predictions with measured compositions on plot of mammal phosphate vs. local rain water composition, showing reasonably good fits. Whales have low $\delta^{18}O$ because they exchange body water with low $\delta^{18}O$ ambient water extremely rapidly. The points for bird phosphate are based on measured body water compositions assuming a fractionation between water and phosphate of 17.5‰. Bird compositions are predicted to be higher than for mammals because they lose a greater proportion of water as transcutaneous vapor (Table 1). Predicted reptile compositions are high because they lose most of their water as transcutaneous vapor (Minnich, 1979), and because as cold-blooded animals their phosphate $\delta^{18}O$ is sensitive to ambient temperature. Data are from Longinelli (1984), Luz et al. (1984), Tatner (1990), Yoshida and Miyazaki (1991), Ayliffe et al. (1992), Barrick et al. (1992), Bryant et al. (1994), Huertas et al. (1995), and Kohn et al. (1996a).

Therefore, if reptile, amphibian, or fish body temperature is on average equal to the average air or water temperature, then the phosphate $\delta^{18}O$ of a cold-blooded animal should tend to be greater than that of a coexisting warm-blooded animal (e.g., reptiles vs. herbivores and fish vs. whales). This effect is magnified at low temperature, and leads to a noticeably shallower slope in Fig. 2 for reptiles vs. mammals or birds, and for fish vs. cetaceans. In the case of fish + amphibians, the resulting line is fortuitously nearly coincident with the curve for thermoregulating animals. Reptiles and amphibians employ many behavioral mechanisms to maintain relatively high and constant body temperatures, and many varieties hibernate (e.g., Alvarado, 1979; Minnich, 1979). Therefore, it is inaccurate to assume that body temperature equals ambient temperature, and these two curves should likely be plotted at lower $\delta^{18}O$. For example, measurements by L. Ayliffe of the $\delta^{18}O$ of Australian reptile bones are 2–3‰ lower than predicted (L. Ayliffe, pers. commun., 1996), which she suggests may be the result of behavioral regulation of body temperature through burrowing, sunbathing, and/or hibernation. The magnitude of the correction over a range of climatic conditions is not presently known and will probably require direct measurements of reptile and amphibian body water or phosphate composition in a variety of settings. In contrast, the fish curve should be more accurate at temperatures above 0°C ($\delta^{18}O$(water) > ~ −13.6‰; Dansgaard, 1964), because water turnover rates are so high (Nagy and Peterson, 1988) and because there is little capability of varying temperature significantly from the surrounding water.

7.2. Dependence of $\delta^{18}O$ on Climatic Factors: Humidity

Two different studies (Ayliffe and Chivas, 1990; Luz et al., 1990) first indicated that local humidity can have an important effect on the $\delta^{18}O$ of biogenic phosphate. These extensive data for macropods and deer (Fig. 3) demonstrate the correlation between humidity and the composition of bone phosphate as corrected for local rainwater composition. For kangaroos and wallabies from Australia, the data of Ayliffe and Chivas (1990) define a steep negative slope on plots of bone $\delta^{18}O$ vs. local humidity ($-25 \pm 4‰ \cdot \Delta h$; h

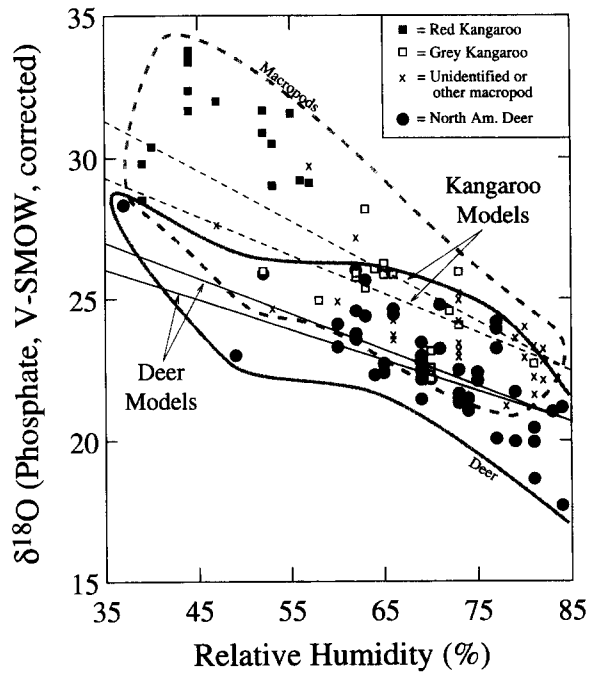

FIG. 3. Comparison of model predictions for kangaroos (thin dashed lines) and North American deer (thin solid lines) with measured compositions on plot of mammal phosphate corrected for local rain water vs. humidity. Thick gray dashed and solid curves outline the two data fields. Shallowly sloped models assume no temperature- or humidity-dependence in cutaneous water vapor loss; more steeply sloped lines assume a twofold increase in cutaneous water vapor loss at the lowest humidities. Data for deer are fit within uncertainty. The strong apparent dependence of kangaroo phosphate composition on humidity is less consistent with the models. Possibly the drinking water composition in hot dry areas of Australia does not correspond to rain water compositions because of preferential evaporative loss of $H_2{}^{16}O$. Data from Ayliffe and Chivas (1990) and Luz et al. (1990).

= relative humidity from 0 to 1). Red kangaroos, which live in hot, dry areas have an average $\delta^{18}O$ that is almost 10‰ higher than grey kangaroos, which live in wetter areas. Ayliffe and Chivas (1990) argued that this compositional difference could not be a result of differences in surface water composition because rainwater composition across Australia is fairly constant. They also argued that the trend could not be due to physiological differences because where red and grey kangaroo ranges overlap, their bone phosphate compositions are similar. For deer from North America, the data of Luz et al. (1990) suggest a dependence of $-17 \pm 4‰ \cdot \Delta h$. In both studies, the source of the humidity dependence of animals has been ascribed to the dependence of food source compositions on humidity according to the Craig-Gordon plant model. Because the Craig-Gordon model accounts for a change in leaf composition of $\sim -30‰ \cdot \Delta h$, it is conceivable that a similar effect could be found in some animals.

The theoretical model developed above allows a test of the humidity hypothesis, and the predicted results are shown as shallowly-sloped lines in Fig. 3. The data for North American deer are fairly scattered, and as described by Luz et al. (1990) the correction for meteoric water is uncertain because animals may have distinct bone-growth seasons, usually in summer when local water has a higher $\delta^{18}O$. The most important issue, however, is whether the slope of the data can be matched. The data suggest a minimum slope of $-13‰ \cdot \Delta h$, whereas the model suggests a slope closer to $-11‰ \cdot \Delta h$. In view of the uncertainties in the measurements and models, this difference is probably not significant. In contrast, the models do not fit the data for kangaroos, and indicate a slope of only $\sim -13‰ \cdot \Delta h$. In general, if the dependence of herbivore isotope composition is solely the result of diet, then because the plant components that are humidity-dependent ordinarily constitute less than 50% of the oxygen input in an animal, plots of herbivore $\delta^{18}O$ vs. humidity should have slopes shallower than $-15‰ \cdot \Delta h$. Consequently, the substantially steeper slope to the kangaroo data cannot be explained by dietary effects alone.

One possible reason for some of the misfit between models and data concerns cutaneous water vapor loss. As described by Hulbert and Dawson (1974), cutaneous water vapor loss from sheep increases by a factor of 2–3 between 20 and 40°C, and transcutaneous water vapor losses in humans show similar increases with increasing temperature and decreasing humidity (Grice et al., 1971, 1972; Appendix B). Such an enhancement in skin water vapor flux might be expected for animals analyzed by Luz et al. (1990) and Ayliffe and Chivas (1990) from dry areas. Because water vapor lost from the skin has one of the lowest $\delta^{18}O$ signatures, expected humidity dependencies might be enhanced through increasing the $\delta^{18}O$ of animals inhabiting dry areas (e.g., Fig. 1f). Increasing water vapor loss by a factor of 2 increases the model kangaroo slope from $-13‰ \cdot \Delta h$ to $-17‰ \cdot \Delta h$ and the deer slope from $-11‰ \cdot \Delta h$ to $-13‰ \cdot \Delta h$ (steeply-sloped lines in Fig. 3). Although this does improve the model fits, the slope for the kangaroos is still not fit well, and there are significant outliers. An additional mechanism likely affects the compositions of some animals.

An additional explanation for the disparity between the models and kangaroo data is the possibility that surface drinking water is not always the same as rainwater (e.g., Ayliffe et al., 1992). Many groundwaters and surface waters in arid areas of Australia have undergone evaporative loss of $H_2{}^{16}O$, and measured $\delta^{18}O$ may be enriched by 5–10‰ over regional precipitation and groundwater sources (Calf et al., 1991; Simpson and Herczeg, 1991a,b; Herczeg et al., 1992). As a result, the assumption that drinking water composition is nearly constant across Australia may be inaccurate. The degree to which drinking water is enriched in ^{18}O would naturally depend on temperature and humidity. As red kangaroos live in hot, dry areas, their drinking water would be most susceptible to evaporative enrichment in ^{18}O and their bone phosphate $\delta^{18}O$ would be higher than for grey kangaroos in cooler, moister areas. This interpretation also allows reevaluation of the herbivore field in Fig. 2, which has an anomalous lobe towards high $\delta^{18}O$ off the trend delineated by other animals. This perturbation is principally defined by elephants that lived in southern Sudan, which has a high average temperature and low average humidity. It is possible that the water the elephants drank and that supported plant growth was also evaporatively enriched in ^{18}O, and that some of the elephant data should be plotted with a higher source water $\delta^{18}O$, closer to the trend of the other data. A similar conclusion regarding uncertainties in drinking water compositions was reached by Bryant and Froelich (1995), Ayliffe et al. (1992), and Luz et al. (1990).

7.3. Dependence of $\delta^{18}O$ on Animal Tribe and Family: Kenyan Herbivores

Both Koch et al. (1990) and Kohn et al. (1996a) found that different herbivorous mammalian tribes and families in Kenya have systematically different oxygen isotope compositions, with differences in a single area of as much as 5–7‰. The $\delta^{18}O$ of phosphate vs. $\delta^{13}C$ is shown in Fig. 4 for these data. Koch et al. (1990) analyzed the structural carbonate component of bone, and a correction of −8.5‰ was applied to obtain the phosphate composition (Longinelli and Nuti, 1973). The differences in composition for the two sets of data largely reflect differences in local drinking water composition. Cerling et al. (1988) and Johnson et al. (1991) report surface water compositions ($\sim +6‰$) for the area in northern Kenya studied by Kohn et al. (1996a). Surface water $\delta^{18}O$ values have not been described for the area in southern Kenya studied by Koch et al. (1990), but based on zebra compositions, drinking water there is probably 0 to 1‰. This estimate is based on a measured carbonate composition for southern zebra of 30.7‰ (Koch et al., 1990), a fractionation of 8.5‰ between structural carbonate and phosphate (Longinelli and Nuti, 1973), a fractionation of 17.5‰ between phosphate and body water (Longinelli and Nuti, 1973; Kolodny et al., 1983; Longinelli, 1984; Luz and Kolodny, 1985), and a 5‰ fractionation between zebra body water and drinking water as deduced from the northern Kenya data. An alternative estimate can be based on the data for hippos. Because hippos spend a very large proportion of their time in water, it is expected that their body water

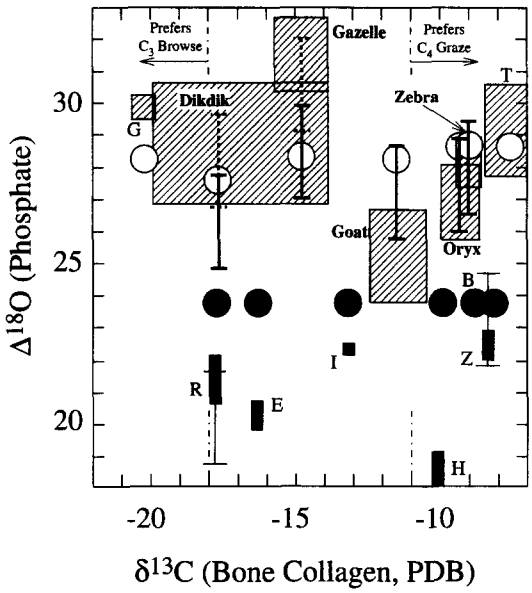

FIG. 4. Summary of $\delta^{18}O$ of herbivore phophate vs. $\delta^{13}C$ determined from data of Koch et al. (1990; southern Kenya, black boxes) and Kohn et al. (1996a; northern Kenya; ruled boxes). Letters correspond to specific animals (G = gerenuk; T = topi; R = rhinoceros; E = elephant; I = impala; B = buffalo; Z = zebra; H = hippopotamus). Diet probably causes the trend towards lower $\delta^{18}O$ with decreasing $\delta^{13}C$ that is observed for goat, oryx, zebra, and topi in northern Kenya, and for southern Kenyan animals (excepting hippopotamus). C4 plants have both high $\delta^{13}C$ and high $\delta^{18}O$ compared with C3 plants. Error bars show theoretical predictions of average phosphate composition using the model developed in this paper. Thin error bars correspond to generalized models of C4 and C3 feeders in southern Kenya, and the difference in predicted $\delta^{18}O$ reflects different diets. Thick error bars correspond to specific genera in northern Kenya, and the differences in predicted $\delta^{18}O$ reflect both diet and physiology. Dashed error bars for dikdik and gazelle show effect of doubling transcutaneous water vapor losses. White and gray dots show theoretical predictions of average tooth composition for animals from northern and southern Kenya respectively using the body-size-dependent equations of Bryant and Froelich (1995). For the size ranges encountered (5–250 kg in northern Kenya; 50–4000 kg in southern Kenya; Estes, 1991), the dependence of $\delta^{18}O$ on body size according to the Bryant and Froelich (1995) model is quite weak. Size of dots and error bars reflects stated uncertainties in predicted $\delta^{18}O$. The range in $\delta^{18}O$ observed for single species in northern Kenya is likely due to seasonal changes in isotope composition (Kohn et al., 1996b). The compositions observed for southern Kenya and for C4 feeders in northern Kenya are predicted well by the model developed in this paper, which accounts for known dietary and physiological differences, but are less well fit by the theoretical model of Bryant and Froelich (1995). The high $\delta^{18}O$ observed for gerenuk, dikdik, and gazelle in northern Kenya are only consistent with the genus-specific models which include additional transcutaneous water vapor loss.

composition should be similar to surface water. The measured structural carbonate composition is ~25.8‰ (Koch et al., 1990), and given the same fractionations among structural carbonate, phosphate, and body water, the calculated surface water composition is again 0 to 1‰. This water composition is of course predicated on the accuracy of the fractionations between the structural carbonate and phosphate components, and any errors in assumed fractionations will propagate into systematic inaccuracies in the calculated water composition.

The data shown in Fig. 4 demonstrate several important isotope trends. The data of Koch et al. (1990) show a positive correlation between oxygen and carbon isotope compositions (except for hippos). This likely reflects the isotope offset between C3 and C4 plants in relatively dry settings, as C4-feeders should have a higher $\delta^{18}O$ (and higher $\delta^{13}C$) than C3-feeders (Fig. 1a; Koch et al., 1990). For example, assuming an "average herbivore" physiology (Appendix C) and a body size similar to the average of the animals analyzed by Koch et al. (1990; ~1000 kg), the predicted compositions corresponding to a C4 and a C3 diet are shown by the thin error bars in Fig. 4. These predictions are in reasonable agreement with the measurements. Many herbivores derive ~30% of their oxygen from leaf cellulose and water, and because the C3–C4 isotope offset is ~10‰ in semiarid settings (Sternberg et al., 1984), diet alone should affect compositions by ~3‰. Predicted compositions for the same animals using the Bryant and Froelich (1995) equations (gray dots, Fig. 4) are essentially constant for all large-bodied animals in the same area, and do not match the data of Koch et al. (1990) as well. The discrepancies between the measured compositions and the predictions based on the equations of Bryant and Froelich (1995) may in part be due to uncertainties in drinking water compositions, but a contributing factor must also be dietary differences, which are not accounted for in their model.

The data of Kohn et al. (1996a) show similar oxygen and carbon isotope trends for either C4-feeders (goat, oryx, zebra, and topi) or for C3-feeders and mixed-feeders (gerenuk, dikdik, and gazelle), but there is an additional oxygen isotope offset between the two groups. Kohn et al. (1996a) ruled out the possibility that the different animal groups were sampling different surface waters because the animals all inhabit the same small area. The possibility of sampling bias was also eliminated because detailed analysis of isotope zoning in teeth indicates that seasonal variations are smaller than the observed isotope differences among the tribes and genera (Kohn et al., 1996b). The most likely explanation involves differing physiologies and diets. Oryx, zebra, and topi all sweat and are not very selective in choosing leaves vs. stems as food, whereas the antelopes (gazelle, dikdik, and gerenuk) pant and select leaves. Both differences should tend to elevate antelope $\delta^{18}O$ over the other animals (Fig. 1b, e). No similar offset would be expected for the data of Koch et al. (1990), which comprises large animals that do not select leaves vs. stems and, excepting impala, do not pant significantly.

For several of the animals (zebra, gazelle, dikdik, goat, and oryx), sufficient data are available to attempt quantitative investigation of the isotope effects of differing physiologies and diets. Parameters used for modeling are listed in detail in Appendix C and illustrate the physiological differences among these herbivores. Compared to many herbivores, these animals are all relatively drought tolerant. Results of applying the methods described above and the mass-dependent equations of Bryant and Froelich (1995) are shown in Fig. 4 by thick error bars and white dots, respec-

tively. As found for the animals in southern Kenya, differences in predicted compositions using the Bryant and Froelich (1995) model are small for the size-range encountered (5–250 kg).

The measured compositions of the C4-feeders (oryx and zebra) are predicted well by the genus-specific model. The $\delta^{18}O$ for goat is somewhat overestimated, but goats are herded in the area, and this likely lowers their $\delta^{18}O$ because they must drink more water (Fig. 1c). An increase in water consumption by goats is consistent with observations that the Turkana goats drink every day, whereas most wild goats drink only every 2–3 days. Halving the water content of their food to account for herding practices allows measured goat compositions to matched exactly. The compositions predicted by the equations of the Bryant and Froelich (1995; white dots, Fig. 4) are similar to the proposed model and are reasonable approximations of compositions, but do not reproduce the dependence of $\delta^{18}O$ on diet as well.

Predictions using the genus-specific model developed in this study underestimate the measured $\delta^{18}O$ values for gazelle and dikdik, but these drought-tolerant animals are especially sensitive to assumed biological fractionations and water flux proportions. For example, simply increasing transcutaneous water vapor losses by a factor of 2, to account for physiological response to heat and low humidity (e.g., Grice et al., 1971, 1972), allows much better correspondence between models (thick dashed error bars, Fig. 4) and the measured gazelle and dikdik compositions. Because no measurements have been published on skin permeabilities or the fractionation of cutaneous water vapor relative to body water for these animals, these modified models of course remain speculative. However, there may be good physiological reasons why antelope $\delta^{18}O$ is so high. The predictions using the Bryant and Froelich (1995) equations (white dots, Fig. 4) are also 1–3‰ too low for gazelle and dikdik, likely as a result of applying a generalized model to animals with atypical physiologies.

8. SEASONALITY AND IMPLICATIONS FOR CLIMATE RESEARCH

The $\delta^{18}O$ values of different teeth in a single jaw and of different positions on a single tooth have been found to vary systematically in herbivores depending on the time of tooth eruption and of enamel mineralization (e.g., Bryant et al., 1996; Fricke and O'Neil, 1996; Kohn et al., 1996b). Explanations for these variations ordinarily invoke seasonality, which includes changes of input isotope composition resulting from seasonal changes of water and plant composition as well as seasonal changes of diet. This interpretation is supported, for example, by measurements of the body water composition of adult birds, which varies during the year according to expected seasonal changes of food and water isotope compositions (Tatner, 1990).

To explore theoretically how seasonality could affect the $\delta^{18}O$ of different animals, two models were constructed using the physiological and dietary parameters for an "average herbivore" and an "average carnivore" (Appendix C), and the climatic and meteoric water compositions for two locations: New Delhi, India, and Rio de Janeiro, Brazil. Monthly meteoric water compositions, humidity, and temperature were obtained from published tabulations (IAEA, 1992; Meteorological Office, 1958, 1983). New Delhi experiences large seasonal changes in humidity and meteoric water $\delta^{18}O$, whereas Rio de Janeiro has a nearly constant humidity and less variable $\delta^{18}O$ throughout the year (Table 3). Results are shown in Fig. 5 and illustrate the importance of local climate, animal physiology, and diet on mammal phosphate compositions.

In New Delhi, most seasonal shifts in mammal $\delta^{18}O$ are driven by changes of meteoric water composition (asterisks in Fig. 5). However, herbivores do not track meteoric water compositions exactly, because herbivore isotope composition is strongly affected by the plants they eat, and plant composition depends on seasonally variable humidity. For example, the elevated herbivore $\delta^{18}O$ between October and June occurs because humidity is much lower, elevating plant $\delta^{18}O$ values. The July-September rainy season not only causes a decrease in meteoric water $\delta^{18}O$, but also increases humidity. Because the enrichment of plant ^{18}O over meteoric water is smaller at this time than during other months, herbivore compositions approach meteoric values more closely. Carnivore compositions are also affected by humidity, because they eat plant-consumers whose compositions are humidity dependent. However, the importance of humidity becomes progressively diminished with increasing trophic level. For example, if a herbivore derives 30% of its oxygen from plants, and carnivores derive 30% of their oxygen from herbivores, then only ~10% of a carnivore's oxygen is plant derived. Consequently, carnivores should track the meteoric water signal more closely than do herbivores. In contrast to New Delhi, the humidity in Rio de Janeiro is high and nearly constant throughout the year, and both herbivores and carnivores are predicted to track meteoric water compositions almost exactly. This is also reflected in the difference in the yearly average composition of a herbivore vs. a carnivore from the two areas. The large and small differences between average herbivore and carnivore compositions in New Delhi and Rio de Janeiro, respectively, reflect the average humidity differences in the two areas.

By varying input humidity and meteoric water composi-

Table 3. Meteorological Data for New Delhi, India, and Rio de Janeiro, Brazil.

New Delhi	Year	Jan	Feb	March	Apr	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Humidity (%)	0.49	0.56	0.51	0.36	0.27	0.28	0.44	0.67	0.72	0.62	0.44	0.41	0.56
Temperature (C)	25.0	13.9	16.7	22.5	28.0	33.3	33.6	31.4	30.0	28.9	26.1	20.0	15.3
Rio de Janeiro													
Humidity (%)	0.81	0.80	0.80	0.81	0.83	0.84	0.83	0.82	0.80	0.80	0.80	0.80	0.80
Temperature (C)	25.3	26.7	26.7	26.7	26.1	25.0	24.2	23.3	23.3	24.2	25.0	25.6	25.8

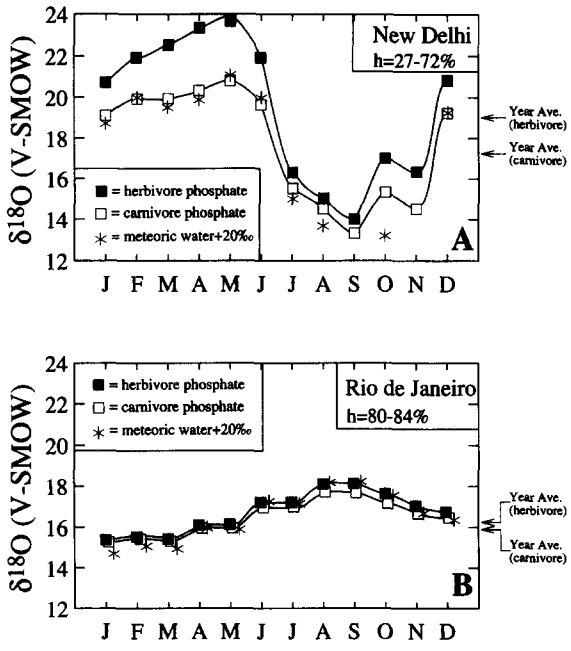

FIG. 5. Predicted $\delta^{18}O$ of an average herbivore and carnivore in two climatically different settings. (a) New Delhi, India, has strong seasonal variations in relative humidity and meteoric water composition. The seasonal changes in predicted phosphate $\delta^{18}O$ largely reflect changes in meteoric water compositions, but the additional enrichment in herbivore $\delta^{18}O$ over carnivores is due to the dependence of herbivores on plants, whose compositions are strongly dependent on humidity. Thus, the seasonal change in offset between herbivore and carnivore $\delta^{18}O$ largely reflects seasonal changes of humidity. (b) Rio de Janeiro, Brazil, has a uniformly high humidity during the year. Symbols have been slightly offset to improve clarity. Compositions of herbivores and carnivores there are predicted to be nearly identical, and to track meteoric water compositions almost exactly. Climatic and isotope input data are from IAEA (1992) and the Meteorological Office (1958, 1983).

tion, and monitoring the variations in predicted animal composition, it is possible to obtain a numerical expression for the dependence of animal composition on climatic factors. For the "average" animals, in temperate climates the approximate equations are

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 26.8 - 8.9h + 0.76SW \quad \text{(Herbivores)} \quad (17)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 21.3 - 3.0h + 0.74SW \quad \text{(Carnivores)} \quad (18)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 29.3 - 8.6h + 0.71SW \quad \text{(Herbivorous Birds)} \quad (19)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 22.7 - 3.9h + 0.64SW \quad \text{(Omnivorous Rodents)} \quad (20)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 34.3 - 3.0h + 0.70SW - 0.23T \quad \text{(Insectivorous Reptiles)} \quad (21)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 25.9 + 1.00SW - 0.23T \quad \text{(Fish + Amphibians)}, \quad (22)$$

where h is relative humidity from 0 to 1, SW is surface water $\delta^{18}O$ (V-SMOW), and T is temperature in °C. The temperature-dependent fish + amphibian calibration was obtained from the phosphate-water fractionation equation of Longinelli and Nuti (1973) and Kolodny et al. (1983), assuming that body water and meteoric water compositions are the same. As described above, the small dependence of carnivore and insectivore compositions on humidity arises from the humidity-dependence of the compositions of the animals they eat.

By comparing one calibration to another, it is possible to evaluate which pairs of animals are best suited for climate studies. For example, despite radically different metabolisms and sizes, typical herbivorous birds and mammals have such similar dependencies on humidity and water composition that together they would not separate climatic factors well. However, there is substantial disparity between herbivores and carnivores, and between cold-blooded and warm-blooded animals. These general pairs are logical choices for paleoclimate studies. When targeting animals for isotope analysis, it is nonetheless important to determine each animal's humidity and temperature dependence. For example, using the data reported in Appendix C for five herbivorous East African genera yields

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 30.4 - 12.9h + 0.68SW \quad \text{(Gazelle)} \quad (23)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 28.6 - 13.5h + 0.64SW \quad \text{(Dikdik)} \quad (24)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 27.2 - 8.9h + 0.72SW \quad \text{(Goat)} \quad (25)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 28.2 - 9.9h + 0.76SW \quad \text{(Zebra)} \quad (26)$$

$$\delta^{18}O\ (\text{Phosphate, ‰}) \sim 28.2 - 10.3h + 0.68SW \quad \text{(Oryx)}. \quad (27)$$

No correction to dikdik or gazelle for potentially different skin permeabilities was made. Not surprisingly, drought tolerance in gazelle and dikdik results in a much stronger dependence on humidity and a lesser dependence on meteoric water composition than for other animals. Thus, a combined analysis of drought tolerant herbivores and carnivores from the same area would best resolve changes of humidity from changes in surface water composition.

9. SUMMARY AND CONCLUSIONS

Isotope modeling is an important means of distinguishing not only the possible, but also the probable causes of observed isotope signals. In the case of biogenic phosphate $\delta^{18}O$, incorporating physiological and dietary differences among animals allows many observed trends and compositional differences to be reproduced accurately for a wide

range of genera, such as the global correlation between phosphate and meteoric water composition, and the dependence of herbivore $\delta^{18}O$ on diet. One disparity between models and measurements involves the high $\delta^{18}O$ observed for red kangaroos from arid Australia. Some of this enrichment may be physiological changes in water vapor losses through the skin in response to heat and humidity, but an additional cause may be an uncorrected increase in ^{18}O of surface waters due to evaporation. A second disparity involves antelopes from East Africa, but this discrepancy can be eliminated by adjusting transcutaneous water vapor fluxes within commonly measured ranges.

The results of this study delineate several fruitful areas of future research. (1) Additional field investigation of physiologically diverse genera in different climates would allow empirical investigation of the dependence of animal $\delta^{18}O$ on humidity and surface water, and the development of a database against which future theoretical models could be evaluated. Such investigations should include measurement not only of animal compositions, but also of the temperature and humidity, surface water compositions, and plant compositions in the area. (2) The accuracies of the fractionation factor for transcutaneous water vapor and its flux should be tested. Transcutaneous water flux has a significant effect on predicted compositions, but is not commonly measured, and data sources for the fractionation are sparse. Development of a database of measurements and characterization of physiological response of skin to climate would substantially decrease modeling uncertainties. (3) Despite much previous research, the causes and predictability of plant $\delta^{18}O$ remain enigmatic, particularly for C4 vs. C3 plants in climatically diverse natural settings. Because plants have a direct impact on animal $\delta^{18}O$ through diet, our ability to infer changes of humidity is limited by our understanding of the differences to which different plants fractionate oxygen isotopes. (4) Any paleoclimate research should include analysis of several genera with clearly different sensitivities to water composition and humidity in order to best separate climatic factors (see also Luz et al., 1990).

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APPENDIX A

Procedure for Applying the Oxygen Isotope Mass Balance Model

Values must first be assigned to the following parameters: average air temperature, average relative humidity, diet (proportions of carbohydrate, protein, and fat), energy extraction efficiency, digestibility, fraction of oxygen taken up in the lungs per breath, free water content of food, water economy index, proportion of oral to nasal breathing (independent of panting), free water content of feces, fraction of water lost as urine (as percentage of total water turnover), skin permeability and area, and the ratio of sweating to panting. Then, the following steps allow oxygen molar amounts to be determined. In the following calculations, roundoff errors make the actual values slightly different than in Table 3.

Terms corresponding to inputs for an average 30 kg herbivore at 15°C and 75% r.h.

1) Assign a daily energy expenditure [$900 \cdot M^{0.73} \sim 10800$ KJ].
2) Based on a known oxygen conversion factor, determine moles of oxygen required from air [10800 KJ · 0.00216 (moles O_2/KJ) ~ 23.3 moles O_2].
3) Based on the assumed fraction of O_2 taken up and the concentration of oxygen in air, determine the amount of air fluxed through the lungs [22.4(l/mole) · 23.3 (moles O_2)/(0.20 · 0.21) ~ 12400 l].
4) From the saturation concentration of H_2O in air at ambient temperature and the assigned relative humidity, determine the amount of H_2O vapor taken into the lungs

$$[0.75 \cdot 10^{(0.686+0.027 \cdot T(^\circ C))} \cdot 12400/(760 \cdot 22.4) \sim 6.74 \text{ moles } H_2O].$$

5) From the daily energy requirement, composition of the food, food component energy values, energy extraction efficiency, and digestibility, determine the mass of food ingested to meet the energy expenditure [10800/{0.7 · 0.9 · (0.85 · 17300 + 0.05 · 39700 + 0.10 · 20100)} ~ 0.91 kg].
6) Determine dry food O_2 and H_2 influxes from the amount of food consumed, food component compositions, digestibility, and energy extraction efficiency [0.7 · 0.9 · 0.91 · ((0.85 · 15.4 + 0.05 · 2 + 0.10 · 3) ~ 7.7 moles O_2; 0.7 · 0.9 · 0.91 · ((0.85 · 30.9 + 0.05 · 60 + 0.10 · 11) ~ 17.4 moles H_2].
7) From the free water content of the food ingested, determine the influx of unbound food H_2O [0.91 kg · 55.56(mo/kg) · 0.65/(1 − 0.65) ~ 97 moles H_2O].
8) From the WEI and assigned daily energy expenditure, determine total water turnover [0.2 · 10800/18(mL/mo) ~ 150 moles H_2O].

9) Determine the amount of drinking water ingested [150 − 97 − 17.4 − 6.74 ~ 29]. If the animal is known not to drink, verify that this term is close to zero.

Terms corresponding to effluxes

1) Determine dry fecal output based on digestibility and amount of food consumed [0.91 · (1 − 0.7) ~ 0.27 kg], and from the H_2O content of feces, determine fecal H_2O loss [0.27kg · 55.56 · 0.6/(1 − 0.6) ~ 22.5 moles H_2O].
2) Determine urinary water lost based on the assigned fraction of urinary H_2O to total water turnover [0.25 · 150 ~ 37.5 moles H_2O].
3) Determine the amount of water exhaled orally during normal breathing, assuming that 50% of normally respired air is expelled orally and is saturated at body temperature (12400 · 0.5 · 0.003 ~ 18.6 moles H_2O).
4) From the saturation concentration of H_2O in air at body temperature (~0.003 moles H_2O/l), the amount of air fluxed through lungs to obtain oxygen, determine the amount of air expired nasally, assuming 50% of air flux is nasal, and that nasal cooling lowers concentration nasally expired water by 50% [12400 · 0.5 · 0.5 · 0.003 ~ 9.3 moles H_2O).
5) From skin area of animal and skin permeability, determine transcutaneous water vapor loss [1.44 · $30^{0.667}$ ~ 13.9 moles H_2O].
6) Determine the amount of water used for heat loss [150 − 18.6 − 13.9 − 9.3 − 37.5 − 22.5 ~ 48.2 moles H_2O], and apportion between panting and sweating according to the assigned panting/sweating ratio [0.5 · 48.2 ~ 24.1 moles H_2O via sweating and 24.1 via panting]. Determine total orally-lost H_2O [24.1 + 18.6 ~ 42.7 moles H_2O].
7) From protein content of food, digestibility, energy extraction efficiency, and amount of food consumed, determine amount of urea (or uric acid for birds) produced [3 · 0.1 · 0.9 · 0.7 · 0.91 ~ 0.17 moles O_2 in urea].
8) Determine CO_2 loss based on the O_2 intake, corrected for the difference between the amounts of bound H_2 and bound O_2 in food, and the C and O losses to urea or uric acid. (Some oxygen is required to oxidize the excess of bound H_2 over bound O_2 in food, and a greater ratio of C to O is lost in urea or uric acid than in CO_2). [23.3 − 0.17 − (17.4/2 − 7.7) ~ 22.13 moles CO_2]. Note that the RQ can be calculated from the CO_2 loss and O_2 intake [22.13/23.3 ~ 0.95].

APPENDIX B

Additional Discussion of the Model Input and Ouput Amounts

Effects of Diet on Oxygen Input Amounts

Once a metabolic requirement is assigned, diet and digestibility allow the amount of food consumed and the oxygen fluxes associated with it to be calculated. For a specific food type, the amount of food an animal must catabolize scales with daily energetic requirements, and the amount of food actually ingested to meet that requirement is then determined by the food digestibility and the efficiency with which energy is extracted. The energetic gain of food catabolization depends on the specific end product. For energy and composition calculations, fats and carbohydrates are assumed to be catabolized entirely to H_2O and CO_2, whereas the nitrogenous endproduct of protein is assumed to be urea (NH_2CONH_2) for mammals and uric acid ($C_5H_4N_3O_3$) for birds. Food energy contents are well known and predictable, and for carbohydrate, fat, and protein catabolization corrected for urea production these are ~17.3, ~39.7, and ~20.1 KJ/kg, respectively (e.g., Kleiber, 1975). Apparent digestibilities are quite variable, ranging from ~40–50% for herbivores consuming nutritionally low-quality grass to greater than 90% for grub-consumers, but can be estimated reasonably accurately for each animal (±5–10%) from field and nutritional studies. Differential digestibility of food components was not considered in the present calculations, but can be easily incorporated. If the energy of urea is subtracted from food energy contents, then energy extraction efficiencies are nearly 100% for carnivores and rodents, but somewhat lower for herbivores and birds, ~90%, in part due to greater energetic losses in methane and in uric acid vs. urea production (Robbins, 1983).

The digestion of food produces metabolic water, in an amount determined from the hydrogen content of the food: 30.9, 60.0, and 11.0 moles H_2/kg for carbohydrate, fat, and protein (Kleiber, 1975). The amount of metabolic water produced from air O_2 is equal to the total amount of metabolic water minus the chemically bound oxygen in the food (15.4, 2.0, and 3.0 moles O_2/kg for carbohydrate, fat, and protein). That is, all the chemically bound oxygen in the digested food is assumed to produce metabolic water, and any remaining hydrogen is assumed to be oxidized by air O_2. The amount of oxygen excreted as urea or uric acid is simply related to the protein content of the diet (6 and 3 moles O_2/kg protein for urea and uric acid, respectively). Fecal water output is determined from the percentage of water in feces (typically 50–60% by mass) and from the amount of feces produced (= [food intake] × [1 − apparent digestibility]).

An alternative approach for assigning some of these parameters is to use representative values for the amount of food digested, its H_2 and O_2 contents, the respiratory quotient, and fecal output (e.g., Bryant and Froelich, 1995). This approach is merely a simplification of the specific dietary approach described above. The digestibility and food component proportions can always be adjusted to obtain such representative values. Including specific dietary terms, however, has the advantage of readily allowing investigation of the isotope effects of different diets.

Assignment of Water Loss Proportions

After subtracting urinary and fecal water losses from total water turnover, the remaining water loss must be apportioned among oral respiration, nasal respiration, transcutaneous water vapor loss, and sweat. For some birds, reptiles, and rodents, these proportions have been quantified and can be explicitly specified. For example, 60% of total water loss in reptiles was assumed to occur through their skin (Minnich, 1979). Based on data for birds (Willoughby and Peaker, 1979), 30% of total water loss was assumed to occur fecally, 50% of the remainder was assumed to be lost through the skin, and after subtracting off a nasal component, the remaining water was assigned an oral route. Although for other animals such proportions are rarely determined, some generalizations are possible.

Quantifiable water loss must occur simply because of breathing, although the precise amount lost depends on relative proportions of oral vs. nasal respiration. Air expired through the mouth is saturated with water at body temperature, whereas air expired through the nose is also saturated, but at a lower temperature. For many herbivorous mammals, respiratory water loss is reduced by ~50% during nasal respiration (e.g., Langman et al., 1979) because water content decreases with lower temperature. This generalization applies to many domestic and wild herbivores (e.g., goats, horses, antelopes, etc.), but should be checked for each species. For example, because of differences in nasal passage length and complexity, the efficiency of cooling air and limiting amounts of expired water is extremely enhanced in kangaroo rats and virtually nonexistent in humans. Because no data were found concerning the relative ratios of nasal vs. oral respiration rates, normal exhalation was proportioned equally between nose and mouth. Air lost through the nose was assumed to be saturated at a temperature halfway between body and ambient temperatures, which typically reduces water loss by ~50%.

Transcutaneous water vapor loss depends on skin permeability and area. Skin permeability is not routinely determined, but many measurements cluster at ~1 mg/cm^2 · h (Campbell, 1977). Elephant ears have extraordinarily high permeabilities (~50 mg/cm^2 · h, Wright and Luck, 1984), humans have variable permeability (0.2–2 mg/cm^2 · h; Grice et al., 1971, 1972; Campbell, 1977), whereas some desert-adapted animals have uniformly low permeabilities (e.g., ostrich ~ 0.2 mg/cm^2 · h; Campbell, 1977). Some data for sheep and humans suggest that vapor loss rates double if skin temperature increases by 5–10°C or if humidity is decreased from 75% to 40% (Grice et al., 1971, 1972; Hulbert and Dawson, 1974). Unless otherwise required by specific measurements, a value of 1 mg/cm^2 · h

was used for thermoregulating animals, and because of the paucity of direct measurements, no explicit temperature or humidity correction was made. Skin area is generally expressed as $k \cdot m^{2/3}$, where k is a proportionality constant known as the Meeh factor (Meeh, 1879) and m is mass. According to Dawson and Hulbert (1970), k is often assumed to be ~1000, and has values of 1100–1200 ($cm^2/kg^{2/3}$) for a variety of marsupials. An intermediate value of 1100 was used, and combined with a permeability of 1 $mg/cm_2 \cdot hr$ results in cutaneous water vapor losses of $\sim 1.45 \cdot m^{2/3}$ moles H_2O/day (mass in kg) for thermoregulators.

After subtracting off the contributions of normal respiration, urinary, fecal, and cutaneous water vapor losses from total water turnover, any remaining water was assumed to be used for heat regulation, and was apportioned between sweating and panting. Only primates and large ungulates commonly sweat for thermoregulation. With a few other exceptions (e.g., kangaroos), most other animal groups rely exclusively on panting, skin vapor loss, or adaptive behavior (burrowing, wallowing, etc.) to maintain constant body temperatures. For animals that both sweat and pant, the ratio of sweating to panting was assigned based on specific studies (e.g., Robertshaw and Taylor, 1969) or on the measured density of sweat glands in the skin.

The overall accuracy of the assumptions for large animals can be checked against birds and rodents, whose water loss mechanisms have been studied in some detail. In moles/day, transcutaneous water loss from birds is $\sim[1.25 - 1.50] \cdot [\text{mass}]^{0.6}$ (Willoughby and Peaker, 1979), similar to the model expression derived independently above. In rodents, relative water losses are approximately equal between pulmonary (30–60%) and transcutaneous (40–70%) avenues (Fyhn, 1979). Using the above set of assumptions, relative respiratory and skin water losses for rodents are modeled as 49 and 51%, respectively, in good agreement with measurements. Additional comparisons for transcutaneous water losses in specific herbivores include sheep with and without sweat glands (Hulbert and Dawson, 1974), and dikdik (Maloiy, 1973; Kamau, 1988). Sheep use panting and sweating approximately equally for thermal regulation (Robertshaw and Taylor, 1969), and Hulbert and Dawson (1974) found that sheep lacking sweat glands had cutaneous water losses that were half that of normal sheep. That is, water vapor accounted for 50% of total cutaneous water loss. Based on the above derivation, transcutaneous water vapor loss for sheep was 44% of total cutaneous losses. For dikdik, fully hydrated animals at 20–25°C lose ~25% of their water cutaneously (Maloiy, 1973), and 60–90% of evaporative heat loss occurs through respiration (Kamau, 1988). The model calculations independently imply cutaneous water losses of 21%, and respiratory heat losses of 73%, in good agreement with the direct measurements.

Appendix C. Values for Parameters Used for Calculations

Inputs (moles)	Herbivore	Carnivore	Bird	Rodent	Reptile	Gazelle	Dikdik	Goat	Zebra	Oryx	Deer	Kangaroo
Mass (kg)	30.00	30.00	0.10	0.05	1.000	50.00	5.00	30.00	250.00	170.00	50.00	30.00
Metab pre-exp	2.96	3.00	2.93	2.54	0.429	2.96	2.96	2.96	2.96	2.96	2.96	2.73
Metab exponent	0.73	0.86	0.75	0.51	0.773	0.73	0.73	0.73	0.73	0.73	0.73	0.64
Energy (KJ)	10688	18677	151	76.45	2.685	15495	2905	10688	49927	37720	15495	4801
O_2 respired (mo)	23.09	43.70	0.34	0.17	5.8e-3	33.47	6.28	23.09	107.84	81.47	33.47	10.37
Humidity (%)	0.75	0.75	0.75	0.75	0.75	0.57	0.57	0.57	0.57	0.57	0.60	0.60
Temperature (C)	15.00	15.00	15.00	15.00	15.00	29.00	29.00	29.00	29.00	29.00	15.00	21.00
Air exchanged (l)	12312	23309	181.2	91.7	3.09	17850	3347	12312	57516	43453	17850	5530
H_2O conc., sat'd. (mmo/l)	0.724	0.724	0.724	0.724	0.724	1.73	1.73	1.73	1.73	1.73	0.724	1.05
Air H_2O (mo)	6.69	12.66	0.10	0.05	1.68e-3	14.51	2.72	10.01	46.76	35.32	7.76	3.49
Rel. Digestibility	0.70	0.90	0.90	0.85	0.850	0.75	0.80	0.75	0.50	0.75	0.70	0.70
Energy extr. efficiency	0.90	1.00	0.90	1.00	0.900	0.90	1.00	0.90	0.90	0.90	0.90	0.90
Food Carbo content (%)	0.85	0.00	0.80	0.40	0.000	0.85	0.75	0.85	0.90	0.85	0.85	0.85
Food Fat content (%)	0.05	0.20	0.05	0.15	0.100	0.05	0.05	0.05	0.05	0.05	0.05	0.05
Food Protein content (%)	0.10	0.80	0.15	0.45	0.900	0.10	0.20	0.10	0.05	0.10	0.10	0.10
MJ energy/kg food	11.78	21.62	15.26	18.63	16.876	12.62	15.18	12.62	8.35	12.62	11.78	11.78
Food ingested (g)	907	864	9.90	4.10	0.159	1230	191	847	5980	2990	1320	407
Moles O_2/kg food	13.49	2.80	12.80	7.81	2.900	13.49	12.25	13.49	14.11	13.49	13.49	13.49
Food O_2 input (mo)	7.71	2.18	0.10	0.03	3.53e-4	11.18	1.88	7.71	37.96	27.21	11.18	3.46
Moles H_2/kg food	30.37	20.80	32.07	26.31	15.900	30.37	28.38	30.37	31.36	30.37	30.37	30.37
Food H_2 (mo)	17.36	16.17	0.26	0.09	1.94e-3	25.16	4.34	17.36	84.36	61.25	25.16	7.80
Free-H_2O in food (%)	0.65	0.65	0.65	0.65	0.650	0.60	0.60	0.60	0.60	0.60	0.65	0.65
Free H_2O in food (mo)	93.61	89.15	1.02	0.42	16.4e-3	102.30	15.95	70.57	498.19	249.04	135.71	42.05
Urea /Uric acid (mo)	0.34	3.73	0.00	0.01	6.57e-4	0.50	0.18	0.34	0.81	1.21	0.50	0.15
WEI (ml/KJ)	0.25	0.25	0.20	0.15	0.250	0.16	0.14	0.20	0.25	0.16	0.20	0.20
Water turnover (mo)	148.44	259.40	1.68	0.64	37.30e-3	141.97	23.01	118.75	693.43	345.62	172.16	53.34
Drinking water (mo)	30.79	141.42	0.30	0.07	17.26e-3	0.00	0.00	20.82	64.12	0.00	3.54	0.01
Total Moles O_2 input	96.34	167.50	1.15	0.47	23.83e-3	103.05	17.48	81.50	450.33	250.87	118.15	36.60
Outputs												
Fecal output (kg, dry)	0.272	0.086	0.001	0.001	2.4e-5	0.307	0.038	0.212	2.989	0.747	0.395	0.122
Fecal H_2O content(%)	0.60	0.60	---	0.60	0.500	0.50	0.40	0.50	0.60	0.60	0.50	0.50
Fecal H_2O (kg)	0.408	0.130	0.002	0.001	2.4e-5	0.307	0.026	0.212	4.483	1.121	0.395	0.122
Fecal H_2O (mo)	22.68	7.20	0.50	0.05	1.33e-3	17.05	1.42	11.76	249.10	62.26	21.92	6.79
Urea or Uric Acid O_2 (mo)	0.17	1.87	0.01	0.00	3.3e-4	0.25	0.09	0.17	0.40	0.61	0.25	0.08
Urine (mo)	37.11	64.85	0.00	0.13	5.60e-3	21.30	3.45	29.69	173.36	51.84	25.82	8.00
Nasal H_2O (mo)	9.32	17.64	0.14	0.07	2.34e-3	13.51	2.53	9.32	43.52	32.88	13.51	4.18
Skin H_2O (mo)	13.90	13.90	0.59	0.20	22.38e-3	19.54	4.21	13.90	57.14	44.19	19.54	13.90
Sweat/(Sweat+pant)	0.50	0.10	0.00	0.00	0.00	0.20	0.10	0.50	0.75	0.75	0.10	0.10

Oral H_2O (mo)	42.03	143.76	0.45	0.19	5.66e-3	61.86	10.76	36.36	107.86	87.93	84.93	19.25
Sweat H_2O (mo)	30.82	12.05	0.00	0.00	0.00	8.71	0.63	17.73	62.46	66.52	6.44	1.21
CO_2 (mo)	21.95	35.93	0.31	0.15	4.86e-3	31.82	5.89	21.95	103.21	77.46	31.82	9.86
RQ (CO_2/O_2)	0.95	0.82	0.91	0.86	0.84	0.95	0.94	0.95	0.96	0.95	0.95	0.95
Total Moles O_2 output	96.34	167.50	1.15	0.47	23.83e-3	103.05	17.48	81.50	450.33	250.87	118.15	36.60
Inputs: composition												
Air O_2	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1	15.1
Meteoric H_2O	-3.25	-3.25	-3.25	-3.25	-3.25	6.00	6.00	6.00	6.00	6.00	-3.25	-4.00
Air H_2O vapor	-13.24	-13.24	-13.24	-13.24	-13.24	-2.84	-2.84	-2.84	-2.84	-2.84	-13.24	-13.47
Leaf H_2O	3.25	---	3.25	3.25	---	19.16	14.16	23.16	24.16	24.16	7.15	6.19
Cellulose	30.25	---	30.25	30.25	---	46.16	41.16	50.16	51.16	51.16	34.15	33.19
Stem H_2O	-3.25	---	-3.25	-3.25	---	6.00	6.00	6.00	6.00	6.00	-3.25	-4.00
Leaf/(Leaf+Stem)	0.50	---	0.50	0.50	---	0.75	0.90	0.50	0.50	0.50	0.50	0.75
Food H_2O	0.00	0.16	0.00	0.08	0.16	15.87	13.35	14.58	15.08	15.08	1.95	3.64
Food O_2	30.25	7.16	30.25	18.71	7.16	46.16	41.16	50.16	51.16	51.16	34.15	33.19
Δ Atm. vapor-SW	-9.99	-9.99	-9.99	-9.99	-9.99	-8.84	-8.84	-8.84	-8.84	-8.84	-9.99	-9.47
Δ Food H_2O-SW	3.25	3.41	3.25	3.33	3.41	9.87	7.35	8.58	9.08	9.08	5.20	7.64
Δ Food O_2 -SW	33.50	10.41	33.50	20.49	10.41	40.16	35.16	44.16	45.16	45.16	37.40	37.19
Outputs: compositions												
Body temperature (K)	311.15	311.15	311.15	311.15	288.15	311.15	311.15	311.15	311.15	311.15	311.15	309.15
Δ Oral H_2O-BW	-8.19	-8.19	-8.19	-8.19	-9.99	-8.19	-8.19	-8.19	-8.19	-8.19	-8.19	-8.32
Δ Nasal H_2O-BW	-17.05	-17.05	-17.05	-17.05	-18.34	-16.34	-16.34	-16.34	-16.34	-16.34	-17.05	-16.85
Δ Skin H_2O-BW	-18.00	-18.00	-18.00	-18.00	-18.00	-18.00	-18.00	-18.00	-18.00	-18.00	-18.00	-18.00
Δ CO_2-BW	38.65	38.65	38.65	38.65	43.16	38.65	38.65	38.65	38.65	38.65	38.65	39.01
Δ Urea-BW	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\Sigma M_\gamma \Delta_{\gamma\text{-}SW}$ (inputs)	376.9	111.6	4.60	1.05	23.31e-3	889.8	112.5	599.1	3769.8	2203.7	732.0	272.9
Moles SW	73.2	123.8	0.81	0.30	18.03e-3	69.6	11.2	58.4	342.5	169.4	84.7	26.2
M(Air O_2) * δ(Air O_2)	348.6	659.9	5.13	2.60	87.59e-3	505.4	94.8	348.6	1628.4	1230.3	505.4	156.6
$\Sigma M_\beta \Delta_{\beta\text{-}BW}$ (outputs)	471.6	524.7	3.62	2.60	-41.49e-3	690.2	124.9	498.1	2677.6	1967.2	591.0	144.1
Moles BW	96.3	167.5	1.15	0.47	23.83e-3	103.0	17.5	81.5	450.3	250.9	118.2	36.6
A:	2.64	1.47	5.30	2.22	6.39	6.84	4.71	5.52	6.04	5.85	5.47	7.80
B:	0.76	0.74	0.71	0.64	0.76	0.68	0.64	0.72	0.76	0.68	0.72	0.72
Phosphate Composition	17.66	16.57	20.51	17.66	26.35	28.39	26.06	27.32	28.10	27.40	20.64	22.46

Note: Energy values are based on allometric equations of Nagy (1987) and Nagy and Peterson (1988). Conversion factor of KJ to moles O_2 is: 0.00216 (herbivores) and 0.00234 (carnivores and insectivores). The composition of H_2O in meat and insects was assumed to be equal to herbivore body water composition. The composition of air O_2 taken up was 15.1‰ based on measured oxygen utilization efficiencies and oxygen uptake fractionations. Final A and B terms are for the relationship between animal body water and surface (drinking) water: BW (‰) = A(‰) + B*SW(‰). Energy extraction efficiency and digestibility based on summaries of Robbins (1983) for various animal groups. Fecal water content based on studies of East African herbivores. Urinary loss based on water turnover studies for East African animals. Digestibilities and food compositions reflect greater leaf consumption by dikdik and gazelle, and consumption of poorer quality food by zebra. Food compositional differences reflect influence of C3 vs. C4 feed. Physiological and dietary data from Taylor (1968), Casebeer and Koss (1970), Shkolnik et al. (1972), Maloiy (1973), Dawson et al. (1975), Denny and Dawson (1975), Nge'the (1976), Nge'the and Box (1976), Hoppe (1977), Hoppe et al. (1977), King et al. (1978), Bentley (1979), Fyhn (1979), Minnich (1979), Willoughby and Peaker (1979), Spinage et al. (1980), Kamau (1988), Maloiy et al. (1988), Hossaini-Hilali et al. (1994). For birds, rodents, and reptiles, the proportions of water losses have been directly measured, and these values were used to derive amounts of respiratory, cutaneous, and fecal water losses.