

Margaret J. Schoeninger · Urszula T. Iwaniec
Leanne T. Nash

Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair

Received: 18 April 1997 / Accepted: 11 August 1997

Abstract Carbon and nitrogen stable isotope ratios were measured in hair samples from two species of *Galago* from Gedi Ruins National Monument in eastern Kenya and from *Lepilemur leucopus* from Beza Mahafaly Special Reserve in southern Madagascar. Forest structure was generally similar in the two areas but average rainfall was lower in Madagascar. Species average $\delta^{13}\text{C}$ values varied with feeding height in the forest canopy and with average rainfall level as expected from reported variation in plant $\delta^{13}\text{C}$ values. *G. garnettii*, which feeds higher in the forest canopy, had less negative $\delta^{13}\text{C}$ values than *G. zanzibaricus*, which spends more time below 5 m. *L. leucopus*, from a drought-afflicted forest, had less negative hair $\delta^{13}\text{C}$ values than the two galago species. The values within the *Lepilemur* sample showed a positive linear relation with percent dependence on a CAM tree species and with xeric conditions within the species reserve. Nitrogen stable isotope ratios varied with trophic level of feeding and with time spent feeding on leguminous plants. The insectivorous galagos had significantly more positive $\delta^{15}\text{N}$ values than the folivorous *L. leucopus*. Within the *Lepilemur* sample, $\delta^{15}\text{N}$ values varied inversely with the percent of feeding time spent on leguminous plants. The range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in each of the prosimian species is larger than reported for animals fed monotonous diets and for New World monkey species. The monkey species feed as groups of individuals whereas the prosimians have solitary feeding habits. The ranges in the prosimian species

apparently reflect the greater variation in diet among individual prosimians compared to individual monkeys. The isotope data reported here are equivalent, on average, to those reported for other arboreal species from similar forest habitats and with similar dietary habits. This supports the use of such data for paleoecological reconstruction of forest and woodland systems and diet reconstruction of extinct primate populations and species.

Key words Primates · Feeding ecology · Stable isotope ratios

Introduction

Ecological data on primate species permit the testing of general evolutionary models for extinct and extant species (Fleagle 1988) and the identification of aspects of human behavior that most endanger or protect extant species (Pulliam and Babbitt 1997). Arboreal primates can be difficult to study when they are nocturnal or inhabit dense forests, so we tested the effectiveness of animal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values¹ as indirect monitors of habitat use and diet. Additionally, we assessed the generality of previous results showing that animal $\delta^{13}\text{C}$ values were correlated with the level of forest cover and $\delta^{15}\text{N}$ values were correlated with feeding on leguminous plants (Schoeninger et al. 1997). The former has potential

M.J. Schoeninger (✉) · U.T. Iwaniec¹
Department of Anthropology, University of Wisconsin,
Madison, WI 53706, USA
e-mail: mjschoen@facstaff.wisc.edu; Fax: (608) 265-4216

L.T. Nash
Department of Anthropology,
Arizona State University,
Tempe, AZ 85287-2402, USA

Present address:

¹Osteoporosis Research Center,
601 N. 30th St., Creighton University, Omaha, NE 68131, USA

¹A δ value is defined as:

$$\delta = \left[\frac{R_{\text{sample}}}{R_{\text{std}}} - 1 \right]$$

× 1000‰ (read as per mil or parts per thousand)

where R is the isotope ratio ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) and the standard is the internationally recognized standard. The international standard for carbon $^{13}\text{C}/^{12}\text{C}$ is Pee Dee Belemnite (PDB), a marine carbonate; the standard for nitrogen $^{15}\text{N}/^{14}\text{N}$ is atmospheric nitrogen or AIR.

for paleoecological reconstructions (e.g., Schoeninger 1995) and the latter for assessing primate diet choice (e.g., Ganzhorn 1988; Oftedal 1991).

Natural abundance stable isotope ratios in plant and animal tissues are being used with increasing frequency to investigate various aspects of plant and animal ecology (Schwarcz and Schoeninger 1991; Association of Applied Biologists 1994; Koch et al. 1994; Lajtha and Michener 1994; Pate 1994) but with little application to non-human primates. We maintain that primates are ideal subjects for the method because their behavioral ecology varies widely. Some species forage in groups while others are solitary and can be expected to differ individually in diet items selected. Species vary in the height within single forest canopies that they occupy and in the types of forest utilized, and can be expected to reflect established variations in plant δ values. In addition, across species there is a wide range of diet types from pure herbivory through omnivory to insectivory which can be traced isotopically.

To this end, we analyzed hair in three species of arboreal, forest-dwelling prosimians living in Kenya and Madagascar which have been subjects of multi-season behavioral studies (Harcourt and Nash 1986; Nash 1994, 1997). The level of canopy cover in the forests was similar to that in two of three regions of central America and South America where hair $\delta^{13}\text{C}$ values in four monkey species correlated with the density of canopy cover (Schoeninger et al. 1997). Prosimians have been separated, phylogenetically, from New World monkeys since the late Eocene or early Oligocene epoch (Simons 1995) and, as such, serve as a taxonomic check on the general nature of the stable isotope approach to studies in primate ecology. The present study focussed on two galago species, *Galago garnettii* (= *Otolemur garnettii*) and *G. zanzibaricus* (= *Galagoides zanzibaricus*) that live sympatrically at Gedi Ruins National Monument in Kenya and *Lepilemur leucopus* from Beza Mahafaly Special Reserve in southern Madagascar. The two areas, characterized as lowland, dry forests, are similar to each other in terms of overall tree height, the layers within the canopy, and the height and thickness of the undergrowth. The Kenyan forest is multistratal with a canopy at 15–20 m, emergents to 25 m, and a thick understory (Harcourt and Nash 1986); these variables were not quantified at the Madagascar forest (Nash 1994), although canopy use was recorded for all three species (Harcourt and Nash 1986; Nash 1997). Annual precipitation in the Kenyan forest is around 1,000 mm (Harcourt and Nash 1986) and around 750 mm in the Madagascar reserve (Nash 1994). Although they vary in average body size (Harcourt and Nash 1986; Nash 1994), all three prosimian species are less than 1.0 kg. Such average body sizes normally correlate with insectivorous frugivory across primate species (Kay 1975, 1984; Kay and Hylander 1978) but *Lepilemur* is a complete folivore (perhaps coprophagous: Hladik and Charles-Dominique 1974; perhaps not: Russell 1977; L.T. Nash, personal observation).

Materials and methods

Stable isotopes and prosimians

Patterned distributions of carbon and nitrogen stable isotope ratios occurring in the biosphere serve as the basis for the stable isotope approach to ecological questions. Across all plants, there is a non-overlapping distribution of $\delta^{13}\text{C}$ values between plants that utilize the C_4 photosynthetic pathway (largely tropical grasses) and other plants such as trees and herbs, the majority of which follow the C_3 pathway (O'Leary 1981, 1988). Herbivore values reflect aspects of their ecosystem because their tissues average the variation in $\delta^{13}\text{C}$ values of plants selected as diet items (DeNiro and Epstein 1978; Bada et al. 1990). The method has commonly been applied to questions involving the feeding on C_3 versus C_4 plants. $\delta^{13}\text{C}$ values faithfully represent the relative amounts of browse versus grass in diet and are useful for animal species where observational data are ambiguous or scanty (Tieszen et al. 1979). As such, the values in human bone collagen track the spread of maize (a C_4 plant) agriculture in the prehistoric New World (Vogel and van der Merwe 1977; Schoeninger and Moore 1992). Similarly, the $\delta^{13}\text{C}$ values in tooth enamel of extinct grazing animals monitor the presence of C_4 grasslands during the Tertiary (Cerling et al. 1993; Kingston et al. 1994; Morgan et al. 1994).

Primates, in general, show little use of C_4 plants (Milton 1987) and the Kenyan and Madagascar forests are comprised mainly of C_3 plants with additional species that utilize the third photosynthetic pathway (i.e., crassulacean acid metabolism or CAM; Kluge and Ting 1978; O'Leary 1981, 1988). Even so, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the prosimians should monitor various ecological variables. *G. zanzibaricus* feeds lower in the canopy and should have more negative $\delta^{13}\text{C}$ values, on average, than *G. garnettii*, as plant leaf $\delta^{13}\text{C}$ values vary with canopy height (Vogel 1978b; van der Merwe and Medina 1989; Broadmeadow et al. 1992; Garten and Taylor 1992), and terrestrial animals have more negative bone collagen $\delta^{13}\text{C}$ values than arboreal ones (van der Merwe and Medina 1991; Ambrose and DeNiro 1986). *Lepilemur* was expected to show less negative $\delta^{13}\text{C}$ values than the galagos because the Beza Mahafaly Special Reserve in southern Madagascar had undergone a severe drought for the 2 years prior to hair collection. The $\delta^{13}\text{C}$ values in C_3 and CAM plants, in contrast to C_4 plants (Marino and McElroy 1991), become less negative under drought conditions (O'Leary 1981; Ting and Gibbs 1982; Garten and Taylor 1992). In terms of animal $\delta^{15}\text{N}$ values, individual *Lepilemur* vary in the amount of time spent feeding on leguminous plants (Nash 1997). Those individuals which spend more time should have lower $\delta^{15}\text{N}$ values than those which spend less time, because leguminous plants, in general, are less positive than non-legumes (Virginia and Delwiche 1982; Shearer et al. 1983; Shearer and Kohl 1986). This pattern identified prehistoric domesticated beans in South America (Hastorf and DeNiro 1985), and the people feeding on them in central America (DeNiro and Epstein 1981). The two galago species are omnivorous (Harcourt and Nash 1986) and should have more positive $\delta^{15}\text{N}$ values than *Lepilemur* which is herbivorous (Nash 1994) reflecting the stepwise increase in $\delta^{15}\text{N}$ from producers to top consumers (Minagawa and Wada 1984; Schoeninger and DeNiro 1984). This "trophic level effect" has identified feeding relationships within single ecosystems (Wada and Minagawa 1983; Peterson and Fry 1987; Hobson et al. 1997) and, possibly, trophic position in less controlled situations (Schoeninger 1985, 1995; Bocherens et al. 1994). Starvation increases endogenous nitrogen turnover (Swick and Benevenga 1977) resulting in ^{15}N enrichment in tissues with rapid turnover (e.g., muscle and bone collagen in growing animals; Hobson et al. 1993), but none of the prosimians showed signs of food stress and this was not expected to be a factor. The effect of the drought on *Lepilemur* $\delta^{15}\text{N}$ values could not be predicted, as elevated animal $\delta^{15}\text{N}$ values correlate with water conservation mechanisms in some (Schoeninger and DeNiro 1984; Ambrose and DeNiro 1986; Heaton et al. 1986) but not all (Ambrose and DeNiro 1986; Sealy et al. 1987; Vogel et al. 1990) situations subject to drought conditions (Cormie and Schwarcz 1996).

Field studies

All behavioral data come from focal individual follows of radio-tracked subjects. At Gedi, focal follow data comprised 130 h on *G. garnettii* (two males, three females) and 178 h on *G. zanzibaricus* (five males, four females). About two-thirds of the follows at Gedi were done between dusk and 0100 hours and the remainder between 0100 and dawn. Approximately 250 h of focal follows were conducted at Beza on *Lepilemur* (equally divided across four males and one female). All follows at Beza were done between dusk and 2400 hours. During focal follows, scan samples of behavior were taken at 5-min intervals recording the individual's substrate, activity and food (when eating). Percent of time at different heights of substrate comes from these scan samples. Due to difficulties in observing galago feeding, most of the information on diet for the galagos comes from analysis of feces from followed subjects and other animals (Harcourt and Nash 1986). The information on diet in *Lepilemur* comes from scans which showed that all feeding was on leaves, stems, or flowers. Also, of 69 *Lepilemur* fecal pellets examined from followed subjects and other animals, seeds were found in only one pellet. In addition, during focal *Lepilemur* follows, throughout each 5-min interval, we noted whether or not particular foods were eaten during that interval (1/0 sampling; Martin and Bateson 1993). The information on diet elements is the percent of all 1/0 intervals when any feeding was seen devoted to *Euphorbia tirucalli* (Euphorbiaceae) or to *Tamarindus indica* (Leguminosae). Additional details on methods can be found in Harcourt and Nash (1986) and Nash (1997).

Several animals of each species were trapped for marking and to attach radio-transmitters for tracking. Trapping and handling of the galagos was accomplished in 1988–1989, following methods described for the genus (Charles-Dominique and Bearder 1979). The animals were sedated with ketamine for handling. Most of the *Lepilemur* subjects were captured by blowgun darts using Telazol (A.H. Robbins, Richmond Va) following published methods (Lemos De Sa and Glander 1993). After darting, animals were caught in a canvas sling as they fell. A few animals were pulled by (gloved) hand from their sleeping holes and then sedated with Telazol for handling. In both studies, animals were released at their trap sites within 4–6 h of capture and there were no fatalities due to trapping procedures. The work on *Lepilemur* was done under a protocol approved by the Institutional Animal Care and Use Committee at Arizona State University. The work on the galagos predated such a requirement, but followed methods that would currently be approved.

Hair analysis

Hair was cut from the back or tail as close to the skin as possible with a pair of fine-tipped surgical scissors. Among the galagos, some of the hair was clipped from the tail as a method of identifying individuals. Hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ reflect the values in the an-

imal's diet (Minson et al. 1975; DeNiro and Epstein 1978, 1981; Vogel 1978a; Jones et al. 1981; Nakamura et al. 1982; Tieszen et al. 1983; White 1993) and the collection of hair is less invasive than for other tissues commonly analyzed (e.g., bone collagen). Hair does not resorb or turn over, thus a specific period of feeding is monitored by each segment of hair analyzed. Among the few species studied, monkeys lose hair in molts (Inagaki and Nigi 1988; Dietz et al. 1995; Isbell 1995) which occur relatively rapidly (4–6 weeks once during the year). Thus, hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values probably correspond to diets taken during a limited portion of the year. Hair growth patterns are less well-known in prosimians. *Lemur catta*, the ringtailed lemur, reportedly shows reduced hair growth during the dry season which is a period of reduced energy expenditure and intake (Pereira 1993). Such a pattern of hair growth should result in hair δ values that are weighted toward wet-season diet values. Neither *Lepilemur* nor *G. garnettii* showed any signs of molt. *G. zanzibaricus* did in some, but not all, individuals. No obvious pattern of seasonality was seen in the molt (L.T. Nash, personal observation).

We analyzed hair from nine individuals from each species. Individual hair samples were cleaned sequentially with water and with acetone and dried at 90°C. Approximately 3 mg was weighed into quartz tubes with excess cupric oxide, copper, and silver. The tubes were sealed under vacuum and the samples combusted at 900°C in a muffle furnace for 2 h. Tubes were allowed to come to room temperature. Carbon dioxide and nitrogen gas were purified sequentially, collected cryogenically on a glass vacuum line, and analyzed on a Finnegan MAT 251. A glycine laboratory standard analyzed repetitively produced a standard deviation of 0.2‰ in $\delta^{13}\text{C}$ and 0.3‰ in $\delta^{15}\text{N}$. Intra-animal variation, determined from several separate samples of hair that were cleaned and prepared from the same animal, showed $\delta^{13}\text{C}$ values within 0.2‰ of each other in eight sets of repetitive samples and $\delta^{15}\text{N}$ values within 0.6‰ of each other in six sets of repetitive samples. This replicability is the same as that reported in previous studies (Schoeninger et al. 1997).

Results

No significant differences in either $\delta^{13}\text{C}$ or in $\delta^{15}\text{N}$ values were found between the sexes and the data were pooled.

Carbon

The galagos were 1.8‰ more negative in $\delta^{13}\text{C}$ values (Table 1, Fig. 1), on average, than *Lepilemur* (significant at the 0.001 level of probability; 25 *df*) even though all three species feed arboreally and most tree species follow the C_3 photosynthetic pathway (O'Leary 1988). The

Table 1 Diet and stable isotope ratios (weight and feeding time values are from Harcourt and Nash 1986, for *Galago*; from Nash 1994, 1997, for *Lepilemur*)

	Weight (kg)	Time feeding	$\delta^{15}\text{N}$ (AIR) (‰)				$\delta^{13}\text{C}$ (PDB) (‰)		
			<i>n</i>	\bar{x}	SD	Range	\bar{x}	SD	Range
<i>Galago zanzibaricus</i>	0.14	30% fruit 70% animal prey 0% leaves	9	7.4	1.2	6.4, 9.4	-23.3	0.2	-23.6, -23.0
<i>Galago garnettii</i>	0.84	50% fruit 50% animal prey 0% leaves	9	7.1	0.9	5.6, 9.0	-22.8	0.2	-23.1, -22.5
<i>Lepilemur leucopus</i>	0.6	0% fruit 0% animal prey 100% leaves	9	5.5	1.0	4.2, 7.3	-21.3	0.8	-22.4, -20.1

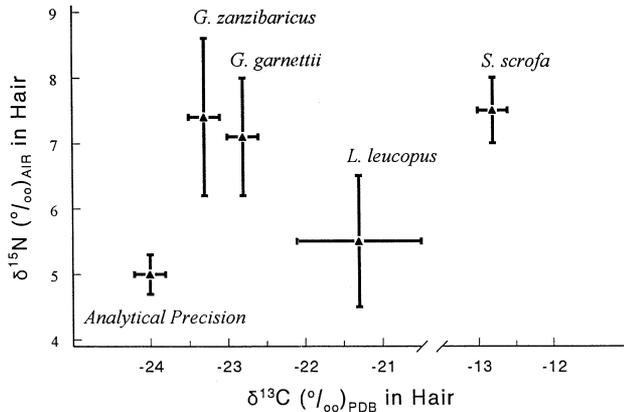


Fig. 1 $\delta^{13}\text{C}$ values plotted against $\delta^{15}\text{N}$ values in hair (mean \pm SD) for two *Galago* species from Kenya, *Lepilemur leucopus* from Madagascar and, for comparison, laboratory-reared *Sus scrofa*. The ten sows were fed a monotonous diet and represent the minimal interanimal variation expected. The offset in $\delta^{13}\text{C}$ values between the two *Galago* species correlates with their feeding position within the canopy. The $\delta^{13}\text{C}$ values in the *Lepilemur* individuals correlates both with the drought conditions in their habitat and with time spent feeding on a CAM plant species. The $\delta^{15}\text{N}$ values among the species correlate with trophic position in feeding and with time spent feeding on leguminous plants among *Lepilemur* individuals

galagos are insectivore-frugivores but insectivory appears unlikely to account for the difference between the genera. Although insects contain significant quantities of lipids, and lipids are depleted in ^{13}C relative to carbohydrates and proteins (DeNiro and Epstein 1977), controlled feeding experiments show no evidence for incorporation of dietary lipid carbon into an animal's proteinaceous tissues (Ambrose and Norr 1993; Tieszen and Fagre 1993). Rather, it appears that a drought effect on CAM and C_3 plants in the Malagasy forest accounts for the difference between *Galago* and *Lepilemur* even though the forest is superficially quite similar to that in Kenya. Several *Lepilemur* individuals were observed feeding on the leaves and branches of *E. tirucalli*, a tall, spindly, succulent tree in both the hot/wet season and the cool/dry season (Nash 1997). Various studies indicate that *E. tirucalli* is a CAM species. Leaf $\delta^{13}\text{C}$ values are less negative than those of C_3 plants (Bender 1971), the Kranz anatomy diagnostic of C_4 plants is lacking (Webster et al. 1975) and Old World succulent species of *Euphorbia* usually have CAM (Kluge and Ting 1978). CAM plant $\delta^{13}\text{C}$ values are determined by the amount of day versus night CO_2 fixation (O'Leary 1981; Ting and Gibbs 1982) which, in turn, is determined by water availability (Kluge and Ting 1978; Ting and Gibbs 1982). Some succulents switch to CAM from C_3 when water-stressed and revert back to C_3 when conditions improve (Ting and Rayder 1982). Of four *Lepilemur* individuals for which we have focal data (see Fig. 2), the two that spent time feeding on *E. tirucalli* have the least negative hair $\delta^{13}\text{C}$ values in the total *Lepilemur* sample. Further, the two individual *Lepilemur* which spent no time feeding on *Euphorbia* have the most negative values in the sample. While these values approach the least

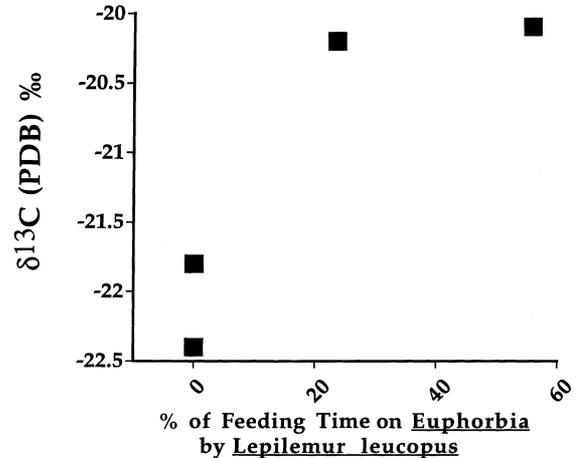


Fig. 2 Observational data of feeding for four individual *L. leucopus* plotted against hair $\delta^{13}\text{C}$ values. There is a positive linear relation with time spent feeding on *Euphorbia tirucalli*, a CAM tree species. One result of the response to water stress in CAM species is that leaf $\delta^{13}\text{C}$ values are less negative than normal (O'Leary 1988). The *Lepilemur* study site in Madagascar had experienced severe drought for 2 years prior to hair collection

negative of the galago hair $\delta^{13}\text{C}$ values they do not overlap them. Within the *Lepilemur* sample there is a tendency for individual $\delta^{13}\text{C}$ values to correlate with a reported vegetation gradient of more mesic to more xeric moving away from a seasonally flowing river (Sussman 1991; Sussman and Rakotozafy 1994). If we eliminate two individuals whose habitats are severely degraded and include a *Euphorbia* stand, individual $\delta^{13}\text{C}$ values approach a significant correlation with the distance of the individual's home range from the seasonal river which forms the eastern border of the roughly rectangular reserve (Spearman's $R = 0.716$, $n = 7$, critical value for $P < 0.05$ is $R = 0.714$). Leaf $\delta^{13}\text{C}$ values in C_3 plants are less negative under drought conditions, an effect exaggerated in xeric areas compared to mesic areas (see Table 2; Garten and Taylor 1992) and there is a clear trend for *Lepilemur* individuals from more xeric ranges to have less negative $\delta^{13}\text{C}$ values.

The two galago species are significantly different from each other in $\delta^{13}\text{C}$ values (Figure 1; 0.02 level of probability, 16 *df*). *G. zanzibaricus* is 0.5‰ more negative than *G. garnettii*. The smaller *G. zanzibaricus* depends to a greater extent on insects than does the larger *G. garnettii* but, as discussed above, this is not the causal variable. The difference between the two galago species is of the same order of magnitude and in the same direction as that between leaves from the base (0–5 m) and the mid-canopy portion in deciduous, tropical forests (see Fig. 3; Broadmeadow et al. 1992). *G. zanzibaricus* spends approximately 70% of its time below 5 m in the canopy whereas *G. garnettii* spends over 50% of the time above 5 m (Harcourt and Nash 1986). The $\delta^{13}\text{C}$ values in leaves from different heights in individual forests are comparable between similar forest habitats (see Table 3) and result from isotope effects (Farquhar et al. 1982). These effects are produced by various fac-

tors (Lajtha and Marshall 1994) including soil-respired ¹²C-enriched CO₂ at the canopy base (Schleser and Jayasekera 1985; Broadmeadow et al. 1992) and high light levels at canopy tops (Yakir and Israeli 1995). The average difference between galagos occurs even though the two species do not completely restrict their movements to one or the other position within the canopy. *Lepilemur*, which occupies the upper level of the canopy in a drought-afflicted forest, also fits the trend. A high light level at the canopy top combines with the drought effect in the latter genus.

Table 2 Effects of water availability on C₃ plant δ¹³C values. Data are from Garten and Taylor (1992), in which habitats labelled 'xeric' are those on hilltops and hillsides and 'mesic' refers to valley bottoms. The same plant species were represented in each habitat

Annual rainfall (mm)	Habitat	
	Xeric δ ¹³ C (PDB) ± SE (‰)	Mesic δ ¹³ C (PDB) ± SE (‰)
500	-28.9 ± 0.2	-29.8 ± 0.2
800	-29.2 ± 0.1	-30.0 ± 0.2
1,000	-29.8 ± 0.1	-30.2 ± 0.2

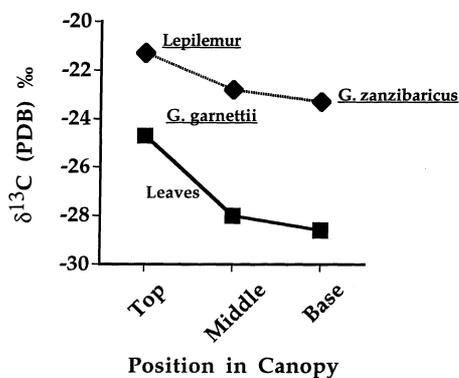


Fig. 3 Average leaf and animal δ¹³C values plotted against vertical position within forest canopies. Leaf data are within level averages reported for a deciduous tropical forest in Trinidad (Broadmeadow et al. 1992). The prosimian species (this study) occupy different levels within their deciduous tropical forests in Kenya (*Galago*) and Madagascar (*Lepilemur*). The primate species data show a similar magnitude of difference in δ¹³C values and the same direction of difference as reported for leaf δ¹³C values

Table 3 Leaf δ¹³C (PDB) varies by position in canopy and by the amount of canopy cover in C₃ plants

Canopy level	Trinidad ^a		Venezuela ^b (3,500 mm rain)		Tennessee ^c	Bavaria ^d
	Deciduous tropical	Semi-evergreen tropical	Evergreen tropical podzol	Evergreen tropical laterite	Deciduous temperate	Deciduous temperate
Top	-24.7‰	-28.4‰			-27.7‰	-27.9‰
Mid	-28.0‰	-28.8‰	-30.5‰	-30.4‰	-29.6‰	-28.8‰
Base	-28.6‰	-31.3‰	-35.2‰	-35.4‰		-31.5‰

^a Data from Broadmeadow et al. (1992)
^b Data from van der Merwe and Medina (1989)
^c Data from Garten and Taylor (1992)
^d Data from Vogel (1978b)

Nitrogen

The two omnivorous galago species differ from each other by only 0.3‰ (insignificant statistically) although *G. zanzibaricus*, which includes more insects in its diet than does *G. garnettii*, shows the more positive value. The two galago species are significantly more positive in hair δ¹⁵N values than the herbivore, *Lepilemur*, on average (significant at the 0.01 level, *df* = 25) as expected based on the difference in trophic position. Yet, the average difference between the two genera is only 1.6‰ whereas the offset between trophic levels (Minagawa and Wada 1984; Schoeninger and DeNiro 1984) and between animals and their diets (DeNiro and Epstein 1981; Hare et al. 1991) is commonly 3‰. Elevated animal δ¹⁵N values correlate with water conservation mechanisms in some situations (Schoeninger and DeNiro 1984; Ambrose and DeNiro 1986; Heaton et al. 1986; Sealy et al. 1987; Cormie and Schwarcz 1996) and it is possible that the *Lepilemur* δ¹⁵N values are elevated as a result of water stress. Further controlled studies are needed in this area.

Within the *Lepilemur* sample there is a negative correlation between hair δ¹⁵N values and the amount of feeding time spent on *T. indica* (kily), a leguminous tree (Fig. 4). Plant δ¹⁵N values vary primarily with soil nitrogen loss rates (Nadelhoffer and Fry 1994) and N₂ fixation by plant species with symbiotic bacteria (Shearer and Kohl 1986; Bowman et al. 1996; Hogberg et al. 1996). Legumes normally show δ¹⁵N values that are less positive than non-legumes (Fig. 5), with the size of the offset indicating the amount of N₂ fixation (Virginia and Delwiche 1982; Shearer et al. 1983; Shearer and Kohl 1986). Among the four *Lepilemur* there is a 3‰ range of variation associated with a maximum difference of 20% in feeding time devoted to leguminous plants. This range encompasses the total range of variation within our *Lepilemur* sample.

The range of variation within each prosimian species is large compared with previously reported data on hair δ¹⁵N values in four New World monkey species. The range of values in the two galago species (3.4‰ and 3.0‰) and in *Lepilemur* (3.1‰) is up to an order of magnitude larger than in four *Cebus* (0.2‰), five *Ateles* (0.6‰), nine *Alouatta* (1.0‰), and seven *Brachyteles*

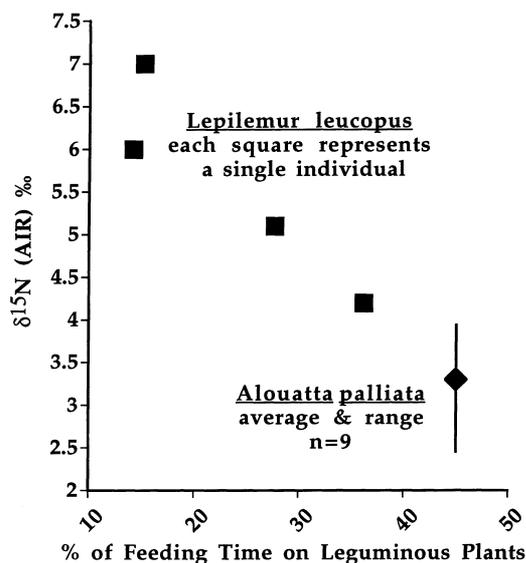


Fig. 4 Observational data of feeding plotted against hair $\delta^{15}\text{N}$ values for four individual *L. leucopus* (this study) and the average for nine *Alouatta palliata* (Schoeninger et al. 1997). Within *Lepilemur*, the stable isotope data show an inverse correlation with time spent feeding on *Tamarindus indica* which is a leguminous tree species. Within *Alouatta*, the population is reported to spend more than 40% of its feeding time on leguminous plants (Glander 1979). Legumes can fix atmospheric N_2 , in which case their tissues have $\delta^{15}\text{N}$ values lower than those in other plants, on average

(1.1‰) (Schoeninger et al. 1997) as well as in five domestic *Sus* fed monotonous diets (1.4‰) (M.J. Schoeninger, U.T. Iwaniec and T. Crenshaw, unpublished data). *Lepilemur*, the prosimian for which we have focal feeding data, shows a range of variation of 14% to 36% of time spent feeding on leguminous plants. *Alouatta* was also reported feeding on leguminous plants (Glander 1979), yet, the range of variation in hair $\delta^{15}\text{N}$ values within *Alouatta* (Schoeninger et al. 1997) is one-third that of *Lepilemur*. In contrast to *Lepilemur*, *Alouatta* forages in groups where individuals often use the same routes for travel following each other in single file (Milton 1980) and presumably eating similar items. *Lepilemur* and the galagos, for which we have no focal feeding data, have solitary feeding habits and presumably vary individually in diet items as reported for *Lepilemur*. We conclude that the large ranges in the three prosimian species are probably due to variation in diet items taken by different individuals and that this parameter is an indirect indicator of species foraging strategy. As such, the species range in $\delta^{15}\text{N}$ values reflects feeding habits while the individual values indicate diet.

Discussion

As expected, average $\delta^{13}\text{C}$ values of species were correlated with the drought in Madagascar and with feeding position in the forest canopy. Average $\delta^{15}\text{N}$ values

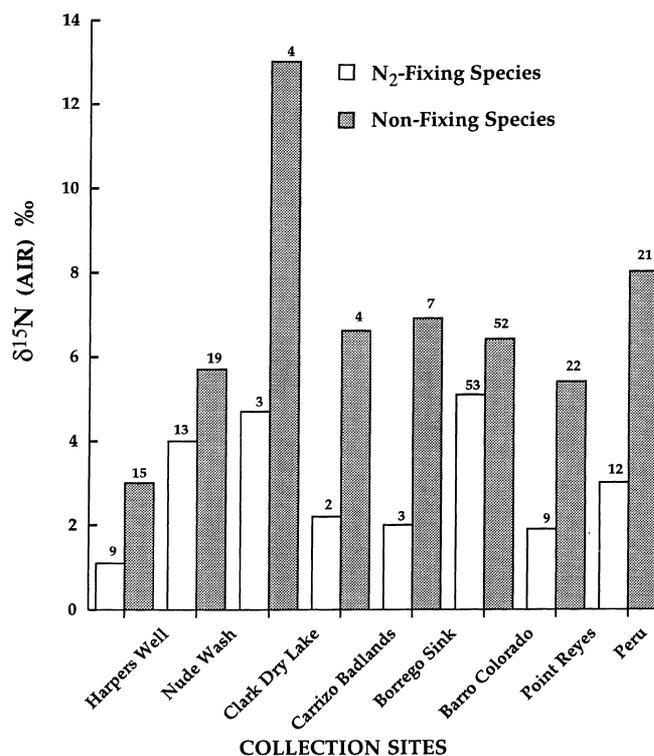


Fig. 5 Average plant $\delta^{15}\text{N}$ values reported for N_2 -fixing species and for non-fixing species (data redrawn from Virginia and Delwiche 1982; Shearer et al. 1983; Shearer and Kohl 1986). The number of species from each collection site is shown above each column. Within each site, the average value for fixing species is always lower than that for non-fixing species although there is variation between sites. For the most part, the $\delta^{15}\text{N}$ values of non-fixing species fall between 6‰ and 7‰ and those of N_2 -fixing species are less than 4‰. The variation is due to differences in source nitrogen (biomass degradation, source rock, or rain in non-fixing species, and N_2 fixation in the others) and nitrogen loss mechanisms in soil (biomass burning, water removal, plant uptake)

correlated with trophic position and time spent feeding on leguminous plants. In addition, the solitary feeding habits of the three species are reflected in the large range of variation within each species when compared with other species that feed as a group.

Of significance is the apparent generality of these findings. We contend that general trends and processes are reflected in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of arboreal primate tissues. Average $\delta^{13}\text{C}$ values in *Galago* hair are very similar to those in two species of New World monkeys living in dry, deciduous forests of Costa Rica and Brazil (Table 4). *L. leucopus* from a drought-afflicted CAM/ C_3 forest has less negative $\delta^{13}\text{C}$ values and two species of New World monkeys from a wetter, closed-canopy C_3 forest in Costa Rica have more negative $\delta^{13}\text{C}$ values.

The $\delta^{15}\text{N}$ values from the species are also comparable. Two disparate genera, *Galago* and *Cebus* (Table 5), the former a prosimian from Kenya and the latter an anthropoid from Costa Rica, are both insectivore-frugivores and have identical average $\delta^{15}\text{N}$ values. There is also congruence in two folivorous species, *L. leucopus*

Table 4 $\delta^{13}\text{C}$ in hair correlates with forest type. [Data for New World monkeys are standardized to PDB (from Schoeninger et al. 1997)]

Tropical forest type (annual rainfall)	Old World prosimians $\delta^{13}\text{C} \pm \text{SD} (n)$	New World monkeys $\delta^{13}\text{C} \pm \text{SD} (n)$
Drought deciduous (<750 mm)	$-21.3 \pm 0.8\text{‰} (9)$	
Deciduous (<1,500 mm)	$-23.1 \pm 0.4\text{‰} (18)$	$-23.5 \pm 0.3\text{‰} (19)$
Evergreen (4,000 mm)		$-24.8 \pm 0.3\text{‰} (9)$

Table 5 $\delta^{15}\text{N}$ in hair correlates with diet [data from Schoeninger et al. (1997)]

	Body weight (kg)	Diet	$\delta^{15}\text{N}$ (AIR) $\pm \text{SD} (n)$
Insectivorous frugivores			
<i>Galago garnettii</i>	0.8	50% animal 50% fruit 0% leaves	$7.1 \pm 0.9\text{‰} (9)$
<i>Cebus capucinus</i>	2.5	20% animal 65% fruit 15% leaves	$7.0 \pm 0.1\text{‰} (4)$
Folivores			
<i>Alouatta palliata</i>	5–7	0% animal 31% fruit 64% leaves (>40% legumes)	$3.3 \pm 0.4\text{‰} (9)$
<i>Lepilemur leucopus</i>	0.6	0% animal 0% fruit 100% leaves (15–35% legumes)	$5.5 \pm 1.0\text{‰} (9)$

and *A. palliata* when plant species data are taken into account (see Fig. 4). Both species are committed folivores based on tooth morphologies (Kay 1975) and gut morphologies (Chivers and Hladik 1980) but *Lepilemur* has average $\delta^{15}\text{N}$ values almost 2‰ more positive than the average for *Alouatta*. The population of *Alouatta* spends over 40% of its feeding time on leguminous plants (Glander 1981), whereas the extreme in *Lepilemur* is 36%. The possibility that some *Lepilemur* $\delta^{15}\text{N}$ values are elevated in response to water stress requires further study.

In combination, these data strongly support the conclusion that hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of forest-dwelling primates accurately reflect general aspects of species habitat utilization and nutritional ecology. As such, the data suggest that the analysis of hair (or other proteinaceous tissues) from museum specimens of forest-dwelling primates can be used in reconstructing general aspects of forest paleoecology, species diet, and species feeding patterns (solitary vs. group feeding) in extinct populations and species. Further analyses of animal tissues from well-studied ecosystems in which diet items are also analyzed can only hasten the full realization of

the enormous potential in this approach to primate ecology, specifically, and to animal ecology, in general.

Acknowledgements We thank Melinda Carter, Jim Moore, Michele Morgan, and an anonymous reviewer for comments on previous versions of the manuscript. Irwin Ting and Marion O'Leary provided helpful discussions regarding *Euphorbia* and CAM plants as did Jim Moore on feeding habits in monkeys and prosimians. The research was supported by the Wisconsin Alumni Research Foundation (to M.J.S) and by the Center for Field Research, Wenner-Gren Foundation, National Geographic Society, and NIMH grant 1 RO3-MH35736-01 (to L.T.N.).

References

- Ambrose SH, DeNiro MJ (1986) The isotopic ecology of East African mammals. *Oecologia* 69: 395–406
- Ambrose SH, Norr L (1993) Experimental evidence for the relationship of carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert JB, Grupe G (eds) Prehistoric human bone: archaeology at the molecular level. Springer, Berlin Heidelberg New York, pp 1–38
- Association of Applied Biologists (1996) Stable isotopes and the integration of biological, ecological and geochemical processes. Association of Applied Biologists Annual Conference in association with The Society for Experimental Biology and the British Ecological Society, University of Newcastle upon Tyne-Conference Proceedings
- Bada JL, Peterson RO, Schimmelmann A, Hedges REM (1990) Moose teeth as monitors of environmental isotopic parameters. *Oecologia* 82: 102–106
- Bender MM (1971) Variations in the ^{13}C and ^{12}C ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. *Phytochemistry* 10: 1239–1244
- Bocherens H, Fizet M, Mariotti A (1994) Diet, physiology, and ecology of fossil mammals as inferred from stable carbon and nitrogen biogeochemistry: implications for Pleistocene bears. *Palaeogeog Palaeoclimatol Palaeoecol* 107: 213–225
- Bowman WD, Scharadt JC, Schmidt SK (1996) Symbiotic N_2 -fixation in alpine tundra: ecosystem input and variation in fixation rates among communities. *Oecologia* 108: 345–350
- Broadmeadow MSJ, Griffiths H, Maxwell C, Borland AM (1992) The carbon isotope ratio of plant organic material reflects temporal and spatial variations in CO_2 within tropical forest formations in Trinidad. *Oecologia* 89: 435–441
- Cerling T, Wang Y, Quade J (1993) Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. *Nature* 361: 344–345
- Charles-Dominique P, Bearder SK (1979) Field studies of loroid behavior: methodological aspects. In: Doyle GA, Martin RD (eds): The study of prosimian behavior. Academic Press, New York, pp 567–629
- Chivers DJ, Hladik CM (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J Morphol* 166: 337–386
- Cormie AB, Schwarcz HB (1996) Effects of climate on deer bone $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$: lack of precipitation effects on $\delta^{15}\text{N}$ for animals consuming low amounts of C4 plants. *Geochim Cosmochim Acta* 60: 4161–4166
- DeNiro MJ, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197: 261–263
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42: 495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45: 341–351
- Dietz JM, Baker AJ, Allendorf TD (1995) Correlates of molt in Golden Lion Tamarins (*Leontopithecus rosalia*). *Am J Primatol* 36: 277–284

- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust J Plant Physiol* 9: 121–137
- Fleagle JG (1988) Primate adaptation and evolution. Academic Press, San Diego
- Ganzhorn JU (1988) Food partitioning among Malagasy primates. *Oecologia* 75: 436–450
- Garten CTJ, Taylor GEJ (1992) Foliar $\delta^{13}\text{C}$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. *Oecologia* 90: 1–7
- Glander KE (1979) Howling monkey feeding behavior and plant secondary compounds: a study of strategies. In: Montgomery GG (eds) *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, DC, pp 561–574
- Glander KE (1981) Feeding patterns in mantled howling monkeys. In: Kamil AC, Sargent TD (eds) *Foraging behavior: ecological, ethological, and psychological approaches*. Garland, New York, pp 231–257
- Harcourt CS, Nash LT (1986) Species differences in substrate use and diet between sympatric Galagos in two Kenyan coastal forests. *Primates* 27: 41–52
- Hare PE, Fogel ML, Stafford TW Jr, Mitchell AD, Hoering TC (1991) The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins. *J Archaeol Sci* 18: 277–292
- Hastorf CA, DeNiro MJ (1985) New isotopic method used to reconstruct prehistoric plant production and cooking processes. *Nature* 315: 489–491
- Heaton THE, Vogel JC, Chevallerie G von la, Gollett G (1986) Climatic influence on the isotopic composition of bone nitrogen. *Nature* 322: 822–823
- Hladik CM, Charles-Dominique P (1974) The behaviour and ecology of the sportive lemur (*Lepilemur mustelinus*) in relation to its dietary peculiarities. In: Martin RD, Doyle GA, Walker AC (eds) *Prosimian biology*. University of Pittsburgh Press, Pittsburgh, pp 17–22
- Hobson KA, Alisauskas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95: 388–394
- Hobson KA, Sease JL, Merrick RL, Piatt JF (1997) Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. *Mar Mamm Sci* 13: 114–132
- Hogberg P, Hogbom L, Schinkel H, Hogberg M, Johannisson C, Wallmark H (1996) ^{15}N abundance of surface soils, roots and mycorrhizas in profiles of European forest soils. *Oecologia* 108: 207–214
- Inagaki H, Nigi H (1988) Annual changes in hair length of the Japanese monkey (*Macaca fuscata fuscata*). *Primates* 29: 81–89
- Isbell LA (1995) Seasonal and social correlates of changes in hair, skin, and scrotal condition in vervet monkeys (*Cercopithecus aethiops*) of Amboseli National Park, Kenya. *Am J Primatol* 36: 61–70
- Jones RJ, Ludlow MM, Troughton JH, Blunt CG (1981) Changes in the natural carbon isotope ratios of the hair from steers fed diets of C_4 , C_3 and C_4 species in sequence. *Search* 12: 85–87
- Kay RF (1975) The functional adaptations of primate molar teeth. *Am J Phys Anthropol* 43: 195–216
- Kay RF (1984) On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH (eds) *Adaptations for foraging in nonhuman primates: contributions to an organismal biology of prosimians, monkeys and apes*. Columbia University Press, New York, pp 21–53
- Kay RF, Hylander WL (1978) The dental structure of mammalian folivores with special reference to primates and Phalangerioidea (Marsupialia). In: Montgomery G (ed) *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, DC, pp 173–191
- Kingston JD, Marino BD, Hill A (1994) Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. *Science* 264: 955–959
- Kluge M, Ting IP (1978) *Crassulacean acid metabolism: analysis of an ecological adaptation*. Springer, Berlin Heidelberg New York
- Koch PL, Fogel ML, Tuross N (1994) Tracing diets of fossil animals using stable isotopes. In: Lajtha K, Michener RH (eds) *Stable isotopes in ecology and environmental science*. Blackwell, Oxford, pp 63–92
- Lajtha K, Marshall JD (1994) Sources of variation in the stable isotopic composition of plants. In: Lajtha K, Michener RH (eds) *Stable isotopes in ecology environmental science*. Blackwell, Berlin, pp 1–21
- Lajtha K, Michener RH (1994) *Stable isotopes in ecology and environmental science*. Blackwell, Berlin
- Lemos De Sa RM, Glander KE (1993) Capture techniques and morphometrics for the Woolly Spider monkey, or Muriqui (*Brachyteles arachnoides*, E. Geoffroy 1806). *Am J Primatol* 29: 145–153
- Marino BD, McElroy MB (1991) Isotopic composition of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. *Nature* 349: 127–131
- Martin P, Bateson P (1993) *Measuring behavior*, 2nd edn. Cambridge University Press, Cambridge, UK
- Merwe NJ van der, Medina E (1989) Photosynthesis and $^{13}\text{C}/^{12}\text{C}$ ratios in Amazonian rain forests. *Geochim Cosmochim Acta* 53: 1091–1094
- Merwe NJ van der, Medina E (1991) The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *J Archaeol Sci* 18: 249–259
- Milton K (1980) *The foraging strategy of howler monkeys: a study in primate economics*. Columbia University Press, New York
- Milton K (1987) Primate diets and gut morphology: implications for hominid evolution. In: Harris M, Ross EB (eds) *Food and evolution*. Temple University Press, Philadelphia, pp 93–115
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48: 1135–1140
- Minson DJ, Ludlow MM, Troughton JH (1975) Differences in natural carbon isotope ratios of milk and hair from cattle grazing tropical and temperate pastures. *Nature* 256: 602
- Morgan ME, Kingston JD, Marino BD (1994) Carbon isotopic evidence for the emergence of C_4 plants in the Neogene from Pakistan and Kenya. *Nature* 367: 162–165
- Nadelhoffer KJ, Fry B (1994) Nitrogen isotope studies in forest ecosystems. In: Lajtha K, Michener RH (eds) *Stable isotopes in ecology and environmental science*. Blackwell, Berlin, pp 22–44
- Nakamura K, Schoeller DA, Winkler FJ, Schmidt HL (1982) Geographical variations in the carbon isotope composition of the diet and hair in contemporary man. *Biomed Mass Spectrom* 9: 390–394
- Nash LT (1994) Behavior and habitat use of *Lepilemur* at Beza Mahafaly Special Reserve, Madagascar. *Am J Primatol* 33: 230
- Nash LT (1997) Vertical clingers and sleepers: seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatol* (in press)
- O'Leary MH (1981) Carbon isotope fractionation in plants. *Phytochemistry* 20: 553–567
- O'Leary MH (1988) Carbon isotopes in photosynthesis. *Bioscience* 38: 328–336
- Oftedal OT (1991) The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. *Phil Trans R Soc Lond B* 334: 161–170
- Pate FD (1994) Bone chemistry and paleodiet. *J Archaeol Method Theor* 1: 161–209
- Pereira ME (1993) Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: Kappeler PM, Ganzhorn JU (eds) *Lemur social systems and their ecological basis*. Plenum, New York, pp 205–221
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18: 293–320

- Pulliam HR, Babbitt B (1997) Science and the protection of endangered species. *Science* 275: 499–500
- Russell RJ (1977) The behavior, ecology, and environmental physiology of a nocturnal primate, *Lepilemur mustelinus* (Strepsirhini, Lemuriformes, Lepilemuridae). PhD dissertation, Duke University, Durham, NC
- Schleser GH, Jayasekera R (1985) $\delta^{13}\text{C}$ variations of leaves in forests as an indication of reassimilated CO_2 from the soil. *Oecologia* 65: 536–542
- Schoeninger MJ (1985) Trophic level effects on $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ ratios in bone collagen and strontium levels in bone mineral. *J Hum Evol* 14: 515–525
- Schoeninger MJ (1995) Stable isotope studies in human evolution. *Evol Anthropol* 4: 83–98
- Schoeninger MJ, DeNiro MJ (1984) Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochim Cosmochim Acta* 48: 625–639
- Schoeninger MJ, Moore K (1992) Bone stable isotope studies in archaeology. *J World Prehist* 6: 247–296
- Schoeninger MJ, Iwaniec UT, Glander KE (1997) Stable isotope ratios monitor diet and habitat use in New World monkeys. *Am J Phys Anthropol* 103: 69–83
- Schwarcz H, Schoeninger MJ (1991) Stable isotope analyses in human nutritional ecology. *Yearb Phys Anthropol* 34: 283–321
- Sealy JC, Merwe NJ van der, Lee Thorp JA, Lanham JL (1987) Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. *Geochim Cosmochim Acta* 51: 2707–2717
- Shearer G, Kohl DH (1986) N_2 -fixation in field settings: estimations based on natural ^{15}N abundance. *Aust J Plant Physiol* 13: 699–756
- Shearer GB, Kohl DH, Virginia RA, Bryan BA, Skeeters JL, Nilsen ET, Sharifi MR, Rundel PW (1983) Estimates of N_2 -fixation from variation in the natural abundance of ^{15}N in Sonoran Desert ecosystem. *Oecologia* 56: 365–373
- Simons EL (1995) Skulls and anterior teeth of *Catopithecus* (Primates: Anthroidea) from the Eocene and anthropoid origins. *Science* 268: 1885–1888
- Sussman RW (1991) Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *Am J Phys Anthropol* 84: 43–58
- Sussman RW, Rakotozafy A (1994) Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. *Biotropica* 26: 241–254
- Swick RW, Benevenga NJ (1977) Labile protein reserves and protein turnover. *J Dairy Sci* 60: 505–515
- Tieszen LL, Fagre T (1993) Effect of diet quality and composition on the isotopic composition of respiratory CO_2 , bone collagen, bioapatite, and soft tissues. In: Lambert JB, Grupe G (eds): Prehistoric human bone: archaeology at the molecular level. Springer, Berlin Heidelberg New York, pp 121–156
- Tieszen LL, Hein D, Qvortrup SA, Troughton JH, Imbamba SK (1979) Use of $\delta^{13}\text{C}$ values to determine vegetation selectivity in East African herbivores. *Oecologia* 37: 337–350
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57: 32–37
- Ting IP, Gibbs M (1982) Crassulacean acid metabolism. Waverly, Baltimore
- Ting IP, Rayder L (1982) Regulation of C_3 to CAM shifts. In: Ting IP, Gibbs M (eds): Crassulacean Acid Metabolism. Waverly, Baltimore, pp 193–207
- Virginia RA, Delwiche CC (1982) Natural ^{15}N abundance of presumed N_2 -fixing and non- N_2 -fixing plants from selected ecosystems. *Oecologia* 54: 317–325
- Vogel JC (1978a) Isotopic assessment of the dietary habits of ungulates. *S Afr J Sci* 74: 298–301
- Vogel JC (1978b) Recycling of carbon in a forest environment. *Oecol Plant* 13: 89–94
- Vogel JC, Merwe NJ van der (1977) Isotopic evidence for early maize cultivation in New York state. *Am Antiq* 42: 238–242
- Vogel JC, Talma AS, Hall-Martin AJ, Viljoen PJ (1990) Carbon and nitrogen isotopes in elephants. *S Afr J Sci* 86: 147–150
- Wada E, Minagawa M (1983) Nitrogen isotope fractionation as a clue to food chain dynamics in marine environments. *Tracer* 8: 2–12
- Webster GL, Brown WV, Smith BN (1975) Systematics of photosynthetic carbon fixation pathways in *Euphorbia*. *Taxon* 24: 27–33
- White CD (1993) Isotopic determination of seasonality in diet and death from Nubian mummy hair. *J Archaeol Sci* 20: 657–666
- Yakir D, Israeli Y (1995) Reduced solar irradiance effects on net primary productivity (NPP) and the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in plantations of *Musa* sp., *Musaceae*. *Geochim Cosmochim Acta* 59: 2149–2151