CARBON ISOTOPIC EVIDENCE FOR DIFFERENT FEEDING PATTERNS IN AN ASIAN ELEPHANT POPULATION

R. SUKUMAR, S. K. BHATTACHARYA* and R. V. KRISHNAMURTHY*

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India.

**Physical Research Laboratory, Navrangpura, Ahmedabad 380 009, India.*

ABSTRACT

Stable carbon isotope ratios ($^{13}C/^{12}C$) in bone collagen of Asian elephants showed a variation in $\delta^{13}C$ value from $-11{\cdot}1$ to $-20{\cdot}8$ per mil. This indicates that individuals within a population vary widely in their dietary intake of C_4 plants (grasses) and C_3 plants (browse), from a predominance of either of these types through intermediate proportions. The difference in feeding pattern may be related to age, with younger elephants preferentially grazing and adults mainly browsing.

INTRODUCTION

During the last few years, stable carbon isotopes are being used to study the feeding patterns of animals. For herbivores this involves determining the $^{13}C/^{12}C$ ratio in plant material collected from the stomach of the animal[1], fecal matter[2], or in an animal tissue such as bone collagen[3-5] and comparing these values with the $^{13}C/^{12}C$ ratios of the potential food plants. It is posssible to estimate the contribution to the diet of two major plant categories, the C_3 and C_4 plants characterized by their different photosynthetic pathways of carbon fixation. The C_3 and C_4 plants have widely differing $\delta^{13}C$ values averaging about -27 per mil and -13 per mil respectively.

$$\delta^{13}C = \left[\frac{(^{13}C/^{12}C)\ \text{sample}}{(^{13}C/^{12}C)\ \text{standard}} - 1 \right] \times 1000 \text{ per mil}$$

For the work reported here, the standard is the Pee Dee belemnite (PDB) carbonate.

Depending on their food preferences, herbivorous mammals may be pure browsers, pure grazers or intermediate feeders to varying degrees on browse and grass. Most of the browse plants are of the C_3 type, while grasses may be either C_3 or C_4 type. Observational methods of determining proportions of browse and grass in the diet usually involve sampling the population at different seasons. Either the stomach contents of shot animals are visually separated into the component browse and grass species or the proportion of time spent by the animal in browsing and grazing recorded. This is time consuming and often difficult when dealing with animals in habitats with poor visibility (or dangerous as when following elephants at close distance). Also individual preferences, if any, are not easily detectable since the sampled animal provides information only on what it has been feeding at the time of observation or in the near past. The estimate of browse-grass proportion is essentially an average for the population as a whole. The analysis of carbon isotopic ratios of stomach contents or fecal matter also provides similar information though in much less time[1,2]. On the other hand, the $\delta^{13}C$ analysis of secondary metabolic products such as collagen provides an estimate of the proportion of C_3 and C_4 plants in the diet which, hopefully, is integrated over the lifetime of the animal.

The elephant is known to be a generalist feeder, consuming a large variety of browse and grass species. African elephants (*Loxodonta africana*) confined to savanna habitats include a large proportion of grasses in the diet, but this is thought to be forced upon them due to elephant and fire-induced conversion of woodland into grassland[6]. Where browse is available in plenty as in bushland or forest, elephants show a markedly lower preference for grass. In South India, the Asian elephant (*Elephas maximus*) ranges predominantly over deciduous forest where both browse and grass are available. This investigation was undertaken to estimate the proportions of C_3 and C_4 plants in the diet of the Asian elephant by measuring the $\delta^{13}C$ value of its bone collagen and relating it to the $\delta^{13}C$ value of the major food plants identified by direct observation[7]

METHODS

Bones from 12 elephants which died due to natural causes or shooting were collected from a single population inhabiting the Forest Divisions of Chamarajanagar, Satyamangalam and Nilgiris in South India. Both male and female elephants of various ages from new-born to adult were represented. The sex and age of the elephant were not known in cases where the carcass had totally decomposed. About 1 gm of powdered bone from each sample was used to extract collagen as a gelatin by a method described previously[8]. Carbon dioxide gas was prepared from the gelatin by a microcombustion procedure[9] and analyzed for $\delta^{13}C$ in a VG Micromass 602D mass spectrometer with a precision of ± 0.2 per mil. The major plants of elephants were similarly dried, combusted to CO_2 gas and analyzed for $\delta^{13}C$ value.

RESULTS AND DISCUSSION

$\delta^{13}C$ values of C_3 and C_4 plants and their classification as browse and grass

Ten species of browse plants from the Leguminosae, Palmae, Malvales and Bambusoideae (Gramineae) were analyzed for $\delta^{13}C$ value. All of them were found to be C_3 plants. Bamboo is botanically a grass, but its growth form resembles a tree. Hence, elephant feeding on bamboo is properly described as browsing. Further, bamboos being C_3 plants it was convenient to classify them along with the remaining C_3 browse plants. The mean $\delta^{13}C$ value of C_3 plants was -27.2 per mil ($\sigma_{n-1} = 1.28$, n = 10, range from -26.1 to -30.1 per mil, 8 out of 10 samples between -26.1 and -27.6 per mil).

All the tall grasses (mainly *Themeda* and *Cymbopogon*) eaten by elephants were found to be C_4 plants. The mean $\delta^{13}C$ value of C_4 grasses was -12.8 per mil ($\sigma_{n-1} = 0.44$, n = 7, range from -12.2 to -13.3 per mil).

Thus, browsing by elephants can be equated with feeding on C_3 plants and grazing with feeding on C_4 plants.

Shift in $\delta^{13}C$ value of secondary metabolites relative to the diet

Before interpreting the $\delta^{13}C$ values of the elephant bone collagen one has to consider the shift in $\delta^{13}C$ value of the collagen fraction relative to the diet due to metabolic effects. This shift has been estimated as averaging $+3.2$ per mil for mice raised experimentally on a known diet[8], about $+5$ per mil for mammals like the giraffe known to have a pure C_3 diet and $+6$ per mil for mammals with essentially pure C_4 diet[5]. The exact amount of this enrichment may depend on the diet as well as the animal species. In the absence of any measured value for elephants, we have adopted a mean value of $+4.7$ per mil. This seems to be the best possible choice at present since adoption of either of the extreme values reported ($+3.2$ or $+6$ per mil) would imply that the indicated percentage of either C_3 or C_4 plants in the diet of some elephants would be close to 100%. Field observations show that such an extreme dependence on one plant type is not likely in our case[7].

$\delta^{13}C$ values of elephant bone collagen and interpretation in relation to diet composition

The $\delta^{13}C$ values for the 12 bone samples along with the inferred proportions of C_3 and C_4 plants in the diet are given in table 1. The variation in the $\delta^{13}C$ value from -11.1 to -20.8 per mil indicates that the ratio of C_3 to C_4 plants in the diet may vary from 21:79 to 87:13 respectively. The carbon isotopic composition of a new-born calf (No. 12) is entirely contributed by its mother, while that of a one-year-old male (No. 11) which would be still

Table 1 *Stable carbon isotopic composition of Asian elephant bone collagen*

No.	Sex and age class of elephant	$\delta^{13}C$ (per mil) collagen	Inferred ratio of C_3.C_4 plants in the diet
1.	Male adult	−19.6	79:21
2.	Male adult	−20.3	83:17
3.	Female adult	−18.5	71:29
4.	Female sub-adult	−12.2	27:29
5.	Female sub-adult	−14.7	44:56
6.	Unsexed sub-adult	−11.1	21:79
7.	Unsexed sub-adult	−12.8	31:69
8.	Not known	−14.6	44:56
9.	Not known	−20.2	83:17
10.	Not known	−12.8	32.68
11.	Male 1 year	−16.5	57:43
12.	Male new-born	−20.8	87:13

Two samples cross checked by Dr Michael DeNiro (University of California, Los Angeles) gave the following $\delta^{13}C$ values (our values are in brackets):
No. 2 = −20.2 per mil (−20.3) No. 3 = −18.1 per mil (−18.5)

suckling also derived largely from the mother. Their $\delta^{13}C$ values thus reflect the diet source of adult female elephants.

The elephants had access to a mosaic of habitat types including (a) short grass areas with predominantly browse plants, (b) deciduous forests with mixed browse and tall grasses and (c) predominantly tall grassland areas. Elephants are far ranging animals. The annual home range area for a number of elephants in this population was estimated[7] to be between 150 and 300 km^2. It can be expected that natural selection has moulded their behaviour such that they utilize the available habitat types with a view to optimizing their dietary intake. A foraging animal may optimize the net energy intake or the best nutrient value by a 'correct' seasonal combination of browse and grass.

The observed variation in the $\delta^{13}C$ value of collagen may be due to one or more of the following reasons. All elephants in a population may not be following a single feeding strategy with respect to browse-grass intake. There could be a strong individual preference for either browse or grass. Such a behavioural heterogeneity is quite likely in a generalist feeder. The observed variation may also be related to a conservative home range dependence. Although an adult male elephant or a female herd may have a large overall home range, it may spend most of its time within one habitat type making movements for only brief periods into other areas. Its feeding would thus be proportional to the availability of plant types within the core home range.

There may be a sex or age specific difference in feeding pattern. Our limited sample does not bring out any clear difference between the sexes, but there is certainly a preliminary case for variation due to age. Consider the change in $\delta^{13}C$ values from new-born to adult stage: New-born calf (-20.8 per mil), one-year-old calf (-16.5 per mil), 5–15 year old sub-adults (-11.1 to -14.7 per mil) and 25–60 year old adults (-18.5 to -20.3 per mil). If adult elephants prefer browse and younger ones grass, then the new-born changes its adult $\delta^{13}C$ value (-20.8 per mil) derived from the mother to around -16.5 per mil in one year since some feeding on plants (grazing) would have already begun in addition to suckling. With a continued preference for grass this value would further alter, perhaps attaining an extreme value of about -11 per mil during sub-adult life. Later, as the proportion of browse intake increases, the $\delta^{13}C$ value may attain an equilibrium between -18 and -21 per mil during adult life.

An important aspect which has not received due attention so far is the rate of metabolic turnover of collagen in the animal. Collagen is preferred for isotopic analysis because it is relatively stable and is also preserved in archaeological bone samples. While it is true that collagen turnover rates are low compared to intra-cellular proteins, they may nevertheless be significant in certain situations. In adult animals collagen is fairly stable in those tissues or organs which have reached their final growth form. But in younger, growing animals the rates of synthesis and resorption of collagen are relatively high[10]. Turnover rates also increase during pathological disorders.

In a long-lived mammal such as the elephant it can be safely assumed that the carbon content of bone collagen in adults represents an accumulation over many years. In sub-adults which are still growing it has to be demonstrated that the carbon isotopic ratio in collagen is not merely a reflection of seasonal feeding (say, during the past 3-4 months). The persistence of this isotopic 'memory' for any biochemical fraction including collagen must be known before conclusions on feeding ecology can be considered totally reliable[11,12].

ACKNOWLEDGEMENTS

We thank Dr Michael DeNiro, University of California, Los Angeles, for cross checking two samples, Dr K. Gopalan for his support, Dr Madhav Gadgil and Dr N. V. Joshi for helpful comments and Mr N. Ramesh for help in extracting collagen.

26 March 1986

1. Tieszen, L. L., Hein, D., Qvortrup, S. A., Troughton, J. H. and Imbamba, S. K., *Oecologia (Berlin)*, 1979, **37**, 351.
2. Tieszen, L. L. and Imbamba, S. K., *Afr. J. Ecol.*, 1980, **18**, 237.
3. Van der Merwe, N. J. and Vogel, J. C., *Nature (London)*, 1978, **276**, 815.
4. DeNiro, M. J. and Epstein, S., *Science*, 1978, **201**, 906.
5. Sullivan, C. H. and Krueger, H. W., *Nature (London)*, 1981 **292**, 333.
6. Laws, R. M., Parker, I. S. C. and Johnstone, R. C. B., *E. Afr. Wildl. J.*, 1970, **8**, 163.

7. Sukumar, R., *Ecology of the Asian elephant (Elephas maximus) and its interaction with man in South India*, Ph. D. thesis, Indian Institute of Science, Bangalore, 1985.
8. DeNiro, M. J. and Epstein, S., *Geochim. Cosmochim. Acta*, 1978, **42**, 495.
9. Stump, R. K. and Frazer, J. W., *Nucl. Sci. Abs.*, 1973, **28**, 7848.
10. Woessner Jr. J. F., In: *Treatise on collagen*, (ed.) B. S. Gould, Academic Press, London, New York, 1968, Vol. 2, p. 253.
11. Tieszen, L. L., *Nature (London)*, 1978, **276**, 97.
12. Lewin, R., *Science*, 1983, **220**, 1369.

NEWS

ANNUAL MEETING OF THE INDIAN NATIONAL SCIENCE ACADEMY

Dr. Awtar Singh Paintal, Director-General of the Indian Council of Medical Research, New Delhi, has been elected as President of the Indian National Science Academy, at the annual meeting of the Academy held recently at the Indian Institute of Science, Bangalore.

During the annual meeting, Prof. C. N. R. Rao, the outgoing president, delivered a lecture on "Electron energy loss spectroscopy: An old technique rediscovered". Prof. Rao in his address appealed to Indian scientists to ensure that their professional contributions were of the highest standards and promoted the much needed excellence to build a vibrant scientific community in the country. Prof. Rao observed that in spite of some of the successes in certain areas of science and technology the scientific scenario in the country was discouraging; though there are a few men and institutions of excellence, the morale and performance of the average working scientist is not very high.

SHANTI SWARUP BHATNAGAR PRIZE FOR SCIENCE AND TECHNOLOGY

Nineteen scientists/technologists have been awarded the Shanti Swarup Bhatnagar Prizes in science and technology for 1985 and 1986. Given for research primarily in India, the award comprises a cash award of Rs. 20,000 and a scroll.

The recipients for 1985 and 1986 are as follows: **Physical Sciences (1985)**: Prof. Narendra Kumar, Indian Institute of Science, Bangalore; Prof. Kehar Singh, Indian Institute of Technology, Delhi; **(1986)**: Prof. P. K. Kaw, Physical Research Laboratory, Ahmedabad. **Biological Sciences (1985)**: Prof. M. Vijayan, Indian Institute of Science, Bangalore; Dr. C. M. Gupta, Central Drug Research Institute, Lucknow; **(1986)** Prof. Madhav Gadgil, Indian Institute of Science, Bangalore. **Engineering Sciences (1985)**: Prof. P. Ramachandra Rao, Banaras Hindu University, Varanasi; **(1986)** Prof. M. L. Munjal, Indian Institute of Science, Bangalore. **Medical Sciences (1985)**: Dr D. K. Ganguly, Indian Institute of Chemical Biology, Calcutta; **(1986)** Dr. S. S. Agarwal, Sanjay Gandhi Post-Graduate Institute of Medical Sciences, Lucknow; Dr Pradeep Seth, All India Institute of Medical Sciences, New Delhi. **Mathematical Sciences (1985)**: Prof. S. K. Malik, Punjab University, Chandigarh; Prof. R. Parthasarathy, Tata Institute of Fundamental Research, Bombay; **(1986)**: Prof. T. Parthasarathy, Indian Statistical Institute, New Delhi; Prof. U. B. Tewari, Indian Institute of Technology, Kanpur. **Earth Sciences (1985)**: Dr R. N. Singh, National Geophysical Research Institute, Hyderabad; **(1986)** Prof. A. K. Gupta, University of Allahabad; Dr. K. Mallick, National Geophysical Research Institute, Hyderabad; **Chemical Sciences: (1986)**: Prof. P. Balaram, Indian Institute of Science, Bangalore.