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ELEPHANT FORAGING : IS BROWSE OR GRASS MORE IMPORTANT ?

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Although it is well known that the elephant is both a browser and a grazer, there is still confusion in the literature about which plant type is more important in its diet. Several studies on elephant foraging through direct observation seem to indicate that grass is the preferred and more important item in the diet.

In this paper, I present results from an analysis of stable carbon isotope ratios in Asian elephant bone collagen, which clearly indicate that browse (of the C3 plant type) contributes on average 70% (range 55-83%) of the organic carbon for protein synthesis, even though it constitutes not more than 50% of the annual quantitative food intake. The reason for this could be the higher mean protein contribution (by a factor of 2 or more) from browse as opposed to grass (C4 plant type) per unit quantity consumed. Additional results from isotope analysis on African elephant populations are also presented to support this observation. Browse then clearly is more important than grass in the elephant's diet. The implications of these results for proper management of the habitat for elephant conservation are discussed.

INTRODUCTION

Although it is well known that the elephant is both a browser and a grazer, there is still confusion in the literature about which plant type is more important in its diet. Several studies on feeding in African elephant (*Loxodonta africana*) and Asian elephant (*Elephas maximus*) indicated that grass constituted by far the predominant component of the diet. For instance, studies in Uganda by Wing and Buss (1970), in Sri Lanka by McKay (1973) and Vancuylenberg (1977) and more recently in southern India by Sivaganesan (1991) all emphasize that over 80% of the time spent feeding is on grass; the implication here is that the elephant is predominantly a grazer.

Some of these results could be seriously biased as the observations have been made largely in grassland or savanna woodland habitat where elephants would in any case eat mostly grass. Elephant occupancy of browse-rich habitats would also have to be taken into account in calculating proportions of the two plant types in the total diet (Sukumar 1989). Other studies in Africa (Sikes 1971, Laws *et al.* 1975, Field and Ross 1976, Barnes 1982) and Asia (Sukumar 1985, 1989) have indicated that browse is at least as important a component of the diet as is grass and is perhaps more important nutritionally.

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The resolution of this question is important for elephant conservation. If the habitat is to be properly managed for elephants, the question is what vegetation type or habitat mosaic has to be promoted in order to ensure a high quality and carrying capacity.

METHODS

Tropical grasses vary in their photosynthetic system of carbon fixation as compared to browse plants (trees and shrubs); the former are known as C4 plants and the latter as C3 plants. These two plant types have very different stable carbon isotope (13C/12C) ratios; the ratios expressed as $\delta^{13}C$ (per mil) average about -13 per mil and -27 per mil for C4 and C3 plants respectively (Smith and Epstein 1971).

The carbon from the diet source can be traced in the tissues of a herbivore feeding on these plant types. Thus, a pure grazer on C4 plants could be expected to have a $\delta^{13}C$ value close to -13 per mil and a pure browser about -27 per mil. In collagen, a bone protein, the values show an enrichment of the heavier isotope by about 4.5 per mil due to isotopic fractionation (DeNiro and Epstein 1978, Sukumar *et al.* 1987, Tieszen *et al.* 1989). Collagen is generally used in the analysis as it is relatively inert and maintains the isotopic "memory" for longer time periods.

Bones (lower jaws) of elephants which died in the Nilgiri-Eastern Ghats tract of southern India were collected for this study. The samples came from elephants which inhabited a wide variety of habitat types including semi-evergreen forest, moist deciduous forest, dry deciduous forest and dry thorn forest. Collagen was extracted from the bone and analyzed in a mass spectrometer for 13C/12C ratios (see Sukumar *et al.* 1987 and Sukumar and Ramesh 1992 for experimental procedures). Although we collected samples from the entire range of age classes (birth to 60 years), only data from adult animals above 25 years are considered for the interpretation here because the isotopic signature in these represents an integration over several years feeding unlike in younger animals whose collagen turns over more rapidly (Sukumar and Ramesh 1992). The mean $\delta^{13}C$ values of commonly consumed C4 and C3 plants in the study area have been earlier established as -12.8 and -27.2 per mil respectively (Sukumar *et al.* 1987). Bamboos being C3 plants and "tree grasses" have been categorized as browse in this study.

RESULTS

The $\delta^{13}C$ values of 16 samples of adult elephants are given in Table 1. The mean value is -18.6 ($\pm$1.36) per mil (range -16.0 to -20.3 per mil). Assuming a shift of 4.5 per mil in the collagen relative to the diet, as mentioned earlier, the mean $\delta^{13}C$ value of -18.6 per mil corresponds to a 71% contribution of organic carbon from C3 (browse) plants and 29% from C4 (grass) plants. The lowest contribution of carbon from C3 plants in the case of a 60-year old adult female from the Biligirirangans still amounts to 54%, while the highest recorded in a 28-year old elephant (of unknown sex) from Mudumalai Sanctuary is 83% of total carbon.

Over all age classes the sample of 56 elephants gave a mean $\delta^{13}C$ value of -16.4 per mil (range -9.4 to -22.7 per mil), corresponding to a 57% carbon contribution from C3 plants. The extreme values from the larger sample may however reflect only seasonal diet and it is thus better to interpret results from adult elephants (Sukumar and Ramesh 1992).

Table 1 compares the results from this study with African elephant populations in a variety of habitat types.

TABLE 1

PERCENTAGE OF C3 PLANTS IN DIET AS INFERRED FROM STABLE CARBON ISOTOPE RATIOS OF BONE COLLAGEN IN AFRICAN ELEPHANT POPULATION

Region/Country	Vegetation type	$\delta^{13}C$ per mil SD	% C3 plants in diet
Nilgiris-E.Ghats, India	Moist & dry deciduous forest	-18.6 ± 1.36 (n=16, adults)	71
		-16.4 ± 3.61 (n=56, all ages)	57
Tsavo, Kenya	Grasslands & dense woodland	-18.4 ± 0.18 (n=65)	75
East Tsavo, Kenya	Grassland	-16.4 ± 0.7 (n=4)	65
Addo, South Africa	Portulacaria thicket	-17.0 ± 0.4 (n=5)	68
Damaraland, Namibia	Semi desert	-19.0 (n=1)	82
Luangwa, Zambia	Mixed woodland with mopane	-17.9 ± 0.2 (n=4)	75
Liwonde, Malawi	Mopane woodland with marsh	-19.3 ± 0.3 (n=3)	85
Kruger, South Africa	Bushveld savanna	-20.8 ± 1.0 (n=34)	97
Kasungu, Malawi	Brachystegia woodland	-19.8 ± 0.3 (n=4)	88
Nazinga, Burkina Faso	Northern guinea savanna	-21.9 (n=2)	100
Parc W., Niger	Northern guinea savanna	-22.0 ± 0.3 (n=5)	100
Shimba Hills, Kenya	Forest-woodland mosaic	-22.2 ± 0.3 (n=4)	100
Knysna, South Africa	Coastal forest	-23.2 (n=1)	100
Gola, Sierra Leone	Rain forest	-24.0 (n=1)	100
Sapo, Liberia	Primary rain forest	-27.3 ± 0.5 (n=8)	100

Based on Sukumar and Ramesh (1992) and Tieszen *et al.* (1989).

DISCUSSION

The carbon isotope analyses clearly show that C3 or browse plants contribute a much higher quantity of carbon for organic growth in elephants. Direct observations in the same region on elephant feeding indicate that on average elephants feed equally on browse and C4 grass on an annual basis (Sukumar 1989, Sukumar and Ramesh 1992). However, what is important in ultimate contribution of protein for growth is not merely the quantity of the two plant types consumed but the relative protein value of these plants. Here, the browse plants are generally of higher quality in terms of crude protein content (range 3-26% dry weight) as opposed to C4 grasses (range 1.5-10%) (for details of nutritive values see Sukumar 1989).

The browse plants are especially important during the dry season when high quality forage is scarce. Observations on body condition in elephant clans ranging over browse-rich habitat versus tall grass forests during the dry season in the Satyamangalam-Chamarajanagar Division indicate that the former were in much better condition as compared to the latter during the peak of the dry period (Sukumar 1985). Although this observation is only qualitative, it nevertheless supports the hypothesis that elephants which obtain their nutrition largely from browse plants are in better body condition than those which predominantly graze.

Isotopic studies by Tieszen *et al.* (1989) on African elephants at Tsavo also gave a mean $\delta^{13}C$ value of -18.4 per mil which is very close to the result obtained for the southern Indian population. This indicates that even in a habitat that has been largely transformed from woodland to grassland, the elephants obtain a substantial amount of their protein needs from trees and shrubs.

The relative contribution of C3 versus C4 plants to the diet of elephants could, of course, be expected to vary across populations depending on environmental and vegetational factors (van der Merwe *et al.* 1988). Here again, it is interesting to note that the $\delta^{13}C$ values of elephant collagen vary from a mean of -16.4 per mil (65% of carbon from C3 plants) to -27.3 per mil (nearly 100% of carbon from C3 plants) across a variety of habitats from semi-arid savanna woodland to primary rain forest. In the moister habitats the grasses may be of the C3 type and thus the relative contribution of grasses versus other herbs and woody plants cannot be separated. However, the importance of C3 plants as a whole to carbon contribution for protein synthesis is indisputable.

The elephants in the southern Indian population that was sampled have access to a wide variety of vegetation types including a choice of both plant types. There is considerable seasonal variation in the average quantities of browse and grass consumed by an elephant population, with predominant browsing during the dry season and grazing during the early wet season (Sukumar 1989), although individual elephant herds or clans may deviate to a certain extent from this pattern due to constraints imposed by their spacing patterns and home ranges. Thus an adult female (about 60 years) from a clan (Clan 1 in Sukumar 1989) that ranged mostly in deciduous forest with tall grass showed the least protein contribution (55%) from browse plants; as opposed to this the contribution was as high as 83% in the case of an elephant from Mudumalai Sanctuary. Overall, the substantially higher average contribution of protein from browse plants to the elephant population is clear.

What are implications of these results for management of elephant habitats? If browse plants make such a major contribution to the nutrition of elephants then obviously it is important to evaluate the type of plants that are favoured by elephants and promote their growth within elephant habitat. As argued elsewhere it is the availability of high quality browse, rather than grass production, that is likely to be a limiting factor for elephants in deciduous forest habitat (Sukumar 1989). The elephant is broad spectrum feeder on a variety of species but nevertheless seems to favour certain taxa both in Africa and Asia. The browse plants that are favoured by elephants generally include those from the botanical order Malvales (including the families Malvaceae, Sterculiaceae and Tiliaceae) and the families Leguminosae (sub-families Papilionoideae, Caesalpinoideae and Mimosoideae), Euphorbiaceae, Moraceae, Anacardiaceae and Palmae, in addition to the bamboos (Gramineae).

The leguminous plants such as *Acacia* spp. are especially rich sources of protein. These plants are characteristic of deciduous woodland habitats with short grasses and relatively low rainfall. In the study area such plants are abundant in parts of the Sigur plateau (along the Avarahalla stream, for instance), the Moyar river valley, the Talamalai plateau and the Araikadavu river (in Satyamangalam division). Such habitats with high soil fertility are usually taken over by agriculture. Livestock grazing and wood cutting are also common here. Degradation of the habitat puts increasing pressure on the elephant to obtain their nutrition. In the Sigur plateau, for instance, elephants resort to scraping the ground with their forefeet to pull out small amounts of short grasses (grazed down to ground level by livestock) causing soil erosion.

Grasses provide bulk forage with minimal costs in preparation. They are also low in plant secondary compounds that are deterrents to herbivore feeding. For this reason they are very much preferred in tropical rain forests (where dicot forage are high in secondary compounds), although the grasses constitute an insignificant proportion of the elephant's diet

(Olivier 1978) as they are relatively rare in such habitats. When tropical moist forest is opened up through logging there is invasion of grasses and consequently are increasingly consumed by elephants. Thus secondary moist forest with grasses and other "weedy" food plants has a higher carrying capacity for elephants than does primary moist forest.

The possibility exists that carbon (fermentation products) from cellulose in grasses could contribute to metabolic functions other than protein synthesis and thus be under - represented in collagen. The C4 grasses should not be considered as nutritionally useless but as inferior to C3 plants as carbon sources for protein synthesis. This is clear from the isotopic data for elephants from a wide range of habitat types.

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