Journal of Human Evolution 55 (2008) 617–626

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Modern macaque dietary heterogeneity assessed using stable isotope analysis of hair and bone

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ARTICLE INFO

Article history:
Received 26 March 2007
Accepted 5 May 2008

Keywords:
Bioapatite
Bone
Carbon
Collagen
Diet
Hair
Keratin
Macaca mulatta
Nitrogen
Stable isotopes

ABSTRACT

Dietary variability might have been a major factor in the dispersal and subsequent persistence of the genus *Macaca* in both tropical and temperate areas. Macaques are found from northern Africa to Japan, yet there have been few systematic attempts to compare diets between different modern populations. Here we have taken a direct approach and sampled museum-curated tissues (hair and bone) of *Macaca mulatta* (rhesus macaques) for carbon and nitrogen stable isotope dietary analyses. Samples from India, Vietnam, and Burma (Myanmar) were taken, representing both tropical and temperate populations. The $\delta^{13}C$ values obtained from hair show that the temperate macaques, particularly those from Uttar Pradesh, have a $\delta^{13}C$ signature that indicates at least some use of C_4 resources, while the tropical individuals have a C_3-based diet. However, $\delta^{13}C$ values from bone bioapatite indicate a C_3-based diet for all specimens and they do not show the C_4 usage seen in the hair of some animals, possibly because bone represents a much longer turnover period than that of hair. The results of $\delta^{15}N$ analyses grouped animals by geographic region of origin, which may be related to local soil nitrogen values. The greatest variation in $\delta^{15}N$ values was seen in the specimens from Burma, which may be partly due to seasonality, as specimens were collected at different times of year. We also investigated the relationship between the hair, bone collagen, and bone bioapatite $\delta^{13}C$ results, and found that they are highly correlated, and that one tissue can be used to extrapolate results for another. However, our results also suggest that hair may pick up discrete feeding traces (such as seasonal usage), which are lost when only bone collagen and bioapatite are examined. This has important implications for dietary reconstructions of archaeological and paleontological populations.

Introduction

The ability to alter dietary components according to resource availability is likely to be a key factor in Old World monkey adaptation to diverse or changing environments. In the geographically widespread and eurytopic monkey genus *Macaca*, the incorporation of a range of foodstuffs into the diet is perceived as being fundamental to success in a wide range of often seasonal habitats (Jablonski et al., 2000). Modern macaque diets are currently known from behavioral and fecal studies but methodological differences between observational studies limit the extent to which the diets of macaque populations can be directly compared using published data, and there is little research that systematically compares intraspecific and environmentally induced variations in diet.

Stable isotope analysis of carbon and nitrogen provides direct evidence for diet in both modern and fossil animals (Vogel, 1978; Rundel et al., 1989; Ambrose, 1993; Hedges et al., 2005). Numerous studies (e.g., Lee-Thorp et al., 1989a, 1994, 2003; Sponheimer and Lee-Thorp, 1999; Codron et al., 2005) have shown the utility of this technique in reconstructing the diets of fossil primates, although, with the exception of the research by Schoeninger et al. (1997, 1998, 1999), Cerling et al. (2004), and Sponheimer et al. (2006), it has been relatively underemployed in studies of modern primate ecology. Isotope analysis of museum specimens allows a range of individuals to be sampled relatively quickly and cheaply without the need for fieldwork. This facilitates comparison of individuals from diverse environments and latitudes, forming a complementary line of dietary evidence on a different temporal and spatial scale to that obtained from behavioral observations. However, because of the destructive nature of the technique, such isotope analyses are rarely performed on primates in museum collections.

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0047-2484/$ – see front matter
doi:10.1016/j.jhevol.2008.05.001

In this paper, we use stable isotope analysis of whole hairs from 15 museum specimens of the widely dispersed macaque species *Macaca mulatta* to reconstruct the diets of individuals from different populations. The utility of hair in isotope studies of living animals (Schoeninger et al., 1997, 1998, 1999; Cerling et al., 2003, 2006; Sponheimer et al., 2003a,b,c, 2006; Mizukami et al., 2005) and archaeological material (O'Connell and Hedges, 1999; Macko et al., 1999) is well established, but hair from museum specimens is rarely used. When using museum specimens, contamination is a potential concern, but it has been demonstrated that isotopic values for hair are not affected by a variety of external chemical treatments (O'Connell, 1996). In order to assess the utility of museum hair as a source of reliable comparative material in future analyses, and to examine the relationships between the data from different tissues and components, we also performed isotope analyses on bone collagen ($n = 13$) and bone bioapatite ($n = 11$) from the same individuals. We tested the hypothesis that the diets of modern *Macaca mulatta* individuals from relatively high latitudes and elevations include a wider spectrum of foods than the diets of their tropical conspecifics.

Macaca *ecology and paleobiology*

Macaca is one of the most widely distributed modern primate genera. It is found throughout much of southern and southeastern Asia, as well as in northern Africa. In the Pleistocene, its geographic distribution was even wider, extending into Europe as far north as Untermassfeld in Germany (Zapfe, 2001) and Hoxne in the United Kingdom (Singer et al., 1982). Although the range of the genus has contracted since the late Pleistocene, several *Macaca* species, including *M. fuscata* (the Japanese macaque), *M. sylvanus* (the Barbary macaque), and *M. mulatta* (the rhesus macaque), still inhabit temperate regions, unlike other modern nonhuman primates, which are confined largely to the tropics. *Macaca mulatta*, the subject of the isotopic analysis reported here, is the most geographically widespread macaque, inhabiting an area that includes India, Afghanistan, Pakistan, Burma (Myanmar), Vietnam, and China (Lindburg, 1971; Qu et al., 1993; Fig. 1), and some populations are found at high elevations (Lindburg, 1971). *Macaca mulatta* populations thus inhabit a variety of environments, many of which experience seasonal variations in climate.

Although primarily known for its captive use in medical research, extensive and detailed fieldwork in northern India (Southwick et al., 1961; Neville, 1968; Lindburg, 1971; Southwick et al., 1983), Pakistan (Goldstein and Richard, 1989), Nepal (Teas et al., 1980), and China (Qu et al., 1993; Southwick et al., 1996, and references cited therein) has resulted in good (but not necessarily directly comparable) dietary data for rhesus macaques living at relatively high latitudes. However, a much smaller amount of work has been undertaken on tropical rhesus macaques. Wild-caught specimens of *M. mulatta* with known provenance (tropical as well as temperate) are well represented in museum collections. Thus, correlations between geography, environment, and diet can be examined using this species. The use of stable isotopes also allows dietary information to be gathered on tropical specimens for which there are fewer published data.

Background to isotopic analysis

Carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotopes in organic components of animal tissues are used for dietary analysis. The $\delta^{13}C$ in animal tissues is directly related to the external environment, photosynthetic pathways of plant matter consumed, and, in the case of carnivores, the plant matter eaten by their prey (for review, see Hedges et al., 2005). Animal tissues reflect the $\delta^{13}C$ values of the plants and animals consumed (plus fractionation) and a distinction

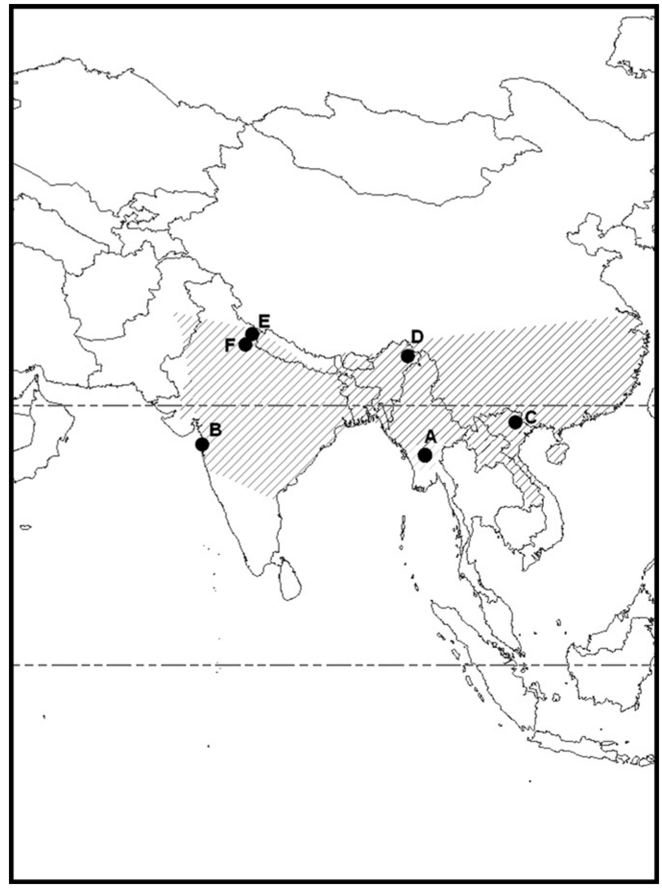

Fig. 1. Modern distribution of *Macaca mulatta* (shaded area). The location of each population sampled for this study is indicated by a black circle and labels correspond with those given in Table 1: A = Burma; B = The Dangs, Gujarat; C = northern Vietnam; D = Arunachal Pradesh; E = Bageswar, Uttar Pradesh; F = Ratighat, Uttar Pradesh.

in $\delta^{13}C$ ($\sim 12‰$) has been observed in tissues between the consumers of the two major plant photosynthetic groups ($C_4 = -15‰$ to $-9‰$; $C_3 = -33‰$ to $-23‰$) (O'Leary, 1988). A third group, CAM (crassulacean acid metabolism) plants, comprises mainly succulents and has an isotopic range that may be intermediate to, or indistinguishable from, C_3 and C_4 plants; these values are dependent on humidity, water availability, salinity, and the diurnal cycle (O'Leary, 1988; Gannes et al., 1998; Winter and Holtum, 2005). All three varieties are found in tropical environments, although the presence of C_4 and CAM plants in temperate latitudes is greatly restricted. C_3 plants include most trees, shrubs, and forbs, while C_4 plants typically include savannah grasses and sedges, which are better adapted to hot, arid conditions (O'Leary, 1988). Environmental factors such as increased shade, lower temperature, and increased moisture result in lower plant $\delta^{13}C$ values (van der Merwe, 1989; Tieszen and Boutton, 1989; Heaton, 1999). Dietary reconstruction may also be complicated by the degree of forest cover in the habitat. This "canopy effect" results in vertical stratification in forest plant $\delta^{13}C$, with forest-floor plants being $2‰$ to $5‰$ lower than those in the upper canopy and in open environments (for review of mechanism, see Koch, 1998; Heaton, 1999). These differences in plant $\delta^{13}C$ can be passed on to animals, as has been shown for Neotropical primates, who in closed-forest conditions have lower $\delta^{13}C$ than those in open environments (Schoeninger et al., 1997). Some altitudinal effects on $\delta^{13}C$ have also been observed in plants, in the order of $+0.5‰$ to $+1.5‰$ increase per 1000 m as the partial pressure of CO_2 changes (Sparks and Ehleringer, 1997; Heaton, 1999).