Isotopic Niche Differentiation Among Mammals from a Rainforest in Peninsular Malaysia

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ISOTOPIC NICHE DIFFERENTIATION AMONG MAMMALS FROM A RAINFOREST IN PENINSULAR MALAYSIA

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ABSTRACT. — We performed stable isotope analysis on eight mammalian species: pig-tailed macaque (*Macaca nemestrina*), long-tailed macaque (*M. fascicularis*), dusky leaf monkey (*Trachypithecus obscurus*), brush-tailed porcupine (*Atherurus macrourus*), wild boar (*Sus scrofa*), lesser mouse-deer (*Tragulus javanicus*), greater mouse-deer (*T. napu*), and barking deer (*Muntiacus muntjac*), to test the hypothesis that the differences in diet and habitat types among species, guilds and foraging strategies are reflected in the $\delta^{15}N$ and $\delta^{13}C$ signatures of their tissues. Whereas the isotopic ratios differed among taxa, the four major isotopic groups observed were: mouse-deer species, primate species, brush-tailed porcupine, and wild boar. The brush-tailed porcupine showed the most divergent isotopic signatures, depleted in both $\delta^{15}N$ and $\delta^{13}C$, and the wild boar had isotopic signatures enriched in both $\delta^{15}N$ and $\delta^{13}C$. Although results are only indicative, the three habitat types occupied by the species were reflected by differences in isotopic signatures, with the ground-dwelling species having the most divergent isotopic values from arboreal and semi-arboreal species. Likewise, among the four different types of dietary lifestyle groups tested, each group showed either significantly different $\delta^{15}N$ or $\delta^{13}C$ from other groups. Omnivores had the highest isotopic values, and bark-eater/frugivores had the lowest. By increasing the sample sizes both within the species and the number of species in future analyses, this isotopic technique provides opportunity to elucidate the diets of their putative predators in the rainforests of Peninsular Malaysia.

KEY WORDS. — stable isotope, Malaysia, niche, rainforest mammal

INTRODUCTION

The niche concept is crucial to our understanding of biological communities. A common definition of niche is the multi-dimensional range of resources utilised by an organism (Hutchinson, 1957). Among other dimensions, species can differ in their ecological niches via spatial separation, temporal avoidance, and dietary differences. Dietary niche is the total sum of food resources used by a species in its habitat (Campbell, 1996).

Although dietary niches are fundamentally important in understanding life history strategies and ecological interactions, they remain poorly described for many mammals,

especially in the tropics. This is due to the challenges of documenting foraging behaviour of elusive species and the physical inaccessibility of the tropical rainforest.

Traditionally, dietary niches are estimated using morphological analysis of food remains in faeces or with direct observation (e.g., Schaller, 1976; Goddard, 1970; Williams & Petrides, 1980; Sankar & Johnsingh, 2002). Other researchers, however, questioned these methods because of the unreliability of the morphological methods used for identifying consumers that deposited the faeces (Putman, 1984; Hansen & Jacobsen, 1999; Davison et al., 2002). Moreover, due to the rapid decomposition rate, low visibility, and the resources required to cover a large area for sufficient number of samples in the tropical evergreen forest (especially in roadless areas), faecal analysis and direct observation may be impractical for examining dietary niches of most species (Kawanishi, 2002).

In contrast, stable isotope analysis might provide a better approach to investigate dietary niches of tropical mammals. This method has long been useful in assessing resources used by a large range of organisms in varied environments (see reviews by Bearhop et al., 2004; Crawford et al., 2008; Newsome et al., 2008). Because stable isotopes occur naturally, they can be used to estimate the contribution of isotopically distinct food items in a consumer's diet (DeNiro & Epstein, 1978, 1981). Specifically, stable isotope ratios, or signatures, of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been widely utilised to examine dietary niche segregation, provided that there are significant differences in the isotopic signatures of the dietary sources (e.g., DeNiro & Epstein 1978, 1981; Stewart et al., 2003; Darimont et al., 2007, 2009). For example, Ambrose & DeNiro (1986) used isotopic analysis to describe foraging strategies of 43 mammalian species of montane forest and grasslands in Kenya and Tanzania, identifying whether animals were grazers or browsers, forest floor or savanna grassland herbivores, carnivores or herbivores, and forest floor or canopy species.

In this study, we performed stable isotope analysis on eight mammalian species of a tropical rainforest in Peninsular Malaysia to test hypotheses regarding niche differentiation. Previously published information on their natural history provides a standard of which to compare our isotopic data. We hypothesize that the presumed differences in diet and habitat types among the species, guilds, and foraging strategies are reflected in their $\delta^{15}N$ and $\delta^{13}C$ signatures.

MATERIAL AND METHODS

Forty-nine hair samples from eight mammalian species were subsampled from carnivore faeces collected from three different sites each of 200 km² in Taman Negara National Park (4°10' to 4°56'N, 102°00' to 103°00'E), Peninsular Malaysia, from Apr.1999 to Aug.2001. Annual rainfall averages 2,500 mm and the average relative humidity is 86% with little seasonal variation. The forest type is broadly classified as

a tropical evergreen moist forest (Whitmore, 1984). The sampling sites were lowland to hill dipterocarp forest ranging in elevation from 70 m to 898 m ASL.

Forty-one faecal samples were identified to depositing predator species using diagnostic species markers amplified from control region mitochondrial DNA (Kawanishi & Sunquist, 2008). Of these, 31 faecal samples were identified as being deposited by dholes (*Cuon alpinus*), five by Asiatic golden cats (*Catopuma temminckii*), four by leopards (*Panthera pardus*), and one by a leopard cat (*Prionailurus bengalensis*). All samples were collected during different months or from a different location. The rapid decomposition rate in the tropical rainforest made the possibility of collecting duplicate faecal samples that contained the remains of the same individual prey unlikely. Following Putman (1984) and Karanth & Sunquist (1995), we identified the hair remains to prey species based on microscopic and macroscopic features such as colour, length, thickness, texture, cuticle patterns, medullary width, and patterns of guard hairs, in comparison with reference hair samples from various body parts of multiple specimens per species collected from the National Zoo of Malaysia, Temerloh mini zoo, and the museum of the Department of Wildlife and National Parks Peninsular Malaysia. Other prey remains such as teeth, pinna, and hooves also aided species identification (Kawanishi & Sunquist, 2008).

Approximately 10–50 guard hairs from each sample were prepared for isotopic analysis. We sonicated hairs in distilled water for 10 minutes to remove residue and contaminants, followed by soaking in chloroform-methanol (2:1) solution for 24 hours to remove surface oils. After drying at 60°C for at least 48 hours, samples were powdered in a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill.). 1 ± 0.1 mg of each sample was loaded into 3.5×5.0 mm tin capsule for continuous-flow isotope ratio mass spectrometry analysis. Analysis was conducted at the stable isotope facility, University of Saskatchewan, Saskatoon, using a Europa Scientific ANCA-NT gas-solid-liquid preparation module coupled to a Europa Scientific Tracer 20-20 mass spectrometer (PDZ Europa, Cheshire, England). Isotope signatures of ^{15}N and ^{13}C are expressed in δ notation as ratios relative to Pee Dee limestone (carbon) and atmospheric N_2 (nitrogen) standards as follows:

$$[1] \quad \delta X = (R_{sample}/R_{standard}) - 1) \, 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

We report both $\delta^{13}C$ and $\delta^{15}N$ values to explore possible dietary niche differences among the mammalian species. We used ANOVA tests to examine the potential differences among guilds and foraging strategies relative to the canopy. Results were interpreted with caution due to uneven and small sample sizes. We then used a MANOVA to identify what species characteristics were best identified by isotopic data. All the statistical analyses were done using SPSS 16.0 (SPSS Inc., Chicago, IL., USA).

Table 1. Presumed diet and habitat type of the eight mammalian species from Malaysia that were investigated in this study as presented in order of similar guilds.

Common name	Scientific name	Diet	Habitat	Reference[*]
lesser mouse-deer	*Tragulus javanicus*	Herbivore, frugivore	Ground-dwelling	1, 2, 3
greater mouse-deer	*Tragulus napu*	Herbivore, frugivore	Ground-dwelling	1, 2, 3
barking deer	*Muntiacus muntjak*	Herbivore, frugivore	Ground-dwelling	1, 2, 3
brush-tailed porcupine	*Atherurus macrourus*	Bark-eater, frugivore	Ground-dwelling	1
wild boar	*Sus scrofa*	Omnivore	Ground-dwelling	1, 2
pig-tailed macaque	*Macaca nemestrina*	Omnivore	Semi-arboreal	1, 2, 3
long-tailed macaque	*Macaca fascicularis*	Omnivore	Semi-arboreal	1, 2, 3
dusky leaf-monkey	*Trachypithecus obscurus*	Folivore	Arboreal	1

*References: [1]Medway, 1978; [2]Payne & Francis, 1985; [3]Yasuda & Andau, 2000.

RESULTS

To facilitate the analyses, and to compare with interpretations of our isotopic data, we summarise general patterns identified in previous studies in Malaysia. Each of the species we sampled is thought to differ in trophic level, guild, and spatial use of habitat (Table 1).

Differences among species. — Species showed a broad range of isotopic signatures, ranging from –26.54‰ to –23.45‰ for $\delta^{15}N$, and 3.37‰ to 9.26‰ for $\delta^{13}C$ (Fig. 1). The two mouse-deer species and the three primate species shared similar isotopic space within the respective groups. The wild boar was enriched in both $\delta^{15}N$ and $\delta^{13}C$, and the brush-tailed porcupine showed the most divergent signatures, depleted in both $\delta^{15}N$ and $\delta^{13}C$ (Fig. 2).

Differences among habitat types. — Species occupying the three habitat types showed differences in $\delta^{15}N$ and $\delta^{13}C$ (Fig. 3). Ground-dwelling species were the most divergent, differing from other habitat types in both isotopes. There was an increase in $\delta^{15}N$ from arboreal to semi-arboreal to ground-dwelling mammals. An opposite pattern was observed for $\delta^{13}C$, though arboreal and semi-arboreal species did not differ significantly.

Differences among dietary lifestyle. — Among different dietary lifestyle groups, species differed in both $\delta^{15}N$ and $\delta^{13}C$ (Fig. 4). In pairwise comparisons, each group had at least one isotope value that was significantly different from the other groups. Omnivorous animals were enriched in both $\delta^{15}N$ and $\delta^{13}C$, and herbivorous/frugivorous animals had generally higher $\delta^{15}N$ than omnivores. Bark-eater/frugivores had the lowest $\delta^{15}N$ and $\delta^{13}C$.

We used a MANOVA to identify what species characteristics were best identified by isotopic data. We found that $\delta^{15}N$ was equally well detected by habitat type and dietary lifestyle (both $P < 0.001$). In contrast, $\delta^{13}C$ better revealed dietary lifestyle ($P < 0.001$) than habitat type ($P = 0.113$).

DISCUSSION

Differences among species. — When the main food sources of two animal species or guilds differ, in general, their isotopic signatures will also vary. Although sample sizes were small and uneven, meaning the results were only suggestive, they did conform to predictions: species of different guilds had little overlapping isotopic signatures, whereas there was overlap within guilds. The four major isotopic groups observed among the eight tropical mammal species studied were: mouse-deer species, primate species, brush-tailed porcupine, and wild boar. Within these four groups, there may be niche differentiation at a finer scale undetectable with isotopes, or they may practice spatial separation and temporal avoidance (Payne & Francis, 1985; Heydon & Bulloh, 1997).

Greater mouse-deer and lesser mouse-deer were isotopically similar in their distribution, indicating that their co-existence may be facilitated by spatial separation and/or temporal avoidance. In Borneo, the greater mouse-deer appear to be more common in upland forest, while the lesser mouse-deer are mostly found in lowland forest (Payne & Francis, 1985). Using the prediction by Millar &Hickling (1990) that larger animals should be able to survive better in periodic food
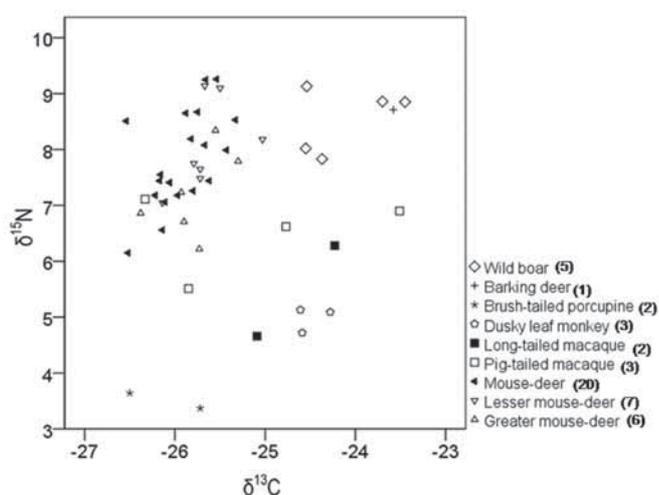

Fig. 1. $\delta^{15}N$ and $\delta^{13}C$ values in hair samples from eight mammalian species of a tropical rainforest in Peninsular Malaysia. The numbers in parentheses indicate sample sizes. Mouse-deer samples that could not be classified to species level were coded as mouse-deer.

scarcity, Heydon & Bulloh (1997) further suggest that the larger body size of the greater mouse-deer gave them an advantage over the lesser mouse-deer during fruit shortages that occur seasonally in the rainforest. The latter's slightly enriched signatures in both $\delta^{15}N$ and $\delta^{13}C$ may suggest a tendency for omnivory.

Although long-tailed macaques, pig-tailed macaques, and dusky leaf-monkeys occurred in similar regions of isotopic niche space, the preliminary results indicated some differences. Dusky leaf-monkeys had a much narrower isotopic distribution than the macaques, which may reflect a narrower dietary niche of the leaf-monkey, though samples sizes of these animals were small. Besides being a dietary specialist, the arboreal leaf-monkey also differs from

macaques in habitat type, with the latter being semi-arboreal species that commonly descend to the ground (Medway, 1978; Francis, 2001).

Long-tailed macaques and pig-tailed macaques with similar dietary lifestyle and habitat had similar isotopic signatures. The relatively wide isotopic ranges of both macaque species may be due to niche variation within each species (Bolnick et al., 2003; Darimont et al., 2009). For long-tailed macaques, although most are segregated in groups when foraging, adult males are sometimes solitary and spend more time in low trees and thick scrub than females and juveniles (Payne & Francis, 1985). In addition, males and females from both species differ in body size and weight, especially in pig-tailed macaques, in which adult females are only half the size of
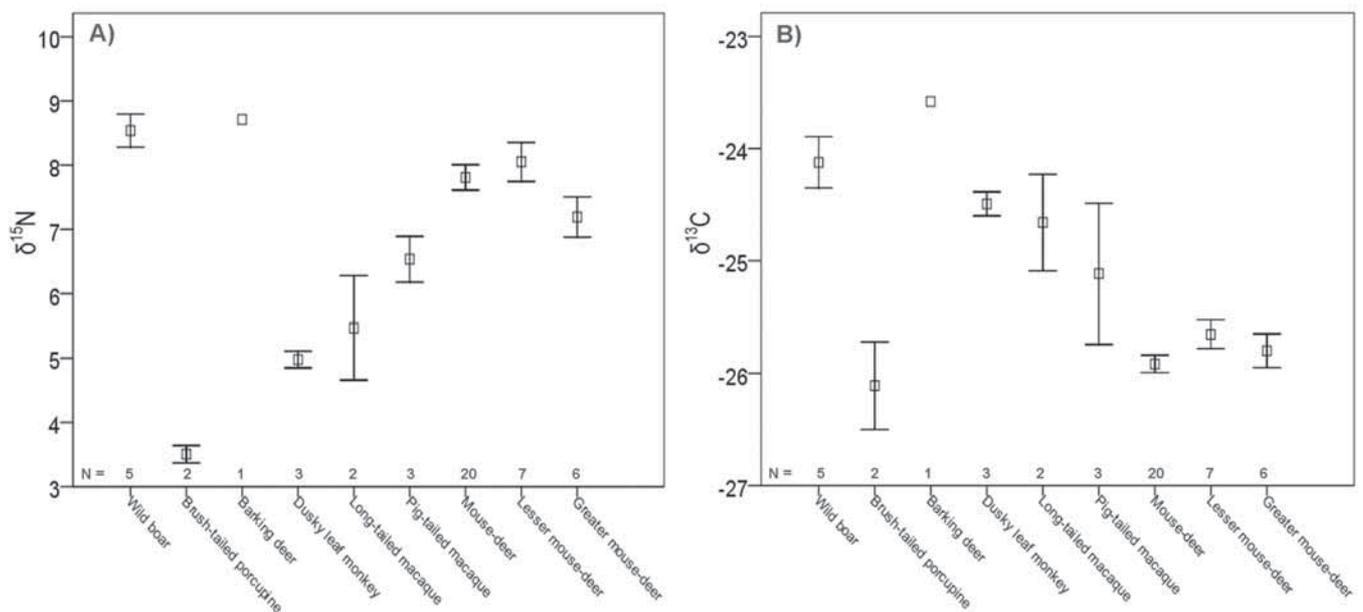

Fig. 2. Differences (mean ± SE) in $\delta^{15}N$ (A) and $\delta^{13}C$ (B) identified in hair samples from eight mammalian species of a tropical rainforest in Peninsular Malaysia. Mouse-deer samples that could not be classified to species level were coded as mouse-deer.
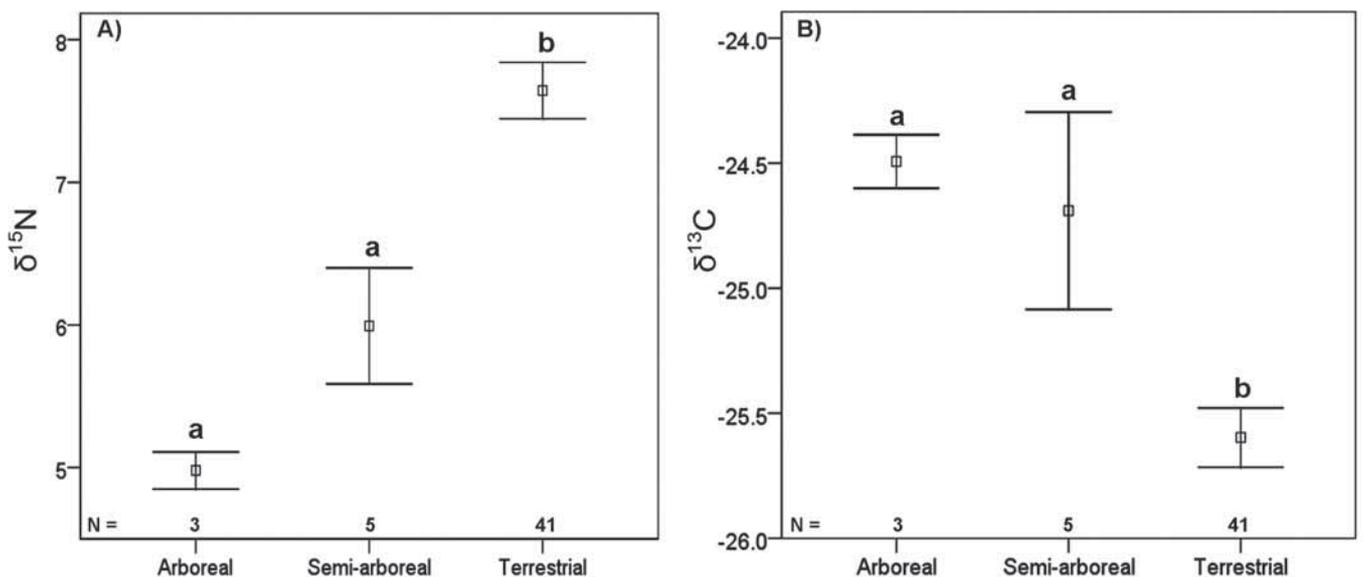

Fig. 3. Differences (mean ± SE) in $\delta^{15}N$ (A: $F_{2,48} = 10.046$; $P < 0.001$) and $\delta^{13}C$ (B: $F_{2,48} = 5.728$; $P = 0.006$) among taxa classified into different habitat types. Tukey's multiple comparison post-hoc groups membership indicated by a and b.

the adult males (Payne & Francis, 1985; Francis, 2001). Such subdivision of the population by sex or age group may be a factor that leads these two macaques to exhibit a wider distribution in their isotopic ratios.

Habitat type. — Only the ground-dwelling species were significantly different in $\delta^{13}C$ from other habitat types. Arboreal species are known to exhibit higher $\delta^{13}C$ than ground-dwelling species in the same guild due to the 'canopy effect' (Medina & Minchin, 1980; Medina et al., 1986), which would have the strongest effect in the tropical rainforest.

The large isotopic overlap between arboreal and semi-arboreal species might be an artifact of small sample sizes or due to the fact that the semi-arboreal long-tailed macaque and pig-tailed macaque, while consuming plant material at the canopy level, also have omnivorous diets (Medway, 1978) high in $\delta^{13}C$. A slight enrichment of $\delta^{13}C$ occurs with higher trophic levels (DeNiro & Epstein, 1978). Furthermore, pig-tailed macaques spend much more time on the ground than long-tailed macaques (Medway, 1978), which might explain the wider distribution of $\delta^{13}C$ found in the former species.

Dietary lifestyle. — Enrichment of $\delta^{13}C$ and especially $\delta^{15}N$ with trophic level are found in many studies (e.g. DeNiro & Epstein, 1978, 1981; Hobson et al., 2000). On average, $\delta^{15}N$ is enriched by 3‰ and $\delta^{13}C$ by 1‰ with trophic level (DeNiro & Epstein, 1978, 1981). Our results, however, did not fully conform to the pattern. Specifically, herbivores and frugivores were similarly enriched in $\delta^{15}N$ as omnivores.

The omnivorous animals at the highest trophic level among the sampled species showed high $\delta^{13}C$ and $\delta^{15}N$ values. Studies have found that $\delta^{13}C$ values of soil organic matter are higher than that of shade flora or fresh litter at ground level (Medina et al*.,* 1986; Balesdent et al., 1993); $\delta^{13}C$ of roots and stems are higher than that of leaves (Medina et

al., 1986); and that ground-dwelling invertebrate-consumers tend to be highly enriched in $\delta^{15}N$ and $\delta^{13}C$ (Kelly, 2000). The only strictly ground-dwelling omnivore in this study, the wild boar, is well known to consume a variety of food items including roots, fallen fruits, tubers, and animal material, especially soil invertebrates (Medway, 1978; Payne & Francis, 1985; Francis, 2001), which was reflected in significantly higher isotopic ratios in both $\delta^{13}C$ and $\delta^{15}N$ than other species. Likewise, the wide range of isotopic ratio in both the omnivorous macaques could be attributed to the diversity of food sources in their diet. Long-tailed macaques eat up to 185 species of fruits, and a wide array of animal material such as insects, frog eggs, crabs, and invertebrates (Payne & Francis, 1985; Lucas & Corlett, 1998), and a similar diversity of food items is consumed by pig-tailed macaques (Francis, 2001).

Surprisingly enriched signatures in the barking deer raise a question about its diet. This presumably herbivorous species has upper canines in adult of both sexes (Francis, 2001). Could this be associated with carnivory? Alternative and common functional explanations of the canines, which are more elongated in adult males, are for fighting for mates and for attacking enemies (Medway, 1978; Francis, 2001). If the canines of barking deer are truly used for obtaining animal material, it explains the enriched signatures in both $\delta^{13}C$ and $\delta^{15}N$. More samples of barking deer as well as studies on their dietary habits in the local rainforest are needed to test the hypothesis that the barking deer is omnivorous.

The result of this study found that the major species groups (mouse-deer species, primate species, brush-tailed porcupine, and wild boar) of the eight mammalian species were different in their isotopic distributions. By increasing the sample sizes both within the species and the number of species in future analyses, this isotopic technique offers a possible method to investigate diets of their putative predators in this rainforest.
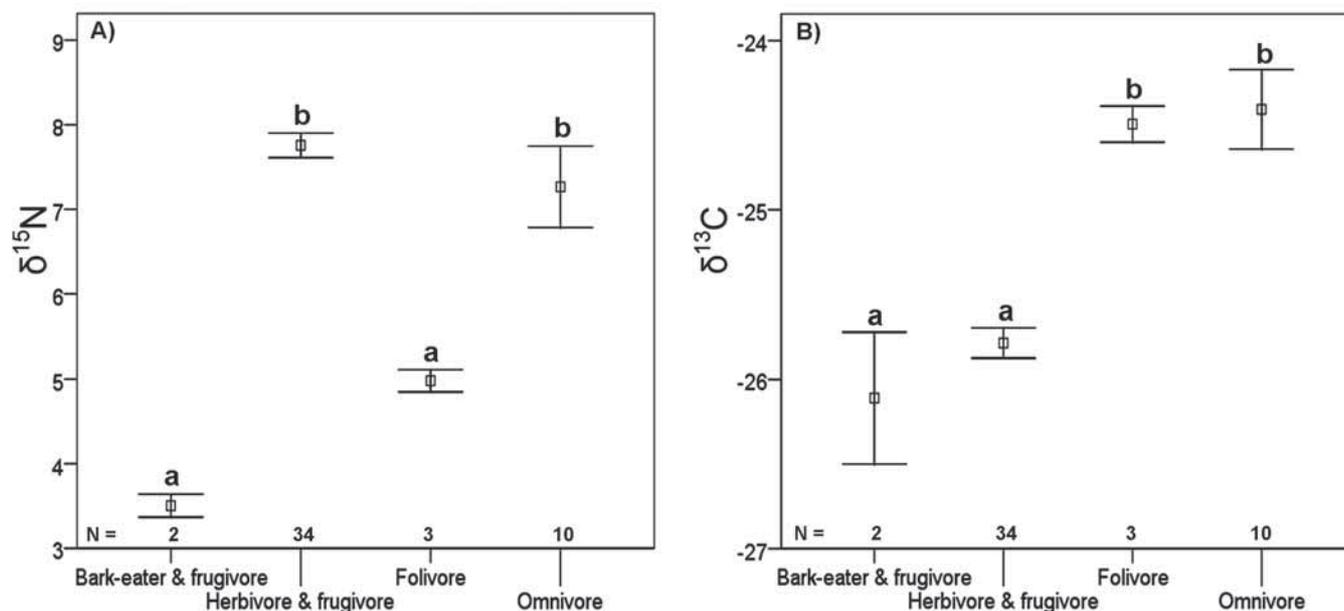

Fig. 4. Differences (mean ± SE) in $\delta^{15}N$ (A: $F_{3, 48} = 17.316$; $P < 0.001$) and $\delta^{13}C$ (B: $F_{3, 48} = 19.100$; $P < 0.001$) in individuals classified into different dietary lifestyle. Tamhane pairwise comparison post-hoc groups membership indicated by a, b, and c.

Additionally, an important management tool made possible by this technique would be to determine the regular diet of predators captured for allegedly having preyed on livestock or attacked humans, both of which commonly show distinct signatures compared to natural prey. Whether the particular predator was a habitual cattle-lifter or man-eater during the month to year of its life prior to the capture can be determined by conducting isotopic analysis on blood plasma or hair samples (e.g. Yeakel et al., 2010). Central to this strategy is assessing the range of isotopic values of natural prey animals, domestic animals, and people in the area.

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