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Nutritional Composition of the Diet of *Alouatta palliata mexicana* Females in Different Reproductive States

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Observational data on the feeding and behavior of a semi free-ranging troop of mantled howler monkeys (*Alouatta palliata mexicana*) were collected and analyzed to determine whether differences exist in the nutritional composition of the diet of females at different reproductive states. The reproductive states selected for study were non-gestation (control), gestation, and lactation. Mean ingestion was calculated in grams/day and in kilocalories for fats, proteins, and moisture, all considered key nutrients in these reproductive conditions. Results showed greater ingestion of fats and proteins by gestating and lactating females than by non-gestating females; however, no significant differences were found between gestating and lactating females. The mean ingestion figure in kilocalories for fats and proteins was similar to the figure reported in other studies. Finally, it is interesting to note that no differences were found in the moisture content of diet according to reproductive state. Zoo Biol 18:507–513, 1999.

Key words: reproductive state; diet; nutrients; howler monkeys

INTRODUCTION

Various studies [Glander, 1981; Seria-Silva, 1996] pointed out that primates need to obtain carbohydrates, amino acids, minerals, vitamins, water, and certain fatty acids in their diet. However, the specific requirements vary among individuals. No two species have identical diets and within a species differences exist among individuals, reproductive states, social groups, and populations. This is owing to the spatial and temporal variation of resources and the physiological and anatomical differences within and among primate species [Oates, 1986].

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The howler monkey (*Alouatta palliata*) is one of the most widely studied primates [Neville et al., 1988]. However, there still exist several uncertainties in relation to its foraging strategies [Milton, 1980]. Although this primate is typically considered to be a folivore-frugivore [Crockett and Eisenberg, 1986], more detailed studies revealed that they consume considerable amounts of ripe fruits in addition to young leaves [Serio-Silva, 1997]. It is evident that this primate exhaustively selects the food it consumes, but much about the role of the nutrients found in the plant species it consumes remains unknown. In an attempt to learn more about the role of these nutrients, Glander [1981] chemically analyzed 62 tree species consumed by howler monkeys. His work demonstrated that the leaves the monkeys consumed contained significantly more water, protein, and amino acids, which were more digestible, and had less fiber than the leaves they did not consume.

Serio-Silva [1996] holds that the *Alouatta palliata mexicana* troop he studied consumed plant parts with significantly higher content levels of moisture, protein, fiber, and ash. However, he suggests that this selection may vary as a result of each individual's physiology, reproductive state, or its social role in the group. An event that is apparently important in *A. palliata mexicana* adult females is the selection of food in the various reproductive states they experience (non-gestation, gestation, lactation). Although nothing is known in reference to howler monkeys, various studies on other mammals, including humans, demonstrated that the periods of gestation and lactation have high energy costs and involve highly specific nutritional needs. In some studies conducted on humans, a comparison of the production and composition of maternal milk with the theoretical requirements of infants showed that there is a limit in protein compounds and energy intake. Likewise, it is estimated that there is a 60% increase in the energy requirements of lactating adult women compared with adult women who are not pregnant or lactating. The transformation of proteins in maternal milk has a significant cost of metabolic energy [Sampson and Jansen, 1984].

Finally, changes in the metabolism of proteins and lipids were reported for rats. During the first 2 weeks of gestation, these nutrients are stored in the mother's tissue and almost 60% of body fat is lost during lactation. When female rats were subjected to a diet deficient in proteins, they lost body protein during lactation [Sampson and Jansen, 1984]. This study on rats suggests that well-fed females store carbohydrates and lipids in their body tissue during gestation and mobilize them for energy and anabolic sustratum in the secretion of milk.

The objective of this study was to investigate whether the composition of the diet of howler monkey (*A. palliata mexicana*) females in different reproductive states varies. Based on the studies cited above, we hypothesized that gestating and lactating females would ingest more fats, proteins, and moisture than non-gestating females, owing the greater contribution of these nutrients required during gestation and lactation. As in the case of other mammals, it was expected that *A. palliata mexicana* females in gestation would increase their ingestion of proteins and fats and thus ensure the development of the embryo and the production of milk during lactation.

METHODS

Site and Group of Study

Agaltepec Island (18°27' - 18°28'N, 95°02'W - 95°03'W; altitude 360 - 390 m above sea level), with a surface of ca. 10 ha (83,719 m2), is the largest of four volca-

nic islands on Lake Catemaco, in southeastern Veracruz, Mexico. The vegetation of the island consists of elements representative of four vegetation associations: tropical subdeciduous forest, riparian vegetation, secondary vegetation, and grazing land. All trees on the island with a diameter at breast height >30 cm were marked. A total of 1,605 trees was recorded on a topographic map and 1,451 of them were identified to species. The identified trees were grouped into 32 families, 58 genera, and 63 species.

The howler monkey population studied was a troop living in semi free-ranging conditions on the island. This group of primates was translocated onto the island as part of a conservation program to protect this threatened species [Rodríguez-Luna et al., 1993]. The troop was made up by 10 individuals (one adult male, eight adult females, and one infant) at the start of the study and has been monitored continuously since then. The data presented here were collected during observations conducted between November 1989 and January 1997.

Sampling and Analysis of Data

The collection of data was done during an annual cycle in which three howler monkey (*A. palliata mexicana*) females asynchronously went through three different reproductive states, and each female was used as its own control in each reproductive state. The reproductive states selected were non-gestating (before copulations resulting in fertilization), gestating (from fertilization to the delivery of young), and lactating (from the delivery of young to approximately 15 months after the birth of young).

The original database was provided by Serio-Silva [1992] and contains records on focal animals [Altmann, 1974] as well as the plant species they consumed (leaf or fruit), number of plant parts they consumed, and the average weight (grams) of the leaves and fruits of each species they consumed. Likewise, nutrient analyses were conducted to determine the content of moisture, fats, protein, carbohydrates, fiber, and ash in the plant species and plant parts consumed by the troop. However, only the moisture, protein, and fat values were considered in the analysis since they are reported in the literature as especially important nutrients during gestation and lactation [Cohelo et al., 1977].

Fat/Protein Index at Each State

For the three selected females, the daily consumption of fruits and leaves from each plant species was determined. The data were converted to real values of grams of fat and protein consumed by each individual from the different plant species and plant parts. These real values were used to calculate the daily value of fats and proteins consumed by each individual in the different reproductive conditions. From the resulting values, an index of the fat/protein proportion was calculated for each female during each reproductive state. An index equivalent to one was interpreted as an equal consumption of fats and proteins, an index greater than one as a greater consumption of fats than of proteins, and an index smaller than one as a greater consumption of proteins than of fats.

Moisture, Fat, and Protein Real Values

Independent of the above information, the daily consumption (in grams) of moisture, fat, and protein was calculated for each female in the different reproductive states. The existence of significant differences among the different consumption values for moisture, fat, and protein, according to reproductive state, was investigated.

Calculation of Kilocalories per Gram of Fat and Protein

The real values obtained for fat and protein were selected for the calculation of the average amount of kilocalories per gram of daily food intake during each reproductive state. We applied a conversion factor of 4 kcal/gram of protein and a factor of 9 kcal/per gram of fat [method in Cohelo et al., 1977].

An analysis of variance, using a generalized linear model (GLIM) [Crawley, 1993; Francis et al., 1993] and assuming a normal distribution of the data as well as a link identity function, was conducted. The null hypothesis proposed that there were no significant differences in the indices and real values for each nutrient according to reproductive state. The significance of the results was tested by using F tables ($P = 0.05$). Likewise, multiple Tukey tests ($P = 0.05$) were performed to determine where the differences lay according to reproductive states and to indices.

RESULTS

Calculation of Indices for Each Reproductive State

Significant differences were found in the fat/protein index for daily consumption by the studied individuals of *A. palliata mexicana* according to the three reproductive states. The index was highest for the lactation state ($F = 6.94$, df = 2,4, $P < 0.05$).

Real Values of the Consumption of Moisture, Fat, and Protein in Each Reproductive State

The real values of each nutrient (including moisture) show differences in the consumption of nutrients according to reproductive state (Fig. 1). No significant differences were found among the reproductive states for mois-

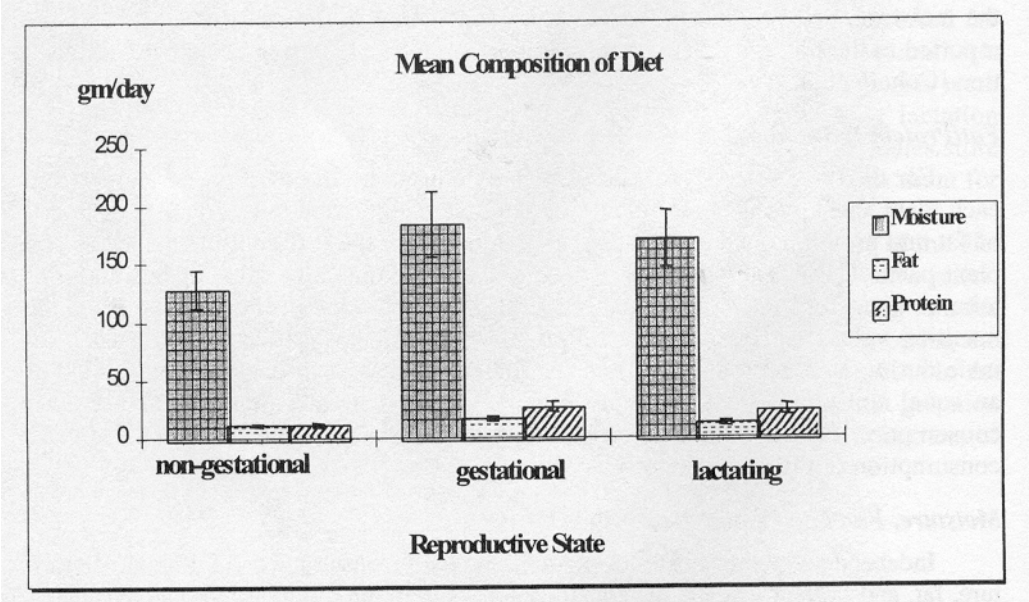

Fig. 1. Real values of the consumption of moisture, fat, and protein by female howler monkeys (*A. palliata mexicana*) in different reproductive states (non-gestation, gestation, and lactation).

ture content (grams/day) ($F = 1.93$, df = 2.54, $P > 0.05$). However, in the case of fat and protein contents (grams/day), significant differences were found ($F = 3.634$, df = 2.54, $P < 0.05$ and $F = 5.880$, df = 2.54, $P < 0.05$, respectively) among the reproductive states. Nevertheless, when comparisons were conducted with GLIM among gestating females and lactating females only, no significant differences were found in the consumption of fat and protein ($F = 2.02$, df = 1,33, $P > 0.05$ and $F = 0.35$, df = 1,33, $P > 0.05$, respectively).

Value of Kilocalories per Gram of Fat and Protein Consumed

Calculated from the daily consumption by the females in each reproductive state, the average value of kilocalories in the diet of gestating females and lactating females was greater than the average value for non-gestating female. This pattern was true for both fat and protein (Table 1).

DISCUSSION

Although the fat/protein index obtained for the lactation state was greater, it required information from the real values because the value of the index masked the real contribution of each nutrient to each of the reproductive states.

The analysis of the real values did not show significant differences in the ingestion of moisture according to reproductive state. Other reports [Kenagy, 1987] suggest that the acquisition rate of moisture in the diet during lactation should be increased. It is possible the *A. palliata mexicana* females at Agaltepec Island inhabit an environment that is exceptionally rich in the production of fruits, which make up their main source of liquids. The presence of numerous species providing succulent fruits (e.g., from the genus *Ficus* in combination with other species) throughout the annual cycle allows for a more equitable distribution of individuals [Serio-Silva, 1996].

Likewise, the obtained data show that gestating females, like lactating females, have a greater amount of fats and proteins in their diet in comparison to the control (non-gestating) females. The females of this species seem to be employing a mechanism of immediate contribution to the energy requirements. This might explain why no differences were detected in the composition of the diet of gestating females and lactating females. These results are similar to those of Cohelo et al. [1977] and McNab [1987]. They suggest that both states (gestation and lactation) are more energy demanding than the non-gestation state. However, these authors did find differences between gestation and lactation with the latter state requiring more energy. The fact that the present study only considered the amount of fats, proteins, and humidity should not be overlooked. Only these nutrients were taken into account because they are considered key nutrients for the development of the embryo and the production of milk. However, the subsequent analysis of other components (such as carbohydrates, ash, and fiber) of the diet of these primates might support the existence of

TABLE 1. Consumption of kilocalories (kcal/day) per gram of nutients (X ± se) by female howler monkeys (*A. palliata mexicana*) in different reproductive states

Nutrient	Non-gestation	Gestation	Lactation	Cohelo et al. [1977]
Fat	99.81 ± 3.1	143.28 ± 5.3	108.27 ± 4.1	—
Protein	42.92 ± 1.4	104.12 ± 2.8	93.56 ± 5.2	—
Total	142.73 ± 4.5	247.4 ± 8.1	201.83 ± 9.3	354.0

differences between the diet of gestating females and lactating females. The value of the kilocalories for the ingestion of fat and protein obtained from the studied females approximated that of Cohelo et al. [1977]. This might be a consequence of the present study not taking into account the kilocalories provided by carbohydrates.

The information obtained in this study showed that once the neonate is present, there is a greater demand for the female to increase her energy intake. Among other things, this is to provide for the adequate production of milk and thermoregulatory conditions to feed the young and ensure its survival [Hill, 1983; Leon et al., 1978; Markussen et al., 1985].

In general, many reports exist on mammals in which the animals begin to accumulate a large amount of lipids in fatty tissues during lactation. These lipids are then used in an efficient manner during lactation [Thompson, 1992]. The data obtained in the present study suggest that gestation and lactation should be considered a continuous process. In this continuous process, the demand for energy-rich nutrients, such as fat and protein, supplement females with the necessary resources to support a new individual from the moment of conception. The dependence of the young on the mother does not end at birth, for the means for obtaining the needed resources are modified.

Similarly, elements of the behavioral plasticity of those species (e.g., shared parental care, building and localization of nests, thermoregulatory characteristics) that might influence the use of energy resources during these reproductive states have been identified.

CONCLUSIONS

1. The results presented here suggest that female howler monkeys (*A. palliata mexicana*) show a greater demand for energy-rich nutrients during costly states such as gestation and lactation.
2. The consumption of energy-rich resources by howler monkeys is indicated by the average values of kilocalories obtained for different reproductive states, making it evident that these values are higher during gestation and lactation than during the non-gestation (control) state.
3. Gestation and lactation should be considered a continuous process in which the demand for nutrients and energy is intensified until the gradual independence of the neonate is reached.

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