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Diet and activity in black howler monkeys (*Alouatta pigra*) in southern Belize: does degree of frugivory influence activity level?

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Abstract This study reports on the diet and activity budgets of Central American black howling monkeys (*Alouatta pigra*) at Monkey River, Belize. This is a previously unstudied population, close to the southern boundary of the species range, and it provides comparative data on *A. pigra* from a new study site. Both diet and activity are within the ranges reported for other *A. pigra* sites and for mantled howlers (*A. palliata*). No age-sex differences could be discerned in either diet or activity, though monthly variation was apparent. The monkeys switch from consuming leaves 86% of the time in January to March to consuming 67% fruit in April to July. This difference was statistically significant, and provided the opportunity to compare activity levels of the monkeys over two dietary periods, one characterized primarily by folivory, the other by frugivory. Howlers are often seen as a relatively inactive species, something that is associated with a low quality, folivorous diet. However, *A. pigra* have been described as being as frugivorous as possible and as folivorous as necessary. Yet, despite the opportunistic consumption of large quantities of high-energy foods, *A. pigra* has been observed as conforming to the howler lifestyle, resting as much as 80% of the day. The data in this paper support both of these reports. Black howlers at Monkey River Belize are typically inactive, maintaining high levels of inactivity even during months characterized by frugivory, suggesting that diet is more flexible and varied than is behavior and calling into question the assumption that howler inactivity is due to the digestion of large quantities of leaves.

Keywords *Alouatta pigra* · Diet and activity · Howler monkeys · Level of frugivory

Introduction

The genus *Alouatta* is among the best known of the neotropical primates. However, most of what is known about howlers derives from work on mantled howlers (*A. palliata*) (e.g., Chivers 1969; Milton et al. 1980; Jones 1985; Glander 1992; Zucker et al. 1997; Clarke et al. 1998) and *A. seniculus* (e.g., Neville 1972; Sekulic 1982; Crockett and Sekulic 1984; Agoramorthy and Rudran 1995; Pope 1990, 2000). Relatively little is known about *A. pigra*, commonly referred to as the Belizean, Guatemalan, or Central American black howler, whose status as a species was only recognized in the early 1970s and whose range is limited to the southern Yucatan peninsula of Mexico, western Guatemala, and Belize (Horwich and Johnson 1986). Information on Central American black howlers is becoming available now due to the increasing body of research on a black howler population at the Community Baboon Sanctuary (CBS) in north central Belize and those transplanted from CBS to Coxcomb Basin Wildlife Sanctuary (CBWS) in south central Belize. These studies, which began in the early 1980s, have served to provide information on several topics including group size and structure (Horwich 1983; Horwich and Johnson 1986; Horwich et al. 2001), dispersal patterns (Brockett et al. 2000b), social interactions (Brockett et al., 1999; 2000c), birth seasonality (Brockett et al., 2000a), territoriality (Horwich and Gebhard 1983), feeding ecology (Silver et al. 1998), and ranging behavior (Ostro et al. 1999). Recently, Cornick and Marowitz (2002) reported on the vocal patterns of *A. pigra* at Lamanai in northern Belize.

Howlers in general have long been known as energy-minimizing folivores (Milton 1980) due to their heavy reliance on leaves and fermentative digestion (Milton and McBee 1983), which is often assumed to be associated with their inactive lifestyle (Horwich et al. 1993). Although most howlers have typically been thought of as the most folivorous new world monkeys (Eisenberg et al. 1972), early research on *A. pigra* described the

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species as frugivorous (Coelho et al. 1976; Schlichte 1978). More recent studies of longer duration have revised this view and *A. pigra* at the CBS is known to have a highly varied diet, largely dependent on the availability of preferred foods. Belizean howlers can survive for long periods on just leaves (Horwich and Lyon 1990), but fruit and other reproductive plant parts are consumed whenever available (Silver et al. 1998, 2000; Ostro et al. 1999). Silver et al. (1998) describe *A. pigra* at CBS as being as frugivorous as possible and as folivorous as necessary. However, despite the opportunistic consumption of large quantities of high-energy foods, Horwich et al. (1993) state that “*A. pigra* conforms to the howler lifestyle, resting as much as 80% of the day.”

The assumption that folivory is associated with high levels of inactivity is challenged by the fact that *A. pigra* maintains an inactive lifestyle despite periods of high fruit availability and consumption. Many primates do, however, demonstrate behavioral changes associated with diet. Recently, Watts and Mitani (2002) reported that colobus hunting by chimpanzees increases during periods of fruit consumption, and the researchers suggest that this may be due to higher levels of energy available during fruit eating seasons, rather than to the dietary needs of the chimpanzees. In other words, colobus hunting may be an energetically expensive “luxury” that the chimps can only afford when fruit is abundant. Another possibility is that chimpanzees only hunt when they are in large groups and large groups only occur when fruit is abundant (C. Chapman, personal communication; Mitani and Watts 1999; Boesch 1996). However, in cebus monkeys at Santa Rosa National Park in Costa Rica the opposite pattern has been reported. Cebus monkeys are much more likely to hunt when fruit is not available, possibly to augment the amount of high quality foods in the diet (Fedigan 1990). In either case, it is clear that the quality of the diet can play a role in the resulting activity patterns of different primates.

This paper has two objectives. First, we report on the diet and activity of a previously unstudied population of Central American black howlers living in a coastal riverine forest in southern Belize in order to help determine the uniformity or variability within the species by providing comparative data from a new site. It is important for our understanding of the level of dietary flexibility and frugivory in the genus *Alouatta* that reported dietary profiles of *A. pigra* can be demonstrated at more than one study site (Silver et al. 1998). The study population inhabits a lowland, semi-evergreen forest, in a subtropical moist life zone, located on the north side of Monkey River (MR) 1 km west of the river mouth (16°21'N, 88°29'W). This represents the southernmost population for which data are available, near the southern boundary of the species range. Second, because the diet of the Monkey River black howler population, like those at the CBS (125 km NW of Monkey River) and the CBSW (53 km NW of Monkey River) (Fig. 1), reflects seasonal variation in fruit availability and consumption, our data

includes months characterized by folivory and months characterized by frugivory. Thus, in addition to describing the diet and activity patterns of this population, we use these data to investigate the relationship between dietary seasons and activity levels in this species.

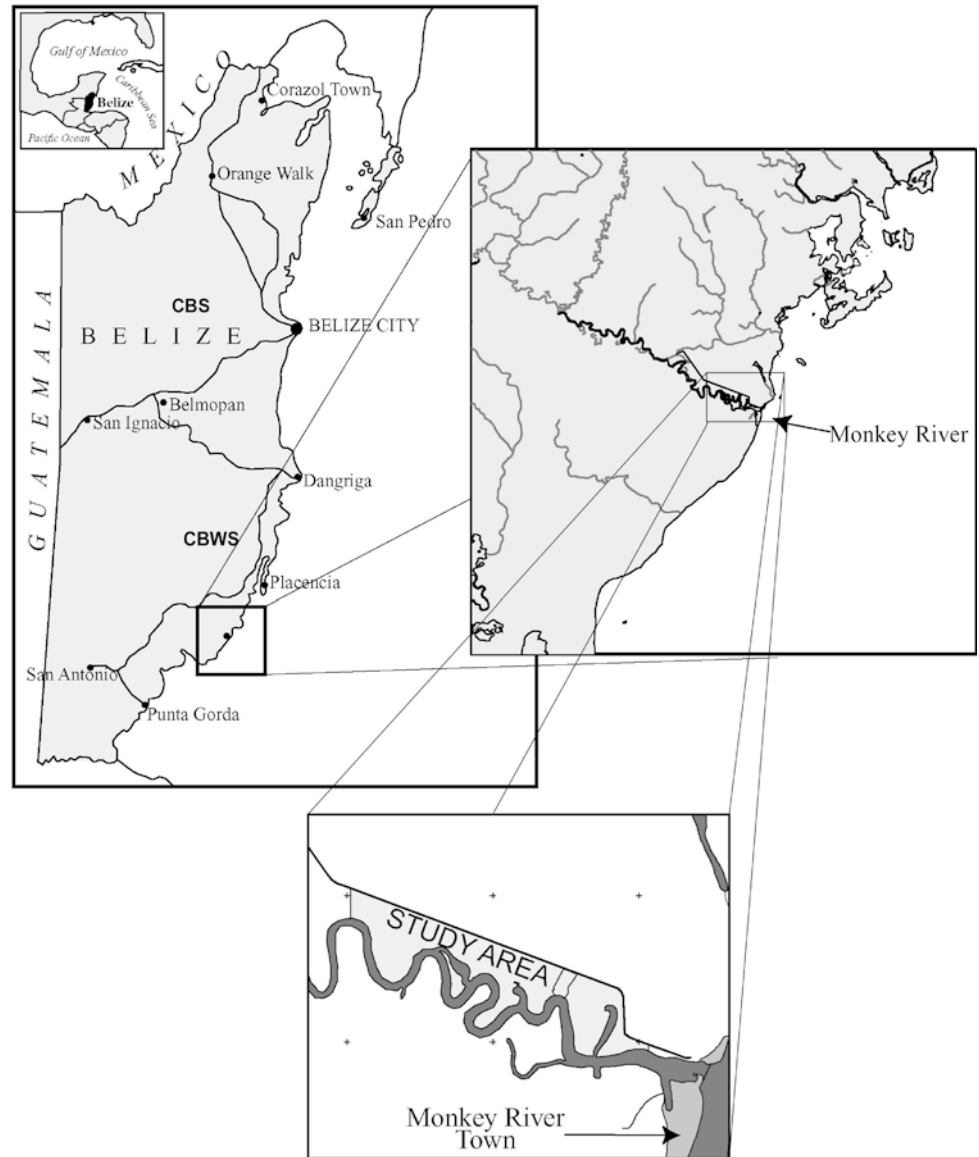
Methods

The study site is a narrow band of forest between the river and the Monkey River road, approximately 2 km in length and averaging 0.25 km in width (Fig. 1). Eight monkey groups inhabiting a 52-ha study area were observed from May to July 1999, February to May 2000 and January to May 2001. January to May is the dry season, with the rainy season beginning in June (Fig. 2). The group size of *Alouatta pigra* in this area ranged from 2 to 10 individuals with a mean group size of 6.6 (Pavelka 2003). Data were collected primarily on four social groups at the east end of the study area, although three groups further west were also occasionally sampled. 662 h of focal animal data were collected over the 3 years. No interannual variation in consumption of leaves versus fruit was noted in the months sampled. Efforts to obtain data from a full annual cycle of feeding and activity data were thwarted by a severe hurricane in 2001, which resulted in long-term alteration in the forest and food supply. The effect of hurricane Iris is currently under study (Pavelka et al. 2003), and descriptions of the pre-hurricane diet and activity are limited to the data described here. Animals were identified at the level of age-sex class, because individuals were not recognizable. Ten-min focal animal samples were obtained on different groups and age-sex classes over the study period so that as many different individuals as possible would be sampled. Different social groups were sampled on different days.

All state and event behaviors were recorded in the focal data but were grouped for this analysis into five activity budget categories: inactive (includes resting, sitting in body contact, and sitting near another individual), locomote, feed, and social (includes grooming and social play behaviors). When animals were feeding, the plant species and part were also obtained. Feeding by plant part was recorded as leaf bud, mature leaf, new leaf, unknown leaf, flower, fruit, seed, and these were categorized for analysis into reproductive plant parts (hereafter referred to as fruit, because flower eating was rare) and leaves. Diet and activity durations were converted to proportions of the time sampled. For the analysis of overall activity budgets, feeding bouts where the plant part was unknown were included as part of the time spent feeding, but these were eliminated for the analysis of diet (fruit versus leaves). We calculated these diet and activity budgets for all animals over the entire study period, as well as by month and by age-sex class. For analysis, all data for each age-sex class were combined for each day of observation and the time spent in each activity was converted to a proportion of time sampled. Combined data for a single day was then used as the unit for analysis. This is justified by the fact that the non-observation period (12–14 h) was greater than the observation period (10–12 h) and, more importantly, by the fact that alternate monkey groups were observed on successive days, resulting in data points that represent data collected on different animals. Nursing infants were excluded from the analysis, as their activity patterns were not independent of their mothers and they rarely foraged. The final data set was comprised of 128 days during which feeding was recorded and plant part was identified.

Potential differences among adult males, adult females, and immatures, in time spent eating fruit and leaves as well as time spent in each of the activity categories were examined using a one-way Anova. We then grouped together the months that showed high levels of leaf consumption (January to March, $n=65$ days) and the months that showed high levels of fruit consumption (April to July, $n=63$ days) and compared activity levels between them. Independent samples *t*-tests were used to test for significant differences between these two dietary seasons in the time spent eating

Fig. 1 Location of the study area



fruit and leaves, and time spent in each of the four activity budget categories. Additionally, because we had 128 independent data points showing time spent eating fruit and time spent inactive, we ran a Pearson's correlation between these two variables to investigate the percent of variation in activity level that is explained by diet.

Results

Overall diet and activity budgets for this population, including all age-sex classes and all months sampled, indicated that the monkeys were inactive for an average of 66.33% of the time, fed for 18.57%, locomoted for 7.49% and were social for 3.67%, with 41.38% of feeding time spent feeding on fruit and 58.62% on leaves. The monkeys were observed feeding on a number of tree species and plant parts. In total, 35 known species of trees and vines were eaten. However, over 60% of the diet is made up of the leaves and reproductive parts of

only five species: sering or white maya (*Miconia argentea*) 15.9%, fig (*Ficus sp*) 13.9%, cochito (*Myrciara floribunda*) 13.1%, strangler fig (*Ficus crassiuscula*) 10.8%, and kaway (*Pterocarpus*) 7%. A comparison of the mean time spent in each diet and activity category among adult males, adult females, and immatures revealed no differences, indicating that during the time sampled, activity budgets and overall diet do not differ among age-sex classes in this population of *A. pigra*. When data from all age sex classes are pooled, monthly variation in diet is immediately apparent (Fig. 3). Corresponding variation, however, is not seen in the monthly activity budgets (Fig. 4).

To compare the effects of diet on activity, we grouped the data from January to March that showed high levels of leaf consumption and the data from April to July that showed high levels of fruit consumption. January, February and March show an average of 13.68% of time spent feeding on fruit and 86.32% on leaves, whereas

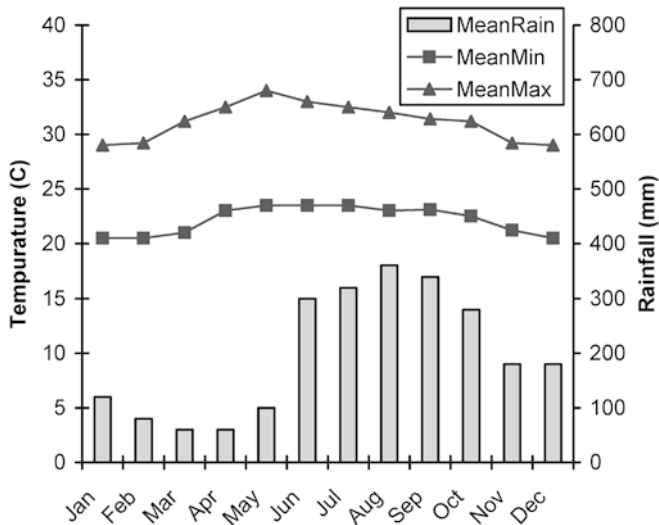


Fig. 2 Climate chart for Savanna Forest Station, 20 km north of the study site. Information obtained from the Land Information Center, Ministry of Natural Resources, the Environment & Industry, Belmopan, Belize. June 2000.

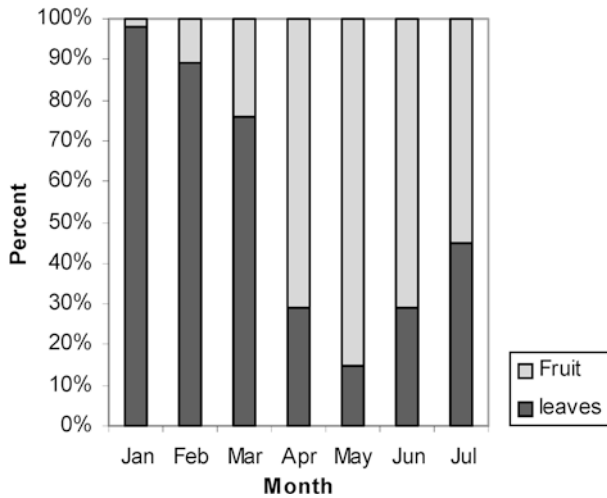


Fig. 3 Amount of frugivory and folivory by black howler monkeys (*Alouatta pigra*) by month

from April to July, fruit was consumed an average of 66.61% of the time and leaves only 33.39% (Fig. 5). As suspected, the change in diet from folivory in the first dietary period to frugivory in the second was confirmed by the significant differences between these two periods in both fruit and leaf consumption ($t = -9.64$, $df = 126$, $P = 0.00$).

Small but significant differences were also found in the time spent locomoting ($t = -2.7$, $df = 126$, $P = 0.007$) and in social behavior ($t = 2.6$, $df = 126$, $P = 0.01$, Fig. 6) between the two dietary seasons. During the folivorous months the monkeys spent 5.45% of their time traveling or locomoting, and this increased to 9.52% during fruit eating months. Time spent in social activity decreased from 5.16% to 2.16% of time sampled when moving

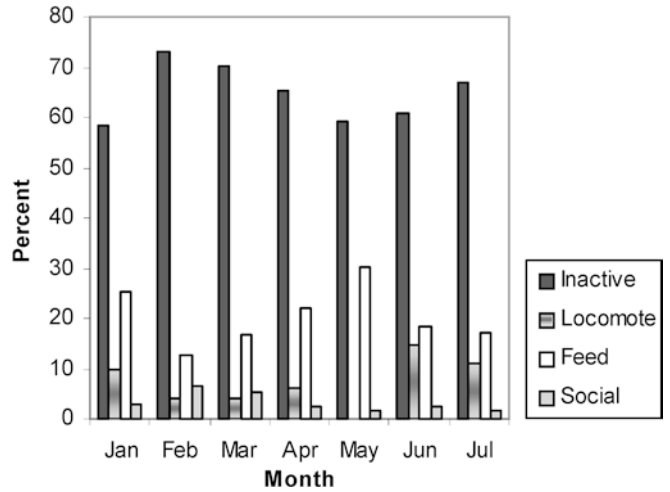


Fig. 4 Activity by month

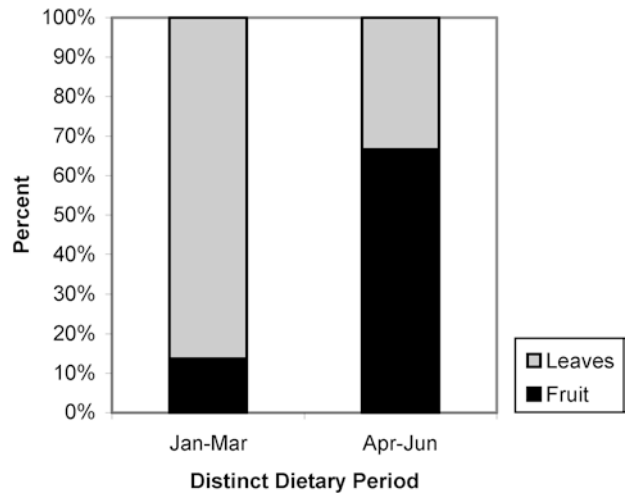


Fig. 5 Amount of frugivory and folivory in January to March compared with April to July

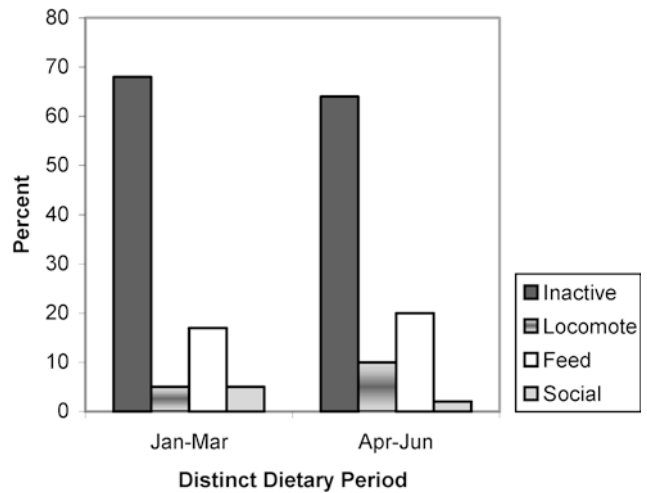


Fig. 6 Activity in January to March compared with April to July

from a leaf to fruit diet. In sum, while feeding on fruit the monkeys spent more time moving and less time socializing. There was no significant difference in time spent inactive when eating predominantly leaves versus predominantly fruit, either in the t-test comparing the two time periods ($t=1.2$, $df=126$, $P=0.20$) or in the Pearson's Correlation ($r=-0.14$, $n=128$, $P=0.13$), which indicates that time spent inactive was not related to the proportion of the diet composed of fruit.

Discussion

The overall activity budget of the Monkey River black howlers follows the typical howler pattern (Horwich et al. 1993; Estrada et al. 1999) and is similar to that reported by Silver et al. (1998) for the population of *A. pigra* at the CBS on the Belize River in north Central Belize. The CBS monkeys spent 61.9% of their time inactive, 9.8% locomoting, 24.4% feeding, 2.3% in social activities, and 1.6% involved in other behaviors. Black howlers at Monkey River are typical of howler monkeys in showing high levels of inactivity, normally associated with a highly folivorous diet. However, *A. pigra* show seasonal variation in diet with months of high levels of frugivory. This is true of both Monkey River and CBS populations, where, at least in terms of fruit versus foliage consumption, overall diet is almost identical. CBS monkeys consume 40.8% fruit and 59.2% leafy plant parts, compared to 41.4% reproductive parts (mostly fruit) and 58.6% leaves at Monkey River.

Both of these studies show *A. pigra* diets higher in frugivory than other howler species. In general, howlers consume between 25% and 35% fruit. For example, populations of *A. palliata* have been reported with frugivory levels at 28.5% (Chapman 1987) and 34.8% (Estrada et al. 1999), brown howlers *A. caraya* at about 30% (Bicca-Marques and Calegario-Marques 1994) and red howlers *A. seniculus* at 25.5% (Julliot 1994). Comparisons between species highlight the relatively frugivorous nature of *A. pigra*, but these differences are not unexpected when one takes into account the diversity of habitats occupied by howlers and resulting differences in fruit availability (Silver et al. 1998).

The results of this study suggest that there are no differences in either diet or activity among age-sex classes in this population of *A. pigra*. Although diet has been shown to be equivalent between age-sex classes for other species of howlers (Bicca-Marques and Calegario-Marques 1994), the activity patterns of these monkeys have, on more than one occasion, been shown to vary significantly between age-sex classes (Bicca-Marques and Calegario-Marques 1994; Glander and Teaford 1995). One would expect that the different requirements of each age sex class (e.g., growth for juveniles, reproduction/lactation for females, and larger body size for males) would lead to variation in diet and activity budgets between the age-sex classes. Indeed, these

differences are exactly what has been invoked as an explanation for such variation when it occurs (Freeland and Janzen 1974; Glander and Teaford 1995). It may be that while there were no differences among age/sex classes in the plant parts selected, differences may exist among the species and parts of plants selected, a possibility that will be explored in future research.

Monthly variations in diet for *A. pigra* at Monkey River are greater than those in activity. Again, these findings are consistent with what has been previously published for this species (Silver et al. 1998). The examination of diet by month at Monkey River has also lent support to the claim by Silver et al. (1998) that *A. pigra* are facultative folivores, eating as much fruit as availability will allow. Qualitative observations at Monkey River suggest that the switch to fruit consumption corresponds with the onset of the fruiting season. We are currently conducting quantitative investigations of the relationship between diet and phenological cycles based on the analysis of vegetation sampled before the hurricane. Data collected from other howler species indicate similar results in terms of seasonal variation in diet and activity. For example, *A. palliata* has also been shown to have an exceptionally varied diet over the course of a year, something that, again, has been related to the availability of preferred foods (Glander 1981; Chapman 1987; Estrada et al. 1999).

The increase in time spent locomoting during the frugivorous season warrants further study. One obvious possible explanation is that the monkeys have more energy when eating higher quality foods, and thus move around more. Another is that they move around more because the distribution of fruit requires it. The overall amount of time spent feeding is not significantly different in these two seasons, but the patterns of animal movement might show differences in the type of ranging and movement that is required based on variation in the distribution of fruit and leaves. It must also be acknowledged that the differences in activity levels between the leaf eating months and the fruit eating months might be due to something other than diet. The increased availability of fruit, which results in the increase in frugivory, is due to seasonal patterns of rainfall. Flowers tend to be produced in the dry season, as flowers would be particularly susceptible to damage from rain, and fruit follows at the end of the dry season (January to May at Monkey River). The activity patterns might be directly affected by these seasonal patterns. Future research will explore in more detail the relationship between animal movement (within versus between patch locomotion), activity and feeding time relative to seasonal changes in rainfall and forest productivity.

Howling monkeys have long been described as energy minimizing folivores whose inactive lifestyle is linked to the fermentative digestion of large quantities of low quality leaves (Milton 1980). *A. pigra*, however, has been described as having a more frugivorous diet yet retaining

the high levels of inactivity. Using the switch from folivory in January through March to frugivory in April through July, we compared activity levels based on diet, and found no significant difference in time spent inactive between these two time periods, and no correlation between time spent eating fruit and time spent inactive on a daily basis. Like the activity profiles of *A. palliata* (Estrada et al. 1999) and *A. pigra* at the Community Baboon Sanctuary in Belize, the Monkey River black howlers appear to be relatively conservative in their activity budgets. This is surprising when one considers that the quality of the diet changes so dramatically over time, and diet is often suggested to have a strong effect on activity. During periods of predominant frugivory, the activity levels remain very howler-like. The similar levels of inactivity whether the monkeys are eating leaves or fruit questions the assumption that howler inactivity is directly linked to the digestion of large quantities of leaves. The data presented here suggest that diet is much more flexible and varied than is behavior in this species, and that activity levels may be more phylogenetically constrained.

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