Chapter 7
Effect of Housing Conditions and Diet on the Behavior of Captive Woolly Monkeys (*Lagothrix*)

Diana Carolina Guzmán-Caro and Pablo R. Stevenson

Abstract The frequent capture of wild individuals and illegal pet trade of woolly monkeys has become one of the main threats for this species in Colombia. As a consequence, these primates frequently arrive at captive centers and zoos, and in captivity they show a high mortality. Finding conditions that promote the expression of natural behaviors in captive animals is considered beneficial for their physical and psychological well-being and a key step in rehabilitation and reintroduction programs. This study evaluates the effect of housing conditions and diet on the behavior of captive woolly monkeys in Colombia. Behaviors were quantified using focal animal sampling and instantaneous records. Comparisons were made to wild behavior patterns. Housing conditions were evaluated in terms of volume, density, and environmental enrichment; and diet was evaluated in terms of consumption quantity, type, and nutrient composition. Results show that enclosures with a larger size and a higher level of environmental enrichment are associated with more natural behavior patterns. Results also suggest that food and nutrient deprivation may have a considerable negative effect on behavior. This study provides valuable knowledge for the conservation of captive woolly monkeys. Results from this study should be implemented into captive well-being and the development of rehabilitation and reintroduction programs for woolly monkeys.

Keywords Captive diet · Captive primates · Environmental enrichment · Housing conditions · Illegal trade · Rehabilitation · Woolly monkeys

7.1 Introduction

Illegal wildlife trade is one of the main threats to primate species in Colombia (Hernandez-Camacho and Cooper 1976; Gómez 2000; Defler 2004, IUCN 2008). Primates are particularly attractive as pets and as laboratory animals (Mancera and

D. C. Guzmán-Caro (✉) · P. R. Stevenson
Universidad de Los Andes, Bogotá, Colombia
e-mail: guzman@asoprimatologicacolombiana.org

P. R. Stevenson
e-mail: pstevens@uniandes.edu.co

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Reyes 2008) and, consequently, large numbers of individuals from different species are constantly captured and removed from their natural habitat (Gómez 2000; Defler 2004). Many of the captured or traded individuals are subsequently confiscated by authorities or voluntarily offered, and sent to or received by centers of wild animal management or zoos, where they usually spend the rest of their lives in captivity. However, the increasing number of captive individuals, the low number of captive centers and zoos in the country, and problems such as lack of space and resources, among others, make it difficult for these centers to provide adequate conditions for captive primates or even accept new individuals (Echeverry, Millan, personal communication).

Illegal trade has thus become a main issue for primate conservation in Colombia that needs to be urgently addressed. The development of breeding, rehabilitation, and reintroduction programs for captive primates is a valuable conservation strategy that urgently needs to be expanded in Colombia. However, few studies have been performed on captive primates in Colombia (Stevenson et al. 2010), and the lack of information on how the species respond to different captive conditions has restrained the development of conservation plans involving captive individuals (but see: Price 1992; Ortíz and Stevenson 2003; Peres 2005).

Providing captive animals with conditions that promote the performance and maintenance of natural behaviors is considered beneficial for captive animals' welfare (i.e., the psychological and physical well-being of animals) and a key step in rehabilitation and reintroduction programs (Redshaw and Mallinson 1991; Shepherdson 1994; Shepherdson et al. 1998; Mellen and Sevenich 2001; Custance et al. 2002; Little and Sommer 2002; Hosey 2005; Seddon et al. 2007; Laule and Whittaker 2007). Environmental enrichment (EE) techniques, in which individuals are exposed to a more naturalistic environment, have been suggested as an adequate approach to stimulate species-typical behaviors in captive primates (Snowdon 1994; Schapiro and Lambeth 2007). However, enrichment methods should be based on adequate knowledge of the species' natural habitat (i.e., functional attributes such as physical complexity and vegetation), and on how individuals interact with it (i.e., patterns of habitat use; Little and Sommer 2002; Hosey 2005). Furthermore, the effectiveness of these techniques in promoting the display of natural behaviors should be evaluated through wild–captive comparisons (Redshaw and Mallinson 1991; Renner et al. 2000; Little and Sommer 2002; Hosey 2005); thus, complete information on the species' natural history and behavior patterns is also required.

Captive primates are usually provided diets that differ greatly from natural diets (Crissey and Pribyl 1997; Hosey 2005). Inadequate diets are often associated with health problems (e.g., nutrient deficiency and obesity) in captive individuals, and may also have negative effects on behavior (Hosey 2005). Providing captive primates with diets similar to the ones they consume in their natural habitats has been proposed as an adequate feeding strategy (Crissey and Pribyl 1997). However, the lack of information on the nutritional composition of their natural diet has made it difficult to determine the proper captive diet. Furthermore, differences in feeding strategies, gut morphology, and nutrient requirements among species indicate that captive feeding approaches must be species specific (Crissey and Pribyl 1997).

Woolly monkeys (*Lagothrix*) represent one of the most widely distributed genera in Colombia (Stevenson et al. 2010), and they have been found to be valuable seed dispersers in Neotropical forests (Stevenson 2000). In Colombia, these valuable monkeys face many threats. Wild populations of woolly monkeys are decreasing because of habitat destruction due to different processes of human expansion in most of the regions they inhabit, as well as hunting, both legal and illegal (Etter and van Wyngarden 2000; Stevenson et al. 2010). These monkeys' large body size not only makes them easy targets for hunters but also a preferred food item for indigenous people (Peres and Palacios 2007). Also, together with *Saimiri, Saguinus,* and *Cebus,* they are particularly threatened by illegal trade due to their popularity as pets and, as a consequence, they frequently arrive at zoos and captive centers (Echeverry, personal communication). Unfortunately, woolly monkeys are threatened in captivity as well, since *ex situ* populations typically sustain high mortality and low breeding success (Debyser 1995; Ange-van Heugten et al. 2008). Studies on captive woolly monkeys have suggested that the leading causes of woolly monkey deaths are related to hypertension complications and undetermined factors during the first year of life (Debyser 1995; Ange-van Heugten et al. 2008, this volume). An inadequate diet has been proposed as a probable cause of health problems, but the link between nutritional problems and mortality has not been identified (Ange-van Heugten et al. 2007). Lastly, the influence of housing conditions and diet on the behavior of captive woolly monkeys has been poorly studied.

This study evaluates how different housing conditions and captive diets affect woolly monkeys' behavior at different zoos and captive centers in Colombia. Through the assessment of behavioral patterns, we determined to what extent the (1) enclosure size, density of individuals within enclosures, and EE and (2) the quantity and composition of the diet affect captive woolly monkeys' behavior. We used the same methods applied for in situ studies to make direct comparisons between captive and wild behavior patterns. Finally, we identified which housing conditions and captive diets seem to be associated with more natural behavior patterns in captive woolly monkeys. This information will be used to propose a preliminary protocol of animal management that establishes which captive conditions should be met to promote improved expression of natural behaviors in captive woolly monkeys. However, the effectiveness of this protocol for promoting natural behavior patterns in these primates should be evaluated experimentally.

7.2 Methods

7.2.1 Study Sites

Our study sites included nine locations with captive woolly monkeys within Colombia (Table 7.1). Data on woolly monkeys' behavior, housing conditions, and captive diet were collected between December 2010 and September 2011 on all woolly

Table 7.1. Type and location of the different study sites

Study site	Type	Location (Department)
Zoológico Santa Cruz	Zoo	Cundinamarca
Zoológico de Piscilago	Zoo	Tolima
Zoológico Jaime Duque	Zoo	Cundinamarca
Zoológico de Cali	Zoo	Valle
Bioparque los Ocarros	Zoo	Meta
Zoológico de Barranquilla	Zoo	Atlántico
Zoológico Cafám	Zoo	Tolima
Fundación El Refugio	Nonprofit organization	Valle
Centro de Atención y Valoración Cortolima	Attention Center for Wild Animals	Tolima

monkey enclosures present at each site. A total of 29 *Lagothrix* individuals and a total of 14 enclosures were sampled (Table 7.2).

7.2.2 Behavior in Captivity

The behavior of all *Lagothrix* individuals present in each enclosure was evaluated through focal sampling methods. Instantaneous samples were taken every 10 min between 0600 and 1800 h for 5 days, per individual. For each instantaneous sample, the following information was collected:

1. Type of activity, using the same categories used by studies on wild woolly monkey populations (Stevenson 2006; González and Stevenson 2010; Zárate 2009; Vargas-Troncoso 2011): (a) feeding, (b) moving, (c) resting, and (d) social interactions (i.e., play, social grooming, mating, or aggression).
2. When the observed activity was feeding, the consumed item was identified and classified according to categories used by previous studies on wild woolly monkey populations (more information on these categories is available in the Captive Diet section below).

7.2.3 Housing Conditions

Housing conditions were studied for all woolly monkey enclosures using three variables: (1) enclosure size, (2) density of individuals in the enclosure, and (3) index of EE, measured as follows:

1. *Enclosure size:* Volume of space in which individuals are kept (in cubic meters).
2. *Density of individuals:* Number of individuals per cubic meter.
3. *Index of EE:* Two EE indexes were constructed using information on surface areas for different types of substrates, weighted by the degree of similarity to substrates used by wild woolly monkeys. Indexes were based on the assumption

Table 7.2. Information on the individuals found in each of the studied enclosures at the different study sites

Study site	Enclosure	Individual	Age–sex class
Zoológico Santa Cruz	SC	Niña	Adult female
		Margarita	Adult female
Zoológico de Piscilago	PL	Calimeño	Adult male
		Juliana	Adult female
		Paulo	Sub-adult male
		Chepe	Sub-adult male
Zoológico Jaime Duque	JD	Pocho	Adult male
		Isabella	Adult female
		Carolina	Sub-adult female
Zoológico de Cali	CA1	Rosita	Adult female
		Margara	Adult female
	CA2	Negro	Sub-adult male
	CA3	Jazmin	Female juvenile
	CA4	Petunia	Adult female
		Acacio	Adult male
	CA5	Rubus	Adult male
Bioparque Los Ocarros	OC	Niño	Adult male
		Paquita	Adult female
		Lina	Adult female
		Tommy	Sub-adult male
Zoológico de Barranquilla	BA	Dave	Adult male
		Mariana	Adult female
		Manu	Female juvenile
Zoológico Cafám	CF	Olivia	Adult female
		Popeye	Adult male
Fundación El Refugio	ER	Manuela	Adult female
Centro de Atención y Valoración Cortolima	CT1	Hembra	Adult female
		Ñato	Adult male
	CT2	Matilde	Sub-adult female

that a complex environment in terms of structure may favor the expression of natural behaviors. Structural complexity was measured in terms of the area of potential supporting structures. However, since different structures are used in different ways by wild woolly monkeys, two criteria were used to weigh the importance of different substrates: diameter and height.

The first index was based only on information on the diameter of the substrates used for moving by the woolly monkeys in Yasuní National Park, Ecuador (Cant et al. 2001). Thus, since woolly monkeys move on substrates of less than 2 cm in diameter 15% of the time, the total area of that type of objects was weighted by this proportion (i.e., multiplied by 0.15). Similarly, substrates between 2 and 5 cm in diameter were used 22% of the time; therefore, the weighted area of that type of substrate was obtained by multiplying the total available area by 0.22 to obtain the relative contribution. The different diameter categories were weighted using the same procedure. Flat surfaces were included in the >20 cm category, which

represents substrates that are rarely used by wild woolly monkeys (4% of the time). The area of diagonal substrates was included without correction, but the area of vertical ropes was estimated as if the monkeys were able to use them at an angle of 45°. The area of large trunks (>40 cm in diameter) was included just as the basal area.

The second index also included the substrate type in the same way described above, but it also included height as an additional weighting variable. For this purpose, we used the patterns of vertical stratification described from woolly monkeys in Tinigua Park, Colombia (Stevenson and Quiñones 1993). In natural conditions, woolly monkeys prefer the lower levels of the canopy, avoid the forest floor, and only use emergent trees occasionally for feeding purposes. This pattern has been explained as a behavioral preference to avoid predation, which may not be too relevant for captive animals, unless they are in a process of rehabilitation for reintroduction. Then, the second index considered the height at which the surfaces were found (i.e., forest floor: 0.1%, >0–3 m: 3%, 3–6 m: 12.9%, 6–9 m: 18.8%, 9–12 m: 25.5%, 12–15 m: 19.8%, 15–18 m: 9.9%, 18–21 m: 5.0%, 21–24 m: 3%, 24–28 m: 1%, >28 m: 0.8%). Both indexes were finally obtained by adding all weighted areas and dividing the total value by the number of individuals that are potentially using those substrates (m^2 per capita). Information on how to calculate these indexes may be provided by the authors upon request.

7.2.4 Captive Diet

Consumption Times

Data on all food items consumed by individuals from 0600 to 1800 h were collected for 5 days per enclosure. Items were individually identified, and the time spent by individuals consuming each item was registered for each feeding event. These data were collected for a maximum of two individuals per day; therefore, for enclosures with more than two individuals, the total number of sampling days per individual was less than 5 (all individuals were sampled for a minimum of 2 days). For comparative purposes, food items were classified according to categories used to study the diet of wild populations (Stevenson 2006; Gonzalez and Stevenson 2010; Zárate 2009; Vargas-Troncoso 2011): (1) fruits, (2) leaves (classified as vegetables in this study), (3) seeds and unripe fruits, (4) flowers (including vegetables such as cauliflower and broccoli), and (5) others (including dairy products, eggs, meats, cereals, bread, cakes, cookies, chips, dog-food, soil, baby-food, marmalade, icecream, and small reptiles).

Consumption Quantities

Data on the type and quantity (in grams) of food items offered daily to *Lagothrix* individuals per enclosure were collected based on information provided at each

site. Additionally, information on the composition (i.e., number and type of items provided) and time of all feeding bouts (i.e., when individuals were provided a particular diet) was collected for 5 days per enclosure. To estimate consumption values for the different items provided, we weighed the remaining items or pieces per day, or per feeding bout when possible. In a few cases, we were only able to weigh the remaining items or pieces for a limited number of days.

Total Daily Consumption

Consumption rates (g/s) for all consumed food items were estimated per enclosure, based on information on daily consumed quantities and daily consumption times. For items for which consumed quantities were unknown, feeding rates of similar items were used. Daily consumed quantities for each item per enclosure were estimated using the calculated consumption rates and daily consumption times.

Nutrient Composition and Consumption

Nutrient composition for the consumed food items was studied as grams of (1) crude fiber, (2) total sugars, (3) crude protein, and (4) crude fat, per gram of food. For each particular type of item ($n=77$), nutrient composition was estimated using databases from Zootrition software (Wildlife Conservation Society 1999) and the online USDA National Nutrient Database for Standard Reference (USDA Agricultural Research Service 2011). When this information was not available for a particular item ($n=10$), the nutrient composition of the most similar item found in the databases was used. Daily nutrient consumption values were estimated using information on nutrient composition and daily consumed quantities for each item.

7.2.5 Data Analyses

Activity and Feeding Behavior Patterns

We estimated the frequency of instantaneous samples on each activity and diet category for each observed individual per day. These frequencies were used as sampling units for further analyses. In order to assess differences between the activity budgets and diet composition, we calculated Chi^2 values by comparing the observed values in captive individuals and the expected frequencies from an average obtained from data on studied wild populations (Stevenson 2006; Zárate 2009; Gonzalez and Stevenson 2010; Vargas-Troncoso 2011). To estimate differences in activity budgets, we included the frequencies for feeding, movement, and resting, but we excluded social interactions. This approach is justified by the fact that increased rates of social interactions do not always represent unnatural behaviors (i.e., more

grooming or play events). To compare feeding behavior patterns between captive and wild woolly monkeys, Chi^2 analyses were performed based on calculated frequencies for the different food categories (fruits, vegetables, seeds and unripe fruits, arthropods, and other items). Expected frequencies were calculated using reported activity and diet percentages for wild woolly monkey populations (Stevenson 2006; Zárate 2009; Gonzalez and Stevenson 2010; Vargas-Troncoso 2011). Chi^2 values were calculated per individual and per enclosure.

Effect of Housing Conditions and Diet on Activity Behavior Patterns

Logarithmic or linear regression analyses (depending on best-fit line) were performed on SPSS software (SPSS Inc. 2006) to evaluate the effect of housing conditions (enclosure volume, density of individuals, and EE indexes) and diet (total consumption and crude fiber, total sugars, crude protein, and crude fat consumption) on the activity Chi^2 value obtained for the different enclosures. Data on volume, the two EE indexes, crude fiber, and crude fat were transformed using the Ln function to obtain a normal distribution.

Effect of Diet on Feeding Behavior Patterns

Given the nonparametric distribution of feeding behavior Chi^2 data, Spearman correlation analyses were performed using SPSS software (SPSS Inc. 2006) to evaluate the relationship between diet (quantity of crude fiber, total sugars, crude protein, and crude fat) and feeding behavior patterns.

Estimation of Adequate Captive Conditions

Minimum values for *adequate* housing conditions and diet (i.e., minimum values that are expected to favor the expression of natural behaviors) were estimated using linear equations from regression analyses between Chi^2 values and the different variables. These values were not estimated for density and crude fiber, since these variables did not show a clear relationship with activity Chi^2 values. Minimum values were estimated as ranges of minimum values, using the highest non-significant activity Chi^2 value to calculate the upper limit, and the lowest significant activity Chi^2 value to calculate the lower limit.

7.3 Results

Woolly monkeys within the same enclosure tend to show similar activity patterns. However, in 4 out of 14 enclosures, individuals showed significant differences in the percentage of time spent feeding. Significant differences between or among

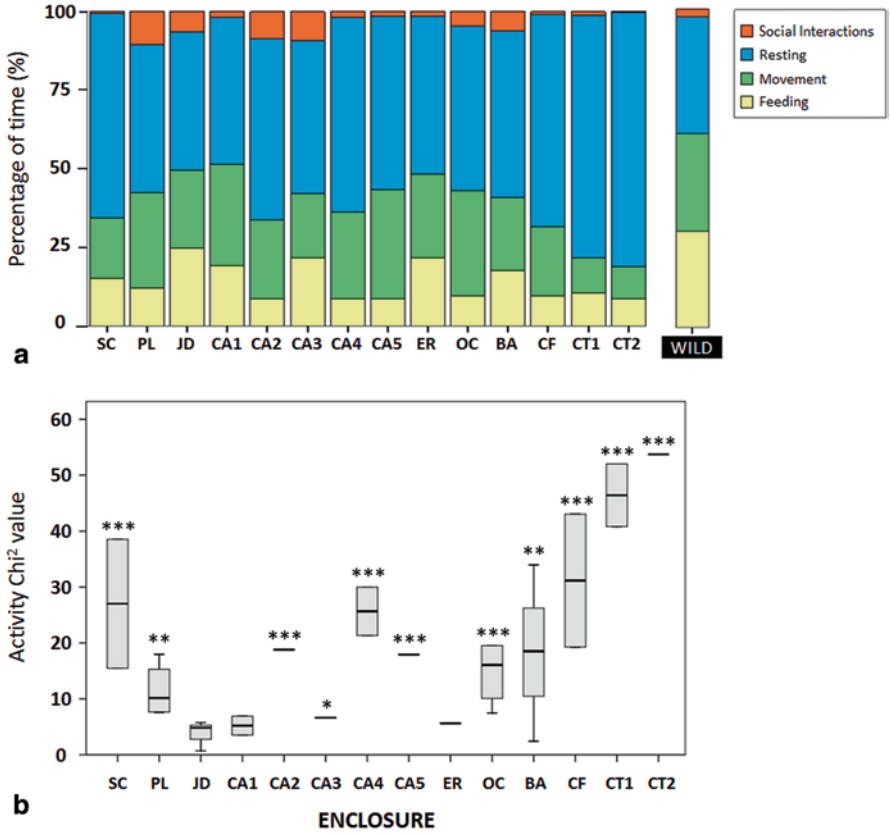

Fig. 7.1 **a** Percentage of time spent by woolly monkeys on the different activities at the different enclosures (*SC* Santa Cruz, *PL* Piscilago, *JD* Jaime Duque, *CA* Cali, *ER* El Refugio, *OC* Ocarros, *BA* Barranquilla, *CF* Cafám, *CT* Cortolima) and in the wild and **b** activity Chi^2 values for the different enclosures. *Boxes* show data distribution from enclosures with more than one individual

individuals were also found in five enclosures for movement, and in three for resting and social interactions (Appendix 7.1). The percentage of time spent by woolly monkeys in the different activities also varied among enclosures and between captive and wild environments (Fig. 7.1a). In general, captive woolly monkeys spend more time resting and less time feeding compared to wild woolly monkeys. However, Chi^2 analyses indicate that the activity behavior patterns found for three of the studied enclosures are not significantly different from patterns found for wild populations (JD, $p=0.272$; CA1, $p=0.082$; ER, $p=0.058$; Fig. 7.1b).

The percentage of time spent by woolly monkeys feeding on the different types of items varies greatly among enclosures and between captive and wild environments (Fig. 7.2b). Accordingly, Chi^2 values for feeding behavior patterns show that, for all enclosures, the time spent by woolly monkeys consuming fruits, vegetables, seeds and unripe fruits, arthropods, flowers, and other items differs significant-

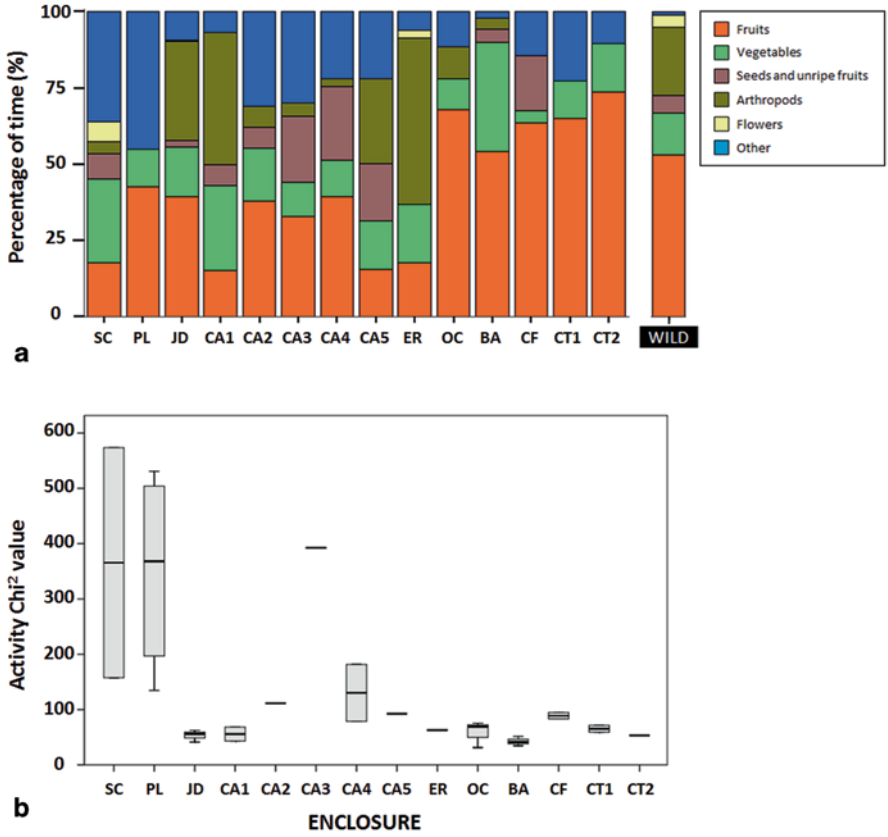

Fig. 7.2 **a** Percentage of time spent by woolly monkeys feeding on the different items at the different enclosures and in the wild and **b** feeding behavior Chi^2 values for the different enclosures. *Boxes* show data distribution from enclosures with more than one individual

ly from the feeding behavior patterns found for wild woolly monkeys ($p<0.05$; Fig. 7.2b). Within this wide variation of feeding patterns, results show a tendency towards a higher consumption of *other* items and a lower consumption of fruits in captive woolly monkeys compared to wild populations.

Total daily food consumption per individual varies among enclosures both in terms of time (Fig. 7.3a) and quantity (Fig. 7.3c). Differences are also observed in the consumption time and quantity for the different item categories (Fig. 7.3b, d). However, the Pearson correlation analysis between total consumption time and quantity did not show a significant relationship (Pearson coefficient = 0.412, $p=0.143$). Therefore, there is considerable variation in consumption rates among enclosures.

Regression analyses between activity Chi^2 values and housing conditions show a tendency towards more natural behavior patterns (lower Chi^2 values) in enclosures with a larger volume of space, lower density of individuals, and higher EE index

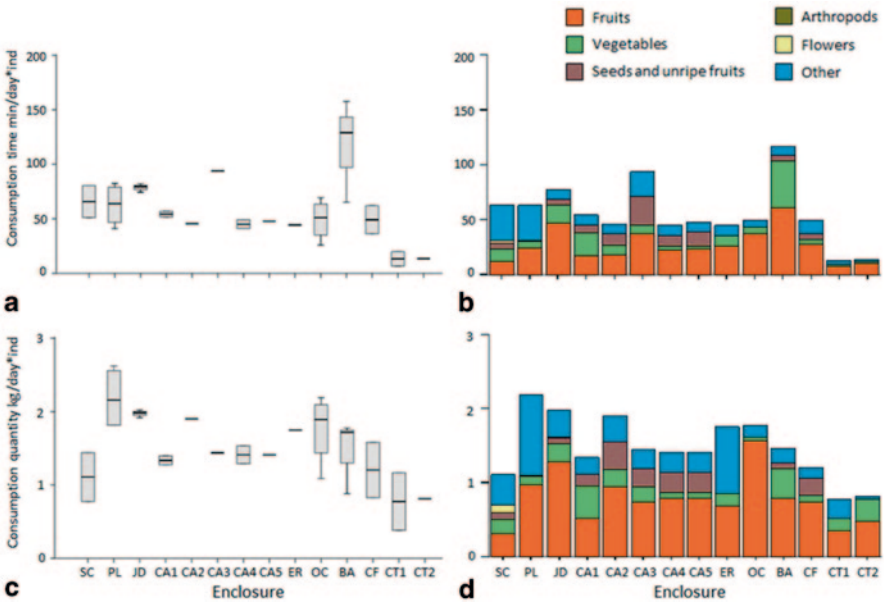

Fig. 7.3 Total consumption of food by captive woolly monkeys in different enclosures, in terms of **a** time and **b** quantity. The colored panels show consumption for the different food categories consumed, in terms of **c** time and **d** quantity, per individual per day. *Boxes* in (**a**) and (**b**) show data distribution from enclosures with more than one individual

values (Fig. 7.4). The logarithmic relationship between Chi^2 values and the two EE indexes was highly significant (Fig. 7.4c, d); therefore, EE seems to have a strong influence on captive woolly monkeys' behavior. Even though the relationship between activity Chi^2 values and enclosure volume was not statistically significant (Fig. 7.4a), the results suggest that this variable can have an important effect on captive woolly monkeys' behavior. On the other hand, although high densities within enclosures seem to have a negative effect on behavior (Fig. 7.4b), this relationship does not show a clear pattern.

Regarding diet variables, results from the regression analyses indicate that captive woolly monkeys tend to display more natural behavior patterns when they consume larger quantities of food and nutrients. The logarithmic relationship between activity Chi^2 values and total food consumption was highly significant (Fig. 7.5). Similarly, the logarithmic relationships between activity Chi^2 values and daily consumption of total sugars, crude protein, and crude fat also show statistically significant patterns (Fig. 7.6b–d). Crude fiber consumption did not show a significant relationship with activity Chi^2 values (Fig. 7.6a). On the other hand, Spearman correlation analyses between nutrient consumption and feeding behavior Chi^2 values indicate that none of the diet variables seems to be related to more natural feeding behavior patterns.

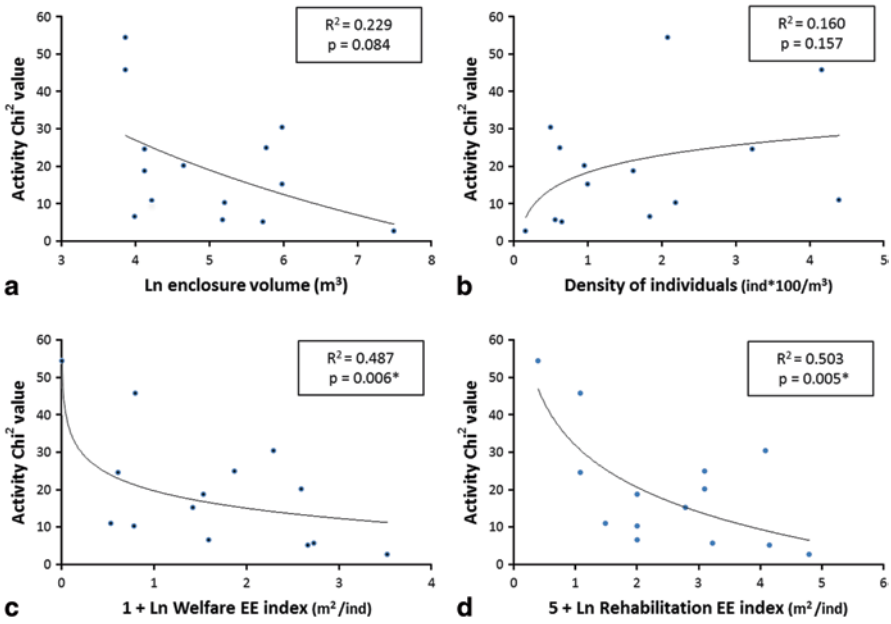

Fig. 7.4 Logarithmic regressions between Chi² values and **a** enclosure volume, **b** density of individuals, **c** welfare, and **d** rehabilitation EE indexes

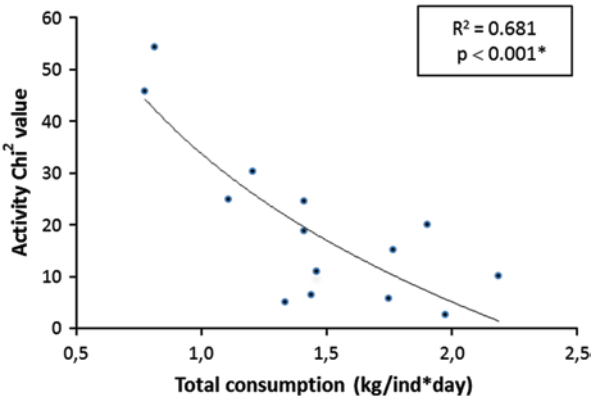

Fig. 7.5 Logarithmic regression between activity Chi² values and total food consumption

Estimated ranges of minimum values for enclosure volume, EE indexes, total consumption, and sugars, protein, and fat consumption required to provide woolly monkeys with *adequate* captive conditions (i.e., housing conditions and diet that are expected to promote the display of natural behaviors) are shown in Table 7.3. The actual minimum value for each variable is expected to lie within the estimated minimum ranges. Even though these ranges were estimated using linear equations, the regression analyses indicate that the relationship between the activity Chi² values and these variables is best represented by a logarithmic model. Therefore, it is expected that variable values above the estimated minimum ranges will represent

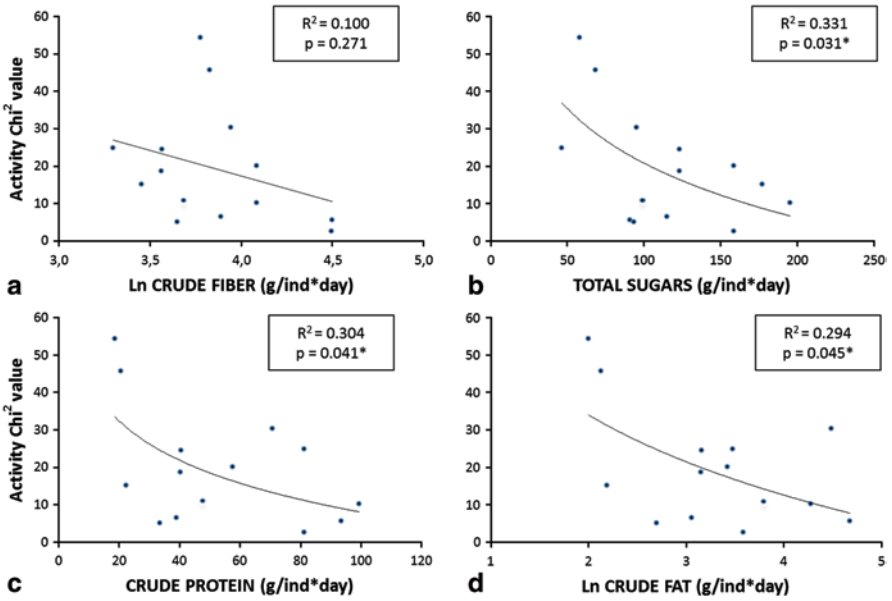

Fig. 7.6 Linear regression between activity Chi^2 values and **a** crude fiber; and logarithmic regressions between activity Chi^2 values and **b** total sugars, **c** crude protein, and **d** crude fat

Table 7.3 Minimum values for the different housing conditions and diet variables, required to provide captive woolly monkeys with *adequate* housing conditions and diet. The actual minimum value for each variable is expected to lie within the shown ranges

	Variable		Minimum range
Housing conditions	Enclosure volume *(m^3)*		1,103.81–1,250.10
	Environmental enrichment *(m^2/ind)*	Welfare Index	9.03–9.94
		Rehabilitation Index	0.80–0.84
Diet	Total consumption *(kg/ind.day)*		1.93–1.96
	Total sugars *(g/ind.day)*		186.88–191.41
	Crude protein *(g/ind.day)*		106.15–103.04
	Crude fat *(g/ind.day)*		118.10–129.50

an improvement in captive conditions until an undetermined stabilizing point is reached (i.e., when an increase in the variable values will not represent a further decrease in the Chi^2 value).

7.4 Discussion

In their natural habitat, woolly monkeys usually have large home ranges (Defler 1996; Stevenson 2006) and show behavior patterns dominated by feeding or foraging activities and movement (Di Fiore 2003; Stevenson 2006). Contrastingly, when

captive, woolly monkeys are largely limited in terms of space and, since most of the food they consume is provided, foraging activities are greatly reduced. Accordingly, the activity percentages obtained for resting and feeding in the different enclosures were always higher and lower, respectively, compared to percentages reported for wild populations (Fig. 7.1a). However, some enclosures showed similar and even higher movement percentages than wild populations, suggesting that movement activities may not be strongly impaired under certain captive conditions. Overall, 11 out of the 14 studied enclosures showed activity budgets that were significantly different from natural patterns, corroborating the prediction that captivity negatively affects woolly monkeys' behavior patterns. Nevertheless, the remaining three enclosures indicate that natural activity patterns can be achieved in captivity and, therefore, this suggests that there are certain captive conditions that enable woolly monkeys to behave naturally in terms of activity budgets.

Captivity usually limits both the diversity and total area of substrates available for individuals to develop natural behavior patterns. The natural habitat of woolly monkeys consists of dense forest vegetation that provides them with a wide range of substrates that can be exploited in numerous ways (i.e., complex patterns of habitat use; Cant et al. 2001). Consequently, the absence of adequate substrates (i.e., similar to substrates used by wild woolly monkeys) may reduce activities such as foraging, and might also prevent individuals from expressing natural locomotor and postural behavior, among others. The significant association found in the regression analyses between the activity Chi^2 values and the two EE indexes supports these predictions. Low EE indexes, indicative of a lower availability of substrates similar to the ones used by wild woolly monkeys, were associated with less natural activity patterns, while higher EE index values were associated with more natural activity patterns (Fig. 7.3). These results therefore indicate that EE has a particularly important effect on behavior, and that substrate-deficient enclosures may hinder the expression of natural behaviors by limiting the range of activities that individuals are able to perform. Additionally, since the EE indexes reflect the degree of similarity with the natural habitat, these results also support the idea that more naturalistic environments help promote the expression of natural behaviors.

Enclosure size had a minor but still considerable effect on captive woolly monkeys' behavior. Individuals in larger enclosures tend to show more natural activity patterns, which once again suggests that space limitation has a negative effect on woolly monkeys' behavior, most likely by causing a reduction in movement. Finally, even though there is a slight tendency towards more natural behaviors in less dense enclosures, woolly monkeys are group-living animals and, therefore, solitary individuals may show abnormal behavior patterns due to the absence of social interactions. Still, captive woolly monkeys live in densities that are far higher than densities reported for wild populations (Stevenson 2007, 2011) and, therefore, this may also have a negative effect on behavior patterns.

Captive diets are rarely similar to natural diets (Crissey and Pribyl 1997; Hosey 2005), and this is also the case for captive woolly monkeys in Colombia, as shown by the results of the Chi^2 analyses (Fig. 7.2b). Wild woolly monkey populations can

feed on fruits of approximately 200 species and plant material from at least 1,000 plant species (Stevenson 2004) and, while the number of potential arthropod species preyed on by woolly monkeys has not been quantified, it might be on the order of thousands in natural forests. Under captive conditions, the opportunity of a diverse diet is greatly reduced. Moreover, while feeding behavior in wild woolly monkeys is usually determined by food availability and preference (Stevenson 2004), in captive woolly monkeys it is mostly determined by food availability, and preference plays a minor role in an individual's feeding decisions. In most enclosures, little or no remaining items or pieces were left; thus, the proportions in which captive individuals consume items of the different categories mostly reflect the proportions in which these items were offered at the different study sites. Even though preference was observed in terms of the order in which the different items were consumed, this did not affect the final consumption proportions obtained for the different food categories. We also noticed that captive woolly monkeys were much less selective in leaf consumption. For instance, the consumption of mature leaves is rare in natural conditions (Stevenson 2006), but many of the studied individuals were observed eating dead leaves of several species that have been not reported in the diet of wild populations (i.e., *Cedrela montana*; Meliaceae).

In general, individuals that consumed larger quantities of food and main nutrients showed more natural activity patterns (Figs. 7.5 and 7.6). This could be related to caloric intake and energy budgets, since in some study sites, the total amount of food provided to individuals may not satisfy the basic caloric and nutritional requirements of the individuals. As a result, nutritionally deficient diets may cause abnormal behavior patterns, such as disproportionately large resting percentages, due to the lack of energy to perform other activities (i.e., movement). Nevertheless, these results have to be interpreted carefully since high sugar and fat consumption has been proposed as a probable cause of health problems in captive woolly monkeys (i.e., hypertension, diabetes; Ange-van Heugten et al. 2008). Therefore, although these results suggest that nutrient deprivation may negatively affect activity patterns in captive woolly monkeys, an excess of food should not be regarded as positive until the effects of diet on health problems and survivability are clarified.

This study suggests that both housing conditions and diet can have strong effects on captive woolly monkeys' behavior. Enclosures with a larger volume of space and a higher availability of substrates similar to the ones used by wild woolly monkeys seem to help promote the display of natural behavior in captive individuals. Thus, this study supports the prediction that housing conditions are crucial for the maintenance of natural activity patterns in captive woolly monkeys, and that more naturalistic environments are beneficial for captive individuals. On the other hand, providing captive woolly monkeys with a diet that satisfies the basic caloric intake and nutrient requirements of individuals is of great importance for individuals to be able to perform natural behaviors. Minimum values for *adequate* housing conditions and diet variables are proposed (Table 7.3). We suggest that in order to promote the expression of natural behaviors in captive individuals, or for the future development of rehabilitation programs, these values should be considered.

7.4.1 Post-Project Follow-up

Results from this study will be used to propose a preliminary protocol of animal management that lists favorable enclosure conditions and diet for the maintenance and rehabilitation of woolly monkeys in captivity. This protocol will be shared with all the participating institutions to encourage its implementation. With this document, institutions will be able to provide woolly monkeys with improved captivity conditions that might promote the maintenance of the natural behaviors. However, for a proper evaluation of the protocol's effectiveness, we intend to develop an experimental study to test whether individuals subjected to the suggested housing conditions and captive diet do, in fact, exhibit a more natural behavior, compared to individuals subjected to conditions indicated as being non-adequate. If the effectiveness of the protocol is confirmed, this would lead the way to the planning and construction of reintroduction projects for the species and, therefore, it would represent a valuable opportunity for conservation efforts.

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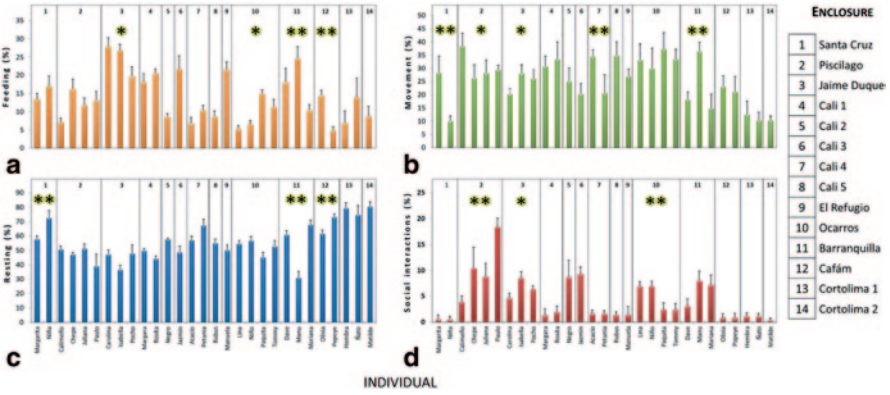
Appendix 7.1



Appendix 1. The figure shows activity budgets in terms of percentage of instantaneous records corresponding to **a** feeding, **b** movement, **c** resting, and **d** social interactions per individual. *Bars* show intraindividual variation. *Dotted lines* indicate group individuals present in the same enclosure. *Asterisks* indicate significant or highly significant statistical differences between activity budgets for individuals within the same enclosure

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