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Abstract Woolly monkeys (Lagothrix lagotricha and L. flavicauda) are threatened species in the wild and in captivity. Numerous zoological institutions have historically kept Lagothrix lagotricha spp., but only a few of them have succeeded in breeding populations. Therefore the majority of institutions that formerly kept Lagothrix lagotricha are no longer able or willing to do so. Captive populations of the species have frequent health problems, most significantly hypertension and related disorders. Researchers have conducted free-ranging dietary and behavior studies with respect to woolly monkeys, but have established no concrete link between diet or nutrients and captive health problems. The available literature we discuss indicates that researchers need to examine the link further. In addition, it is critical to the survival of the primates to be able to keep breeding populations in captivity owing to increasing natural pressures such as deforestation and hunting. Therefore, better understanding of the captive and free-ranging behavior and health parameters of the species is vital to ensure their survival and to maintain forest health and diversity. Researchers need to conduct large-scale research studies comparing the health and complete diet of individuals in the wild and captivity to resolve health problems facing the species in captivity.

Keywords diet · health · hypertension · primate · woolly monkey

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Introduction

Woolly monkeys (*Lagothrix* spp.) are one of the largest South American primates, with reported dimensions of 508–686 mm in head-to-body length and 5.5–10.8 kg in body mass (Nowak 1999). There are 2 species: *Lagothrix lagotricha* and *L. flavicauda* (*cf. Oreonax flavicauda*). *Lagothrix lagotricha* has 4 subspecies: *L. l. cana, L. l. lagotricha, L.l. lugens, and L. l. poeppigii*— inhabiting the eastern Andes in Columbia, the Rio Tapajos, and the Mato Grosso in central Brazil, and eastern Perú and Ecuador. *Lagothrix flavicauda* resides primarily in the eastern slope of Cordillera Central in northern Perú (Nowak 1999).

Woolly monkeys are threatened species, with *Lagothrix flavicauda* listed as critically endangered by the World Conservation Union (IUCN 2006), as endangered by the United States Department of Interior (USDI 2006), and on Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2006). *Lagothrix lagotricha* is listed on Appendix 2 of CITES, and of the 4 subspecies, *L. l. lugens* is considered vulnerable by IUCN (IUCN 2006; Nowak 1999). CITES, IUCN, and USDI have repeatedly changed the status of woolly monkey taxa on their scales of endangerment. Research is needed to identify the specific reasons why they are threatened with extinction. In some South American countries the threat is more severe than in others; for example, a Peruvian census in 1998 did not include woolly monkeys because they were rarely seen (Bennett *et al.* 2001). In addition, researchers have reported that woolly monkeys have a low r_{max} (intrinsic rate of natural increase). A low r_{max} correlates highly with the likelihood of specific extinction (Bodmer *et al.* 1997).

Woolly monkeys are often a source of food and commerce (Peres 1991; Shephard 2002). In addition, *Lagothrix* has a large span between offspring and reproduce for a shorter period of their lives compared to many non-ape primates (Mooney and Lee 1999; Nishimura *et al.* 1992). Further, *Lagothrix* have a comparatively large body size and low tolerance to habitat destruction, and are thus especially vulnerable. In addition, the introduction of firearms in the 21st century to hunt woolly monkeys makes them a threatened species (Peres 1991; Shephard 2002).

The situation for *Lagothrix* in captivity is thus precarious. In an attempt to conserve the species, numerous zoos have tried to develop and to maintain breeding populations. However, most institutions have not been able to replenish their own populations successfully. Very few institutions are currently able or willing to house *Lagothrix*. The most commonly reported causes of death in captivity include pregnancy complications and hypertension-related conditions. In fact, the European Endangered Species Program (EEP) showed that the captive woolly monkey population was reduced by 16% in 1 yr (1998). Owing to the limitations of importing wild animals and the problems associated with breeding, woolly monkey survivability in the wild and in captivity is of utmost concern. According to the last count, there were 107 captive woolly monkeys worldwide (www.ISIS.org; EEP 2003). Approximately half of the individuals currently in captivity are subspecific hybrids and therefore some of the subspecific information relevant in the wild may not be valid in captive populations.

General Behavior versus that of Other Nonhuman Primates

Researchers have studied *Lagothrix lagotricha* sspp. in their natural habitats since initial reports by Bates (1864). Historically, they have been harder to maintain in captivity than closely related spider monkeys are. Woolly monkeys are unique in that dominant males are very friendly toward subordinate males in their groups and all individuals have a chance to mate (Defler 1995). In addition, males are excellent protectors: they accompany their mates after the birth of young and follow them and the offspring everywhere. They are tolerant of young monkeys and occasionally carry infants on their backs (Defler 1995).

Female woolly monkeys with dependent infants are more efficient foragers than adult males are, and females do not necessarily sexually prefer the largest dominant males (Stevenson 2002). Woolly monkeys live as solitary males or in solitary male groups but never as solitary females or in female-only groups (Di Fiore 2002). Populations of wild woolly monkeys are genetically very diverse. They may have social patterns more similar to those of chimpanzees than of other ateline primates (Di Fiore 2002).

Woolly monkeys, squirrel monkeys, and capuchins forage together. Typically numerous birds, deer, and peccaries follow them through the forest and eat fruits and leaves that the monkeys leave behind. Therefore, woolly monkeys are a vital part of the ecosystem and efforts to conserve them are essential for their own well-being and of their ecosystem. Woolly monkeys share many of their habitats with the following primate species: *Saguinus fuscicollis* (saddleback tamarin), *Saimiri boliviensis* (Bolivian squirrel monkey), *Pithecia monachus* (monk saki), *Cebus albifrons* (white-fronted capuchin), *Cebus apella* (brown capuchin), and *Alouatta seniculus* (howler).

Woolly monkey group sizes vary drastically but range from 10 to 49 individuals at the Tinigua National Park in Columbia and in Amazonian Ecuador (Dew 2005; Stevenson and Castellanos 1999). Stevenson and Castellanos (1999) showed that woolly monkey groups that are either very large or very small may be less successful in foraging. Very large groups have to travel more kilometers per day to obtain their food, and very small groups may travel more as a defense mechanism. Woolly monkeys prefer to rest and travel in the middle to upper canopy of the forest. They do not reside as high as many other primate species, e.g., spider monkeys (*Ateles belzebuth belzebuth*), do (Dew 2005). Woolly monkeys seldom venture to the ground.

Diets

Free-ranging Subjects

Compared to other primates, woolly monkeys spend a large amount of time eating and moving in pursuit of food (*ca.* 60–75%; Dew 2005; Di Fiore 2004; Di Fiore and Rodman 2001). They typically cover 2 km/d moving and foraging (Defler and Defler 1996; Dew 2005). One acre of tropical rain forest typically has >200 species of trees, and because the woolly monkeys consume fruits from the majority of them as they travel through the forest they are one of the most important links to maintain

forest diversity (Defler 1995). Fruits consumed by woolly monkey are typically characterized by tough leathery outer shells with 1 or 2 large seeds in the middle with small fleshy parts adhering to each seed. For monkeys to eat the fleshy part they also must consume the seeds or spend time picking them out. Their vernacular name is macaco barrigudo (barrel or belly monkey) because after feeding on the ripe fruits and seeds their stomachs distend so that they appear to be pregnant (Bates 1864; Defler 1995).

Defler and Defler (1996) studied the diet of the wild Lagothrix lagotricha lagotricha in southeastern Colombia in an undisturbed rain forest at Estacion Biologica Caparu (EBC)). They reported daily food consumption of 23 woolly monkeys in a single troop for ca. 2400 h between January 1985 and September 1987. Defler and Defler (1996) recorded a total of 2243 woolly monkey foraging bouts and identified the food items in 1719 cases. The monkeys consumed fleshy fruits as 78.9% of their diets, leaves (primarily new growth) as 11.4%, seeds as 4.3%, invertebrates (termites and katydids) as 4.9%, bark as 0.3%, flowers as 0.1%, and tendrils as 0.1%. The majority of the fruits consumed were very tough (could not be easily opened by human hands) and had seeds that the monkeys seemed to swallow completely. The fruits comprised 183 plant species, with 44% of them from the Moraceae, Sapotaceae, and Leguminosae. Sapotaceae was the most consumed. Chrvsophyllum amazonicum and Manilkara amazonica were the 2 most consumed fruit species and they each accounted for $\geq 5\%$ of the fruit total. There was considerable variation in diets of woolly monkeys among months and years. They consumed fruits of Iriartea ventricosa and immature seeds of Micrandra spruceana when there was little else to eat.

In a 1-yr feeding behavior study in Amazonian Ecuador, Dew (2005) reported results similar to those of Defler and Defler (1996). However, the woolly monkeys in Ecuador ate more insects (6%), and 12% of the total diet items where unknown because their foraging behavior made exact recordings impossible for the researchers. Though unconfirmed, much of the unknown percentage was probably insects and prey items. Di Fiore (2003) had previously reported that woolly monkeys there seemed to forage and travel to locations where higher densities of prey live. Dew (2005) also reported that the woolly monkeys selected food items by discriminatively picking items for seeds that they wanted to swallow. Dew's research showed that although woolly and spider monkeys often live in the same regions, the woolly monkeys eat different diets than those of closely related spider monkeys. They tended to eat fruits that were lower in fat and higher in both sugar and water than the spider monkeys at the same location. In addition, woolly monkeys prefer harder fruits, consume more vegetative matter, spend more of their time eating, forage in larger groups, and never forage from the ground versus spider monkeys. The woolly monkeys did not drink water in the year-long study whereas the spider monkeys did. The information is important for captive feeding of woolly monkeys and shows that though 2 species may be very closely related, their dietary needs may differ substantially.

Researchers believe that the 4 woolly monkey subspecies play a vital role in seed dispersal and increased germination for the forest plants on which they feed (Defler and Defler 1996; Dew 2005; Stevenson *et al.* 2002; Yumoto *et al.* 1999). Di Fiore (2004) described the diet and feeding ecology of a population of *Lagothrix* Springer

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lagotricha poeppigii in Yasuní National Park, Ecuador in the western Amazon Basin. The main constituent of the diet was ripe fruits, varying between 64% and 89% of the monthly diet. Fruits, including exudates, comprised an average of 76.2% of the diet; immature seeds, leaves, and other nonreproductive plant parts comprised 10.6%, flowers 3.6% and animal prey 9.6% of the diet. The 3123 fruit feeding records in the study represent a minimum of 147 plants belonging to \geq 80 different genera and 45 different families. The top 3 genera —*Inga* (Fabaceae), *Ficus* (Moraceae), and *Spondias* (Anarcardiaceae)— each accounted for \geq 5% of all feeding records.

Yumoto *et al.* (1999) showed that woolly monkeys were especially important with regard to seed dispersal because they ate primarily fruit and also traveled in a larger area during the day than howlers did (17.2 ha vs. 69.8 ha, respectively). The average gastrointestinal retention time for the seeds they consumed was 2.0–6.1 h. The researchers studied retention times in the field and therefore used feeding bouts and the appearance of seeds in the feces to determine retention times instead of standard markers. Yumoto *et al.* (1999) also showed that woolly monkeys in the La Macarena Forest in Columbia divided their foraging time as follows: fruit, 81.5%; leaves, 4.4%; and insects (primarily ants: *Crematogaster* spp. and *Eciton* sp., 14.1%).

Defler and Defler (1996) reported that 3 woolly monkey subspecies —*Lagothrix lagotricha cana, L. l. poeppiggi,* and *L. l. lugens*— similarly consume the majority of their diets as fruits (77%, 73.6%, and 60%, respectively). The Anacardiaceae, Arecaceae, Fabaceae, Leguminosae, Moraceae, and Sapotaceae provide the most important food sources for woolly monkeys regardless of their subspecies or test site (Defler and Defler 1996; Dew 2005; Di Fiore 2004, Iwanaga and Ferrari 2001, Peres 1994). The test sites for the 4 subspecies differ greatly with respect to rainfall, food availability, and soil quality. Though woolly monkey subspecies appear to have foraging preferences, they are commonly reported to sample items from numerous species. In fact, Peres (1994) reported that in 11 mo a large (39–41 members) group of *Lagothrix lagotricha cana* ate from 225 species of plants. During times of very low fruit availability members of the group seemed to prefer young seeds, young foliage, and exudates of mature seed pods of *Parkia* instead of insects (Peres 1994).

Research varies widely with regard to the amount of time that woolly monkeys spend trying to catch animal prey (Di Fiore 2003; Di Fiore and Rodman 2001). Depending on the study, woolly monkeys have reportedly spent between 0.1 and 36.2% of their time either trying to capture or consuming animal prey (Defler and Defler 1996; Di Fiore and Rodman 2001; Peres 1994, Stevenson et al. 1994, 1998). Researchers have suggested that some woolly monkey subspecies preferentially spend more time trying to catch animal prey when there is an abundance of fruit available. The time allows them to store fat reserves for enhanced survival when food is less available. Lagothrix lagotricha cana and L. l. lagotricha consume less animal matter than the other 2 subspecies, though they are larger (by 30-65%) than L. l. lagotricha and L. l. lugens (Di Fiore and Rodman 2001). Larger individuals may be less able to catch large enough quantities of insects to fulfill their protein requirements. Overall, it seems that woolly monkeys (regardless of location or subspecies) preferentially consume ripe fruits and that the majority of the differences in their foraging habits are likely a response to habitat quality, available food sources, and body size. When food sources are scarce, woolly monkeys do not D Springer

forage over large ranges. Instead they appear to forage longer in certain areas and therefore conserve energy that they would otherwise need to move around to more trees (Di Fiore 2001).

Researchers have infrequently noted that woolly monkeys chase frogs and larger animals or are very interested in bird nests (Stearns *et al.* 1988). Captives have preyed on birds. It may be an opportunistic way for them to eat additional calories in the wild, though it occurs at such a low level that it is not easily noticed (Stearns *et al.* 1988).

Defler and Defler (1996) reported that the majority of consumed fruits were yellow-to-orange. The finding is surprising because they are 75% dichromatic — unable to use color vision— and perhaps color in their captive diet may be an important yet often ignored concept (Jacobs and Deegan 2001). Finally, researchers have suggested that some primates ingest the seeds of some fruits to rid their gastrointestinal systems of parasites. However, Stevenson *et al.* (2005) did not report this during woolly monkey observations in Columbia.

Captive Subjects

Owing to the health problems and low reproductive success of captive woolly monkeys, their captive diet is a major concern. Wiltevenn et al. (1999) measured the captive diet of one of the largest captive populations of woolly monkeys; it appeared sufficient in all essential nutrients versus the 1978 National Research Council nutritional requirements for New World monkeys. The diet did not appear to be a risk factor for hypertension when compared to human standards (Wilteveen et al. 1999). However, our review of captive diets for them indicated that there are few dietary similarities between institutions and that most institutional diets do not meet the current National Research Council estimated requirements for New World primates (Ange-van Heugten et al. 2007; Timmer 2006; Timmer and Ange-van Heugten 2006; Timmer et al. 2005). In addition, many institutions overfeed their subjects and offer huge daily variations of fruits and vegetables while potentially underfeeding them insects. Thus, the fat and sugars offered widely differ in both type and quantity. Large-scale studies of captive and wild populations are needed for comparisons of nutrient supply and possible natural supplements to the diet that may be missing in captivity as well as comparisons with the updated New World monkey nutrient requirements.

Health Problems in Captivity

The captive management of *Lagothrix lagotricha* sspp. is a major concern. There is a breeding program but it is in peril owing to the shrinking number of captive individuals, poor reproductive performance, and high infant mortality. Many females have a reduced body mass during pregnancy and often abort without obvious reasons. Offspring frequently die young. Body sizes of the young woolly monkeys are considered of normal size. Müller *et al.* (1989) found that a high incidence of stillbirth, premature birth, and abortion coincided with a high incidence of renal disease in mothers. A healthy pregnancy is difficult to maintain because of the \oint Springer

decrease in body mass and because of the high incidence of abortions (Mooney and Lee 1999). Thus, individuals do not eat sufficient quantities of nutrients to maintain or increase body mass during pregnancy. The severe complications that may arise in breeding individuals are often similar to those of diabetes mellitus and hypertension in humans and other primates and ultimately include congestive heart failure, renal failure, and aneurysm (Giddens *et al.* 1987; Miller *et al.* 1995). The complications are often pronounced during pregnancy and also may result in very large, difficult to deliver infants (Lloyd *et al.* 1995). They can ultimately result in arteriosclerotic changes in the placenta that lead to nutrient and metabolic insufficiencies with severe consequences for the fetus. Hypertension is of multifactorial origin. Stress may play a role, along with obesity and genetic predisposition (Debyser 1995). All of the factors may be associated with the shrinking number of captive woolly monkeys.

Hypertension-specific Health Problems

Captive woolly monkeys have a high incidence of primary systemic hypertension: a blood pressure of >140 (systolic)/90 mm Hg (diastolic; Giddens et al. 1987; Miller et al. 1995; Muller et al. 1989; Wagner et al. 1984). Hypertension in woolly monkeys appears to be a multifactorial disease, and affected captive primates may die from congestive heart failure, renal failure, and aneurysms. Some of the underlying causes of the disease in woolly monkeys may be age, obesity caused by restricted physical activity, unnatural captive diets, sex, and psychological and physical stress including pregnancy (Muller et al. 1989). Giddens et al. (1987) diagnosed hypertension in woolly monkeys via a direct measure: arteriolar puncture while anesthetized with ketamine, of systolic and diastolic blood pressure in 15 captive apparently healthy woolly monkeys (systolic and diastolic blood pressure measures from 194 mm Hg and 136 mm Hg, respectively) Giddens et al. (1987) also showed that systolic and diastolic blood pressures of the captive woolly monkeys were significantly higher than those of captive baboons (Papio cynocephalus), pigtailed macaques (Macaca nemestrina), and crab-eating macaques (Macaca fasicularis). Another group of 17 apparently healthy woolly monkeys had elevated pressures (176/116 mg Hg) while anesthetized (Miller et al. 1995; Wagner et al. 1984).

Arteriolar nephrosclerosis is the first lesion associated with hypertension in woolly monkeys (Giddens et al. 1987; Miller *et al.* 1995). The most common causes of death in captive woolly monkeys are congestive heart failure, renal diseases and failure, and cardiovascular failures (Brown *et al.* 2000; Giddens *et al.* 1987; Henderson *et al.* 1970; Miller *et al.* 1995). Giddens *et al.* (1987) showed that direct arterial blood pressure in woolly monkeys increases by 16 mm Hg per kg of additional body mass for systolic pressure and 10 mm Hg per kg for diastolic pressure. The correlation has led many investigators to believe that the increase in mass with age exacerbates hypertension in woolly monkeys. However, young woolly monkeys that have healthy body masses have also been diagnosed as hypertensive.

Female woolly monkeys (80%) are more likely than males (20%) to become hypertensive (Muller *et al.* 1989). In addition, there are reports of atherosclerosis in woolly monkeys, though they are rarer than reports of hypertension (Giddens *et al.*

1987; Henderson *et al.* 1970). It is currently unknown whether woolly monkeys develop hypertension in the wild or if it is only a problem in captivity. It is very important to study hypertension-related problems in both captive and wild individuals. The survival of the species depends on further research.

Successful treatment of woolly monkeys with hypertension is still needed. Poor treatment success may be due to the late diagnosis of the condition. Oral furosemide and β -blockers have not been as effective in treating hypertension in woolly monkeys as they are in humans. Antihypertensive therapy with diltiazem given simultaneously with furosemide has reduced blood pressure in a woolly monkey (Miller *et al.* 1995). Researchers believe that captive woolly monkeys are extremely stress sensitive and that making their enclosures more similar to their natural environments and providing a seasonal change in diet may help to decrease their hypertension. In support of the theory, fecal cortisol measurements are 10–30 times higher for captive woolly monkeys versus their free-ranging counterparts, though Ziegler (2001) did not report their behavior, gender, age, hypertension status, and social grouping.

Hepatitis Health Concerns

Woolly monkeys at the Louisville Zoo (13 of 16 individuals tested) were the first to be diagnosed with woolly monkey hepadnavirus (WMHBV, which is related to human hepatitis B) infections (Lanford *et al.* 1998). Researchers have since studied and reported the virus in other captive woolly monkey populations though the association between WMHBV and potential health problems is not well understood.

Toxoplasmosis and Related Health Concerns

Woolly monkeys are especially susceptible to the protozoan *Toxoplasma gondii* while Old World primates seem to be immune to it (Bouer *et al.* 1999; Hessler *et al.* 1971). In all captive situations, animal keepers should be very careful to limit the possible exposure of woolly monkeys to the protozoa. For example, woolly monkey cages should be thoroughly cleaned and kept as far from felines as possible. Felines are the only animals known to pass *Toxoplasma gondii* oocyctes in their feces. Therefore, feline care staff should not care for woolly monkeys at the same institution. Amebiasis, demodectic acariasis, *Klebsiella* infection, and salmonellosis are also especially problematic for captive woolly monkey populations (Peddle and Larson 1971; Schiefer and Loew 1978).

Bone Formation Health Concerns

Rickets and osteomalacia have occurred in woolly monkeys. In fact, the condition is so well known that many clinicians refer to the condition as woolly monkey syndrome (NRC 2003). Dew (2005) reported that Amazonian soil is very rich in calcium, and in addition free-ranging diets are likely also to be high in phosphorus from consumed insects. Therefore, it is vital to make sure that captive diets have adequate levels of calcium and phosphorus as well as proper calcium-to-phosphorus ratios. In addition, woolly monkeys should either have sunlight or proper artificial Despringer

wavelength exposure to produce the vitamin D metabolites needed for normal bone mineralization as well as proper vitamin D_3 concentrations in their diets (NRC 2003). It is not known if the bone formation problems noted in captivity are also problems in free-ranging populations. Research is critically needed in this area to ascertain if the problems are in captive populations only and, if so, how we can best prevent them from occurring.

Reproduction Facts and Challenges

Institutions have had difficulty breeding captive woolly monkeys, and the individuals have not been able to replace themselves in sufficient numbers (Mooney and Lee 1999). One study reports an infant mortality rate of 50% in captive woolly monkeys, with infant mortality increasing if the infant is a male or if it is the first pregnancy (Debyser 1995). Debyser (1995) also reported that there is increased risk of pregnancy complications if the social group is unstable and if the mother is captive born. Debyser (1995), Muller *et al.* (1989), and Ruedi and Heldstab (1980) have associated the high incidence of woolly monkey stillbirths, premature births, and spontaneous abortions with renal disease and hypertension in the mothers. Hypertension is accompanied by arteriosclerotic changes in the placenta that lead to placental insufficiency and detrimental effects, possibly death, to the fetus (Debyser 1995). Debyser (1995) and Ruedi and Heldstab (1980) have also linked dystocia, *Klebsiella* infections, septicemia, and meningitis to infant deaths in woolly monkeys.

Free-ranging woolly monkeys live in large heterosexual groups with *ca.* 10–49 individuals/group (Mooney and Lee 1999; Stevenson and Castelanons 2000). Members of both sexes are sexually mature between 4 and 5 yr of age and the females have a 21-d ovarian cycle. On average, wild females have their last offspring at 20 yr (Mooney and Lee 1999; Robinson and Redford 1986). The annual birth rate in free-ranging monkeys is reported as 0.29 or an interbirth interval of 37 mo (Nishimura 2003; Robinson and Redford 1986). The gestation period lasts 225 d, with infants born at *ca.* 10% of their adult mass (Mooney and Lee 1999). Mothers typically nurse infants for 18–24 mo (Mooney and Lee 1999). Captive woolly monkeys reach reproductive maturity later than their free-ranging counterparts do (averages of 6–7 yr vs. 4–5) and reproductive females have a mean life longevity of 13 yr versus a much longer life span for both free-ranging individuals that are able to reproduce have a much shorter life span.

Alternative Research

The Apenheul Zoo in The Netherlands has used herb gardens to introduce Amazonian herbs from many plant families. They are useful for health problems related to high blood pressure, liver deficiencies, and diarrhea (Vermeer 1994a). Therefore they may also benefit woolly monkeys. Other zoological institutions have similarly incorporated feeding over-the-counter Amazonian herbs (Amazon Heart Support and Graviola, Raintree Nutrition, Inc., Carson City, NV, 89701) in hopes of Despringer

decreasing hypertension and health problems in captive woolly monkeys (Ange-van Heugten *et al.* 2007). There is no publication on medical effects of the supplements.

Several institutions holding woolly monkeys have instituted feeding schedules to deliver sugar loads gradually throughout the day to combat potential diabetic-like conditions (Vermeer 1994b). In addition, many institutions have taken woolly monkeys off exhibit to reduce stress and have stopped breeding in order not to sacrifice the current individuals to potential pregnancy-related health problems. The method is obviously problematic, and a short-term solution at best.

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