

Use of Mineral Licks by White-Bellied Spider Monkeys (Ateles belzebuth) and Red Howler Monkeys (Alouatta seniculus) in Eastern Ecuador

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Abstract Geophagy occurs in all primate groups and is particularly common in species that consume greater quantities of plant material, i.e., leaves, fruit. The function of geophagy is not fully understood and likely varies over space and time, perhaps in connection with changes in diet. Central to a better understanding of geophagy in primate ecology is knowledge of the occurrence of such behavior among different species and seasons. We used camera traps triggered by heat and motion to document the use of mineral licks by primates over a 3-yr period at a lowland forest site in eastern Ecuador (Tiputini Biodiversity Station). Such mineral licks can be important sources of minerals, nutrients, and other compounds for a wide range of species in Amazonian forests. Although 10 species of primates are known from the study site, we obtained photographs of only 2 species, Ateles belzebuth (white-bellied spider monkey) and Alouatta seniculus (red howler) at 2 of 4 saladeros surveyed. From late December 2004 through early January 2008, we recorded 192 photographs with a total of 318 Ateles belzebuth representing ≥ 66 separate visits. Comparable numbers for *Alouatta seniculus* were 80, 121, and 37. We recorded both species visiting a mineral lick at the same time on ≥ 7 occasions. Use of mineral licks varied across months; we recorded more visits from November through February, the drier period at Tiputini. Visits also varied by hour, with no visits before 0830 or after 1630; Ateles belzebuth showed a stronger mid-day peak in visits. Average visit length (calculated as the time between the first and last

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photographs of a given visit) was similar between the 2 species but median visit length was more than twice as long for Ateles belzebuth (15 min) as for Alouatta seniculus (6 min). Results indicate that mineral licks are important in the ecology of these species, but further studies are needed to determine the precise benefit(s) obtained and how benefits may vary with diet and other factors.

Keywords A louatta \cdot Ateles \cdot camera trap \cdot Ecuador \cdot geophagy \cdot mineral lick

Introduction

Researchers have reported consumption of soil (geophagy) in many mammals and birds (Abrahams and Parsons [1996;](#page-10-0) Diamond et al. [1999](#page-11-0); Dominy et al. [2004;](#page-11-0) Matsubayashi *et al.* [2007\)](#page-11-0) and appears particularly common in more herbivorous species (Kreulen [1985](#page-11-0); Krishnamani and Mahaney [2000](#page-11-0)). Suggested benefits of geophagy include mineral supplementation, detoxification of plant secondary compounds, or alleviation of digestive disorders (Atwood and Weeks [2002](#page-10-0), [2003;](#page-10-0) Davies and Baillie [1988](#page-10-0); Mahaney et al. [1995;](#page-11-0) Voros et al. [2001](#page-12-0)). However, a full explanation for geophagy has not been achieved (Ferrari et al. [2008\)](#page-11-0), perhaps because geophagy has multiple causes that may vary geographically, seasonally, and among groups (Davies and Baillie [1988;](#page-10-0) Setz et al. [1999\)](#page-12-0).

Researchers have reported geophagy for all primate groups, including strep-sirhines (Britt et al. [2002;](#page-10-0) Norscia et al. [2005\)](#page-11-0), apes (Ketch et al. [2001;](#page-11-0) Mahaney et al. [1995\)](#page-11-0), Old World monkeys (Pages et al. [2005;](#page-11-0) Voros et al. [2001\)](#page-12-0), and New World monkeys (Dew [2005;](#page-10-0) Izawa [1993](#page-11-0); Müller et al. [1997;](#page-11-0) Setz et al. [1999\)](#page-12-0). A diet rich in leaves and fruits is characteristic of species reported to eat soil on a regular basis (Britt et al. [2002](#page-10-0); Krishnamani and Mahaney [2000](#page-11-0); Stevenson et al. [2000\)](#page-12-0). Sources of soil for ingestion vary among groups and species. New World monkeys often consume soil from arboreal sources, such as termite nests, e.g., Pithecia pithecia, (Setz et al. [1999](#page-12-0)); Alouatta belzebul (De Souza et al. [2002\)](#page-10-0); Chiropotes satanas (Veiga and Ferrari [2007\)](#page-12-0), or other sources (Bicca-Marques and Calegaro-Marques [1994](#page-10-0)). Although use of terrestrial sources is more common in Old World monkeys (Krishnamani and Mahaney [2000\)](#page-11-0), consumption of soil from ant mounds of *Atta* and other terrestrial sources has been reported for several New World species, e.g., Callicebus personatus (Müller et al. [1997\)](#page-11-0); Saguinus mystax (Heyman and Hartmann [1991\)](#page-11-0); see Ferrari et al. [2008,](#page-11-0) for a recent review.

Mineral licks (known as saladeros in Ecuador) are sites where many mammals and birds come to obtain minerals or other compounds by eating soil or drinking water (Abrahams and Parsons [1996;](#page-10-0) Krishnamani and Mahaney [2000\)](#page-11-0). Use of mineral licks along river banks by macaws and other parrots has received much attention (Brightsmith [2004;](#page-10-0) Brightsmith and Muñoz-Najar [2004](#page-10-0); Burger and Gochfeld [2003](#page-10-0); Gilardi *et al.* [1999\)](#page-11-0) at least partially because of the importance of such sites for ecotourism. Mineral licks also occur within forests, well away from river banks (Clayton and MacDonald [1999;](#page-10-0) Lizcano and Cavelier [2004;](#page-11-0) Matsubayashi et al. [2007\)](#page-11-0). Such licks typically occur in sites with eroded soil layers, often along small drainages or intermittent stream courses; they are visited by a variety of birds, e.g., guans, pigeons, and mammals, e.g., bats, primates,

rodents, ungulates (Brightsmith [2004](#page-10-0); Ferrari et al. [2008](#page-11-0); Krishnamani and Mahaney [2000;](#page-11-0) Lizcano and Cavelier [2000,](#page-11-0) [2004](#page-11-0); Voigt et al. [2007\)](#page-12-0). Long-term studies, i.e., studies encompassing >1 yr, at saladeros are lacking but are needed to understand the ecological role and importance of such sites (Brightsmith [2004\)](#page-10-0) and how their importance may vary seasonally. Geophagy may, e.g., be more pronounced in the dry season, perhaps in relation to changes in diet (Mahaney et al. [1995](#page-11-0)), although not all studies have supported this idea (Setz et al. [1999\)](#page-12-0).

Soil or water from mineral licks may provide a dietary supplement or may help detoxify plant secondary compounds ingested as part of the diet (Dominy *et al.*) [2004;](#page-11-0) Ferrari et al. [2008;](#page-11-0) Mahaney et al. [1995;](#page-11-0) Voigt et al. [2007](#page-12-0), [2008\)](#page-12-0). For example, mountain tapirs (*Tapirus pinchaque*) use licks where water has a higher sodium and nitrogen content (Lizcano and Cavelier [2004\)](#page-11-0), suggesting that use of such sites may be beneficial when such minerals are low in concentration in the environment (Brightsmith and Muñoz-Najar [2004](#page-10-0); Emmons and Stark [1979;](#page-11-0) Matsubayashi et al. [2007](#page-11-0)). Use of mineral licks by animals often tends to be associated with diets rich in secondary compounds (Diamond et al. [1999;](#page-11-0) Gilardi et al. [1999](#page-11-0)) and may allow species to exploit a wider array of plants with a diverse array of toxins (Norconk et al. [1997\)](#page-11-0).

Among New World monkeys, use of terrestrial mineral licks has been reported most frequently for Ateles spp. and Alouatta spp. (Dew [2005](#page-10-0); Emmons [1997](#page-11-0); Izawa [1993;](#page-11-0) Stevenson et al. [2000](#page-12-0)), although frequency of use varies geographically. For example, Alouatta frequently consumes soil at sites in Amazonia but not in Central America (Ferrari et al. [2008\)](#page-11-0). Both Ateles and Alouatta species are known to eat a wide variety of fruits and other plant material (Defler [2004\)](#page-10-0). Ateles is, overall, more frugivorous and Alouatta more folivorous (Stevenson et al. [2000\)](#page-12-0). Here, we report on use of mineral licks (saladeros) by Ateles belzebuth (white-bellied spider monkeys) and *Alouatta seniculus* (red howlers) at a site in eastern Ecuador. Both species are common at the study site but differ in diets, home ranges, and patterns of movement (Di Fiore and Suarez [2007;](#page-12-0) Schmitz et al. 2007; A. Link and A. Di Fiore unpubl. data). The major objectives of this study, then, were to determine how use of saladeros varied among hours of the day and among months of the year and whether such use varied between species. By documenting use of saladeros over a 3-yr period, we hope to shed additional light on variability in use of such sites for soil consumption.

Methods

Study Site

We conducted our research at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (ca. 0°37′S, 76°10′W, 190–270 m elevation). TBS was founded in 1994 by the Universidad San Francisco de Quito (USFQ) on a tract of undisturbed lowland rainforest within the ca. 1.7-million ha Yasuní Biosphere Reserve, a region noted for its biodiversity (Valencia *et al.* [2004\)](#page-12-0). At least 10 species of primates are known to occur at the station: pygmy marmosets (*Cebuella pygmaea*), goldenmantle tamarins (Saguinus tripartitus), noisy night monkeys (Aotus vociferans),

dusky titi monkeys (Callicebus discolor), common squirrel monkeys (Saimiri macrodon), white-fronted capuchins (Cebus albifrons), equatorial saki monkeys (Pithecia aequatorialis), red howlers (Alouatta seniculus), common wooly monkeys (Lagothrix poeppigii), and white-bellied spider monkeys (Ateles belzebuth). The station and nearby areas contain a variety of habitats including terra firme and várzea forest, palm swamps and other wetlands, as well as areas of natural succession. The mean annual precipitation is ca. 2800 mm. There is a rainy season from April to early August, when $>65\%$ of the annual rain falls (monthly average ca. 385 mm); 15% occurs from November to February (monthly average ca. 140 mm; based on data from 1998 to 2002; Karubian et al. [2005](#page-11-0)). January often is particularly dry (pers. obs.).

We documented use of 4 saladeros—Chorongo, Harpia, Harpia Parcela, Puma located in old-growth forest. Saladeros were located ca. 0.5 km (Chorongo) to ca. 1.5 km (Harpia, Puma) north of the Tiputini River. Farthest distance between saladeros (Puma, Harpia Parcela) was ca. 2.7 km. All 4 sites were used by many of the same species, e.g., peccaries *Tayassu* spp., tapir *Tapirus terrestris*, red brocket deer Mazama americana, piping guans Aburria cumanata, plumbeous pigeons Patagoienas plumbea) on a regular basis, as evidenced by presence of well-used trails leading into the sites, tracks within the sites, direct observations of animals in the sites, and photographs obtained as part of this study. Trees on the borders of 2 of the saladeros (Puma, Harpia) were known to be used by primates to descend to the ground (F. Narváez, pers. comm.). With the exception of a recent record of two Ateles belzebuth (October 2008) at the Chorongo saladero, we have no records of primates using the Chorongo and Harpia Parcela saladeros and we do not consider them further here. Puma and Harpia saladeros were ca. 1.6 km apart. Soil was continually moist at the Puma saladero but running water was not always present (depending on rainfall). Water was typically present at the Harpia saladero; after heavy rains, water covered most of the saladero floor often with a noticeable flow.

Focal Species

Ateles belzebuth and Alouatta seniculus are widely distributed across the Amazon in northern South America, with the latter species having a wider range north of the Amazon (Emmons [1997\)](#page-11-0). Ateles belzebuth typically occurs in social groups of 20– 40 that split apart into smaller groups of 1–9 for foraging (Defler [2004](#page-10-0); de la Torre [2000;](#page-10-0) Dew [2005](#page-11-0); Russo *et al.* 2005). Group home ranges vary from ca . 100 to ca . 400 ha (Defler [2004\)](#page-10-0). In Yasuní National Park, near the current study site, home ranges were from 266 to *ca*. 300 ha (Di Fiore and Suarez [2007](#page-11-0)). Daily movements range up to several km/d (Dew [2005](#page-10-0)). Ateles belzebuth is one of the most frugivorous primates, with fruit comprising up to 87% of the items ingested (Dew [2005;](#page-10-0) Russo *et al.* [2005](#page-11-0)); leaves made up *ca.* 9% of the diet in Yasuni (Dew [2005\)](#page-10-0). Alouatta seniculus, in contrast, typically occurs in groups of 3–9, with home ranges < ca. 10 ha (Defler [2004;](#page-10-0) de la Torre [2000](#page-10-0); Emmons [1997\)](#page-11-0). Alouatta seniculus can be characterized as a folivore/frugivore, with a diet that is ca. 50% or more leaves and ca. 40% fruit (Defler [2004;](#page-10-0) Stevenson et al. [2000](#page-12-0)). Partly as a result of the reliance on leaves, daily movements are ca 0.6 km/d (Stevenson *et al.* [2000\)](#page-12-0), considerably less than in Ateles belzebuth.

We used both digital (Snapshot Sniper, LLC) and film-based (Highlander PhotoscoutTM, PTC Technologies) camera traps triggered by an infrared motion-and-heat detector to document use of saladeros. We placed cameras at edges of each saladero, ca. 1 m above ground surface. We positioned one camera at each site (Puma and Harpia saladeros) to face the tree that was used by primates. Cameras remained continuously activated, except when batteries failed or other malfunctions occurred; date and time were automatically stamped on each photograph. We set cameras with a minimum time between photographs of 5 min. We checked cameras at ca. 7- to 10 day intervals to replace film, batteries, memory sticks, and desiccant. Rolls of film (36 exposure, 400 ASA, Kodak Gold) often were used up within 1 wk. We labeled all images with location, camera, date, time, and species.

Analyses

We summarized images by species, hour, and date. We classified photographs with either (or both) primate species as belonging to independent visits if >1 h had elapsed between consecutive photographs. Joint visits by groups of the 2 species were indicated by presence of both species in one photograph or interspersion of animals of the 2 species in consecutive photographs within the same visit time frame. We calculated a minimum visit duration by using the time difference between the first and last photographs of an independent visit by ≥ 1 animals. Although it is possible to identify some animals by distinctive markings, e.g., botfly scars, facial markings, we were not able to identify animals in most cases. Thus, length of visits reflects occurrence of ≥ 1 animal but we do not have data to document how long a given animal spent at a saladero during a visit.

We used numbers of animals in photographs summed across photographs or number of independent visits to evaluate temporal (hourly, monthly) variation in use of saladeros by each species separately. Given that we did not individually identify primates, number of animals does not refer to number of animals, as the same animals could occur in >1 photograph during a particular visit. Thus, we base most of our comparisons on numbers of visits, although results of numbers of animals are presented when appropriate. We compared observed numbers of visits to expected numbers via χ^2 tests (Whitlock and Schluter [2009](#page-12-0)). To compare use by hour, we based expected values on an even distribution during the hours of the day when photographs were taken; we categorized photographs by hour considering photographs from 30 min before to 30 after the hour. When photographs from a visit spanned >1 h, the visit was considered to be during the hour with the most photographs. Given that number of visits recorded depends on the number of days that cameras were active, we calculated expected numbers based on number of trap-days cameras were operational during each month (summed across years) and using a null expectation of even distribution among months. Thus, expected number of visits/ month was standardized by sample effort. We calculated number of trap-days from the time the camera was placed in operation to the time the film was replaced, i.e., starting a new sequence, or last photograph was taken, based on the date and time stamp on the photographs. In some cases, all film was exposed or flash card filled before checking; in other cases, malfunctions or battery failure occurred before replacement. At each site, the camera facing the tree used by primates recorded most photographs so number of trap-days was based on that camera.

We compared use between species with contingency table tests, i.e., comparing number of visits by hour, month, or saladero and correlation (Pearson's) analyses. For the latter, we correlated numbers of visits between species by month, with months summed across years, i.e., $n=12$, for the 2 species. When monkeys descended to the saladero, they sometimes left the tree and moved out onto the soil surface. Thus, we classified animals as either remaining in contact with the tree or not and compared the distribution between species, i.e., in contact or not, via contingency table tests.

We checked data for assumptions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) before we applied parametric tests. We conducted all analyses via STATISTIX Ver. 8.0 (Analytical Software [2003](#page-10-0)) or SPSS, Ver. 16 (SPSS, Inc. [2007\)](#page-12-0).

Results

We obtained 192 photographs with *Ateles belzebuth* (Slide 1) and 80 with *Alouatta* seniculus (Slide [2](#page-7-0)); photos included 318 Ateles belzebuth and 121 Alouatta seniculus (not counting infants separately; Table I). These records represented, at a minimum, 66 independent visits for Ateles belzebuth and 37 for Alouatta seniculus. On 7 separate occasions, both species used the same saladero at the same time, as indicated by simultaneous, alternating, or immediately successive photographs of both species within the same event period. Seven photographs contained ≥ 1 animals of both species (Slide 3). We photographed both species at both Puma and Harpia saladeros, but there was only 1 photograph (*Alouatta seniculus*) of either species at

Site	Year	Days	Ateles belzebuth			Alouatta seniculus		
			Photos	Animals	Visits	Photos	Animals	Visits
Puma	2005^{a}	349	45	109	8	42	59	13
	2006	179	$\mathbf{0}$			1		
	2007	178	$\mathbf{0}$			$\mathbf{0}$		
Harpia	2005	292	60	66	19	8	12	3
	2006	142	54	84	25	11	27	8
	2007	184	29	51	11	18	22	12
	2008	17	$\overline{4}$	8	3	$\mathbf{0}$		
Totals			192	318	66	80	121	37

Table I Summary of number of days camera traps were operated at each of 2 saladeros (Puma, Harpia), Tiputini Biodiversity Station, Ecuador

Number of photos, number of animals (total of animals in all photographs), and number of independent visits (see Methods) are given for each species

^a Includes 6 d from December 2004

Puma after 2005. Use of the Harpia saladero continued throughout the study period (Table [I\)](#page-5-0). Consequently, analyses that consider use of Puma saladero in relation to sample effort, e.g., photographs in relation to number of trap-days, are based only on data from late 2004 (December) through 2005.

Most photographs were of a single animal (Fig. 1); the maximum number of animals in a single photograph was 3 for Alouatta seniculus and 8 (1 photograph) for Ateles belzebuth. Number of photographs per visit ranged from 1 to 7 for Alouatta seniculus and 1 to 9 for *Ateles belzebuth*. Visit length (time between first and last photograph in a visit with >1 photograph) ranged from 6 to 31 minutes for Alouatta seniculus, 5 to 59 for Ateles belzebuth, and from 26 to 77 minutes when both species were present. Mean visit length was similar between species $(14.2 \pm 11.7 \text{ SD min}$ for Alouatta seniculus, 17.8 ± 12.0 min for *Ateles belzebuth*) but median visit length was greater for *Ateles belzebuth* (15 min) than for *Alouatta seniculus* (6 min).

Number of animals recorded in different hours of the day varied for both species with *Ateles belzebuth* appearing to show a more pronounced peak in activity, from about 1100 h to 1300 h (Fig. [2](#page-7-0)). Number of independent visits also varied over time for each species (χ^2 =12.5, 13.8, df=7, 0.10>p>0.05) (Fig. [2\)](#page-7-0), but distribution of visits among hours did not differ significantly between species (χ^2 =4.87, df=7, p= 0.68). We did not photograph either species before 0830 h or after 1630 h.

Use of saladeros, as measured by number of animals in photographs or number of visits, varied across months (Fig. [3\)](#page-8-0). In both species, number of visits was not evenly distributed throughout the year (Ateles belzebuth: χ^2 =35.6, df=11, p<0.001; Alouatta seniculus: χ^2 =16.5, df=11, p<0.001; calculations based on trap-days per month). November through February was the peak period for both species (Ateles belzebuth: χ^2 =19.7, df=1, p<0.001; Alouatta seniculus: χ^2 =7.3, df=1, p<0.01; comparing number of visits from November–February to number from March–October; calculations based on trap-days per month); we did not photograph either species in August and recorded no Alouatta seniculus in September. Although monthly activity was somewhat more variable for *Ateles belzebuth*, numbers of visits per month correlate highly between the 2 species (Pearson's $r=0.83$, $n=12$, $p<0.001$).

Fig. 1 Percentage of photos with \geq 1 *Alouatta seniculus* or *Ateles belzebuth* from camera traps at 2 saladeros at Tiputini Biodiversity Station, Ecuador. Number of photographs is given above the bars.

Animals descended to the base of trees to consume soil or water and, in some cases, left contact with the tree and moved out onto the surface of the saladero to drink, bathe, or cross to a different location. Ateles belzebuth were more likely to leave the base of access trees than were *Alouatta seniculus*. There were 212 Ateles belzebuth (67%) photographed away from trees and 63 (52%) Alouatta seniculus $(\chi^2 = 7.5, df = 1, p < 0.01).$

Discussion

At least 10 species of monkeys are known to occur at Tiputini Biodiversity Station, but only Ateles belzebuth and Alouatta seniculus were photographed at saladeros, in agreement with previous conclusions that use of terrestrial mineral licks appears to be common only in *Ateles* spp. and *Alouatta* spp. (Campbell *et al.* [2005](#page-10-0); De Souza *et* al. [2002](#page-10-0); Dew [2005](#page-10-0); Izawa [1993](#page-11-0); Izawa and Lozano [1990;](#page-11-0) Stevenson et al. [2000\)](#page-12-0). Use of specific sites, such as saladeros, for geophagy suggests that soils at such sites are higher in compounds needed to aid digestion or help detoxify secondary compounds (Ferrari et al. [2008](#page-11-0); Krishnamani and Mahaney [2000;](#page-11-0) Mahaney et al. [1995;](#page-11-0) Wakibara et al. [2001\)](#page-12-0) than are soils at other locations (Emmons and Stark

Fig. 3 Number of animals and independent visits (see text) by month, for *Alouatta seniculus* and *Ateles* belzebuth, from camera traps at 2 saladeros at Tiputini Biodiversity Station, Ecuador.

[1979;](#page-11-0) Mahaney et al. [1997](#page-11-0); Izawa [1993](#page-11-0); Lizcano and Cavelier [2004](#page-11-0)). If true, such differences might account for use of some sites and not others. Although we did not sample soils during our study, ongoing studies focused on use of saladeros by bats (Voigt et al. [2007,](#page-12-0) [2008](#page-12-0)) suggest that saladero soils are more mineral-rich than soils at control locations in the forest (C. Voigt, pers. comm.). Of the 4 saladeros sampled with cameras in this study, only Puma and Harpia were used on a regular basis, with Harpia receiving more visits. Yet, a previous study at Tiputini found no significant differences in mineral content among 10 saladeros (J. Fabara, unpubl. undergraduate thesis, Universidad San Francisco de Quito), suggesting that use of particular saladeros may be related to factors other than mineral content. As an alternative, Izawa ([1993\)](#page-11-0) suggested that arboreal primates may descend to the ground at sites that are, for one reason or the other, safer from predators, given that arboreal primates are especially vulnerable to predators, e.g., felids, snakes, when on the ground (Di Fiore [2002](#page-11-0); Matsuda and Izawa [2008](#page-11-0)). Risk of predation may help explain why, at saladeros, monkeys often remained close to the base of the access trees, where they could reach soil, and sometimes water, without losing contact with the tree. This was particularly true at the Puma saladero for *Alouatta seniculus*. However, on a number of occasions, animals moved out onto the soil surface where they appeared to be drinking or traveling from one side of the saladero to the other. This behavior was seen mostly in *Ateles belzebuth*; *Ateles belzebuth* also may have used the water and water-mud mixture for bathing, as several animals were photographed covered in water and mud.

Although we photographed both Ateles belzebuth and Alouatta seniculus at both saladeros, patterns of use varied during the day and across months. Overall, Ateles belzebuth visited saladeros more often (more independent visits) than did *Alouatta* seniculus, likely a reflection of the larger number of the former species in the area and the fact that subgroups likely travel over wider areas than do *Alouatta seniculus*. We photographed both species from about 0830 h until about 1630 h, but *Ateles* belzebuth showed a more pronounced peak of activity during midday. Although most studies do not report time of day for soil eating, Müller *et al.* ([1997\)](#page-11-0) noted that all instances of Callicebus personatus descending to the ground to eat soil occurred from 1000 h to 1600 h. Reasons for the hourly variation are unknown but may relate to predator avoidance, e.g., felids may be less active during the middle of the day (unpubl. data from camera traps at Tiputini), movement of troops, or timing of feeding. For example, Ateles belzebuth troops are known to follow regular pathways when moving through their home range (Di Fiore and Suarez [2007](#page-11-0)) and timing of appearance at saladeros may reflect movement along such pathways. Alouatta seniculus, in contrast, has smaller home ranges and likely moves shorter distances than do Ateles; thus, use of saladeros may be less tied to movement patterns and more related to diet. Feeding activity likely is high in early morning (Robinson [1984;](#page-11-0) Wallace [2001\)](#page-12-0), which may account for the absence of primates at saladeros before 0830 h. If geophagy reflects a need to obtain minerals or other compounds to aid digestion, then timing of visits to saladeros may be a response to patterns of feeding.

Both species showed a generally similar pattern of increased use of saladeros during the drier months compared to wetter months. De Souza *et al.* ([2002\)](#page-10-0) recorded Alouatta belzebul ingesting soil from termitaria in central Amazonia but only during the dry season, when leaves made up 78% of the diet; leaves made up only 41% of the diet during the wet season. The difference likely reflects increased digestive costs associated with the higher percentage of leaves. Similarly, an increase in geophagy during the dry season by *Gorilla gorilla beringei* likely was in response to increased use of plant foods known to have more toxins (Mahaney *et al.* [1995](#page-11-0)). In contrast, Setz et al. [\(1999](#page-12-0)) reported that Pithecia pithecia chrysocephala consumed soil most frequently during the rainy season (25 of 26 observations) and concluded that use of soil was not in response to consumption of leaves or a need for mineral supplementation. Instead, they suggested that geophagy may be related to rare or occasional dietary components.

Ateles and *Alouatta* are sympatric in many areas of both Central and South America, but previous studies have not reported simultaneous use of saladeros. Although not common, such behavior was noted on \geq 7 occasions during the present study, i.e. ca. 11% of *Ateles belzebuth* visits and ca. 19% of *Alouatta seniculus*. Whether such behavior is a result of chance encounters at the few saladeros present at Tiputini or whether some other factor is involved, is not known. Given the relatively few visits recorded during the course of this study, the probability that both species would visit the same site at the same time by chance is not high. Further, that both species use the same sites for soil and water does suggest that both species derive similar benefits or are acquiring similar compounds. More detailed studies that include behavioral observations of the 2 species are needed to determine the potential benefits for joint use of saladeros.

Although mineral licks clearly are important in the ecology of these and other primates, a full understanding of the factors that influence use of particular sites and of the benefits obtained from the soil and water will require further study. However, as pointed out by Davies and Baillie (1988), it is entirely likely that there may be multiple, perhaps complementary, reasons for such behavior.

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