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Characteristics of natural salt licks located in the Colombian Amazon foothills

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Abstract Salt licks are key places for the ecological dynamics of wildlife communities around the world and are locations where animals develop geophagical behaviours. Geophagy is a method for animals to supplement their diets or facilitate their digestive processes and is related to the health of individuals and populations. This study characterises a series of salt licks located in the Colombian Amazon foothills and describes their structural, mineralogical and physicochemical properties, as well as the fauna that visit these locations. The results are analysed in reference to the geological characteristics of the study area and in relation to the role of the salt lick in the nutritional ecology of the Amazonian fauna. Located in the study area are two types of salt licks that are significantly different in composition. These salt licks are located in an area where young geological materials have been exposed. The characteristics of the salt licks supports the hypothesis that they are used to solve nutritional problems that result from herbivorous diets. The clear importance of salt licks in the ecology of several Amazonian animal species emphasises the need to prioritise conservation areas by maximising the complementarities of salt lick sites.

Keywords Salt licks · Geophagy · Nutritional ecology · Wildlife management · Amazonia

Introduction

Salt licks are well-defined landscape elements that are present in both temperate and tropical ecosystems. In these locations, species with diets based on plant materials, particularly birds and mammals, exhibit geophagical behaviours (Powell et al. 2009; Blake et al. 2010). The frequent use of these places by wildlife has resulted in many studies since the beginning of the last century to the present day in several localities around the world. These studies describe salt licks properties, patterns of use and explanations regarding why these places are frequently visited (Knight and Mudge 1967; Weeks 1978; Tracy and McNaughton 1995; Brightsmith 2004; Bravo et al. 2008; Poole et al. 2010; Edwards et al. 2012; Panichev et al. 2012).

As a result of these previous studies, non-exclusive hypotheses have been proposed stating that geophagy could be a strategy for supplementing the diet with several nutrients, such as N, Ca, C, P, Mg, N, K, Fe, Cu, Zn, Cl or I (Setz et al. 1999; Holdo et al. 2002;

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Brightsmith and Aramburu 2004; Lizcano and Cavalier 2004; Symes et al. 2006; Ayotte et al. 2006; Matsubayashi et al. 2007; Mills and Milewski 2007; Powell et al. 2009). Another hypothesis states that the consumption of certain types of clay present in the salt licks, such as kaolinite, aids the digestive process of granivorous and herbivorous species through both the adsorption of dietary toxins (Kreulen 1985; Klaus et al. 1998; Diamond et al. 1999; Giraldi et al. 1999; Brightsmith et al. 2008; Ferrari et al. 2008) and buffering capacity (Kreulen 1985; Krishnamani and Mahaney 2000; Ayotte et al. 2006).

According to these hypotheses, salt licks can provide resources for animals that would otherwise be difficult to obtain. Therefore, salt licks have been classified as important places within landscapes (Montenegro 2004) and, as suggested by Klaus et al. (1998), may both affect the density and structure of animal populations and influence the carrying capacity of these areas, particularly in areas with poor soil and, consequently, plant materials with low nutritional properties, similar to the situation found in the Amazon Basin.

The documented importance of salt licks makes their study and proper management a matter of great interest in strategic conservation planning. This study presents the results of a structural, physicochemical and mineralogical characterisation of a group of natural salt licks locates in the Colombian Amazon foothills. There are no previously published studies regarding this area that aid in understanding the ecological dynamics of these locations.

Study area

The study was performed at the San Miguel indigenous reservation and surrounding areas between 200 and 600 masl in the southern sector of the buffer zone of the Parque Nacional Natural Alto Fragua Indi Wasi (PNNAFIW), Caquetá Province, in the Colombian Amazon foothills (Fig. 1). This area has been recognised as an important centre of endemism with considerable diversity of flora and fauna species, many of which are endangered because of the high rates of deforestation during recent decades (Sarmiento and Alzate 2004). This area is characterised by the presence of indigenous groups who practice traditional subsistence hunting (UAESPNN et al. 2006).

In this area, the forest has multiple strata and is of the Ecuadorian Jungle type. The watercourses in the area are tributaries of the Caquetá River, including the Fragua, Fragua Chorroso, Fragua and Fragüita. The area has a rainfall pattern that features a dry season between December and February with rainfall that does not exceed 260 mm per month. The majority of rainfall occurs from March to November, reaching values of up to 478 mm per month. The average annual temperature is 25 °C and has an inverse relationship to precipitation. The lowest temperatures of approximately 23 °C occur during mid-year, and the highest temperatures, which are close to 26 °C, occur during the end of the year (IGAC 1993).

In the study area, there are two different types of geomorphological units. Transitional foothills, where the salt licks characterised in this study are located, are situated between the steep slopes of the Andes and the Amazonian plains and are marked by denudation processes, although local reliefs can be notably prominent. The second type of geomorphological unit, the Amazonian plains, does not show evidence of orogenic activity except at a few locations where the edges of terraces experience erosion (IGAC 1993; Ingeominas 2003). These geomorphological units correspond to two sedimentary basins, the Upper Magdalena Valley (UMV) and the Caguan-Putumayo (CP) (Barrero et al. 2007). The UMV is an intermontane basin located in the upper reaches of the Magdalena River from the Amazonian foothills to the Eastern Andean Cordillera. The CP extends from the foothills over the Amazonian plains.

Although Ingeominas (2003), the governmental institution responsible for the generation of geological information in Colombia, states that there are not enough detailed criteria regarding the stratigraphic sequence, palaeontology, genesis and age of the formations of the Cretaceous, Paleogene and Neogene eras in the study area, in this study, we have provided brief descriptions of the geological formations. These descriptions are based on materials developed by Ingeominas at a 1:100,000 scale. We complement these descriptions with additional information from Mora et al. (1998), Galvis and Pinto (1999) and Higley (2001).

One of the two geological formations found at the study area is the Rumiyaco formation from the late Cretaceous (146–65 ma) to early Paleogene era. This formation is the result of the accumulation of fine

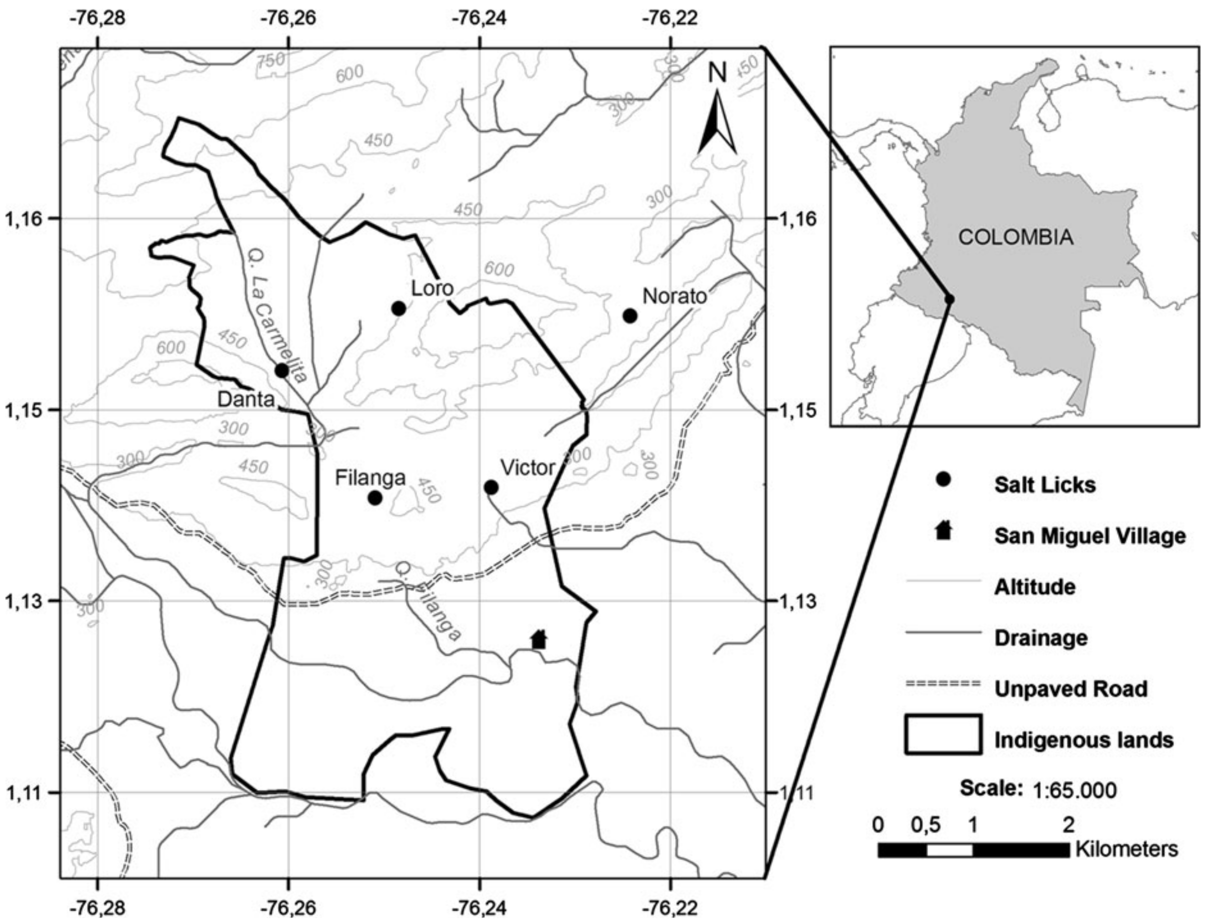

Fig. 1 Location of salt licks used by the Inga community of the San Miguel Reservation. Coordinates are given in decimal degrees

sediments in shallow bottoms and is well oxygenated, which allows for an abundance of organisms. This formation is also characterised by the presence of sedimentary rocks and clay materials with a thickness that usually exceeds 2 m but can reach hundreds of metres. The Rumiyaco formation is composed of red and grey mudstones and lutites with moderate to high bioperturbation, between which are thin intercalated layers with quartz and lithic sandstones. The quartz sandstones have reddish colourations, whereas the lithic sandstones are grey with greenish tones. Petrographically, the rocks of this formation are classified as lithic sandstones with high compositional variability, although they commonly have a low quartz content. In certain areas, the rocks have sedimentary lithics or chert. Calcareous, ferruginous cement is also present.

Also in the study area are two of the three branches of the Pepino formation, the middle and inferior, from the Tertiary period, specifically the Neogene (24–1.8 my) (Ingeominas 2003). The inferior branch of this formation has thick layers containing polymictic conglomerates composed of 70–80 % clasts with diameters up to 15 cm. These clasts contain chert, volcanic rocks and metamorphic quartz supported by both lithic and sublithic sandstones, which have variable texture and are cemented with silica. The materials of this branch have colours ranging from dark grey to dark brown. From a petrographic point of view, the lithic sandstones of the Pepino formation inferior branch have macroscopic contents of quartz (16 %), feldspar (1 %), sedimentary lithics, primarily chert (21 %), metamorphic lithics and volcanic lithics (10 %). These lithic sandstones are immature rocks with low porosity and contain more ferruginous cement than calcareous, yielding a reddish colouration. The matrix is muddy, which is a notable feature of the places at which geophagy is observed.

In the middle branch of the Pepino formation, mudstones and clay stones are the representative rock types, rather than the conglomerates of the inferior branch. Sandstones are common. The sandstones are grey to green mottled and have intense bioperturbation. The rocks are notably similar to those of the lower branch, but the grain is finer. The sedimentary lithics are grey to red. Petrographically, the materials of the Pepino formation middle branch are classified as fractured siliceous mudstone with a greyish colouration and the presence of some isolated grains of thin sand and clay structures. There is no bioperturbation. Microscopically, the materials are primarily mudstones (82 %) with high porosity.

Materials and methods

Location and characterisation of the salt licks

The salt licks were located with the help of the indigenous community from the San Miguel reservation, particularly the elders and hunters. Each place was visited, and the geographic location was recorded on a GPS (Garmin ExTrex®) using the WGS 84 geographic coordinate system with an accuracy of at least 5 m. A structural characterisation of the area was also performed. The area and perimeter of each salt lick were calculated, taking into account the structural effects of large on the location. In addition, we estimated the size of the sites currently used for geophagy.

Salt lick characterisation

At the study area, there are two types of salt licks based on the structural characteristics of the locations. In wall salt licks, animals consume materials from vertical surfaces, such as cut banks. This activity eventually forms small caves located at varying depths. In the second type of salt lick, mud salt licks, the animals consume mud or muddy water on the surface of the terrain. The substrate of the mud salt licks was muddy, whereas that of the wall salt licks was more similar to rock.

Following the recommendations of Mahaney and Krishnamani (2003), 1-kg samples of material were collected in areas with high levels of geophagy at each salt lick. The wall salt lick samples were obtained by scraping the walls of the small caves formed in the areas at which geophagical behaviours are developed. The mud lick samples consisted of the muddy substrate that is consumed by the salt lick users. The analyses performed in this study refer to the soil content, and although these data provide clues regarding the availability of minerals, they are not direct measurements of this variable. Other studies have used these types of analyses demonstrating that they can be useful (i.e. Emmons and Stark 1979; Matsubayashi et al. 2007; Brightsmith et al. 2008; Powell et al. 2009). The analyses were performed at the Soil Laboratory of the Instituto Geográfico Agustín Codazzi following the standard analysis methodologies of the United States Department of Agriculture (USDA) (Soil Survey Staff 2011; IGAC 2006).

Cation exchange capacity (CEC) and saturation of exchangeable bases (Ca, Mg, K and Na) were determined using ammonium acetate (1 normal and neutral). Electrical conductivity (EC) was determined in a saturation extract, and particle size (texture) identification was performed using the Bouyoucos method. Phosphorus (P) was determined using the Bray II method. Trace elements (Fe, Cu, Mn, and Zn and B) were extracted with DTPA. Organic carbon concentration was determined by the Walkley–Black method. The pH was also determined for each sample. The results of these analyses were compared to the control samples ($n = 7$) that were obtained from 50 cm below the soil surface in places where there was no evidence of geophagy.

Optical mineralogical analysis was conducted using a petrographic microscope to determine the mineral composition of the sand (0.05–2 mm particles) and clay (<0.002 mm) fractions of the samples collected from three of the six salt licks analysed. The sampled salt licks were selected to obtain data of the different geological formations in the study area. The clay and sand fractions are the sources of the particular minerals sought by the animals at the salt licks to meet their long- and short-term nutritional needs, respectively. To identify differences among the composition of the different salt licks and control soils, the salt lick samples were divided into wall and mud salt licks according to the structural characteristics of each. The differentiation of these two types of salt licks allowed us to understand the materials and nature of the salt licks better. The physical and chemical variables were compared among the soil samples from the controls ($n = 7$), mud and wall salt licks ($n = 8$ and 3, respectively) using a Kruskal–Wallis test. The type of sample (mud, wall or control) was included as a factor. In addition, the Tukey–Kramer HSD post hoc test was performed to identify the soil classes with significant differences.

Species inventory and visit frequency

To complement the characterisation of the salt lick structure and the materials that were the object of geophagy, an inventory of the species that used each salt lick was performed. The species were identified from footprints, faeces, hair, direct sightings and camera trapping (RECONYX RapidFire 3.1®). The cameras were installed during different periods of time at five of the six salt licks in some of the sites with geophagy. There were different sampling efforts for the camera days per site (71 for Filanga, 43 for Danta, 65 for Loro_1, 25 for Loro_2 and 23 for Victor salt lick). The cameras were programmed to take photos 24 h/day with a rest period of 2 min between shots, making it possible to determine the number of days with visits by different species at each salt lick. The cameras were checked every 15 days to replace the batteries and memory card. The data regarding the species that visited all of the monitored salt licks were used to determine the relationships between the physicochemical and mineralogical characteristics of the salt licks and the animal visit frequency using a Pearson correlation analysis with the significance set at the $P = 0.05$ level. An emphasis was placed on those elements that were considered relevant to the ecophysiology of the animals. The frequency of visits of each species was calculated as the number of days with a record (picture) of at least one individual divided by the total number of days for which the camera was active at that particular salt lick (days with pictures/total active camera days).

Results

Description of salt lick sites

Five salt licks were identified for this study, and all were associated with a watercourse (Fig. 1). Loro's salt lick, a wall salt lick, has a set of sites at which geophagical behaviours are evident. These sites are arranged in two adjacent areas located on the border of a continuously flowing brook. Although it is possible to identify signs of geophagy on the brook floor, animal signs were primarily located in these areas, which are similar in size to each other but larger than those present at the other wall salt licks. Moreover, landslides along the river slopes have led to changes in the number of these areas. During the study, it was possible to identify eight of these areas at depths of 260 and 760 cm below the terrain surface. This salt lick is the largest of the five sites identified in this study, even when its two sections are considered independently (Table 1).

Filanga's salt lick is another wall salt lick and is the closest to the town of San Miguel (Fig. 1). This salt lick is characterised by large animal trails and a sparse canopy and is one of the largest ones within the studied sites (Table 1). The salt lick has only one small active geophagical site, which is located on the edge of one of the branches of the Filanga brook 180 cm below the surface under five layers of clay material (Table 1).

Danta's salt lick is a mud salt lick, which is bounded on one side by a small permanent stream and on the other side by a seasonal stream. These two streams separate two active sites, where the salt lick users ingest either muddy water or mud. Signs of past use are not highly conspicuous at this salt lick. Therefore, the areas of the sites were estimated, taking into account past animal use as reported by the local people (Table 1). The thickness of the mud layer is <20 cm.

Don Víctor's salt lick is the second mud salt lick that is located in a valley, and a stream demarcates one of the boundaries. According to the calculated area, this salt lick is the third largest one identified in this study (Table 1). The location is moderately sloped, and the two edges of the valley have a height difference of approximately 10 m. This salt lick has only one active geophagical site with an approximate area of 3.2 m^2 and a depth of 30 cm. The material under the salt lick is rocky.

Norato's salt lick is the third mud salt lick and is located outside the indigenous lands. This salt lick is located in a plain embedded in a section of steep slope near a rock wall, out of which a stream flows. The stream runs to two active geophagical sites. There is evidence of disturbance by cattle, which use the salt lick to escape from the heat and also as a drinking site.

Table 1 Geometrical characteristics of *scratch* and *lick spots* identified at each salt lick

Salt lick	Geophagical spot	Dimensions (cm)			Area (m^2)	Perimeter (m)	Depth from soil surface (cm)
		Width	Height	Depth			
Loro _1	1	300	500	100	1,816	193	270
	2	80	120	80			470
	3	110	120	40			NA
	4	NA	NA	NA			260
Loro_2	1	40	80	60	227	67	450
	2	70	130	90			360
	3	45	200	25			450
	4	70	140	100			NA
Filanga	5	20	70	20	972	126	180
Don Víctor	1	200	NA	200	555	98	0
Norato	1	200	NA	150	218	70	0
	2	400	NA	300			0
Danta	1	500	NA	400	373	86	0
	2	100	NA	100			0

In the "lick spots," the mud layer is nearly 30 cm deep, under which are rock and gravel substrates.

Geological, mineralogical, physical and chemical properties of salt licks

The salt licks analysed in this study have similar properties to other salt licks located in the Amazon Basin. With respect to the particle size, the mud salt licks have less clays than sand or silt, and on average, this category constitutes more than a quarter of the samples and is similar to other salt licks (Table 2). The wall salt licks are more similar to the salt licks located in Peru and display high levels of clays (Table 2). Our salt licks also have similar mineral contents compared to other salt licks from the Amazon, although the Na concentration was the lowest, and the Fe and P concentrations were the highest reported (Table 2).

Based on the work of Ingeominas (2003), Loro's salt lick is on the Rumiyaco formation from the Cretaceous Period (146–65 ma). The other salt licks identified in this study are located on one of the branches of the Pepino formation, which contains materials from the Neogene–Palaeogene Period. In the clay fraction from Loro's salt lick, which is located on the Rumiyaco geological formation, the mineralogical analyses indicate the presence of illites, a phyllosilicate that can retain cations by adsorption. Kaolinite and quartz are predominant at the Filanga and Danta salt licks, which are both located on the Pepino formation. At the Filanga salt lick, smectites, another phyllosilicate capable of retaining cations, was also observed (Table 3). In the sand fraction, there is a remarkable level of quartz, magnetite and haematite. These minerals do not provide abundant nutrients because they are either the final products of weathering processes or because they are minerals dominated by a single element (magnetite–haematite). Although diopside and hornblende could be sources of certain minerals, they were found at low percentages (Fig. 2).

The physicochemical analysis indicates that the wall salt licks generally contain more clay than the control samples but not more than the mud salt licks (Table 4). By measuring the electrical conductivity (EC), it is possible to differentiate the materials from mud salt licks and control samples from the materials from wall salt licks. The wall salt lick samples exhibited the highest EC values, whereas the control samples showed the lowest average EC (Table 4). The wall salt licks are saturated with base, and this saturation contrasts with the control soils, which had moderate ECs despite having a low exchange capacity. Similar results were also observed when the exchangeable bases content was evaluated. This content tended to be higher in the salt licks than control soils.

Table 2 Physicochemical properties of salt licks located in the Amazon Basin

Locality	Granule class (%)			CEC	Exchange complex (mq/100 g)				Minor elements (ppm)				pH	P (ppm)	Reference
	Sand	Silt	Clay		Ca	Mg	K	Na	Mn	Fe	Zn	Cu			
San Miguel Reservation Caqueta Department, Colombia	50.57	23.37	26.10	22.83	7.60	4.68	0.28	0.13	16.13	200.13	2.01	0.65	5.10	44.80	This study
	34.66	21.89	43.50	21.03	12.50	3.27	0.57	4.67	19.56	30.79	2.30	0.80	7.86	512.23	
Manu National Park, Peru	–	–	–	–	7.09	8.15	0.70	4.43	0.81	3.30	0.83	0.68	7.80	–	Adapted from: Emmons and Stark (1979)
Tinigua National Park, Colombia	–	–	–	–	0.46	0.83	0.41	0.96	–	–	–	–	4.75	–	Adapted from: Izawa (1993)
	–	–	–	–	0.70	0.78	0.61	1.30	–	–	–	–	5.17	–	
Manu National Park, Peru	4.64	37.90	57.40	28.00	1.97	4.21	0.26	5.07	35.90	21.30	1.86	0.33	–	0.30	Adapted from: Giraldi et al. (1999)
Tambopata Natural Reserve Buffer Zone, Peru	17.20	47.10	35.70	15.44	1.24	4.59	0.27	1.10	–	–	–	–	–	–	Adapted from: Brightsmith and Aramburu (2004)
Yavarí-Mirí River, Peru	–	–	–	22.17	21.20	6.11	9.78	0.37	19.33	95.51	2.17	3.08	7.18	84.23	Adapted from: Montenegro (2004)
Tambopata Research Centre, Peru	11.00	29.00	60.00	17.90	2.13	2.13	0.36	5.92	16.90	119.00	2.30	0.73	8.70		Adapted from: Brightsmith et al. (2008)

Table 3 Clay fraction and cation exchange capacity (CEC) of several of the salt licks identified

Salt lick	Geological formation	Composition (%)						CEC (meq/100 g)
		Illite	Kaolinite	Quartz	Smectite	Chlorite	Goethite	
Loro	Rumiyaco	7	31	60	–	–	–	20.50
Danta	Lower Pepino	–	64	31	–	tr	tr	12.70
Filanga	Upper Pepino	–	28	59	11	tr	–	28.50

Although sodium (Na) was present at concentrations that were statistically equivalent between the control and mud salt lick samples, the calcium (Ca), magnesium (Mg) and potassium (K) concentrations were significantly higher in the two types of salt licks soils compared to the controls (Table 4).

Compared to the mud salt licks, the wall salt licks contained higher nutrient levels. This observation is particularly true for K and Na, which were present at values that were high for Amazonian soils. A slightly greater accumulation of Mn, Zn, Cu and B was also observed in the scratch spots, although these were not always significantly different. By contrast, the Fe and organic carbon content were significantly lower in the wall salt licks compared to the mud salt licks. The phosphorus content was extremely high at several of the wall salt licks (Table 4), and the Ca and Mg contents, which have previously been reported to be elevated at salt licks, were statistically similar between the two types of salt licks (Tables 4).

Frequency of wildlife visitation to salt licks

Birds and mammals visited the salt licks at all hours of the day and night, and the events were consistent with the activity periods of the different species. *Cuniculus*

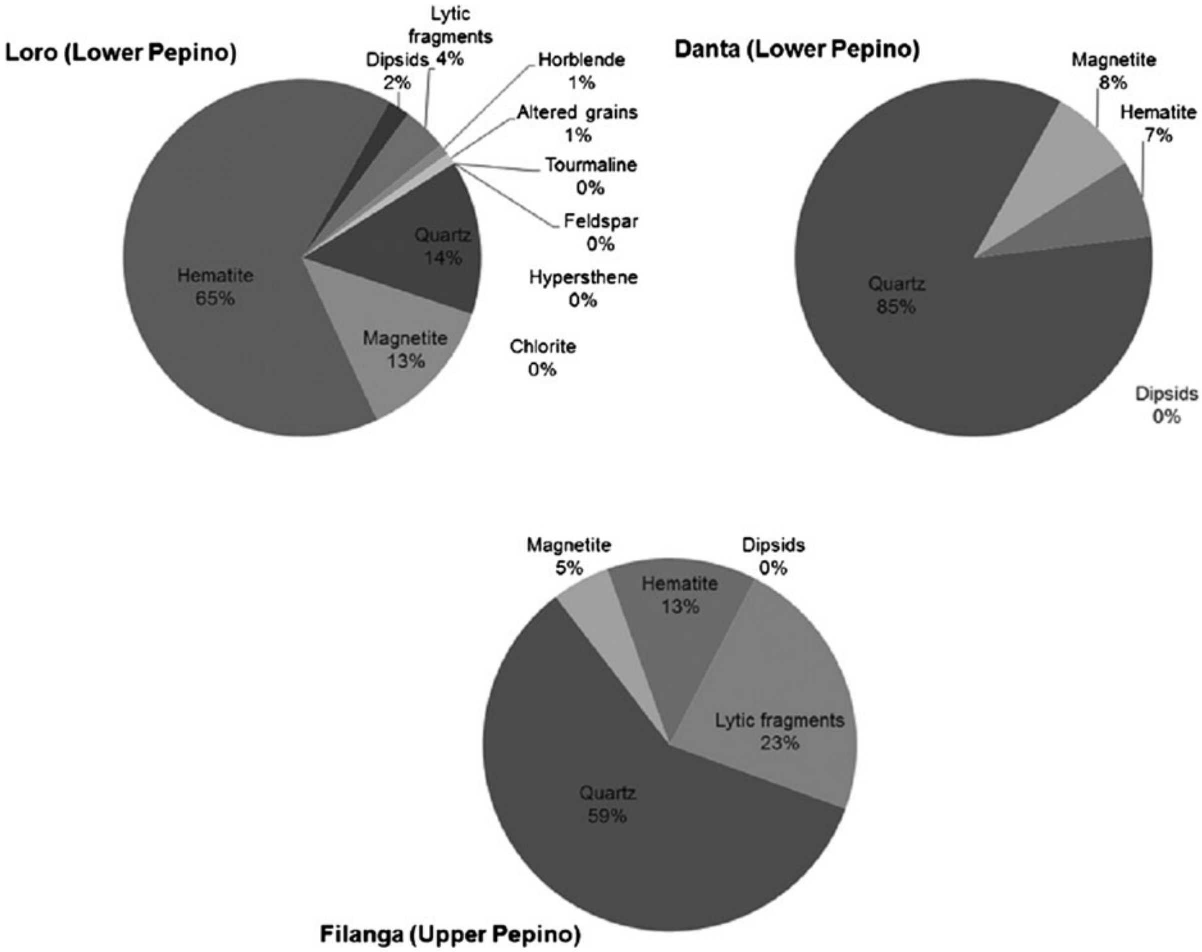

Fig. 2 Sand fraction of salt lick materials. When only trace amounts were found, a value of 0 % is reported

paca and *Coendou prehensilis,* which were exclusively nocturnal visitors, and *Dasyprocta* sp, which was exclusively diurnal, were the most frequent terrestrial mammal species that visited the salt licks (Table 5). Bats, which visited the salt licks at night and dusk, and pigeons and parrots, which were daytime visitors, were the most frequent volant species. Other species recorded during the day, although at much lower frequencies, included *Pecari tajacu, Alouatta seniculus* and *Aburria aburri,* all of which visited the salt licks at dawn. *Tamandua tetradactyla, Didelphis marsupialis* and *Dasypus novemcinctus*, which were relatively rare visitors, visited the salt licks only at night.

For the bats, parrots and small non-flying mammals, achieving a species-level identification of the individuals that visited the salt licks was impossible. Although non-flying small mammals were also present at three salt licks, they were not considered in the analysis because it is likely that the visits did not correspond to individuals of the same species. *Cun. paca* and *Coe. prehensilis* used the majority of the salt lick sites, whereas bats, *Dasyprocta* sp., *D. marsupialis* and *A. seniculus* used only a limited number of the licks. Guans were observed at only one of the eight geophagical sites at Loro's salt lick, and pigeons were identified at Danta's salt lick and at one of the geophagical sites of Loro's salt lick, where parrots were also present in mixed flocks (Table 5). Variation in visit frequencies to the salt licks by the animals was correlated with differences in the physicochemical properties of the salt licks. For example, visits of *Coe. prehensilis* were correlated with changes in the contents of Mg ($r^2 = 0.77$; $P = 0.05$), K ($r^2 = 0.83$;

Table 4 Physical and chemical properties (average values) of the collected material from salt licks and control samples. Parentheses show the standard deviations

Descriptor	Granule class (%)			CEC (mq/100 g)	Bases Saturation (%)	Exchange cations (mq/100 g)				Minor elements (ppm)					Organic carbon (%)	pH	P (ppm)	EC (dS/m)
	Sand	Silt	Clay			Ca	Mg	K	Na	Mn	Fe	Zn	Cu	B				
Mud salt licks ($n = 3$)	50.57	23.37^{b}	26.1^{ab}	22.83	58.87^{b}	7.6^{a}	4.68^{a}	0.28^{ab}	0.13^{b}	16.13^{a}	200.13	2.01	0.65	0.31^{b}	1.87^{a}	5.10^{b}	44.8^{ab}	0.13^{b}
	(6.27)	(9.39)	(15.55)	(8.87)	(39.66)	(7.90)	(3.73)	(0.10)	(0.04)	(14.33)	(234.21)	(2.29)	(0.66)	(0.20)	(3.06)	(0.35)	(36.89)	(0.06)
Wall salt licks ($n = 8$)	34.66	21.89^{b}	43.50^{a}	21.03	99.17^{a}	12.5^{a}	3.27^{a}	0.57^{a}	4.67^{a}	19.56^{a}	30.79	2.28	0.81	1.14^{a}	0.07^{a}	7.86^{a}	512.23^{a}	0.73^{a}
	(14.68)	(10.03)	(6.25)	(3.48)	(2.19)	(2.59)	(2.60)	(0.24)	(2.79)	(9.82)	(22.21)	(4.82)	(0.64)	(0.55)	(0.06)	(0.75)	(490.83)	(0.37)
Controls ($n = 7$)	21.00	57.83^{a}	21.17^{b}	3.7	53.63^{b}	0.25^{b}	0.11^{b}	0.07^{b}	0.20^{b}	0.57^{b}	45.83	0.43	0.44	0.17^{a}	1.31^{a}	4.18^{b}	1.20^{b}	0.09^{b}
	(20.50)	(20.10)	(13.45)	(ND)	(18.13)	(0.02)	(0.04)	(0.04)	(0.08)	(0.38)	(19.73)	(0.23)	(0.39)	(0.17)	(0.56)	(0.16)	(0.52)	(0.02)
Chi Square	3.665	6.969	9.274	2.783	12.585	12.06	11.737	12.733	11.468	11.91	5.397	2.62	3.436	10.833	9.162	13.76	13.21	11.089
P	0.16	0.031	0.01	0.249	0.002	0.02	0.003	0.002	0.003	0.003	0.067	0.27	0.179	0.004	0.01	0.001	0.001	0.004

The chi-square and "*P*" values correspond to the Kruskal–Wallis test; "*"marks the statistical significance. The super index letters mark the group samples types with statistically significant differences according to a Tukey–Kramer HSD post hoc test

EC electrical conductivity, *CEC* cation exchange capacity, *ND* No Data

$P = 0.03$) and sand ($r^2 = 0.78$; $P = 0.05$). Visits by *Cun. paca* were correlated with Mg ($r^2 = 0.82$; $P = 0.03$), K ($r^2 = 0.97$; $P = 0.001$), Na ($r^2 = 0.82$; $P = 0.03$) and P ($r^2 = 0.84$; $P = 0.03$), whereas the activity of *Dasyprocta* sp. at the salt licks was correlated with Zn ($r^2 = 0.93$; $P = 0.01$). Finally, visits by *P. tajacu* were correlated with the salt licks content of Mn ($r^2 = 0.90$; $P = 0.01$). Several other variables were independent to the visit frequency to the salt licks similar to that reported by (Molina 2010).

Discussion

All the locations identified as salt licks have characteristics consistent with those reported for other salt licks. The salt licks are visited by various animal species, almost exclusively herbivores and frugivores, and these animals exhibit geophagy at two particular types of salt licks, designated in this study as wall and mud salt licks, which may be equivalent to the two types of salt licks described by Matsubayashi et al. (2007) and Brightsmith (2004), respectively. The variability in the physicochemical characteristics of the mud and wall salt licks analysed in this study could be perceived as a reflex of variability shown by the salt licks located in the Amazon Basin (Table 2), which could be consequence of the diversity of geological histories that occur both locally and regionally.

Variation in the sizes of the geophagical sites at the wall and mud salt licks (Table 1) may result from the visits of different species to each salt lick (Table 5), which could have a long-term effect on the shape and structure of the salt lick. This variation in visitor composition and the consequent geometric characteristics of the salt licks may be related to the location of the salt lick, topography, surrounding forest structure and other factors related to the natural history of each visitor in addition to the diet supplementation. At Loro's salt lick, the understory density can be considered a habitat characteristic that determines the presence or absence of a particular species. In the largest geophagical site, located on top of a ravine, only birds and primates were observed. By contrast, at another site located at the same salt lick but on the bed of the creek, other terrestrial species, such as *T. tetradactyla*, *D. marsupialis*, *C. paca*, and *P. tajacu*, were identified (Table 5).

Table 5 Fauna associated with identify salt licks

Common name	Scientific name	Loro	Filanga	Don Víctor	Norato	Danta
Parrots	Psittacidae*	X	–	–	–	X
Wattled Guans	*Aburria aburri**	X	–	–	–	–
Wading bird	Birds*	–	–	X	–	–
Pigeons	Birds*	–	–	X	–	X
Red howler monkey	*Alouatta seniculus***	X	–	–	–	–
Black-eared opossum,	*Didelphis marsupialis***	X	–	–	–	–
Spotted paca	*Cuniculis paca***	X	X	X	X	X
Agouti	*Dasyprocta sp.**	–	X	X	X	X
Armadillo	*Dasypus novemcinctus***	X	–	X	–	–
Collared peccary	*Pecari tajacu**	X	X	X	X	X
Tamandua	*Tamandua tetradactyla**		–	–	–	–
Brazilian porcupine	*Coendou prehensilis***	–	X	X	–	X
NFSM	Rodentia**	X	–	X	X	X
cf. Ocelot	Felidae	–	–	–	X	–
Bats	Chiróptera**	–	–	–	–	X

NFSM, morph species of non-flying small mammals

* Species that visit the salt lick during the day; ** Species that visit the salt lick overnight

The fact that the salt licks were associated with materials located under a variable number of soil horizons and the congruence between the data reported regarding the study area by Ingeominas (2003), which observed parental materials with high clay content and those related to other Amazonian salt lick properties, as well our results from the physico-chemical analyses led us to the conclusion that the salt licks in this study are sites where geological materials have been exposed. In addition, these locations have more than a quarter of their material as clays in the case of mud salt licks and almost a half as clays in wall salt licks. The differences in clay content could be a result of the mixed structure of the mud salt licks, which continuously receive eroded materials from other components of the habitat both in and above the surface soil.

The importance of a salt lick's proximity to watercourses and steep slopes should be emphasised because of the direct relationship of this variable to erosion processes and therefore to the exposure of the salt lick materials. This relationship was evident at Loro's salt lick, where landslides along the river slopes changed the number of geophagical sites during the study.

The salt licks identified in this study are located over two of the youngest geological formations in the study area, which is consistent with Lee et al. (2009), who show that salt licks in South America are associated with geological materials that originated during the Tertiary and Quaternary Periods. However, in the southern sector of the study area, where plains predominate, the underlying geological formations are even younger, and the local people are unaware of any salt licks in the area. This lack of awareness could be a consequence of the small size of the study area, which could lead to the underrepresentation of the physiographic elements present in the area, including salt licks, which are not rare in the other plains of the Amazon Basin that are also associated with watercourses (Cabrera 2012; Montenegro 2004; Sarmiento 2007). This finding is consistent with the hypothesis that erosion drives the determinants of the spatial dynamics of salt licks.

At Loro's salt lick, the presence of illites in the clay fraction (Table 3) may explain the frequency of visits by many different species because this phyllosilicate can adsorb cations, which accounts for its high CEC. Indeed, the results confirm that the average CEC of the wall salt licks have medium to high values for the Amazon region, which is consistent with the range of 10–40 meq/100 gr described by Cortés and Malagón (1984) for illites and with the values reported for other salt licks in the Amazon Basin (Table 2). Of great importance are the data collected from Filanga's salt lick in which a mineralogical composition of clay materials, particularly smectites, was observed. The CEC and total bases are quite high in absolute terms, confirming the influence of the mineralogy of these materials on the availability of nutrients.

By contrast, the absence of illites or smectitic clays and the predominance of silicates, such as kaolinite and quartz, in the clay fraction of the materials from Danta's salt lick do not satisfactorily explain the high nutrient contents found because these deposits do not offer elements for vegetal or animal nutrition. The CEC at Danta's salt lick was low, although the base saturation was 76 % due to the calcium and magnesium contents (4.4 meq/100 gr and 4.9 meq/100 gr, respectively). Because kaolinites are used for the control of diarrhoea in animals (Krishnamani and Mahaney 2000; Klaus et al. 1998) and because this material is present in high levels at Danta's salt lick, it is possible that animals visit this particular salt lick to mitigate gastrointestinal problems.

Minerals that constitute the sand fraction of soils are associated with their long-term potential fertility as a consequence of the weathering of its own materials (Cortés and Malagón 1984). This weathering could increase due to the geophagical activity that progressively exposes the materials, and it could influence the potential of a salt lick to continuously provide nutrients to different animal species. The predominance of such minerals as quartz and magnetite means that at least at the study area, the wall salt licks can supply elements during both the short and medium term, depending on the intensity of use by wildlife and depletion of the clay fraction. The low content of diopside or hornblende, which is useful for obtaining magnesium and Na or calcium, magnesium, aluminium and iron, respectively, also supports the low probability that the sand fraction would be a future source of nutrients in the salt licks (Fig. 2). The low nutrient potential of the salt licks could be interpreted as one possible explanation for the abandonment of several old sites that were identified by the San Miguel reservation inhabitants and evident during field work in the vicinity of Loro's salt lick.

To analyse the physicochemical characteristics of salt licks, it must be clear that the analyses performed in this study refer to the soil content. Therefore, the analyses provide clues regarding the availability of minerals, but are not a direct measurement of this variable. Another methodological scheme must be selected to obtain values of nutrient availability, such as those used by Giraldi et al. (1999). Because of the differences in mineral composition between the wall and mud salt licks and control samples, the geological material characteristics seem to be evident directly at the wall salt licks and indirectly at the mud salt licks and show a dilution effect for the second group. The textural differences between mud salt licks and the sandy and clayey wall salt licks could be explained in terms of the nature of the source materials and some geomorphological events that occurred at these locations. The clayey texture of the wall salt licks results primarily from the geological material, but the texture of the mud salt licks exhibits both the geological material characteristics and those contributions by other sources, such as the erosion of surface soils or sediments transported by water that is associated with the salt licks.

Although the EC values were far from what is considered high salinity in the agronomic sense, the salinity at the wall salt licks exceed those of the mud salt licks, suggesting that dilution effects exist at the mud salt licks. The results for ICC, base saturation and the concentration of exchangeable bases can be analysed in the same manner. Therefore, the complete base saturation at the wall salt licks corresponds to materials that are gradually exposed and constantly renewed due to the occurrence of geophagy on them. By contrast, the lower base saturation of the mud salt licks may be observed because their materials are continually subjected to intense washing that is characteristic of wet forests.

The lower organic matter content at the wall salt licks is logical because these materials are exposed on steep slopes, where there is no possibility of accumulation. The high content of interchangeable phosphorus is comparable to that reported in "*Terra preta dos Indios*" and for dark soils located in the Amazon Basin. However, in our study area, high phosphorus levels are difficult to explain because there is no human activity at the salt licks, which is usually associated with the genesis and evolution of the Terra Preta formations (León 1992). Furthermore, there was no significant phosphorous content during the mineralogical examination. However, phosphorous may be linked to minerals that were not identified in the mineralogical characterisation and may have exhibited a controlled release dynamic because of the pH, which was significantly higher at the wall salt licks.

The clear importance of salt licks to the wildlife communities is evidenced here and in other localities by their frequent use (Burger and Gochfeld 2003; Brightsmith 2004; Montenegro 2004; Ferrari et al. 2008; Tobler et al. 2009; Cabrera 2012) and emphasises the need to prioritise conservation areas by maximising the complementarities of lick sites. With sufficient information concerning salt lick use and composition, the protection and use of salt licks can be a criterion for territorial planning in the Amazon Basin and specifically in the Amazon foothills, a zone with active immigration and landscape transformations (Sarmiento and Alzate 2004). Successful implementation of these strategies may be indicated by the good health of populations of different species that use salt licks and the maintenance of ecological functions of the forest, thus making possible the conservation of traditional practices, such as sustainable subsistence hunting by rural communities.

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