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Ingeniería en Ecosistemas

**Salt lick characterization and their relation with
visiting fauna in Amazonia**

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26 de febrero 2020, ciudad de Tena, Napo, Ecuador

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Resumen.

Los saladeros son sitios clave en el bosque, a los que una gran diversidad de mamíferos y aves visitan frecuentemente para consumir barro. Se han propuesto algunas hipótesis para explicar este comportamiento de geofagia, siendo la suplementación de minerales y la desintoxicación dos de las hipótesis más estudiadas. Sin embargo, las razones principales que expliquen el consumo de barro en saladeros siguen sin estar claras. El objetivo del presente estudio se centra en la caracterización físico-química de saladeros con diferentes grados de intervención y en evaluar la relación de estas características con las visitas de fauna. Durante la estación seca, del 24 de octubre al 8 de diciembre de 2019, se seleccionaron 13 saladeros dentro del Parque Nacional Yasuní, Ecuador. Se documentó la concentración de Na, K, Ca y Mg por medio de cromatografía iónica con una columna de intercambio catiónico de alta capacidad (HPLC). Se registró las visitas de fauna utilizando cámaras trampa con un esfuerzo de muestreo total de 256 trampas/noche (con un promedio de 25 trampas/noche por saladero). Se registraron 13 especies de mamíferos y 10 especies de aves asociadas a los saladeros muestreados. Las concentraciones de Na fueron típicamente más altas en las muestras de saladeros en comparación con los sitios de control. Usando modelos explicativos se observó que el número de eventos de depredación y el nivel de intervención antropogénica pueden tener una gran influencia en la frecuencia de visita en los saladeros. Las altas concentraciones de Na parecen estar más asociados a las visitas de ungulados como *Tapirus terrestris* y *Tayassu pecari*. Estas dos, junto con *Mazama americana* y *Ara macao* fueron las especies más frecuentemente registradas (mayores al 11% de la tasa total de visitas). A pesar de las altas concentraciones de Na en los saladeros, el suelo no es el único factor que determina la frecuencia de visitas, por lo que es necesario vincular investigaciones multidisciplinarias que incluyan enfoques ecológicos y geoquímicos. Estos resultados son relevantes para comprender el papel de los saladeros y la influencia del entorno en las especies que los visitan, siendo información importante para programas de conservación a nivel de paisaje, o áreas de alta prioridad de conservación como el Parque Nacional Yasuní.

Palabras clave: Tasa de visita, suplementación mineral, depredación, Perturbation, geofagia.

Abstract.

Salt licks are key areas the forests, where a great diversity of mammals and birds frequently visit them to consume clay. Some hypotheses have been proposed to explain this geophagic behaviour, mineral supply and detoxify are the two more studied. However, the principal reasons that explain soil consumption at salt licks remains unclear. The aim of this study is the physic - chemical characterization of salt licks with different levels of intervention and to asses, their relation with fauna visits. During dry season, from October 24 to December 8 in 2019, 13 salt licks was select at Yasuní National Park. Na, K, Ca and Mg concentration was determined, by ion chromatography with a high-capacity cation-exchange column (HPLC). Visits of fauna for each salt lick was also recorded using camera traps with a total sample effort of 256 trap/nights (with a mean of 25 trap/nights per salt lick). A total of 13 mammals and 10 birds species associated to salt licks was recorded. Na concentrations were typically higher at all salt licks samples in contrast with control sites. Using guidance models a great influence was observed from number of predation events and disturbance level on the frequency of animals visit to salt licks. High Na concentrations appears to be more associated to ungulates visits as *Tapirus terrestris* and *Tayassu pecari*, both with *Mazama americana* and *Ara macao* were frequently recorded species (with visit rates higher than 11%). Although high Na concentration at salt licks, soil chemical composition is not the only factor that determine visit frequency, therefore it is necessary to link multidisciplinary research that includes ecological and geochemical approaches. These results are relevant to understand the role of salt licks and the influence of environment on the species that visit them, being important information for conservation programs at landscape level or areas of high conservation priority such as Yasuní National Park.

Key words: Visit rate, mineral supply, predation, disturbance, geophagy.

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1. INTRODUCTION

Salt licks are sites within forests frequently visited by a great number of animal species to consume soil. This behaviour is called geophagy, and has been reported in several species of mammals and birds (Klaus & Schmidg 1993, Abrahams & Parsons 1996, Young *et al.* 2011). Considering the great diversity of animals that practice geophagy in natural salt licks, hypotheses have been proposed; linking the consumption of soil with 1) supplementation of minerals that are difficult to found in daily diet (Hebert & Cowan 1971, Kennedy *et al.* 1995, Pebsworth *et al.* 2019, Robbins 2012, Slabach *et al.* 2015) and 2) protection or detoxification of the organism from secondary plant (Pebsworth *et al.* 2019).

To response to these hypotheses, there are salt licks studies with different approaches in tropical, neo-tropical and temperate ecosystems around the world (Hebert & Cowan 1971, Klaus & Schmidg 1993, Kennedy *et al.* 1995, Abrahams & Parsons 1996, Abrahams 1999). In Amazonia, salt licks have been characterize in studies in South of Peru (Brightsmith & Muñoz 2004, Montenegro 2004, Brightsmith *et al.* 2008, Powell *et al.* 2009, Lee *et al.* 2010, Bravo *et al.* 2012, Fack *et al.* 2020), in Brazil and Colombia (Lips & Duivenvoorden, 1991; Narvaez & Olmos, 1990; Molina, León & Armenteras, 2013; Lozano, 2006). In Ecuador, studies have been carried out on the use and activity patterns around salt licks in the northern Amazon (Blake *et al.* 2010, 2011a, Link *et al.* 2011, Blake *et al.* 2013) and few studies have focused on the relationship between fauna visits and soil chemistry (Voigt *et al.* 2008, Jaramillo 2010).

In Amazon forest, high precipitations rates make easier the mineral leaching and hindering mineral nutrition in many wildlife species, specially for species in which their only source of minerals are plants (Robbins 2012). The content of macro and micronutrients is an important factor in cell processes as pH balance, osmotic pressure regulation, hormones production, organs and tissues (Underwood & Suttle 1999). Deficits in mineral supply can directly influence in efficiency of absorption and nutrient retention, imbalance within other minerals or dietary elements, feeding strategies, damage in metabolic routes and other effects (Rode *et al.* 2003, Robbins 2012). According to Pebsworth *et al.* (2019), several nutrients (i.e. As, B, Ba, Br, N, Ca, Cr, Na, K, Fe, Cu, Zn, Mg, P, S and Zn) have been analyzed in geophagic soils in contrast to control non-ingested samples. These authors suggest that

soil consumption in salt licks is related to the presence of these minerals. However, elements as Na, K, Ca and Mg are reported with highest concentrations in salt licks (Pebsworth *et al.* 2019), linking these principal elements as motivators for geophagy site selection. Other studies in northwestern Amazonia, such as Montenegro (1998) and Wilms (1999) suggest specifically that Na is the mineral that seems to attract animals to the salt licks. In Ecuador, Voigt, et al. (2008), concluded that there was a higher concentration of Na, K, Ca, Mg and Fe in salt licks than in the bat's diet (fruits and insects), suggesting an important dietary nutrition supplementary role of salt licks. Some studies, as Ayotte *et al.* 2006, besides remark the special function of salt licks as concentrated sources of Na and Mg, specially in mammals -in some specific stages-- which could be related to the important role of Na in regulation the osmolality, or the essential process in enzyme activation related to energy metabolism, where Mg is involve (Robbins 2012).

In relation with the mineral composition of soil in this region, it is important to consider that dynamics of terrestrial habitats on Amazonia are the result of the variety of fluvial environments and its formation (Toivonen *et al.* 2007). Some studies, as Lee *et al.* (2010), have also associated salt licks occurrence in western Amazonia with a riverine formation that existed around ~14 Million years: Lake Pebas (Hoorn *et al.* 2010). In this sense, sedimentation, migration of lateral river-channel, deposition of different materials and other factors, such as historical geomorphology, influence on riverine ecosystems (Toivonen et al. 2007), linked with Amazonia soil salt licks and their structural composition and soil morphology (Lee, et al 2010)

Considering the diversity of salt lick formations, the geomorphology of these particular sites can also influence in the type of fauna that visit them. According to Montenegro (2004) and Molina *et al.* (2014), it is possible to classify the salt licks by their structural characteristics, between “open”, “wall” or “caves” salt licks and for their association with water as “wet” or “dry” salt licks. Some studies have investigated the relationship between salt licks and visiting fauna on a temporal and spatial level (Link *et al.* 2011). The composition of the visiting species and the frequency of these visits have been found to differ from one salt lick to another (Tobler *et al.* 2009, Blake *et al.* 2010). Between habitat types and based on the availability of salt licks in different ecosystems (Blake *et al.* 2011a), such as wall salt licks, or those located at great heights, which are more frequently visited by bird species,

like parrots and macaws (Montenegro 2004, Lee *et al.* 2010). Just in the Ecuadorian Amazon, at least 56 species of mammals (31 bats species) (Voigt *et al.* 2008, Blake *et al.* 2011a) and more than 15 species of birds, were recorded visiting salt licks (Blake *et al.* 2011a). The patterns of these visits and their regularity also depended on the type of fauna, for example, parrots usually visit these sites every morning, whereas some species of primates visit sporadically during the week (Blake *et al.* 2011a, Link *et al.* 2011).

Salt licks visits can also be influenced by climate, variations in feeding behavior and threat of predation (Blake *et al.* 2011a, Link *et al.* 2011). It has been reported that some species as spider monkeys and howler monkeys, use a lot of time in salt licks, with more frequency during dry season and in conditions of sunny and dry weather (Jones & Hanson, 1985; Blake *et al.* 2010, Link *et al.* 2011). These results appears to be explained by a seasonal variation in animal diet (possibly in function of fruit availability). Additionally, the need of mineral supply for some animals at certain times of their life, as pregnancy or lactation, seems to be related with high frequency of visits (Brightsmith 2004, Montenegro 2008, Voigt *et al.* 2007). On the other hand, it has also been reported that spider and howler monkeys, spend a lot of time near to the salt lick before to eat soil (Izawa 1993, Blake *et al.* 2010, Link *et al.* 2011), suggesting that this behaviour and soil intake can changes in response to predators. Predation risk, can influence not only in the activity patterns at salt licks, but also can motivate the generation of behavioral strategies to mitigate the threat (Link *et al.* 2011). However, there are different kind of predator pressures, and the response to changing predation risk depends on different variables (Miller 2002). Additionally, predation patterns can be significant altered by anthropogenic impact in different levels (Ferrari 2009).

The effect of anthropogenic disturbance on mineral licks also have been studied in Amazonia. Ghanem & Voigt (2014), study salt licks deterioration in terms of hunting pressure and accessibility to this sites. They used distances to roads, oils extraction sites and communities to estimate de disturbance in each salt lick. They concluded that high levels of disturbance deteriorate salt licks characteristics and also negative affect the fauna associated to them, reducing significantly the activity rate of animals, not only in large mammals (Blake *et al.* 2013, Ghanem & Voigt 2014).

Although it is known that ecological role of salt licks in a forest is fundamental, it is still unclear why animals invest so much energy to visit these sites. Salt licks studies in Ecuador are limited, as well to the characterization of its physical and chemical composition. In addition, official documented information within this field in public institutions in Ecuador is also restricted. It is necessary to develop researches that include each of these components, linking the characterization of these sites with the ecosystem and the ecological importance that they have as a hotspots for conservation programs.

The aim of this study are (1) to characterize salt licks in terms of soil chemistry composition, fauna visiting (frequency, abundancy, diversity and predator visits), and level of intervention and (2) to analyse the relation between salt licks characteristics and the animals that visit them. A higher mineral supply in geophagic soils in contrast with control ones is expected, according to nutrient deficiency hypothesis. Besides, it is hypothesized a higher visit rate in salt licks with high concentration of minerals, but with a lower level of perturbation and predation presence.

2. METHODS

2.1 Study site

The research project was conducted in lowland Amazon basin (Figure 1), specifically in the protected area Yasuní National Park, site with a global conservation significance and one of the most biodiversity areas on the world (Bass *et al.* 2010). The area include both non-inundated forest (*terra firme*) and temporarily inundated forest (*várzea*). Sediments of piedmont plains, whose valleys open, cover the northwestern basin with the formation of meandric channels. The basin has numerous sandy-silty terraces and the principal contributors, including the Napo River, determine the main hydrographic networks of the western zone (Narvaez & Olmos, 1990).

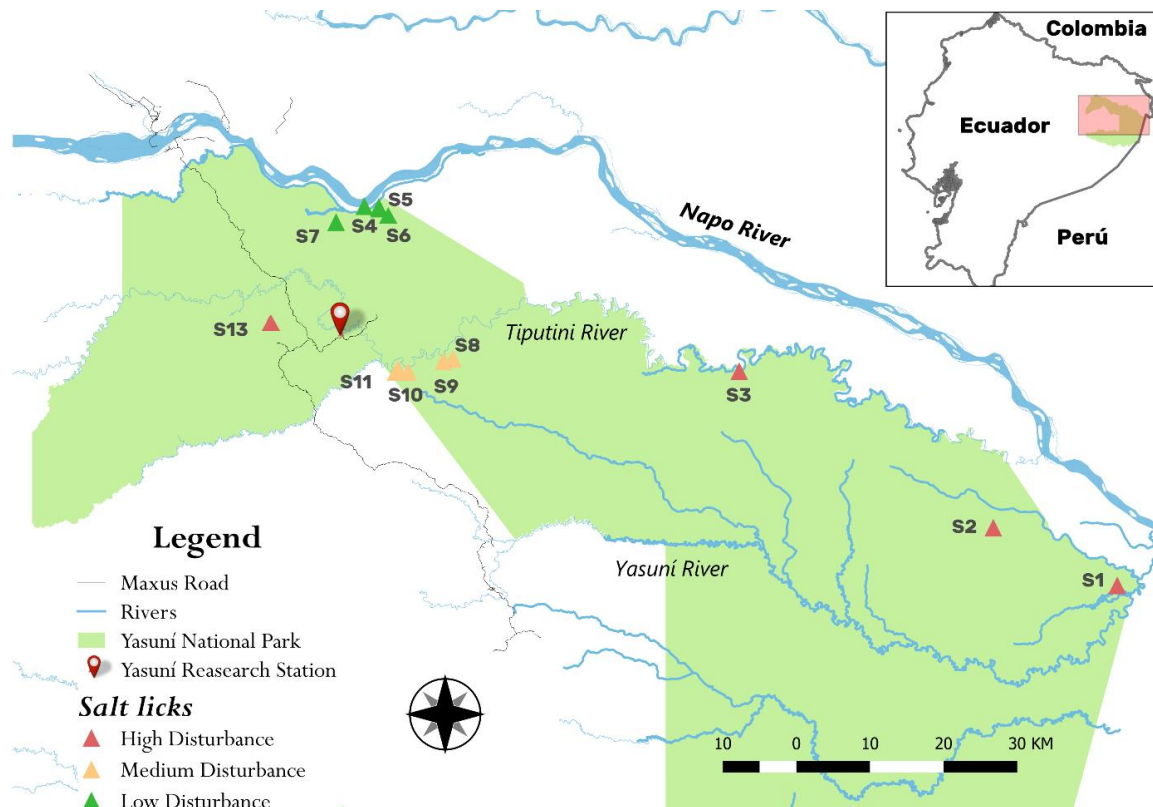


Figure 1. Study site. Location of the salt licks in the north region of Yasuní National Park.

The study site has marked dry and wet season. Dry season register in the protected area is consider between October and February with an approximated monthly mean of precipitation of 140 ± 21 mm and the wet season (from April to August) reach the 383 ± 11 mm of mean monthly precipitation (Karubian *et al.* 2009). Fieldwork and all data collection was carried out during dry season to standardize and compare the results and because the activity in salt licks is greater during the drier months compared to wetter months (Mahaney *et al.* 1990, Blake *et al.* 2010, Link *et al.* 2011).

I compiled a database based on scientific reports, secondary information, and from the Environmental Ministry. From this database, 13 salt licks was selected in function of its accessibility and classification (“wall” or “open”), just open and mud salt licks were used for the study. The salt licks selected are distributed in diverse localities across the protected area, with different levels of disturbance (see Table 1). In this way, salt licks 1 (close to a bordering zone with Perú, with more commercial traits and hunting pressure), 2, 3 (within an oil blocks) and 13 (close to Maxus road, an oil pipeline road) are located in zones with a high anthropogenic impact; them were considered as high level of disturbance. Salt licks 8-12 are located in Yasuní Research Station area, where scientific research is the principal

approach; despite this, they are located in Huaorani zone (hunting communities), but their access is only by river (see Figure 1.); these ones were considered as mid level of disturbance. Finally, salt licks 4-7, are located within a communal territory (Añangu) with an ecotourism strict politics (i.e. hunting is forbidden); those were considered as low level of disturbance.

Table 1. Characteristics of salt licks selected for study / * = Salt licks near to a road

<i>Salt lick</i>	<i>Location</i>	<i>Anthropogenic interaction</i>	<i>Coordinates</i>		<i>~ Area (m²)</i>	<i>Disturbance level</i>
			<i>Latitude</i>	<i>Longitude</i>		
<i>S1</i>	Tambococha	Limit zone / Hunting	0° 59' 0.6072" S	75° 27' 1.62" W	600	High
<i>S2*</i>	Block 43 - PAM	Oil block/ Road	0° 54' 45.7704" S	75° 36' 6.6384" W	50	High
<i>S3*</i>	Block 31 - PAM		0° 43' 13.9908" S	75° 54' 43.6176" W	300	High
<i>S4</i>	Añangu Community	Eco-tourism	0° 31' 14.7432" S	76° 21' 5.04" W	150	Low
<i>S5</i>	Añangu Community		0° 31' 8.9472" S	76° 21' 8.1792" W	35	Low
<i>S6</i>	Añangu Community		0° 31' 4.116" S	76° 22' 11.7372" W	260	Low
<i>S7</i>	Añangu Community		0° 32' 14.7768" S	76° 24' 15.858" W	200	Low
<i>S8</i>	Yasuni Research Station		0° 42' 18.3348" S	76° 15' 41.6196" W	241	Medium
<i>S9</i>	Yasuni Research Station		0° 42' 29.232" S	76° 16' 23.5776" W	80	Medium
<i>S10</i>	Yasuni Research Station	Scientific research / Hunting	0° 43' 17.1516" S	76° 18' 59.3388" W	70	Medium
<i>S11</i>	Yasuni Research Station		0° 43' 17.0868" S	76° 18' 59.274" W	243	Medium
<i>S12</i>	Yasuni Research Station		0° 43' 11.7984" S	76° 19' 41.5812" W	260	Medium
<i>S13*</i>	Maxus Road	Oil zone/Hunting /Chakra	0°43'11.8"S	76°19'41.6"W	60	High

2.2 Soil sample collection

All sample collection was carried out from October 24 to December 8 in 2019. In each salt lick, a data matrix with key information was filled from each location: "Salt lick Name" (common name used by local inhabitants), "Area" (calculate with the maximum length and width of each one), "Trap station" associated with the salt lick, "Responsible" and "Observations". All the salt licks included in this study were classified as "open" and "wet" type, but two of them (S4 and S5, table 1) also included a cave.

Using an experimental paired design, one control site per salt lick was identify. For salt lick samples, three compound samples of soil (three repetitions), with evidences of geophagy (scratches or bite marks) (Mahaney & Krishnamani 2003), were taken in each salt licks for a better characterization of the whole specific area delimited, considering the possible internal variation in the geophagic zone (Klaus & Schmidg 1998). Each compound sample (each one of 1 kg) was taken with 5 subsamples mixture. Control sites was located in the

same physiographic units, with edaphic characteristics similar to salt licks but without any geophagic evidence (Molina et al. 2014), paying close attention to soil texture (Mahaney & Krishnamani 2003). Each control site was located between 150-250 m away from the border of the geophagic point, according to Tapirus and Linneo (2007), Mahaney and Krishnamani (2003). Considering the great heterogeneity of the soil, control samples just have one repetition, because each one is a different non-salt lick soil with possible totally different characteristics in the same area as to average (Klaus & Schmidg 1993).

The samples were stored in plastic covers to elude exposure to light. This procedure, avoid natural drying of samples that could increase the cementation, affecting granulometric analysis, or the high temperatures that could produce changes in the oxidation state of the elements and in the potassium exchange (Fraser *et al.* 1980). All the samples were kept in a plastic and hermetic container, during all the transport from field to laboratory, to avoid contamination.

2.3 Soil chemical composition

For the soil analysis, each collected sample was homogenized, weighed and dried at 104°C for 24h on the stove. The minerals Na, K, Ca and Mg was selected because of its importance in the cell processes but also because they are highly frequently reported in salt licks and have been linked with geophagy (Pebsworth *et al.* 2019). The concentration each mineral was determined by ion chromatography with a high-capacity cation-exchange column (HPLC) according to Thomas *et al.* (2002) protocol, at National Water Reference Laboratory at Universidad Regional Amazónica Ikiám. Each sample was digested with methanesulfonic acid using 10g of soil and 50ml of methanesulfonic acid. Considering the high levels of mineral concentration, an aliquot from the sample was transferred to a 2ml vial and then injected with the standards in the HPLC using a Shim-pack GIS C18, 4- μ L column. Dilutions of the standard at different concentrations were used to quantify all the samples.

2.4 Camera Trapping

I used Bushnell Trophy Cam HD and Reconyx HyperFire 2 HF2X cameras activated by a temperature and movement sensor to register the visit of fauna in each salt lick. Each camera remained active for a record time of at least 30 days in each station. The camera

was located near to the edge of the salt lick, between 0.5-0.75 meters from the ground, directed towards the evidence of excavation trails or other activities in the place. The camera traps were set with the minimum time between photographs with three photographs per shoot. Independent events were considered as each set of consecutive photographs of the same specie that differ more than 30 minutes from the next set of photographs (Blake et al., 2011). Consecutive photos from more than one species also considered an independent event. After the data collection, the photographs were grouped by species and events, considering the date and time of activation. The methodology for fauna monitoring and visit patterns have been widely applied in salt licks, general considerations mentioned above for photo-trap was used here (Tobler *et al.* 2009, Blake *et al.* 2011a, Link *et al.* 2011, Blake *et al.* 2013, Fack *et al.* 2020).

Visits rate was calculate as a number of events per species/sample effort * 100 (Mandujano and Pérez, 2019). The classification and management of the photos was carried out using Wild ID 0.9.30 software. Predation variable was taken summarizing the number of total events with a predator presence for each salt lick.

Bats were not included because of the difficulty for identification. Cameras from sites 2 and 10 were excluded because of malfunctioning problems and site 12 because the camera memory was stolen during the sampling period. Sampling effort differ among salt licks because of these camera problems (Table 3).

2.5 Statistic analysis: Salt licks characteristics and fauna visit rates

Statistical analysis were performance-using R. 3.6.2, from specific package and libraries (vegan, dplyr, biodiversityR, iNEXT, ggplot).

Kruskall Wallis test was used to assess whether the mineral concentration in the three internal repetitions of salt licks samples do no present significant differences (to avoid type II error, the mean of these values was used as one salt lick replicate, n =13). Wilcoxon test was applied also, to contrast the differences between the mean values of these three repetitions of salt lick soils and control ones. This was realized for each mineral, Na, K, Ca and Mg for all samples taken. To difference each mineral concentration in function of the level of perturbation in each salt lick, a Kruskal-Wallis test was realized. Index of Diversity

of Simpson, Shannon and the coefficient of similarity of Jaccard were applied to assess diversity results between salt licks with high, mid and low perturbation.

Finally, to evaluate the relationship between salt licks characteristics and its fauna visiting rates, a generalized linear model was generated. Identity family was used, as a guidance tool (considering the sample size) and the model was applied to understand the interaction between both soil and fauna visiting patterns, involving environmental factors. To build the model, *visits rate* was used as the dependent variable, and all other factors determined as independent variables. The total of co-variables were: *Na*, *K*, *Ca* and *Mg* concentration (ppm) as soil chemical composition variables and *Predation events*, *Disturbance* (high, medium or low) and *Area* as physical variables of each salt licks, that were used to evaluate the influence of soil minerals concentration and some environmental factors on the visits frequency to salt licks. A Spearman correlation analysis was realized to avoid collinearity and select the variables of soil to include in the model. The variables were selected by their ecological importance and its effect on the model. These same variables were also applied for generate a specific model for the most common species (one for each specie) recorded visiting the salt lick, using only the visit rate of the selected specie as dependent variable. The species selected to apply the model was those which the highest visit rates, above 11% of the total of visit in all sample period.

3. RESULTS

3.1 Soil composition

Concentration (ppm) of Na, K Ca and Mg for salt licks and control sites are shown in Table 2. Mineral concentration did not show significant differences between salt lick soil repetitions (chi-squared = 12, df = 12, *p-value* = 0.4457).

Table 2: Soil chemical concentration (ppm) (\pm Standard deviation of the mean values) for each salt lick. Each value represent the mineral concentration in ppm for each sample taken. Each one is considered as one replica of the two type samples: Salt lick geophagic soils and control unconsumed soils.

<i>Salt lick</i>	<i>Location</i>	<i>Type sample</i>	<i>Na</i>	<i>K</i>	<i>Mg</i>	<i>Ca</i>
S1	Tambococha	Salt lick	8.9853 \pm 0.1932	7.5060 \pm 0.0505	18.3263 \pm 0.0741	9.6787 \pm 0.1923
		Control Site	1.1480	12.2230	12.1410	29.6460
S2	43 Block	Salt lick	3.1017 \pm 0.2817	4.5177 \pm 0.2652	4.8060 \pm 0.1599	66.2730 \pm 1.3091
		Control Site	3.5540	6.5230	2.9960	96.1600
S3	31 Block	Salt lick	3.4227 \pm 0.0749	4.5943 \pm 0.0387	4.9773 \pm 0.0186	71.6917 \pm 0.1053
		Control Site	1.0860	3.7470	7.7910	34.6380
S4	Añangu	Salt lick	23.6713 \pm 0.1017	6.1560 \pm 1.7636	5.2507 \pm 0.0225	49.7833 \pm 0.0301
		Control Site	0.0610	3.9080	8.2440	54.2930
S5		Salt lick	18.6533 \pm 0.0550	5.5930 \pm 0.0616	5.4093 \pm 0.0480	86.0683 \pm 0.2644
		Control Site	2.8080	6.8320	4.9950	61.7640
S6		Salt lick	5.3017 \pm 0.0878	6.5773 \pm 0.0377	6.5917 \pm 0.0672	60.0563 \pm 0.3820
		Control Site	1.0420	5.5290	8.6390	59.6930
S7		Salt lick	25.4893 \pm 0.0964	4.8613 \pm 0.0587	6.5557 \pm 0.0090	38.9213 \pm 0.2368
		Control Site	0.4050	5.9650	6.8950	57.8500
S8	Yasuni	Salt lick	11.7553 \pm 0.1034	3.8777 \pm 0.0965	4.7790 \pm 0.1071	57.7340 \pm 0.1098
		Control Site	5.3120	4.8170	7.9310	68.5960
S9	Research Station	Salt lick	13.7793 \pm 0.1546	5.0133 \pm 0.0486	7.3193 \pm 0.0616	53.8047 \pm 0.3431
		Control Site	1.3430	3.0760	9.1200	61.1750
S10		Salt lick	23.3640 \pm 0.1225	5.6143 \pm 0.1384	9.4177 \pm 0.0936	56.9170 \pm 0.5162
		Control Site	0.2030	6.3250	8.0520	25.9150
S11		Salt lick	35.8430 \pm 0.1412	5.8913 \pm 0.1770	10.0313 \pm 0.0649	53.1053 \pm 4.2803
		Control Site	0.6270	5.6620	8.1840	45.6760
S12		Salt lick	21.7353 \pm 0.2017	1.9550 \pm 0.0431	6.2593 \pm 0.0862	20.4620 \pm 3.5089
		Control Site	1.1050	4.0800	13.5680	47.5990
S13	Maxus road	Salt lick	0.7147 \pm 0.0871	4.9037 \pm 0.1068	5.5363 \pm 0.0774	169.3117 \pm 0.9673
		Control Site	0.3470	4.9670	9.6220	56.4140

We found significant differences in Na concentration between salt licks and control sites, ($Z=3.04$, p -value < 0.005) and non statistical differences on Mg, Ca and K (Mg: $Z= -1.223$, p -value = 0.2213; Ca: $Z= 0.2446$, p -value = 0.086; and K: $Z= -0.87357$, p -value = 0.3824; Figure 2).

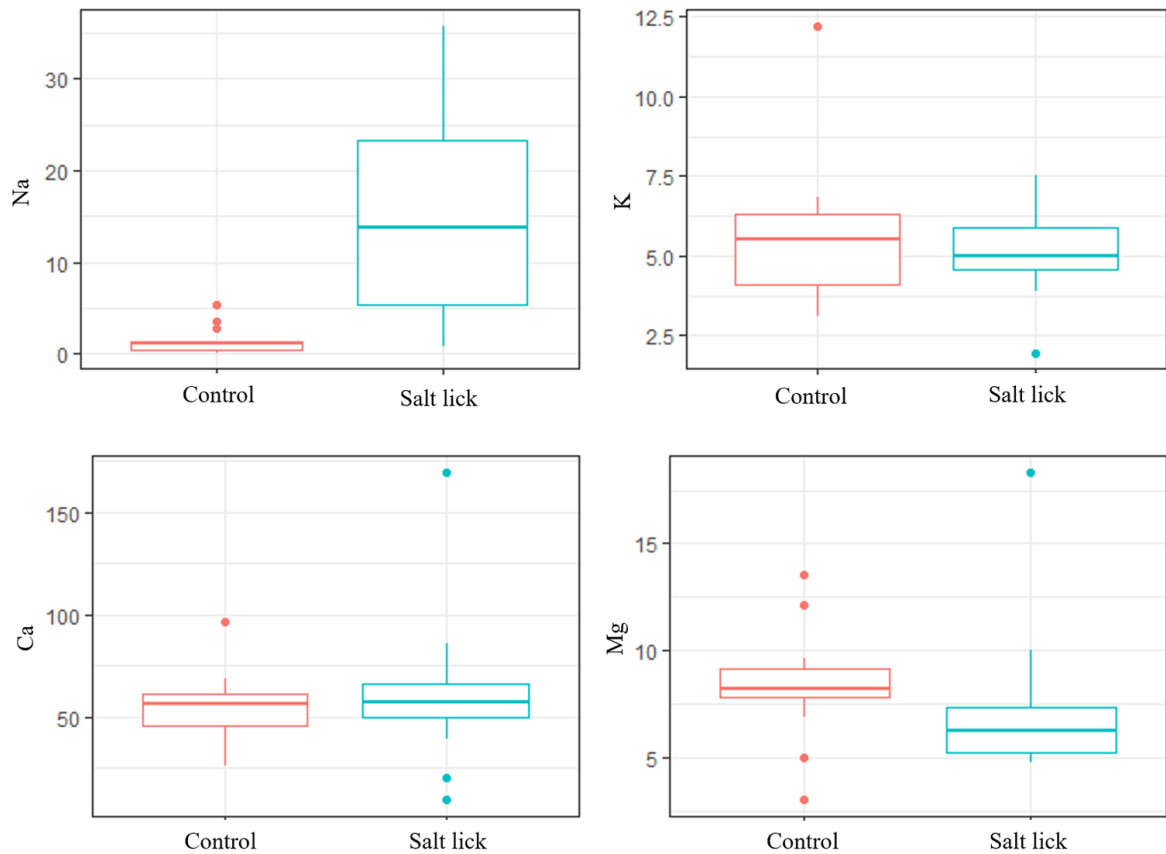


Figure 2. Boxplot of mineral concentration (ppm) between control and salt licks samples. The most representative differences are observed in Na and Mg concentrations.

Specifically, Na concentration in most salt licks soils was higher than in control sites. This pattern repeat in all sites with exception of S2 and S13, with non-different values, being the lowest Na values throughout the study (Figure 3).

In relation with Mg concentration, it can be observed that some of the salt licks present lower levels than the control site, but there is not an evident pattern. According to the concentration of Ca and K, differences in the concentrations between salt lick and control sites was not clear, although for some salt lick such as S13 the level of Ca was significantly higher, and in case of S1 the level of K was higher within control site (Figure 3).

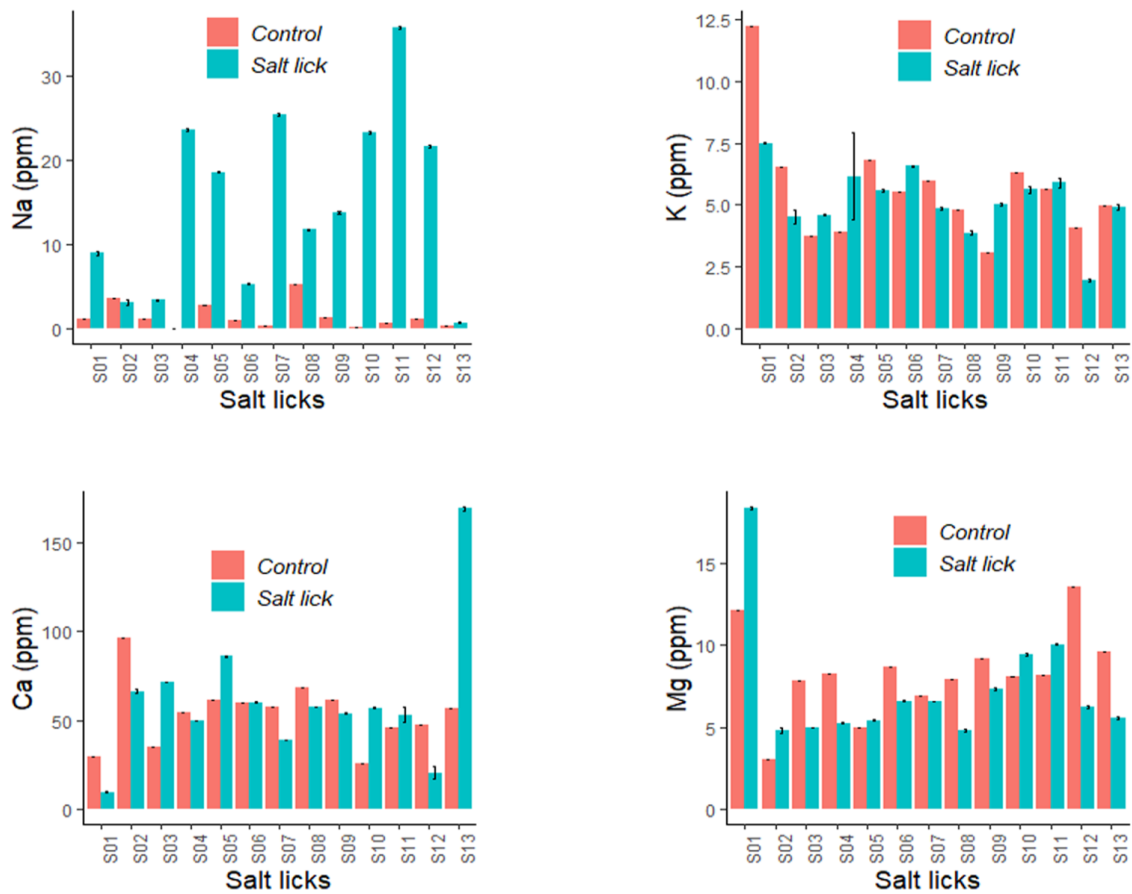




Figure 3. Soil chemic composition: Concentration (ppm) of each mineral analyzed per site. The scale vary in function of the concentration range to a better contrast between salt lick and control site in each mineral.

3.2 Visits of fauna

A total of 567 independent events was recorded (433 from mammals and 134 from birds); 23 species of animals was identified by camera traps, 13 species of mammals and 10 species of birds (see Table 3). The higher number of events (155 and 134 respectively) was recorded in salt licks 7 and 9 (see Table 3) respectively.

Table 3. Species recorded per each salt lick and sample effort / * Event species that we confirm geophagy

	S1	S3	S4	S5	S6	S7	S8	S9	S11	S13
 <i>Mammals</i>										
<i>Ateles belzebuth</i> *	-	-	-	-	-	-	-	1	1	-
<i>Alouata seniculus</i> *	-	-	6	11	4	-	2	1	-	-
<i>Cuniculus paca</i>	-	-	-	-	1	-	-	2	-	-
<i>Coendou prehensilis</i> *	-	-	-	-	-	-	4	16	-	-
<i>Dasyprocta fuliginosa</i> *	-	-	-	-	2	-	4	-	-	-
<i>Dasybus spp.</i>	-	-	-	-	-	-	-	-	-	2
<i>Leopardus pardalis</i>	-	-	2	1	3	-	-	2	-	-
<i>Leopardus wiedii</i>	-	-	-	1	-	-	-	-	-	-
<i>Mazama americana</i> *	-	2	11	-	12	67	-	25	-	1
<i>Panthera onca</i>	-	-	-	2	-	-	-	-	-	-
<i>Pecari tajacu</i> *	-	2	-	-	-	9	2	4	-	6
<i>Tayassu pecari</i> *	45	9	4	-	-	19	-	6	-	7
<i>Tapirus terrestris</i> *	43	1	6	-	15	58	-	2	-	3
	S1	S3	S4	S5	S6	S7	S8	S9	S11	S13
 <i>Birds</i>										
<i>Ara macao</i> *	-	-	-	-	-	-	2	64	-	-
<i>Mitu salvini</i> *	-	-	-	1	1	1	-	1	-	-
<i>Geotrygon montana</i>	2	-	-	-	-	-	-	-	1	4
<i>Ortalis guttata</i> *	-	-	-	-	-	-	-	-	-	12
<i>Pyrrhula barrabandi</i> *	-	-	-	-	-	-	-	2	4	-
<i>Penelope jacquacu</i>	-	1	-	-	-	-	-	-	-	-
<i>Pipile cumanensis</i> *	1	-	-	-	3	1	1	7	3	9
<i>Aramides cajanea</i>	-	-	-	-	-	-	-	-	-	1
<i>Leptotila rufaxilla</i>	-	-	-	-	-	-	-	-	4	7
<i>Psophia crepitans</i>	-	-	-	-	-	-	-	-	-	5
SAMPLING EFFORT	31	30	28	37	20	22	7	38	12	31

Most of mammals' species (8 of 13 species) were recorded only in mid and low-perturbed (S=0.9, H=2.3) salt licks, being the high perturbed (S=0.8, H=1.6) salt licks the less mammals diverse. In birds, just 3 of the 10 species were recorded only in mid (S=0.83, H=1.91) and low-perturbed (S=0.5, H=0.69) zones, while high perturbed (S=0.85, H=1.94) salt licks recorded more birds species (Table 3). From the total species registered (including mammals and birds) calculating the index of diversity of Simpson and Shannon, salt licks with a medium level of perturbed salt licks are quite most diverse recorded (S=0.78, H=1.9), in contrast to low (S=0.73, H=1.6) and high (S=0.75, H=1.7) perturbed salt licks. The

coefficient of Jaccard (0.73) also estimate that both high and low perturbed salt licks are similar in relation with their diversity. About predator species, low (S=0.49, H=0.84) perturbed salt licks presented the higher diversity because were the only salt licks with predator presence, except for S9 (see Table 3).

Among mammals, ungulates had the largest number of visits throughout the study, *Tapirus terrestris* with the 22.57%, *Mazama americana* with 21.86% and *Tayassu pecari* with the 15.87% of the total events. Consequently, these species had the highest visitation rates with respect to all salt licks (see Figure 4). For birds, *Ara macao* was the most common species reaching 11.64% of total events.

At least 8 species of mammals and 5 species of birds were recorded eating clay, thus it was considered at least 422 and 97 events of mammals and birds (respectively) linking with this behaviour. However, we evidenced other inter – specific ecological interactions in the salt licks visits, such as predation. There was a clear predation event from an ocelot eating a bat in S5 and several straight events on different days. Three species of predators were registered in the sample period in four salt licks. Thus, salt licks S4 and S5 presented two and five predators events (respectively), while S6 and S9 present only one event each one. All other salt licks did not present any event with predators.

In addition, species as *Alouatta seniculus*, *Ateles belzebuth*, *Coendou prehensilis*, *Pecari tajacu* and *Tayassu pecari* was registered in groups visiting salt licks, even with their younglings. *Tapirus terrestris* was often recorded visiting in couples for more than 60 minutes.

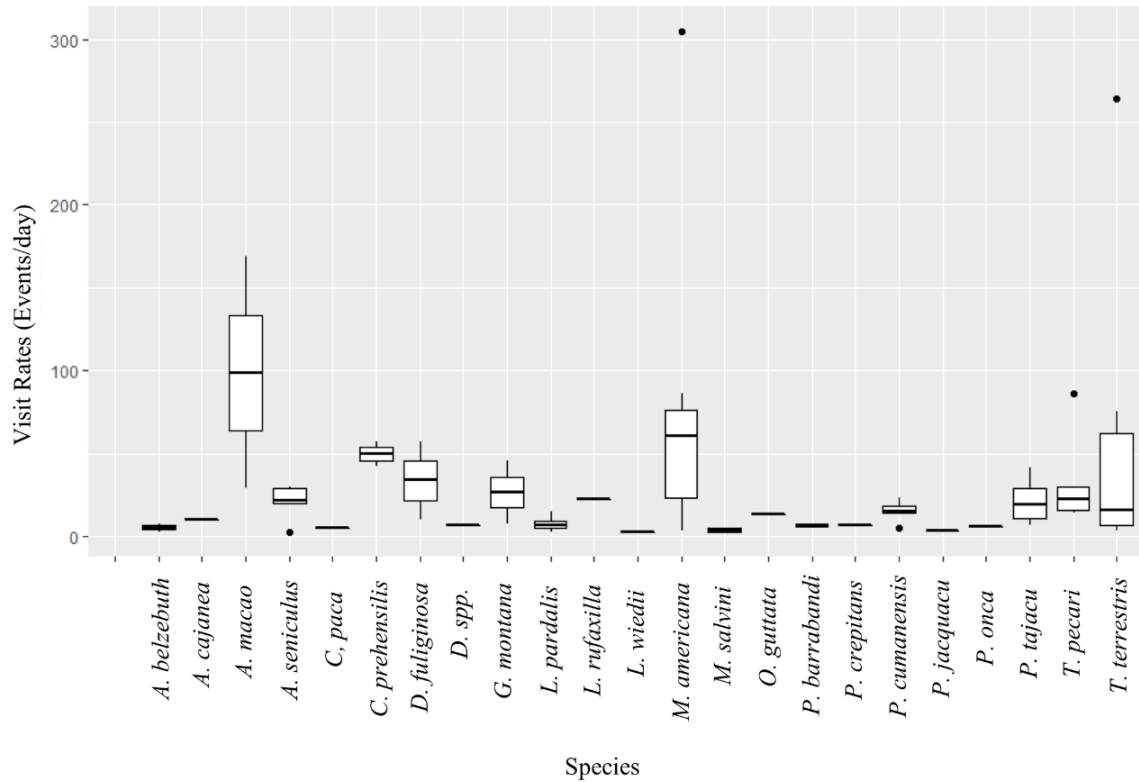


Figure 4. Visit rates (number of events / 100 trap-days) per species in all salt licks.

3.3 Fauna and salt licks characteristics

Results of each mineral concentration were compared between low, mid and high-perturbed areas. There was not a statistically significant difference between different levels of perturbed salt lick in and soils chemical composition (Na: chi-square=4.7, p-value = 0.09; K: chi-square = 0.89, p-value = 0.6; Ca: chi-square = 0.33, p-value = 0.84; Mg: chi-square = 0.2, p-value = 0.9), although we can observe a tendency in Na, with lower levels in high perturbation.

The correlation test between soil variables (Supporting Information Figure S1) shows that there could be a collinearity effects between concentration variables of Na and Ca ($R = -0.61$, $p\text{-value} = 0.02$), and also within K and Mg ($R = 0.64$, $p\text{-value} = 0.01$). Na, besides, was the variables that better represented the differences between saltlicks and control soils (Figure 2). Based on correlation and ecological relevance of variables, Na concentration was used as the soil composition variables in the model for assess soil composition.

A group of possible models, using identity link function, was constructed (Supporting information Table 1) and the best model was selected based, additionally, on collinearity (described above) and ecological criteria. This general model is presented in Figure 5, whose represent the interaction of *Na concentration*, *Depredators* and *Perturbation* variables with the total frequency of visits in each salt lick. *Area*, as a physical variable, was delete from the model due to its low effect on *visist rates* (estimate = 0.10, p-value = 0.83). The model constructed suggest a negative effect (estimate = -1.85, p-value = 0.83) from Na concentration (ppm) and a strong negative effect (estimate = -94.32, p-value = 0.14) from number of predation events above total visit rate (events/day). Conversely, there is a clear positive effect of low perturbation (estimate = 300.5, p-value = 0.2) on the total visit rates.

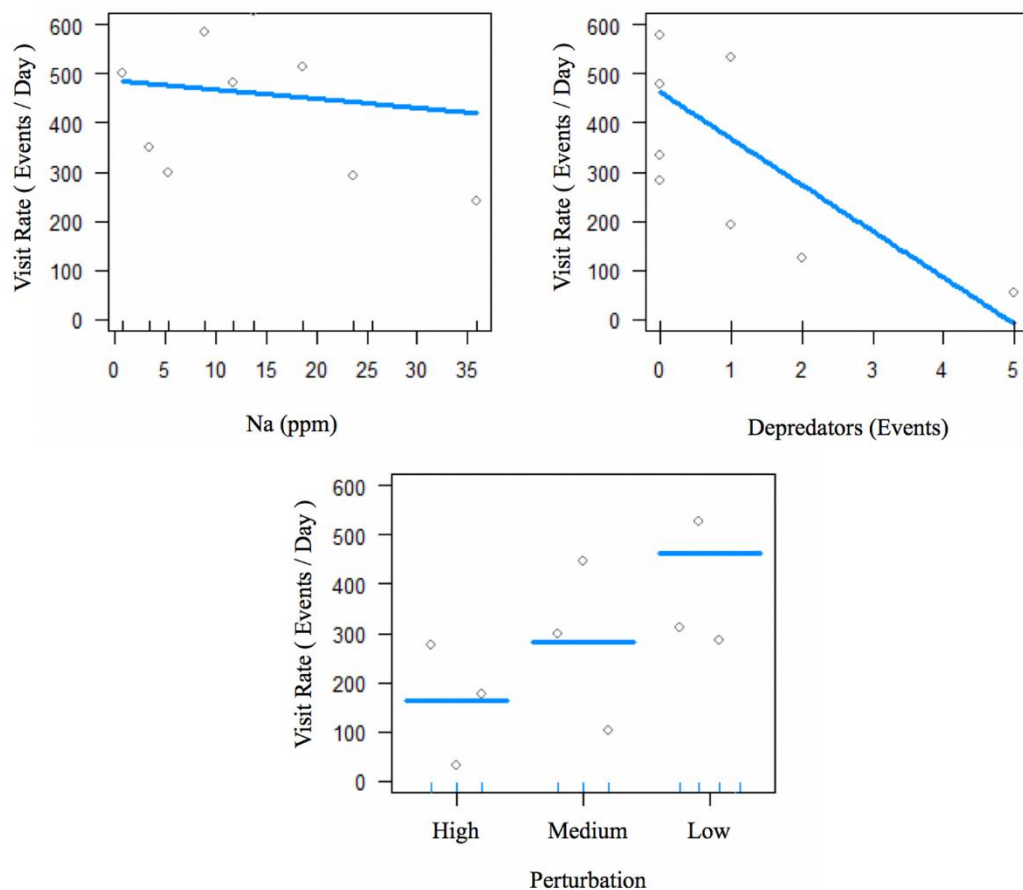


Figure 5. Graphic visualization of general model using the total fauna visit rate (Number of events / 100 trap days) of salt licks. a) Na soil concentration effect (ppm) b) Depredators (Number of predators events recorded) effect c) Perturbation (Low, mid and high in function of salt licks anthropogenic impacts). The model consider as variable *Perturbation Low* and *Perturbation Medium*.

The same model it is also presented for the most common species (*T. terrestris*, *M. americana*, *T. pecari* and *A. macao*) recorded visiting salt licks. At species level the *Na concentration* effect above *Visit rate*, change to positive (in contrast with the *Na concentration* effect in the first model) for *T. terrestris* (estimate = 2.07, p-value = 0.5) and *T. pecari* (estimate = 1.68, p-value = 0.4) with an exception in *M. americana* (estimate = 0.17, p-value = 0.9), where the effect is not clear. However, the effect of this variable on *A. macao* (estimate = -2.73, p-value = 0.3) visit rate is negative. Predation events effect in visit rates remain negative for all the mammal species (*T. terrestris*: estimate = -39.8, p-value = 0.09; *M. americana*: estimate = -44.49, p-value = 0.08); *T. pecari*: estimate = 1.68, p-value = 0.40), although is positive for *A. macao* (estimate = 6.01, p-value = 0.66), while perturbation level change between each one. The effect of low perturbation levels (salt licks remote from roads and less accessible) is positive just for *T. terrestris* (estimate = 90.32, p-value = 0.3), *M. americana* (estimate = 112.46, p-value = 0.2) and *A. macao* (estimate = 16.78, p-value = 0.7), while for *T. pecari* the effect is negative (estimate = -43.64, p-value = 0.4) (Figure 6).

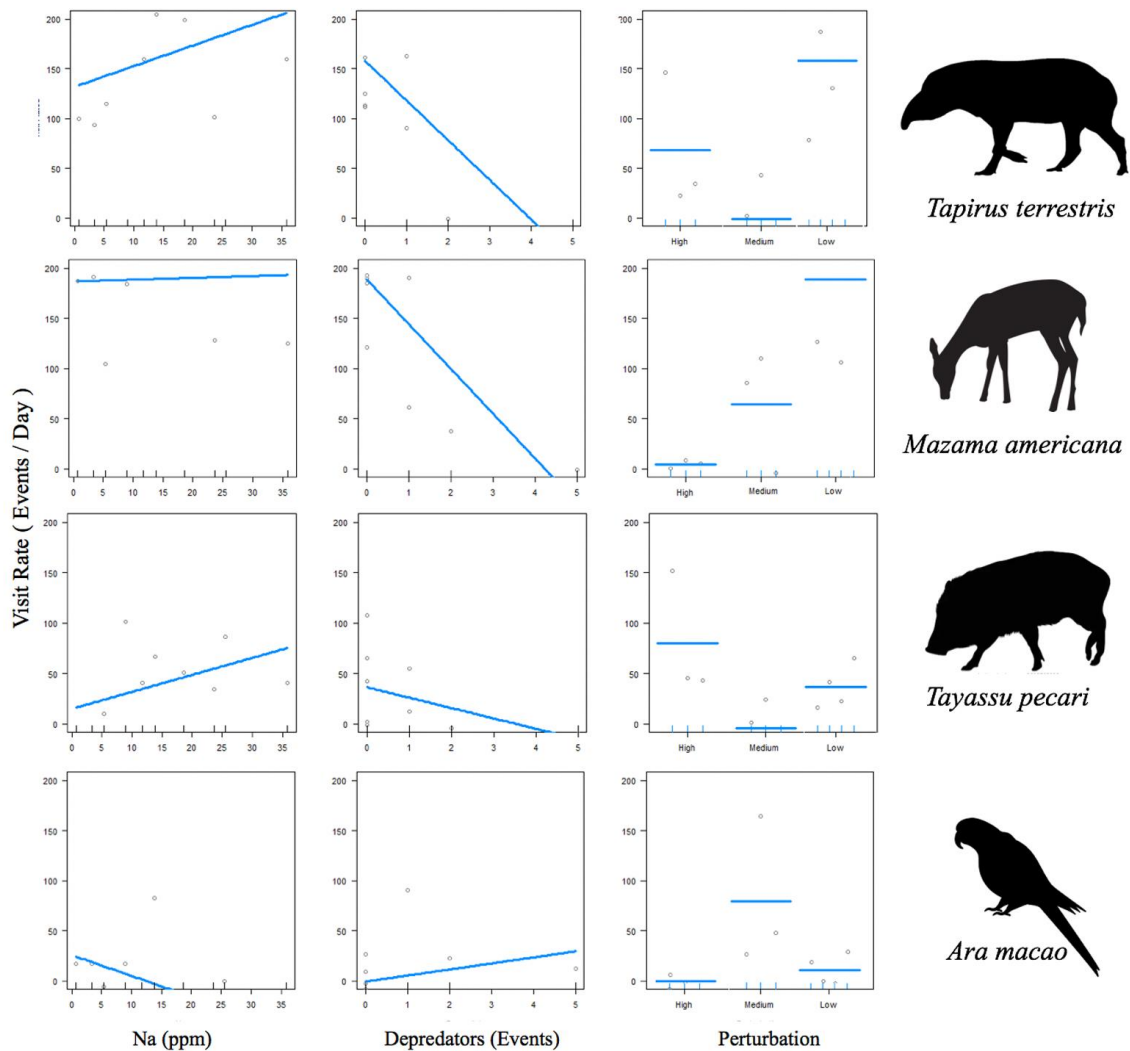


Figure 6. Effect of variables in generalized linear model for visit rates (Events/100 trap-days) from each of the most common species at salt licks. **Variables:** Na concentration (ppm), Depredators (Number of predator events) and Perturbation (Level of disturbance high/medium/low)

4. DISCUSSION

Salt licks are key areas for conservation in tropical forest. Animals invest a great amount of energy visiting salt licks to swallow soil. The multiple hypotheses about soil consumption generate more questions about what makes these places so particular. In this research, the physical and chemical characterization and animal visit rates were analyzed among 13 salt licks that are distributed in Yasuní National Park (YNP), Amazonia of Ecuador.

According to soil chemical composition of salt licks studied, Na concentrations is commonly higher in geophagic soils compared with control samples (adjacent non-ingested soil). These results suggest that Na concentration could be a key component for selection of soil consumed by animals. Agreeing with to mineral supply hypothesis about salt licks (Young *et al.* 2011), Na have been reported as the most consistently mineral present in high concentrations, in contrast of non-lick soils (Klein & Thing 1989, Kennedy *et al.* 1995, Abrahams 1999, Pebsworth *et al.* 2019). Na concentration levels in the organism drive directly regulation of fluid volume and osmolarity, acid-base balance and tissue pH, muscle contraction and nerve impulse transmission (Robbins 2012). In spite of this, some studies did not find representative difference in Na concentration among salt lick and non-ingested soil (Gilardi *et al.*, 1999; Molina, León & Armenteras, 2014). In Ecuador, there is just one research (Jaramillo, 2010) that compared salt licks soil composition with control sites and they neither found higher Na concentrations in salt licks studied, in contrast with this study.

It is important to consider that most of soil composition studies (including this) determine the total concentration of soil mineral elements, ignore their bioavailability (Wilson 2003); for this reason, the patterns found need to consider this possible overestimation. Compounds bioavailable to organism are normally much lower than total concentration measure (Wilson 2003), so without physiological conditions simulations in geophagic animals, mineral supplementation explanation remains speculative. In addition, soil chemical composition also presents low Ca concentration results in both salt lick samples and control ones, thus as this mineral is similar within the salt lick and in control sites, it suggests that the Ca is not a mineral which influence in visiting fauna.

It is possible to estimate slight differences in Mg concentration within some salt licks and control sites (see Figure 3). Despite of this, our results showed that these differences was not statistically significant among total salt licks. Mg concentration is not consistent pattern among all salt licks, some of them have found with higher Mg concentration and others with lower concentration of it. In the same way, K concentration have the similar inconsistent pattern within control and lick soils, being higher in some salt licks as S1 and S12, and lower in some ones other as S2 and S3. Studies as Lavelle *et al.* 2014 and Fack *et al.* 2020 have reported similar results soil salt licks composition. In our results, Mg and K concentration variables presented a high correlation value, both minerals are typically

mobile in soil but they tend to recombine to form clay minerals (Quesada *et al.* 2010), this could explain the similarities on its behaviour.

Respect to visiting fauna to salt licks, 567 events of visits from 13 species of mammals (433 events) and 10 species of birds (134 events) was recorded. Contrasting with other studies in salt licks from YNP, Blake *et al.* 2011 found 25 species of mammals (excluding bats) with an effort of 494 traps/night, coinciding with 12 of our results. Just *Panthera onca* was a new register, but a lower sample effort was used in this study (256 traps/night). In relation with birds, they found 15 species of birds, and additionally, we found *Ortalis guttata*, *Pyrilia barrabandi* and *Aramides cajanea* (*Pipile cumanensis* was register by Blake *et al.* (2011) as *Pipile pipile*, but according to Lentino (1975) and Crespo (2010), this specie and its distribution coincide with *Pipile cumanensis*).

Additionally, according to Salas-Correa & Mancera-Rodríguez (2020), species as *Aramides cajaneus* can be good ecological indicator of successional stages of a secondary forest. This specie was registered only in S13 (Table 3). This results can be implicated with the location of salt lick since this is in the middle of a local Huaorani agricultural system (communal chakra), also the salt lick closer to the community and to the road.

Only in areas with low and medium perturbation were records of predators at salt licks. Species as *Panthera onca* (top predator) could be a great biological indicator of a high diverse forest (Sergio *et al.* 2005) and consequently of a low disturbance. In this sense, our results suggest that salt licks classified as low-perturbed have a higher richness of predators. In addition, some records of carnivorous visiting salt licks also was recorded hunting. An event from *Leopardus pardalis* hunting a chiropter was registered at its peak of activity at night. We also recorded two additional hunting events, but without hunting success. *Leopardus pardalis* bat consume has been poorly reported in its diet (Emmons 1987, Moreno *et al.* 2006, Tinoco-Lopez & Camacho 2015), where it was assumed it hunting in the bats roots, and not in high activity places, as salt licks are considered (Voigt *et al.* 2007, 2008). These results are important because it evidences the use of salt licks, in addition to soil consumption, as key hunting sites to primary predators, as others studies have been reported before to another carnivores (Matsuda & Izawa 2008).

Most species frequently recorded in all salt licks (*T. pecari* and *T. terrestris*) are classified globally (IUCN) as Vulnerable (*T. pecari*: Keuroghlian *et al.* 2013; *T. terrestris*: Varela *et al.* 2019) and Endangered in Ecuador (*T. pecari*: Tirira & Zapata Ríos 2011; *T. terrestris*: Nogales *et al.* 2011), both were the principal salt licks visitors that stay for long periods (greater to 30min) and repeatedly times. These results suggest a high dependency of the soil intake from this two species and coincide with other reports (Lozano 2006, Tobler *et al.* 2009). However, species such as the *Ateles belzebuth* that is endangered according to IUCN (Link, *et al.* 2019) and it has been frequently recorded visiting salt licks (Blake *et al.* 2011; Link *et al.* 2013), are not recorded as much here. In these sense, patterns of visitation in salt licks (as biodiversity hotspots), could be used as indicators of the quality of a forest (King, *et al.*, 2016).

The general model (Figure 5) does not reflect an influence of Na concentration on frequency of fauna visits (Visit rates), considering predators events and perturbation levels variables. However, it has been widely reported for ungulate species, that intake of soil at salt licks is strongly related with the sought of Na (Fraser *et al.* 1980, Ayotte *et al.* 2006, Tobler *et al.* 2009, Poole *et al.* 2010). At a species level, within the results of this research, the specific models agreeing with this hypothesis with two from four most common species recorded, *T. terrestris* and *T. pecari*. There was found a positive effect of Na concentration above visit rates of these two ungulates (see Figure 6). Fruits, leaves and steams are the principal items of *T. terrestris* (Salas & Fuller 1996, François & Sabatier 2000, Galetti *et al.* 2001, Chalukian *et al.* 2013) and *T. pecari* diet (Altrichter *et al.* 2000, Perez-Cortez & Reyna-Hurtado 2008). Na concentrations is also related with dry season in terms of fruit production, founding low Na levels in plant resources in this season Haugaasen & Peres (2007). Most of the species registered at salt licks in this study are frugivorous and/or herbivorous. Fack *et al.* (2020), also evidence an increment of geophagy activity during dry season in Perú. This means a change for frugivorous/herbivorous animals and their mineral nutrition, probably reason why it has found more than 500 visiting events, most of them frugivorous and herbivorous. This decompensation of mineral supply, Na specifically, could be seriously harmful for many frugivorous and herbivorous species. Sodium participates with regulation of blood pressure, muscle contraction and conduction of nerve impulses,

and it contributes with more than 90% of extracellular fluid (Randall, Burggren & French, 1997).

In the case of *A. macao* the effect from Na concentration above the visit rate of the specie is negative. There have reported also that parrots and birds in general are strongly attracted by clay percentage at salt licks (Brightsmith & Muñoz 2004, Brightsmith *et al.* 2008, Powell *et al.* 2009). The high percent of clay in salt licks, link with other characteristics, are predicted to be correlate with adsorption of toxins. This is important especially for birds, because are most able to eat a great diversity of plants with different toxic secondary compounds (Oates 1978, Gilardi *et al.* 1999). Gilardi *et al.* (1999) also evidence the increment of secondary plant compounds at the dry season, suggesting the relation of salt lick visits in this season with clay content for detoxification more than a mineral supply.

However, Na can reach very low level in some ecosystems (Klaus & Schmidg 1993) and is one of the most mobile metals being easily weathered on the soil (Quesada *et al.* 2010). Considering this, and high levels of precipitation in western Amazonia, even in dry season (Karubian *et al.* 2009) it is necessary a greater number of salt lick sampled and control repetitions for a better understanding of the pattern.

About the number of predator events, the effect of the variable in the total visits rate does not change greatly in the species-specific models, except for *A. macao*. There is a negative effect of *depredators* variable on the visit frequency of the three most-frequent species, *M. americana* has the largest size effect, probable because with *T. terrestris* and *T. pecari*, *M. americana* is an smaller prey and not is founded in social groups (Bitetti *et al.* 2008). For *A. macao*, the effect remains negative probably because the predators founded are associated frequently with mammals prey (Moreno *et al.* 2006). In contrast, the effect of the perturbation level does change from general to specific models. The general model also describe a greater frequency of visit events in low-perturbed areas and less in high perturbed sites (Figure 5), while in the specific models this effect change in function of each species. *T. terrestris* visit rate appears to have a positive effect from low perturbation threats, but this does not change a lot in high perturbed salt licks. According to Teixeira-Santos *et al.* (2020) and Alvarez-Solas *et al* (data in prep.), *T. terrestris* probably has a great ecological plasticity, this means that this specie has an evolutionary adaptation to

environmental variations. Thus, it is understandable register of high visit rates in high and low-perturbed salt licks. Hunting is the greater threat to tapirs in Amazonia (Tobler *et al.* 2014) however, this pressure is commonly addressed to smaller species considering the accessibility of all study sites. For example, *M. americana* and *A. macao*, registered a positive effect of visit rates at low-perturbed salt licks. Both species have been reported commonly in well-preserved areas due to its vulnerability to anthropogenic threats. The principal threat to *M. americana* is hunting pressure, in consequence, they are likely to avoid deforested and agricultural zones (Weber 2015; Bitetti *et al.* 2008) that was the characteristics of the high-perturbed salt licks. Additionally, their high risk of threat to *A. macao* is its farming and nest destruction by poachers (Berkunsky *et al.* 2017; Dear *et al.* 2010), that is also associated with the accessibility to salt licks. Finally, *T. pecari*, present a negative effect of low Perturbation, despite of being also a hunting target in the zone. This pattern could be due to congregate in social groups (reaching 300 individuals), thus their priority are areas with high accessibility to fruits and food, since this diet is highly dependent of abundant plant production (Perez-Cortez & Reyna-Hurtado 2008) .

Considering all results described herein, the kind of model presented are just explicative estimations of the resulting information about this data. It could be improving in future line researches with a higher sample sizes and non-classic approaches (as Bayesian statistics) that had better address this ecological patterns with the sample size used. However, these models can be useful as a baseline and guidance for suggest the effect of variables above visit rates in this context.

In overview, there is not an only reason for explain geophagy in the wild but according to the history of it research, is widely associated with physiological stress of the species in function of their habitat. As conclusions of this research, salt lick have been characterized due to: (1) high soil Na concentration and high visit rates of different species of mammals and birds, and (2) a specific interaction between salt lick visits frequency and the Na concentration, the predation presence and the different levels of anthropogenic intervention, especially for some species. In this sense, it is clear the difference between salt licks soil Na concentration and unconsumed soil, but it is not quite related with a higher total visit rate. This specific relation is clearer at a specie level, specially in ungulates where higher Na concentration appear to influence the salt licks visits. On the other hand, in the

case of birds (*A. macao*), Na concentrations do not appear to influence salt lick selection. Besides, analysing its biological interactions, salt licks could lead to determine the distribution of predators in a specific zone or being key places to record unique behavioral factors within geophagic and non-geophagic species. In addition, the remarkable frequencies of threatened species that are visiting salt licks, and the constantly high richness of fauna, evidence their great importance in terms of conservation and their high vulnerability in front anthropogenic treats as accessibility and hunting. For all these reasons, it is important to develop multi-disciplinary studies that include ecological and geochemical approaches but also generate conservation programs with this information, with emphasis in landscape planning and management of protected area, as occurs in the Yasuní National Park.

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6. SUPPORTING INFORMATION

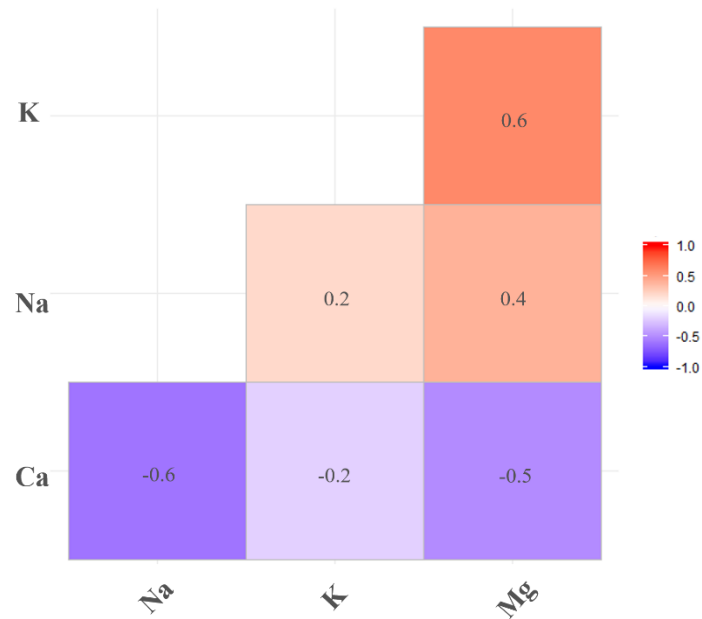


Figure S1. Correlation between mineral concentration in salt licks. Higher 0.5/-.05 values show a possible collinearity between variables and, in consequences, one must be reduced.

Table S1. Generalized linear model. (lineal regression, link function = identity).

Dependent Variable	Model	Variables in model	Df	AIC
<i>Visit rate</i>	Best	Na + Depredators + Perturbation	6	140.1
<i>Visit rate</i>	1	Na + Mg + Area+ Depredators + Perturbation	5	141.8
<i>Visit rate</i>	Full	All	3	144.5
<i>Visit rate</i>	Null	-	9	137.3

Table S2. Specific models for the four most common species.





Species	Predictor variables	β	SE	t value	P
 <i>Tapirus terrestris</i>	Soil Na concentration (ppm)	2.071	2.944	0.704	0.5131
	Depredators (Events)	-39.836	19.479	-2.045	0.0962
	Low perturbation level	90.32	81.56	1.107	0.3185
	Medium perturbation level	-68.852	77.584	-0.887	0.4155
 <i>Mazama americana</i>	Soil Na concentration (ppm)	0.1775	3.1652	0.056	0.9575
	Depredators (Events)	-44.4927	20.9448	-2.124	0.087
	Low perturbation level	112.462	90.6872	1.24	0.261
	Medium perturbation level	59.1799	83.4211	0.709	0.5098
 <i>Tayassu pecari</i>	Soil Na concentration (ppm)	1.683	1.868	0.901	0.4089
	Depredators (Events)	-10.256	12.358	-0.83	0.4444
	Low perturbation level	-43.636	51.745	-0.843	0.4375
	Medium perturbation level	-84.298	49.221	-1.713	0.1475
 <i>Ara macao</i>	Soil Na concentration (ppm)	-2.073	2	-1.037	0.347
	Depredators (Events)	6.017	13.236	0.455	0.668
	Low perturbation level	16.798	55.421	0.303	0.774
	Medium perturbation level	97.01	52.717	1.84	0.125



Figure S2. *Tapirus terrestris* at salt lick S1 (up) and S6 (down).

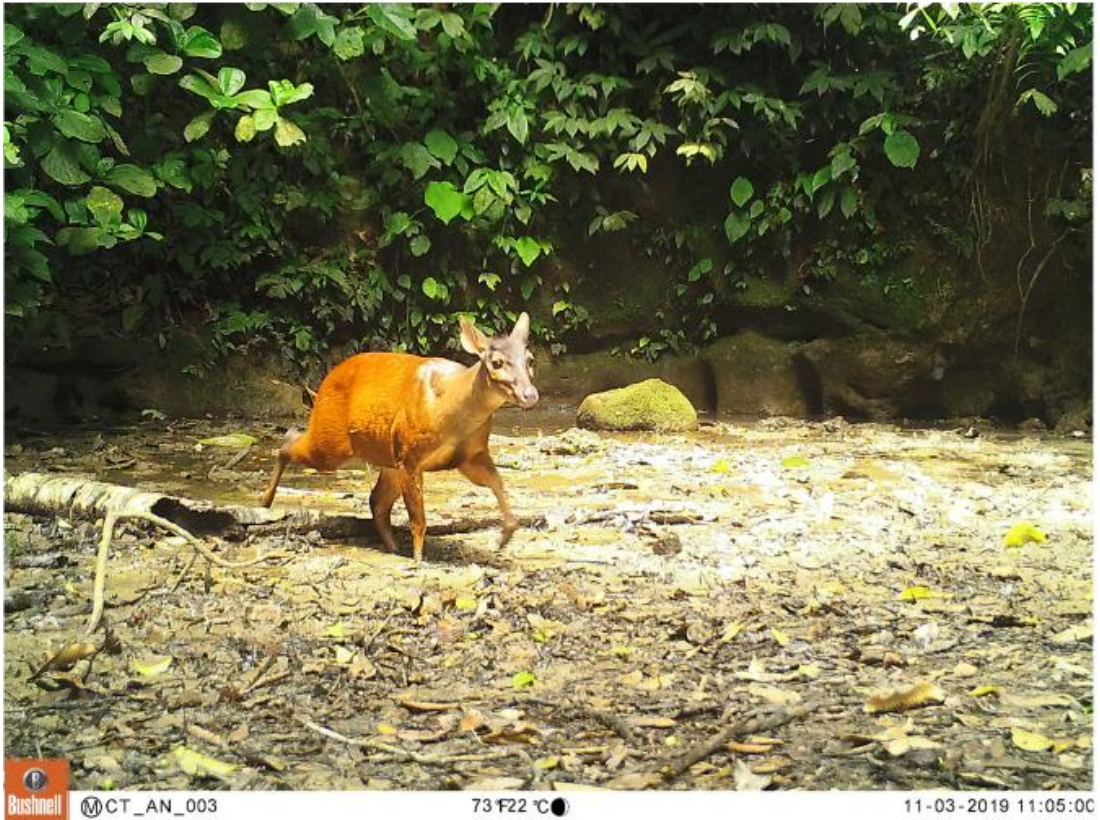


Figure S3. *Mazama americana* at salt lick S6. Near to Añangu communal



Figure S4. *Tayassu pecari* eating soil at salt lick S1, in Tambocochoa.



Figure S5. Group of *Ara macao* at salt lick S09.



Figure S6. Event of *Panthera onca* visiting salt lick S05.



11-07-2019 19:53:01



11-07-2019 19:56:59

Figure S7. Predation event by a *Leopardus pardalis* at salt lick S06.