



Parrot claylick distribution in South America: do patterns of “where” help answer the question “why”?

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Geophagy is well known among some Neotropical parrots. The clay apparently adsorbs dietary toxins and/or provides supplemental nutrients. We used location data and 23 environmental layers to develop a predictive model of claylick distribution using Maxent software. We related species characteristics to claylick use and examined how parrot assemblages using claylicks changed with distance from the centre of claylick distribution. Fifty-two parrot claylicks were reported from an area of ca 4 million km² but over 50% were restricted to a 35 000 km² region of southeast Peru and northern Bolivia. Claylicks were strongly associated with moist forest on younger (<65 millions of yr) geological formations and exposed river banks. The predictive model of claylick distribution matched our reported range well, with precipitation of warmest quarter, land cover, temperature seasonality, and distance from the ocean being most important predictors of claylick presence. Twenty-six of the region's 46 parrot species visited claylicks. Species differed greatly in their lick use, but body size, dietary breadth, abundance and other traits were poor predictors of lick use. We are confident that our survey identified the distribution of major parrot claylicks in South America, although less conspicuous parrot geophagy may occur elsewhere. We suggest that claylick distribution reflects both underlying geology (allowing claylick formation in only some regions) and the physiological need for geophagy among parrots in different parts of the continent. Data on the latter are inconclusive, but we argue that parrot claylick distribution supports the contention that geophagy is related more to sodium deficiencies than to protection from dietary toxins.

Geophagy, the intentional consumption of soil, occurs in a range of animal taxa on all continents, except Antarctica (Brightsmith 2004). In the Neotropics, large flocks of parrots visit claylicks on a regular basis to ingest soil at clearly defined claylicks (Gilardi and Munn 1998, Brightsmith 2004). Most studies of parrot claylicks in South America originate from study sites in Peru (Emmons and Stark 1979, Gilardi et al. 1999, Burger and Gochfeld 2003, Brightsmith and Munoz-Najar 2004) with the exception of single sites in Bolivia (Mee et al. 2005), eastern Ecuador (Duffie 2003), and southern Amazonian Brazil (Roth 1984). Parrot geophagy sites have also been recorded in Mexico (Valdés-Peña et al. 2008), the African Congo (May 2001) and Papua New Guinea (Diamond et al. 1999, Symes et al. 2006).

The reasons for avian geophagy have been extensively discussed elsewhere (Wink et al. 1993, Diamond et al. 1999, Sanders and Jarvis 2000, Symes et al. 2006). Many bird species consume grit for mechanical digestion of seeds and insects (Verbreeck 1994, Gionfriddo and Best 1995, Lopez-Calleja et al. 2000), whereas two hypotheses

have been proposed to explain the consumption of fine clay soils: 1) clay protects the birds from toxins and/or digestion inhibiting plant secondary compounds in their diets (Diamond et al. 1999, Gilardi et al. 1999) and 2) clay is a source of essential minerals such as sodium (March and Sadleir 1975, Brightsmith and Munoz-Najar 2004). Soils with high sodium may have relatively high magnesium, but levels of tested soil from southeastern Peru are five times less than the total magnesium concentration in foods of parrots (Brightsmith et al. 2008, Powell et al. 2009). Both toxin adsorption and sodium supplementation may be important (Brightsmith et al. 2008), but it is unclear if one of these physiological drives results in the daily phenomenon of many parrots descending to claylicks. It is these regularly visited sites, whether visited by parrots only, or a mixture of mammals and parrots, which are the focus of this study.

No study has looked at claylick use and distribution at a regional or continent-wide scale. We collate information on parrot geophagy sites across South America to

examine 1) claylick distributions, 2) claylick characteristics, 3) differences in the parrot assemblages using claylicks, and, 4) characteristics of individual species that use clay licks. We attempt to explain why geophagy sites are distributed as they are in respect to environmental factors, site availability and the physiological need for geophagy.

Methods

Survey of claylick locations

Information on South American claylick distribution was collected from March to August 2007 through a formal survey of ornithological experts via personal contact and posting on popular forums (see Acknowledgements for respondents' names). Published scientists and bird tour operators from all major South American countries were contacted (except French Guiana). Respondents were asked for the following information: 1) local name of the claylick; 2) geographical location; 3) the position of the claylick (major riverbank, stream or within forest); 4) height and width of the exposed soil surface; 5) number of visits made by respondent to the claylick; 6) the largest number of parrots recorded on the claylick; 7) species observed on the claylick. We excluded sites that were used by only one parrot individual as they fall outside the scope of regular avian geophagy.

Generic search engines (e.g. Google) were used to search for instances of the words: colpa, collpa, lick, saladero, barreiro, parrot and macaw. Trip reports for South American countries from the birding portal <www.travellingbirder.com> were also searched.

Where GPS coordinates were not provided information from nearest towns, rivers and associated travel times were used to calculate approximate locations. Information provided was either useful simply as location data that was used for distribution modelling, while a smaller subset of responses included species claylick use data that included information on local site conditions and associated species assemblages.

Environmental variables and claylick distribution

Claylick locations were mapped using Arc GIS ver. 9.2 (ESRI, Redlands, CA, USA). 100% minimum convex polygons (MCPs), as well as 75, 50 and 25% MCPs, were mapped for claylicks based on a system of elimination of the furthest outlying locations. A "centre of distribution" for claylicks was calculated by selectively rejecting outlying claylicks using MCP tools until a cluster of six claylicks within 25 km of each other was reached. A GIS database (Hearn et al. 2000) was used to overlay geographical information on the claylick locations to determine their distribution in terms of the following: 14 major habitats (relatively large areas of land or water that share a large majority of their species, dynamics, and environmental conditions), 25 land cover types (derived from the U.S. Geological Survey's "Global Land Cover Characteristics" database), 29 geological ages and 90 geological provinces. The geological provinces can be

broadly grouped into basins, which represent 24% of South America, and shields and other provinces which represent 26% (Hearn et al. 2000). Chi-squared tests were used to compare the observed and expected claylick distribution between geological age groups and between shields and basins.

Predicting claylick distribution

We used the machine learning method Maxent (Phillips 2005) to predict the spatial distribution of claylicks across South America. Maxent has been used in many areas of species distribution modelling based on locations; for example, locality information from herbarium specimens (Dudík et al. 2004, Phillips et al. 2006, Phillips and Dudík 2008), and we extend this use to claylick locations. Maxent can handle continuous and categorical variables, and non-linearity and interactions among predictors, making it well-suited for species distribution modelling (Phillips et al. 2006), especially with small sample sizes (Hernandez et al. 2006). Maxent identifies cells with suitable conditions for occurrence (Phillips et al. 2006), with the importance of individual environmental variables (training gains) based on decreases in gains when that predictor is omitted from the predictor set.

We used 19 bioclimatic variables from WorldClim database (Hijmans et al. 2005). These Bioclim variables (~1 km spatial resolution), were generated from monthly averages of minimum, maximum, and mean temperatures, and average precipitation for the period 1950–2000 (Nix 1986, Hijmans et al. 2005). We used vegetation continuous field (VCF) products generated using optical remote sensing data from the Moderate Resolution Imaging Spectroradiometer (MODIS) (Hansen et al. 2000). We used Advanced Very High Resolution Radiometer (AVHRR) land use and land cover map as a categorical predictor (Hansen et al. 2003). In addition, we included U.S. Geological Survey's Hydro-1K variables elevation, slope, aspect, flow accumulation, flow direction and compound topographic index (Supplementary material Table S1). We converted aspect into two linear and orthogonal gradients- northness (cos (aspect)) and eastness (sin(aspect)) (Kumar et al. 2006). We calculated Euclidean distance from the Pacific and the Atlantic oceans as a surrogate for the influence of nutrient deposition from precipitation events using a South American continent boundary shapefile in Arc Map using "Euclidean distance" function in spatial analyst. Variables that had different spatial resolution (e.g. MODIS data; 500 m resolution) from Bioclim variables were resampled to ~1 km resolution (using bilinear method) to match the resolution for Maxent analysis.

We distilled the 40 data layers to a set of less correlated variables, after assessing cross-correlations (Pearson product-moment correlation coefficient, r) among predictors (Neter et al. 1996) based on 1050 localities – 50 claylick locations and 1000 randomly generated points from the northern half of South America (Buermann et al. 2008). Only one variable from a set of highly correlated ($r \geq 0.90$) variables was used in the analyses. The decision to drop or include a variable was made by considering the

ease of interpretation and the biological relevance with the claylick distribution. We retained 23 environmental layers (Supplementary material Table S1), mainly to aid interpretation as Maxent is largely robust to covariance among predictors.

Correlates of claylick use by parrots

Parrot species range maps from Juniper and Parr (1998) were overlaid onto the location of each claylick to provide a comparable measure of a claylick's potential species richness. Although not entirely accurate for all species, these are consistent and considered superior to other similar sources in a recent macroecological mapping exercise (Blackburn et al. 2004, Mathias et al. 2004).

For each parrot species whose distributions overlapped at least one claylick, range size data was obtained from BirdLife International species accounts (BirdLife International 2007). This information was not available for the Amazonian parrotlet *Nannopsittaca dachilleae*, so range size was calculated by remapping the species map in Juniper and Parr (1998) with Arc GIS. A measure of relative abundance was calculated for each species as follows: rare = 1, uncommon = 2, common = 3, and abundant = 4 (BirdLife International 2007). An index of habitat breadth (excluding urban) was created by summing the species' presence according to Juniper and Parr (1998) in the following six categories: 1) Andean foothills or cloud forest; 2) lowland and humid forest including Atlantic rainforest, varzea and terra firme; 3) gallery forest; 4) savanna; 5) cultivated; 6) woodland including cerrado, caatinga, chaco and deciduous forest. An index of dietary breadth was calculated by summing, for each species, the incidences of known feeding on the following ten dietary categories as listed in Juniper and Parr (1998): palm (fruit pulp and or seeds); other nuts; miscellaneous (leaf or flower) buds; berries; fruit; seeds; flowers including blossoms or nectaries; grain crops; insects; other (e.g. bark, leaves). These data were supplemented with field observations from Peru for black-capped *Pyrrhura rupicola* parakeet and blue-headed macaw *Primolius couloni* (Lee and Brightsmith unpubl.), for which Juniper and Parr (1998) listed no information. Mean weight for species was obtained from Dunning (2008).

Mann-Whitney U-tests were used to compare species attributes (body weight, range size, ranked abundance, habitat and dietary breadth) for claylick users and non claylick users. Spearman's rank correlations were used to look for relationships between the proportion of licks used by lick users and body weight, abundance, range size, number of licks within range, and dietary and habitat breadth.

Parrot community analysis

A non-metric multidimensional scaling analysis (NMDS: CAP, Pisces Conservation 2002) was used to compare parrot community composition across claylicks. NMDS maximizes rank-order correlation between distance measures and distance in ordination space. NMDS has several advantages over other ordination methods, since

it does not assume linearity of the data and it does not require data transformation (Clarke 1993). Analysis was run using the Sørensen index as the distance measure, a principal component analysis (PCA) starting configuration (maximum of six axes and 200 iterations), and a final solution (number of axes) determined by minimising stress (McCune and Grace 2002). A Spearman's rank correlation analysis was performed between the scores on axes 1 and 2 and distance from the centre of distribution (see earlier) of the claylick.

Results

Claylick locations

Locations of 62 claylicks were received. One response, providing the locations of 33 claylicks from the Los Amigos river system in southeast Peru, was excluded to avoid any adverse effects upon modelling results through sample selection bias (Phillips 2008). Birdwatching trip reports yielded no additional claylicks, but internet searches led to the location of two additional claylicks. Ten locations were discarded due to potential location repetition or poor data quality, leaving 52 claylick locations (Fig. 1). Two locations were removed during GIS analyses to maintain only one presence location within a 1 × 1 km pixel (i.e. spatial resolution of predictor variables).

Reported distribution of claylicks

Claylicks occurred in Paraguay, Peru, Bolivia, Brazil and Ecuador, and were concentrated along the eastern base of the Andes in Ecuador and Peru. No parrot geophagy sites were reported from the following areas, and their absence was checked with the following individuals: Argentina (E. H. Bucher and J. F. Masello pers. comm.); Atlantic rainforest (M. A. Pizo and S. Marsden pers. comm.);

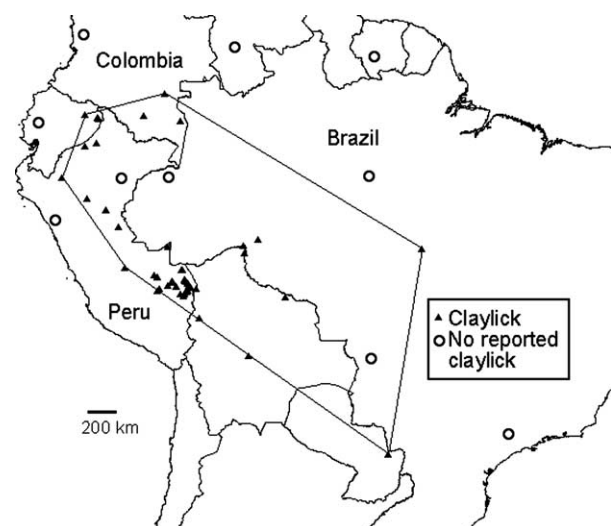


Figure 1. Distribution of known parrot claylicks in South America (with 100% minimum convex polygon) in relation to topographical relief and areas with no parrot claylicks. For 25 claylicks at known altitudes, all are below 1000 m and all but three are below 500 m.

central Amazonian Brazil (A. Whittacker pers. comm.); the Pantanal region (I. Pfeifer pers. comm.); Suriname (J. H. Ribot pers. comm.); and Venezuela (D. Ascanio and S. Beissinger pers. comm.).

All reported claylicks were within the “tropical and subtropical moist broadleaf forest” (TSMBF) habitat type, with all but one claylick occurring in the “evergreen broadleaf forest” land cover type (a single claylick in Bolivia was in “deciduous broadleaf forest”).

The 100% minimum convex polygon (MCP) which contained all claylicks was 3.87 M km². The 75% MCP was only 0.60 M km² (15.6% the area of the 100% MCP), and the 50% MCP was just 0.035 M km² (<1% of the 100% MCP). Most claylicks were found in southeast Peru (Fig. 1). The 100% MCP covered 18 geological provinces, of which nine contain claylicks. More claylicks than expected (43) occur within geological basins than on shields ($\chi^2 = 29.4$, $p < 0.001$), when considered as a proportion of the total area of TSMBF. The 100% MCP included 17 different geological ages as classified by Hearn et al. (2000), but claylicks were found in only seven. More claylicks than expected ($\chi^2 = 12.5$, $p = 0.002$) occurred in younger geological age groups (<65 million yr old), which contain 43 (83%) of the claylicks yet covered only 60% of the total area (Table 1).

Predicted distribution of parrot claylicks

The Maxent predicted distribution of claylicks (Fig. 2) showed broad agreement with their known distributions, suggesting that our sampling was adequate for predicting the current distribution. Bio18 (precipitation of warmest quarter; 31.3%), land cover (20.4%), Bio 4 (temperature seasonality; 12.1%), distance from ocean (7.2%), and MODIS herbaceous cover (4.8%) contributed most to the Maxent prediction. We used area under the receiver operating characteristic curve (AUC), to evaluate performance of the model at all possible thresholds, and to compare among algorithms (Phillips et al. 2006). We created 10 random subsets of the data with 80% of the data (40 records) used for training the model and 20% of the data (10 records) used for testing the model performance. The average test AUC was 0.94 (AUC range 0.85–0.99), which shows that the model predictions would be correct 94% of the time in finding claylicks at locations where they are predicted to be present. The final model was run using all the data (50 records) (Fig. 2).

Physical characteristics of claylicks used by parrots

Physical attributes of claylicks were reported for 27 sites (Table 2), of which 74% (20) were located on the

banks of large rivers, 19% (5) on stream banks and 7% (2) in forest interiors. Mean claylick height was 10.8 ± 9 m ($n = 26$) and width was 91 ± 139 m ($n = 26$), indicating much variation in dimension across sites. Where height was less than one meter in cases where parrots had been recorded on typical mammal claylicks, the area was calculated as the square of the reported width, or length and breadth where this information was provided.

There was a significant positive correlation between number of monitoring visits and number of parrot species recorded at claylicks ($r_s = 0.51$, $p = 0.01$, $n = 25$), so we included only the 18 claylicks that had been visited nine or more times in the subsequent analyses (the correlation between species richness and visitation was no longer significant at this level; $r_s = 0.33$, $p = 0.19$, $n = 18$). There were significant positive correlations between claylick area and species richness ($r_s = 0.501$, $p = 0.034$, $n = 18$) and maximum number of individuals recorded ($r_s = 0.74$, $p = 0.001$, $n = 17$). Maximum number of parrots was correlated with distance to centre of distribution ($r_s = 0.53$, $p = 0.029$, $n = 17$), but not with distance to Atlantic Ocean ($r_s = 0.382$, $p = 0.13$, $n = 17$).

Correlates of claylick use among parrots

Twenty-six of a potential 46 species (57%) (13 of 17 genera) whose range overlapped with at least one claylick were reported as using one or more claylicks (Supplementary material Table S2). Of the genera with more than three species (*Amazona*, *Ara*, *Aratinga*, *Brotogeris* and *Pyrrhura*), half or more of all species visited claylicks, except for *Amazona* (three from eight). All five *Ara* species visited claylicks.

Species using claylicks had larger ranges than non-users (claylick users: $4.25 \text{ M} \pm 2.99 \text{ M km}^2$, non-users: $2.12 \text{ M} \pm 1.58 \text{ M km}^2$; $U = 142$, $Z = 2.19$, $p = 0.029$). Users tend to be larger than non-users, but this difference was not significant (claylick users: 322 ± 378 g, non-users: 192 ± 118 g; $U = 244$, $Z = 0.069$, $p = 0.95$). There was no difference between users and non-users in terms of habitat breadth (claylick users: 2.8 ± 1.3 , non-users: 2.9 ± 1.4 ; $U = 257$, $Z = 0.07$, $p = 0.95$), dietary breadth (claylick users: 3 ± 1.1 , non-users: 2.7 ± 1.1 ; $U = 187$, $Z = 0.99$, $p = 0.33$), or ranked abundance (claylick users: 2.9 ± 0.7 , non-users: 2.9 ± 0.7 ; $U = 245$, $Z = -0.06$, $p = 0.95$). Within those 26 species using claylicks, the mean proportion of available claylicks used was 0.44 ± 0.24 , with proportion of claylicks used significantly correlated with habitat breadth ($r_s = +0.40$, $p = 0.045$), but not with range size ($r_s = +0.18$, $p = 0.37$), ranked abundance ($r_s = +0.06$, $p = 0.77$), or dietary breadth ($r_s = +0.29$, $p = 0.17$).

Table 1. Age of geologic settings for South American claylicks. The proportional area of South America is from Hearn et al. (2000). Significantly more claylicks than expected occur in Quaternary and Tertiary regions than in older age groups ($\chi^2 = 12.5$, $p = 0.002$).

Age grouping	Age range (millions of yr)	Proportional area of South America	Reported claylicks	Expected claylicks
Quaternary	1.8–0	0.31	20	16
Tertiary	65–1.8	0.29	23	15
Precambrian to Tertiary	4500–65	0.40	8	20

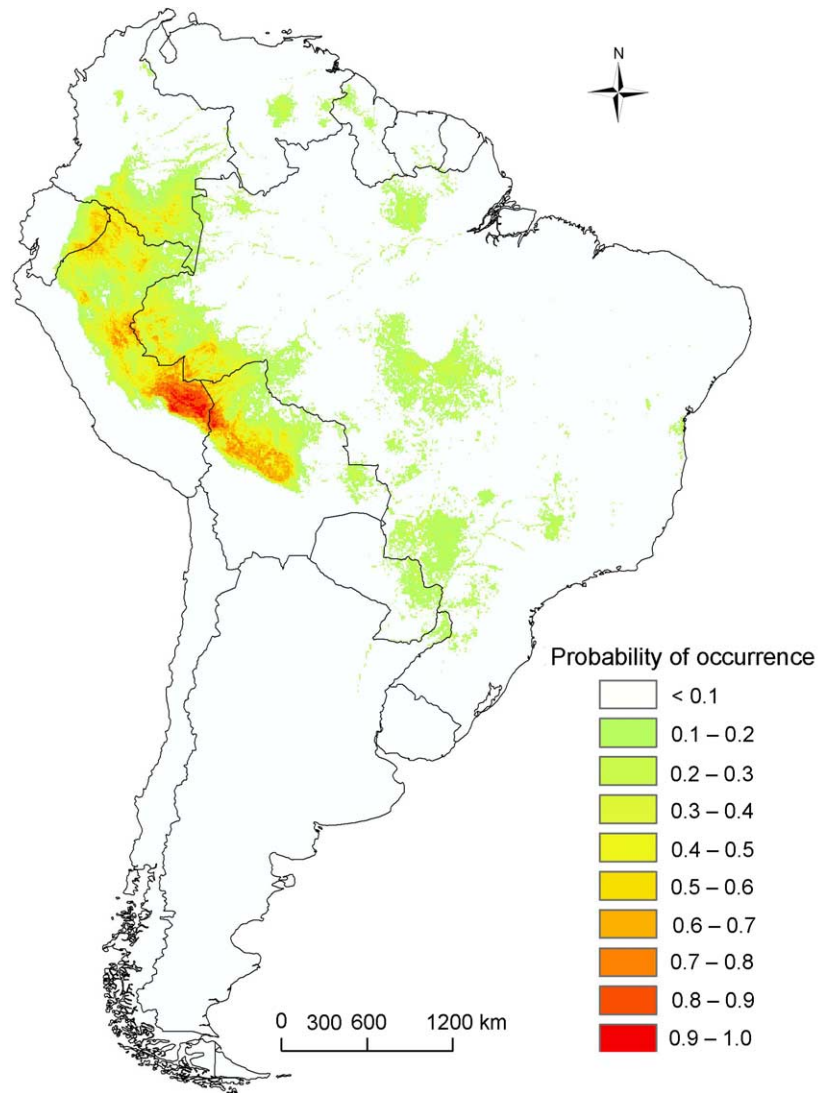


Figure 2. Predicted probability of occurrence of parrot claylicks in South America as determined by Maxent model using 23 environmental variables (Supplementary material Table S1). Red regions are areas with highest probability of claylick occurrence.

Differences in parrot community composition across claylicks

Claylicks and their species composition range from unique single species claylicks to multi-species claylicks with member species represented at most claylicks. The assemblages of claylick using parrots varied significantly with distance from the claylick centre of distribution (axis 1: $r_s = 0.42$, $p = 0.037$, $n = 25$; axis 2: $r_s = 0.42$, $p = 0.037$). Licks near the centre had higher diversity while most outlying claylicks were used by relatively few species (Fig. 3).

Discussion

Did our survey capture claylick distribution across South America?

Most parrot claylicks were reported from the forest ecozones of the western Amazon basin in Bolivia, Peru,

Ecuador, Brazil and Colombia. The claylick locations we received may be biased due to a range of issues including site accessibility, survey outreach, and associated demographics of respondents. However, extensive efforts were made to follow up on regions where no claylicks were reported. We received few responses from Colombia and large claylicks may exist unreported in this country. Isolated geophagy incidents occur outside the range reported here, for instance green-rumped parrotlet *Forpus passerinus* eat soil in Venezuela, but this is rare and unusual (S. Beissinger pers. comm.). Overall, we are confident that regular parrot geophagy is a western Amazon phenomenon.

The analysis captured the distribution well enough because predicted distribution with $>70\%$ probability and real location data did not differ greatly. The Maxent model predicted little extension of the reported range, apart from extrapolations into “data poor” areas such as northern Bolivia and the Brazilian province of Acre. A degree of overprediction in the Maxent model (but at probabilities $<20\%$) occurred for some regions where we are confident there were no claylicks (around Iquitos in Peru, in

Table 2. Claylick physical and bird use characteristics for sites where detailed information was available. No map references are given in order to protect sensitive sites. * Sites in regions with Miocene marine deposits.

Name	Country	Type	Lick height (m)	Lick width (m)	Max no. birds seen	Total number of species on lick	Potential no. of parrot species in lick area	Distance to centre of distribution
Vallee de la Luna ¹	Bolivia	River	35	150	1044	6	15	700
Flor de Oro ^{2*}	Bolivia	Forest	0.5	25	5	1	25	250
Tuichi ³	Bolivia	River	10	20		1	22	200
Cristalino Saliero ⁴	Brazil	Stream	0.2	25	10	1	21	1800
Rio Madeira ^{5*}	Brazil	River	10	15	200	3	19	500
Aripuana ⁶	Brazil	River			1000	5	20	1200
Yasuni ⁷	Ecuador	River	15	30	80	2	20	1550
Saladero de las loras ⁸	Ecuador	River	7	2	20	3	21	1450
Tiputini colpa de loras ⁹	Ecuador	River	8	6	30	2	21	1450
Tiputini colpita de pericos ⁹	Ecuador	River	10	15	100	6	21	1450
Mbaracuya ¹⁰	Paraguay	Forest	1	12		1	13	1900
Heath ^{11*}	Peru/Bolivia	River	6.25	44.5	350	12	24	50
Pantiacolla ^{12*}	Peru	River	20	200	500	9	21	200
Blanquillo ^{13*}	Peru	River	20	40	100	8	21	150
Mascoitania ^{14*}	Peru	River	25	55	100	11	21	250
Rio Blanco ^{15*}	Peru	River	4	12	150	10	21	150
Explorer's Inn ^{16*}	Peru	River	4	10	180	11	21	50
Colpa Hermosa ^{17*}	Peru	River	10	30	350	12	21	50
Manu ^{18*}	Peru	River	12	350	600	10	21	150
Colpa Chuncho ^{17*}	Peru	River	10	400	800	13	21	50
La Cachuela ^{17*}	Peru	River	10	300	250	5	21	0
El Gato ^{19*}	Peru	Stream	12	50	150	12	21	50
Colpita Posada ^{20*}	Peru	Stream	5	20	150	10	21	50
Piedras LPBS ^{21*}	Peru	River	18	28	400	12	21	50
Refugio ^{22*}	Peru	Stream	1	25	20	2	21	50
Colpa Colorado ^{23*}	Peru	River	27	500	1400	16	21	100
Tarapoto ²⁴	Peru	Stream	1	2	25	2	20	1000

Respondent or paper: ¹Mee et al. (2005), ²R. Wallace, B. Hennessey, ³B. Hennessey, ⁴A. Lees, ⁵M. Cohn-Haft, ⁶Roth (1984), ⁷D. Luther, ⁸G. Banda-Cruz, ⁹J. Fabara, ¹⁰M. A. Morales, ¹¹P. Nunez, C. Kirkby, P. Donahue, O. Doest, M. Berrocal, ¹²W. ten Haven, ¹³B. Quispe Estrada, H. Lloyd, ¹⁴C. Torres, ¹⁵O. Doest, ¹⁶V. Vysna, ¹⁷A. Lee, ¹⁸Burger and Gochfeld (2003), ¹⁹Hammer, A. Lee, ²⁰Y. Quispe, ²¹E. Hume, ²²C. Cosmopolis, ²³K. Quinteros, ²⁴R. Ahlman.

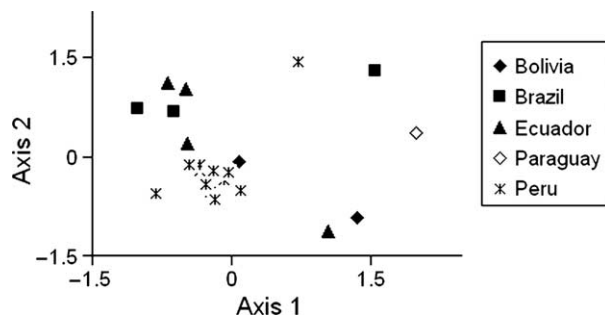


Figure 3. Non-metric multidimensional scaling (NMDS) visual interpretation of scaled distances (axis 1 vs axis 2) for 25 claylicks based on similarity of species composition (STRESS = 0.17). Claylicks are defined by country as an indication of spatial proximity. The only major cluster indicating a community relationship is based around the claylicks of Peru, Ecuador and western Brazil. Outliers are typified by claylicks with low species richness.

Venezuela, the Brazilian Atlantic Forest and in northern Brazil south of Guyana and Suriname, Fig. 2).

We are less sure that we know about all the parrot species that use claylicks. Parrot species richness increases with observer effort and few claylicks have been the subject of ongoing investigations. Parrot species with ranges in southwest Amazon and adjacent Andes, such as green-cheeked parakeet *Pyrrhura molinae*, may engage in geophagy unreported as of yet.

Characteristics of the parrot community that use claylicks

Our analyses showed that parrot claylicks are strongly associated with tropical forest areas. Community analysis indicated that claylick parrot assemblages are largely similar within the core zone of claylick distribution. In turn, we suggest that tropical forest parrots appear to have a greater need to engage in geophagy than communities associated with savanna or other biomes where no parrots have been reported using mammalian geophagy sites, for example, in the Pantanal, Brazil (de Oliveira et al. 2006).

Life history characteristics were poor correlates of claylick use among parrots. Although Diamond (1999) reported a trend towards larger species of birds eating clay in New Guinea, median parrot weight was not significantly higher for South America claylick users compared to non-users. The lack of strong life history correlates of claylick usage among parrots coupled with the strong spatial autocorrelation among parrot communities using claylicks may indicate a general need for geophagy among the group as a whole within specific regions rather than a requirement by some species across larger geographical areas. For instance, the large *Ara* spp. although found across the continent, consume soil nowhere else in their range except in southeast Peru, where they are joined by a host of other species. If true, it may indicate that the drive to consume soil may be more a product of a general dietary deficit across the group, rather than a specific need for detoxification which is more likely to be species-specific as diets differ

widely across parrot species within a given area (Ragusa-Netto 2007, Matuzak et al. 2008).

Conditions needed for claylick formation

The presence of soils suitable for geophagy requires the deposition and subsequent exposure of clays, such as smectites, which retain sodium and bind toxins (Levy et al. 1998), so the white sand deposits from Suriname would be unsuitable for parrot geophagy. The Amazonian basin encompasses several Cenozoic sub-basins delimited by structural or morphologic arches (Roddaz et al. 2005). Geophagy sites were strongly correlated with basins and younger geological types in the western Amazon, which are regarded as eutrophic compared to northern, central and southern Amazon (Tuomisto 2007). Geophagy is rare on the Guiana and Brazilian shields, whose soils are mostly nutrient poor (Stark 1970, Haridasan 2001). However, sediments of the lower Amazon River have a high content of smectites (Guyota et al. 2007). Smectites are also found in Paraiba (Rodrigues 2003) and Para, Brazil (Guerra et al. 2006) and other regions where no parrot geophagy is reported.

The role of local geology needs to be investigated further as sedimentation and lateral river-channel migration directly influence the patterns of riverine ecosystems in Amazonia (Toivonen et al. 2007). A claylick on the Tambopata River occurs on Miocene tidal deposits (Brightsmith 2004) associated with a large lake (Lake Pebas) that existed in western Amazonia around 11–18 million yr ago (Hoorn et al. 1995) that disappeared with Andean uplift and sedimentation (Räsänen et al. 1995). Other claylicks on this river system are on fluvial sediments downstream of these deposits (Lee unpubl.). Fluvial sediments of suspension rich rivers of Andean origin are rich in their extractable mineral nutrient content (Kalliola et al. 1993). In contrast, to the north the Marañon basin experienced the emersion of a forebulge that induced the retreat of Lake Pebas and is associated with the deposition of the “White Sand” deposits (Roddaz et al. 2005). These sandy deposits mean that the clays necessary for the formation of claylicks are not readily available, part explaining the lack of claylicks around the Iquitos area (Escamilo and Pérez 2005).

Depositions of suitable sediments need to be exposed and visible to parrots in order to be found and consumed. Geophagy is not observed along the course of the Amazon River from Iquitos to beyond Manaus, Brazil where the flooding regimes of Igapo and várzea forests inundate suitable soils (Worbes 1985). In contrast, southeast Peru, where the highest number of claylicks are reported, is characterized by tectonic uplift and downcutting rivers that expose large expanses of river bank (Puhakka et al. 1992). These continue to be exposed during the wet season when visitation rates by macaws and large parrots are at their highest (Brightsmith 2004).

What drives geophagy among Neotropical parrots?

Claylick soils are known to provide protection against alkaloid toxins, which has led to the theory that parrots

consume soil predominantly as a protection from dietary toxins (Gilardi et al. 1999), as parrots consume nutritionally rich but potentially highly toxic foods, especially during the dry season when food is limiting (Terborgh 1986). Identifying potentially toxic compounds in seeds is not sufficient to demonstrate toxicity, as toxicity is a dosage- and animal-specific trait (Janzen et al. 1986). For example, the Hawaiian palila *Loxioides bailleui* specialize on seed embryos of the tree *Sophora chrysophylla*, which contain potentially toxic alkaloids (Banko et al. 2002). We are unaware of studies which look at the toxicity of Neotropical parrot diets and none that explore the geographical variation in toxicity. In fact there is limited study of potential toxins in the seeds of most tropical plants. However, seeds from a range of Costa Rican members of the Fabaceae family, identified as an important food family for parrots (Matuzak et al. 2008), contain multiple defensive compounds that can potentially reduce seed predation (Janzen et al. 1986). Most leaves in tropical forests are defended by a wide variety of secondary metabolites (Coley and Barone 1996) and some of these compounds are found in immature fruit and seeds. In general, better plant defences are associated with plants on poor soils (Janzen 1974, McKey et al. 1978, Coley and Barone 1996). If protection from toxins was driving claylick use, we would predict high levels of geophagy in nutrient poor areas such as the Guiana and Brazilian shields (Haridasan 2001). Instead, parrot claylicks are centred on the nutrient rich deposits at the base of the Andes and we argue that this is not what we would expect if geophagy was driven by the need for protection from dietary toxins. Ultimately, parrots are a family of birds renowned for their ability to consume “toxic” food sources wherever they are found (Juniper and Parr 1998), with *Amazona* spp. requiring fifty-times the human dose of quinidine to attain similar circulating levels of the drug (Gilardi 1996). The predation risks and time investments associated with claylick visitation can provide only little, if any, extra benefit in extending their capacity to deal with unripe fruit or seeds for which there are limited ecological avian competitors.

Due to the physiological importance of sodium and its relative scarcity in many ecosystems, the regulation of sodium levels and sodium seeking behaviour are under tight hormonal control (Schulkin 1991). If sodium deficits are a potential driver of geophagy in this system, we would predict that claylick use would be greatest in areas with the lowest sodium concentrations in the food supply. Claylick use was concentrated in tropical moist forest areas where turnover of sodium is very rapid, as ecosystems do not conserve this element (Whittaker et al. 1979) and absent from temperate and more arid areas where leaching and weathering are reduced, and sodium concentrations usually higher (Levy et al. 1998).

Claylick use increases with distance from oceanic influences. Seasalt aerosol influx in rainfall is an important source of ecosystem sodium, and deposition decreases with distance from the coast. Inputs close to the coast can be as high as 65 kg ha⁻¹ (Heartsill-Scalley et al. 2007) compared

to the Amazon average of 3 kg ha⁻¹ (Mortatti and Probst 2003). The Andes form a barrier to Pacific rainfall influences to the Amazon basin (Strecker et al. 2007), so oceanic influence is from the eastern sea bodies of the Caribbean and Atlantic Oceans. Geophagy is conspicuously absent from coastal forests such as the Atlantic rainforests and basins of northeast Brazil and instead found in the western Amazon where sodium hunger is predicted to be greatest.

Comparisons with mammalian geophagy

To date, no study has attempted to map mammalian geophagy at a landscape level in South America. Most studies focus on a few species at a small number of sites (Ferrari et al. 2008). However, the literature suggests that patterns of mammalian geophagy may mirror those of avian geophagy with some simple differences. In general, mammalian geophagy is apparently more common and more widespread as mammals are less restricted as to the types of sites they can use (parrots use mostly river banks sites while mammals use river banks along with areas in the forest). Mammals which remove more soil than birds may also be more capable of excavating new sites and maintaining old sites free of vegetation. Mammals (including tapir *Tapirus terrestris*, collared peccary *Tayassu tajacu*, red brocket deer *Mazama americana*, red howler monkey *Alouatta seniculus*, brown agouti *Dasyprocta variegata*, southern Amazonian red squirrel *Sciurus spadiceus* and capybara *Hydrochoerus hydrochaeris*) have been observed feeding at several parrot claylicks in southeastern Peru (Kyle 2001, Lee and Brightsmith unpubl.). In addition, recent reports on bat geophagy are in the area where parrot geophagy is observed most (Bravo et al. 2008, Voigt et al. 2008), suggesting that characteristics of the soil appear to be attractive to both mammals and birds.

A review of primate geophagy in South America highlights its occurrence in the Amazon, with relatively few reports from the Brazilian Atlantic forest (Ferrari et al. 2008). Spider monkey *Ateles* spp. in Ecuador and Peru came to the ground more often to eat soil, rotten wood or termitaria compared to four sites in Central America where sodium is higher and we would predict geophagy to be lower (Campbell et al. 2005). Where geophagy at ant heaps has been observed in the coastal species masked-titi monkeys *Callicebus personatus* (Müller et al. 1997) and red-handed howler monkeys *Alouatta belzebul* (de Souza et al. 2002) sodium was not considered the cause of geophagy, although in neither of these reports could geophagy considered to be regular. Moustached tamarin *Saguinus mystax* from Peru (Heymann and Hartmann 1991) and red howler monkey *Alouatta seniculus* from Colombia (Izawa 1993) have also been recorded eating soil in the western Amazon. Sodium is the most common reason cited for geophagy world wide, so future studies could test the hypotheses proposed here for birds, using regular geophagy by mammals. Attempts to distinguish between causes of “regular geophagy” and “incidental geophagy” may be enlightening.

The distribution of parrot claylicks across South America has important community and conservation implications for parrot populations. The western Amazon has until now been little impacted by anthropogenic change but now faces increasing infrastructure development with associated conservation implications, including colonisation, deforestation and forest fragmentation. Sites in southeast Peru recording up to 20 parrot species are an anomaly in the trend of decreasing parrot species richness across South America from the northeast to southwest (Blackburn et al. 2004). If the presence of geophagy sites aid the persistence of marginalized species in this region remains to be seen, but the impact of increased disturbance on parrot activity at riverside geophagy sites needs to be investigated. The distribution of parrot claylicks across South America lends strength to the theory that the need for sodium results in one of the western Amazon's most interesting ornithological phenomena, yet much still needs to be understood on the factors, both human and ecological, that influence parrot geophagy across South America.

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