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Avian Geophagy and Soil Characteristics in Southeastern Peru[1]

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ABSTRACT

We observed ten species of psittacids, three species of columbids, and two species of cracids consuming soil from banks of the lower Tambopata River in southeastern Peru. Our study used observations and soil analyses from eight exposed riverbank sections to test the predictions of three models to determine why birds consume clay: mechanical aid to digestion (grit), adsorption of dietary toxins, and mineral supplementation. We found that preferred soils were deficient in particles large enough to aid in the mechanical breakdown of food and help digestion. Percent clay content and cation exchange capacity (CEC), both predicted to correlate with adsorption of toxins, did not differ between used and unused sites as had been found in a similar study. Instead, preferred soils were more saline and had higher concentrations of exchangeable sodium. This suggests that the choice of soils at our site was based primarily on sodium content. Birds may be using the heavy, plastic texture of soils rich in clays and high in exchangeable sodium as a proximal cue for soil selection. Our findings suggest that avian soil selection decisions depend on the range of available soil characteristics.

RESUMEN

Observamos diez especies de Psittasidos, trés especies de Columbidos, y dos especies de Cracidos consumiendo suelo de los bancos del bajo Río Tambopata en el sureste del Perú. Nuestro estudio utiliza observaciones de aves y análisis de suelos de ocho secciones expuestas de los bancos de río para probar las predicciones de tres modelos de porque las aves consumen arcilla: ayuda mecánica para la digestión (arena triturada), adsorción de toxinas en la dieta y suplemento mineral. Encontramos que los suelos preferidos eran deficientes en partículas lo suficientemente grandes como para ayudar en la trituración mecánica del alimento y ayudar a la digestión. El porcentaje de contenido de arcilla y la capacidad de intercambio catiónico (CIC), ambos esperados para correlacionar con la adsorción de toxinas, no varió entre sitios usados y no usados como ha sido encontrado en un estudio similar. En cambio, los suelos preferidos fueron más salinos y con mayor concentracion de sodio intercambiable. Esto sugiere que la selección de suelos en nuestro sitio de estudio está basado principalmente en el contenido de sodio. Las aves pueden estar usando las texturas densas y plásticas de los suelos ricos en arcillas con alto contenido de sodio intercambiable como una señal próxima para la selección del suelo. Nuestros resultados sugieren que las decisiones de selección de suelos por las aves depende del rango de características de suelos disponibles.

Key words: *cation exchange capacity; geophagy; macaw; moist tropical forest; parrot; particle size; Peru; Psittacidae; salinity; sodium.*

Geophagy, the intentional consumption of soil by vertebrates, has been recorded for a wide range of bird and mammal taxa. In birds, geophagy is known for geese, parrots, cockatoos, pigeons, cracids, passeriforms, hornbills, cassuaries (Emmons & Stark 1979, Wink *et al.* 1993, Diamond *et al.* 1999, Burger & Gotchfeld, in press), and even the extinct Carolina Parakeet (Jones & Hanson 1985). Among mammals, a wide variety of taxa including human and nonhuman primates have been found consuming soil on all continents except Antarctica (Daykin 1960, Oates 1978, Jones & Hanson 1985, Klaus & Schmid 1998, Wiley & Katz 1998, Krishnamani & Mahaney 2000). A variety of theories have been proposed to explain geophagy, including mineral supplementation (reviews in Kreulen & Jaeger 1984, Klaus & Schmid 1998), mechanical aid to digestion (Best & Gionfriddo 1991), pH buffering (Kreulen 1985, Mahaney *et al.* 1999), relief from diarrhea (Oates 1978; Vermeer & Ferrell 1985, Mahaney, Aufreiter *et al.* 1995, Mahaney *et al.* 1996), treatment for endoparasites (Mahaney, Stambolic *et al.* 1995, Knezevich 1998), and

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adsorption of dietary toxins (Kreulen 1985, Diamond *et al.* 1999, Gilardi *et al.* 1999, Mahaney *et al.* 1999). It seems that all of these theories have merit in at least some taxa although the reasons why a given taxon consumes a given soil at a given time is poorly understood for most species and may require a complex combination of the above theories.

In the western Amazon basin of Peru, avian geophagy is relatively common, with hundreds of individuals of more than 20 bird species ingesting soil daily at dozens of different sites (Emmons & Stark 1979, Gilardi & Munn 1998, Brightsmith in press, Burger & Gotchfeld in press). Physiological studies have shown that the soils chosen by birds in Peru significantly reduce the toxicity of some secondary plant compounds (Gilardi *et al.* 1999). Gilardi *et al.* (1999) also showed that the soils (1) are not useful mechanical aids for grinding food; (2) are not ingested by individuals suffering from diarrhea; (3) do not provide significant sources of minerals except possibly sodium; and (4) do not buffer gastric pH. This leaves adsorption of toxins as the primary reason for geophagy among parrots and other birds in Neotropical environments. The mechanism by which adsorption of toxins is thought to occur is that positively charged toxins (especially alkaloids) bind to negatively charged cation exchange sites on the very fine (<2 μm) clay particles (Burchill *et al.* 1981, Gilardi *et al.* 1999). Data from wild birds support this theory as soils consumed by birds had higher clay content and cation exchange capacity (CEC; Gilardi *et al.* 1999).

Our study used a series of eight adjacent exposed riverbank sites to determine which soil characteristics were associated with high rates of geophagy among parrots in the western Amazon basin. These observations are designed to test the following hypotheses; (1) if birds eat soil to aid in mechanical digestion, they would favor soils with particles large enough to aid in grinding food (>0.5 mm; Best & Gionfriddo 1991); (2) if birds ingest soils to adsorb dietary toxins, they would choose soils with the high CEC and clay content; and (3) if birds consume soils to provide extra nutrients like sodium, they would choose soils with the highest concentrations of these nutrients.

METHODS

STUDY SITE.—This study was conducted in the Native Community of Infierno, located in the buffer zone of the Tambopata National Reserve, 26 km southwest of Puerto Maldonado, in southeastern Peru (12°48′S, 69°18′W; 195 m elev.). The area is at the moist tropical/subtropical vegetation boundary (Holdridge 1967). Rainfall is *ca* 2810 mm per year (Pearson & Derr 1986). The dry season starts in April and ends in October (Pearson & Derr 1986; and D. Brightsmith, pers. obs. from Tambopata Research Center 50 km southwest). The surrounding area is made up of a mix of floodplain and *terra firme* forests. The 10,000 ha Native Community of Infierno remains more than 92 percent forested, with deforestation concentrated along the river edges (? Hepworth, pers. comm.). The geophagy areas (henceforth referred to as lick sections) studied here are protected from hunting as they lie within the 4000 ha ecological reserve that was established by the members of the Native Community of Infierno in the early 1990s.

The lick sections are exposed areas of soil along the left bank of the lower Tambopata River near the Posada Amazonas Lodge. Periodic flooding of the Tambopata River causes erosion of the banks and keeps the lick sections free of vegetation. The study site is located 65 km from the base of the Andes Mts. and river waters can rise and fall as much as 5 m in 48 hours (D. Brightsmith, pers. obs.).

SAMPLE COLLECTION.—Samples were collected from each of eight lick sections on 8 August 2001. At sections where little or no bird activity was recorded, one sample was taken from approximately the middle of that section. From sections where bird activity was regularly recorded, samples were collected from spots where bird beak marks were present to ensure that the soil sampled was one that was actually eaten by the birds. In two sections, birds ate from two distinct locations and both of these locations were sampled. In this way, ten soil samples were taken from eight lick sections. The samples were dry when collected and were stored in zipper- lock plastic bags until analysis.

SOIL ANALYSES.—Soil analyses were preformed at the Laboratorio de Análysis de Suelos of the Universidad Nacional Agraria La Molina, Peru. The percent dry weight (fraction) of soil in seven different size categories clay (<0.002 mm diam), silt (0.002–0.05 mm), very fine sand (0.05–0.1 mm), fine sand (0.1–0.25 mm), medium sand (0.25–0.5 mm), thick sand (0.5–1 mm), and very thick sand (>1 mm) were determined by dry filtering the sand fraction through a series of progressively finer filters and weighing each fraction. The remaining silt and clay was suspended in dilute sodium hexametaphosphate and sampled at a fixed depth and time to determine the clay content (Tan 1996). The silt fraction was then calculated by subtraction.

The cation exchange capacity (CEC) was calculated using the ammonium acetate method (Tan 1996). The soil complex was saturated with the ammonium cation (NH^{4+}) washed with ethanol and the adsorbed NH^{4+} was qualitatively determined by titration. The amount of exchangeable cations Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+} were calculated by replacement with ammonium acetate, washing with 95 percent ethanol, and the concentrations of the resulting cations were measured using atomic absorption spectrophotometry (Tan 1996). Results were calculated in milliequivalents/100g of soil. The pH of each sample was determined in the lab by suspending 20 g of soil in 20 ml of distilled water, agitating 30 minutes, then letting it settle for 30 minutes and reading the pH of the resulting solution (Tan 1996).

The available phosphorus was determined using the Olsen method by extraction with 0.5 M $NaHCO^{3+}$ at pH 8.5 and results given in ppm (Tan 1996). The concentrations of available Cu, Zn, Mn, and Fe were determined by extraction with $NaHCO^{3+}$ EDTA and quantified by atomic adsorption photometry. Results are presented in ppm.

Bird observations.—Observations of the lick sections were conducted from a point on the far side of the river *ca* 250 m away. The observation point was located near the center of the 370 m spanned by the eight exposed lick sections under study. During observations, each lick section was scanned every five minutes using a Bushnell Spacemaster telescope with a 20–60x eyepiece and the number of birds was recorded. Observations were conducted during 23 early mornings (0500–0700h), 17 late mornings (0700–1200h), and 13 afternoons between 4 April and 9 August 2001 (included in this are 8 full days when the lick was observed from *ca* 0500h until 1730h).

Lick site description.—The length and height of each lick section were measured, but this was not found to accurately reflect the area of the exposed soil due to the large amount of vegetation that encroached from all sides. For this reason, photos of the lick taken on 29 March 2001 were used to estimate the amount of exposed soil at each riverbank section. The photos were reclassified in Adobe Photoshop to make all exposed soil white and all vegetation black. The number of white pixels was then summed. The number of pixels was then converted to square meters by calculating the length in pixels of a 1 m pole that appeared in the photo.

Statistics.—The rank lick size and rank bird use were compared using Spearman's rank correlation (Gibbons 1985). Areas that received bird visits on more than 10 percent of the days when birds were recorded were classified as used and the rest were classified as unused. All samples from used sections showed bird beak marks when collected while none from unused sections showed such beak marks. Soil characteristics were compared between used and unused soil samples. The small number of soil samples analyzed (N = 10 total) prohibited the use of multivaritate techniques, so each soil characteristic was analyzed separately using *t*-tests (Gibbons 1985). The *P*-values for these tests are reported as "raw *P*-values" in the tables. To reduce the probability type I errors inherent in running large numbers of univariate tests, stepwise Bonferroni corrections were run independently for the 7 soil particle sizes categories and 13 soil characteristics (Sokal & Rohlf 1995). The results of these corrections are presented in the tables as the corrected *P*-values. Variation around the mean is described with the standard deviation.

RESULTS

Bird use.—Fifteen species of birds and two mammals were recorded during 191 hours of observation. Birds of the family Psittacidae (parrots, macaws, and parakeets) dominated the sample in both number of individuals and number of species (Table 1). Other species recorded included three pigeons (Columbidae: *Patagioenas* spp.), one guan, and one chachalaca (both family Cracidae). Birds were recorded on 21 of the 25 days. Bird use varied significantly among sections (X^2 = 47.3, df = 5, $P < 0.00001$ for the number of days each spot was used). The three indices of bird use, sum of daily maxima, total bird minutes, and number of days each spot was used, produced nearly identical rankings among the sections (Table 2). Section number 7 received the vast majority of bird use according to all three measures. It had 85 percent of the total bird minutes recorded, a sum of daily maxima ten times more than the next most used lick, and received bird visits on 21 different days. Sections 9 and 6 were next in the ranking and received nearly identical use. Sections 4 and 8c each received one

TABLE 1. *Bird species' use of geophagy sites along the Tambopata River in Southeastern Peru. The total bird minutes is the sum of the number of individuals seen during five-minute scan of the lick. The sum of the maximum number of individuals is the maximum number of individuals seen of a single species on each day summed across the 21 days of observation. See footer for description of days seen.*

Species	Days on each section								Days seen[a]	Total bird min	Sum max individuals
	4	5	6	7	8a	8b	8c	9			
Ara chloroptera (Red-and-green Macaw)	0	1	0	9	0	0	0	0	9	386	80
A. macao (Scarlet Meacaw)	0	3	0	3	0	0	0	0	5	50	19
A. severa (Chestnut-fronted Macaw)	0	0	4	7	0	0	0	2	12	225	104
Amazona farinosa (Mealy Parrot)	0	1	0	5	0	0	0	1	6	181	76
A. ochrocephala (Yellow-crowned Parrot)	0	2	5	8	0	0	1	3	14	477	210
Pionus menstruus (Blue-headed Parrot)	0	0	3	14	0	0	0	2	15	413	211
Pionopsitta barrabandi (Orange-cheeked Parrot)	0	0	0	11	0	0	0	0	11	48	32
Aratinga weddellii (Dusky-headed Parakeet)	0	0	0	12	0	0	0	1	12	2055	648
A. leucopthalmus (White-eyed Parakeet)	0	0	0	1	0	0	0	0	1	2	2
Pyrrhura rupicola (Black-capped Parakeet)	0	0	0	1	0	0	0	0	1	107	20
Patagioenas 3 spp. (pigeons)	0	0	0	13	0	0	0	0	13	359	48
Penelope jacquacu (Spix's Guan)	1	2	0	1	0	0	0	0	4	23	7
Ortalis guttata (Speckled Chachalaca)	0	0	0	3	0	0	0	0	3	10	5
Total[a]	1	4	5	21	0	0	1	4	21	4334	1462

[a] The days seen is the number of different days on which birds were seen using the clay lick.

TABLE 2. *Bird use and size of exposed riverbank geophagy sites at Posada Amazonas along the lower Tambopata River in southeastern Peru. Bird data were collected from 4 April to 9 August 20001. Three measures of bird use are presented: the sum of the maximum number of each species seen on each day; the number of days on which the section was use; and the total number of birds that were recorded during the five-minute scans. The final column shows the approximate surface area of exposed soil for each lick section. There was no significant correlation between the size of the lick and its bird use (Spearman's rank correlation,* P = *0.22).*

Section	Sum daily maxima	Days	Total bird min	Average rank	Size (m^2)
4	2	1	2	5.83	19
5	33	4	67	3.77	62
6	162	5	246	2.33	115
7	1104	21	3706	1.00	36
8a	0	0	0	7.50	50
8b	0	0	0	7.50	16
8c	5	1	5	5.20	14
9	156	4	308	2.77	134
Total	1462	21	4334		56

brief visit while 8a and 8b received no bird visits. Mammal use consisted of a 15 minute visit by a single red howler monkey (*Alouatta seniculus*) and a less than 10 minute visit by an Amazon red squirrel (*Sciurus spadiceus*).

The data suggest that bird species differ in their preference for lick sections as 100 percent of pigeon ($N = 13$ lick visits) and Orange-cheeked Parrot ($N = 11$ lick visits) sightings were on spot 7, while only 42 percent of sightings of Yellow-crowned Parrot ($N = 19$ lick visits) sighting were on lick 7. The sample sizes were too small to permit statistical testing; interspecific patterns will be addressed in future papers.

Site characteristics.—The lick sections ranged from 5 to 38 m long and 3 to 12 m tall. Vegetation covered the majority of many sections, making these sizes biologically irrelevant. As a result, the total amount of exposed soil in each section was used as a measure of size for each section. This ranged from 14 to 134 m^2 ($x = 56$ $m^2 \pm 45.9$) . There was no significant correlation between the amount of exposed soil in each section and the total bird use (Table 2; Spearman's rank correlation, $F = 1.91$, df = 1, 6, $P = 0.22$).

Soil particle size.—Birds ate soils with significantly less very thick sand (particle size >1 mm, $x_{used} = 1.6\% \pm 1.3$, $x_{unused} = 6.5\% \pm 2.9$; raw $P = 0.006$, corrected $P = 0.044$) and significantly more silt (particles between 0.002 and 0.05 mm, $x_{used} = 47.1\% \pm 8.6$, $x_{unused} = 28.6\% \pm 4.0$; raw $P = 0.002$, corrected $P = 0.016$; Table 3). The consumed soils also had less thick sand (particle size between 0.5 and 1 mm) but this trend did not hold when P-values were Bonferroni-corrected (particles between 0.5 mm and 1.0 mm, $x_{used} = 1.8\% \pm 1.2$, $x_{unused} = 4.1\% \pm 1.8$; raw $P = 0.04$, corrected $P = 0.2$; Table 3). There were no detectable differences for the other particle sizes analyzed (Table 3).

Soil Geochemistry.—The concentration of exchangeable sodium ions averaged more than seven times greater in consumed soils than in unconsumed soils ($x_{used} = 253$ ppm $\pm$ 49.8, $x_{unused} = 34.4$ ppm $\pm$ 9.0; raw $P < 0.0001$, corrected $P = 0.001$; Table 4). The electrical conductivity, a measure of total salinity, for consumed soils was over 20 times greater than unconsumed soils. There was no overlap in salinity between used and unused soils. This trend was significant based on raw P-values but it did not hold up after using the Bonferroni corrections, due in part to the high variation within used soils ($x_{used} = 1.74$ dS/m $\pm$ 1.47, $x_{unused} = 0.08$ dS/m $\pm$ 0.09; raw $P = 0.04$, corrected P-value = 0.36; Table 4). Consumed soils also contained lower concentrations of aluminum cations and hydrogen ions but this did not hold up statistically after the P-values were corrected ($x_{used} = 222$ ppm $\pm$ 232, $x_{unused} = 658$ ppm $\pm$ 269; raw $P = 0.03$, corrected $P = 0.27$; Table 4). None of the other ten soil properties tested (CEC, Ca^{2+}, Mg^{2+}, K^+, Cu, Zn, Mn, Fe, pH, and available P) showed significant differences between the consumed and unconsumed soils (Table 4). Soils consumed by birds included a range of types including silty clay ($N = 2$), silty clay loam ($N = 1$), loam ($N = 2$), and clay ($N = 1$), while soils that were not consumed included clay loam ($N = 3$) and clay ($N = 1$; soil types from Tan 1996).

TABLE 3. *Particle size percentages for used and unused soils at avian geophagy sites in southeastern Peru. Raw P-values are calculated using t-tests and then these P-values are corrected using a stepwise Bonferroni correction for season tests.*

Sample	Bird use	Very thick sand >1mm	Thick sand 0.5–1.0 mm	Medium sand 0.25–0.50 mm	Fine sand 0.10–0.25 mm	Very fine sand 0.05–0.10 mm	Silt 0.002–0.05 mm	Clay <0.002 mm
5 (1)	Yes	0.7	1.3	1.3	1.2	1.7	50.0	43.8
5 (2)	Yes	1.0	1.4	1.2	0.8	5.2	62.6	27.8
6	Yes	0.8	0.7	0.6	0.4	0.5	43.0	54.1
7 (1)	Yes	1.9	2.0	1.8	2.3	26.4	46.0	19.7
7 (2)	Yes	4.1	4.1	3.9	3.3	20.7	43.4	20.5
9	Yes	1.1	1.6	1.6	1.7	8.4	37.4	48.2
4	No	5.9	4.9	3.2	4.0	19.7	31.0	31.2
8A	No	7.2	3.4	3.2	11.9	12.4	23.2	38.7
8B	No	10.0	6.0	3.6	3.4	14.7	32.1	30.3
8C	No	2.9	2.0	1.6	1.4	2.8	28.0	61.4
$\bar{x}_{used}$	Yes	1.6	1.8	1.7	1.6	10.5	47.1	35.7
SD_{used}	Yes	1.30	1.20	1.16	1.07	10.62	8.65	14.89
$\bar{x}_{unused}$	No	6.5	4.1	2.9	5.2	12.4	28.6	40.4
SD_{unused}	No	2.94	1.77	0.88	4.63	7.09	3.99	14.50
P_{raw}		0.006	0.04	0.13	0.22	0.76	0.002	0.64
$P_{corrected}$		0.038	0.20	0.42	0.52	0.76	0.016	0.87

DISCUSSION

Site characteristics and bird use.—The fact that the spot the birds used most was one of the smallest and most enclosed suggests that the size of the exposed area of soil is not driving the choice of geophagy sites by these birds. This was not what we predicted at the outset of this study. Behavioral observations have shown that birds are extremely cautious as they approach the lick sections and fly up repeatedly, even after they have started consuming the soil (Burger & Gochfeld in press). These behaviors are most likely due to caution associated with predation risks. This caution may be adaptive as raptors do occasionally capture birds at licks and this predation may be more common in areas with much vegetation (D. Brightsmith, pers. obs.). It is also suspected that humans and other mammalian hunters kill birds at licks (Burger & Gochfeld in press). For this reason, we expected that birds would prefer to use the most open and exposed sections from which they could see approaching mammals and raptors and be able to take flight easily. This prediction was not supported by the data; however, Burger and Gochfeld (in press) report that clearing riverbank vegetation in a known geophagy area resulted in the immediate use of this section by birds. DB has heard of similar phenomena at two other licks in southeastern Peru. As a result, future work could use controlled experiments to investigate how physical characteristics and the amount of vegetation influence bird use of geophagy sites.

Mechanical aids to digestion.—Our finding that birds avoid soils with the highest concentration of large sand particles supports the idea that these birds do not consume soils to provide a mechanical aid to digestion (Diamond *et al.* 1999, Gilardi *et al.* 1999). Soil particles ingested for grinding purposes among cornfield birds in NA usually range from 0.5 to 3.5 mm (Best & Gionfriddo 1991), much larger than the silt and clay particles (<0.05 mm) that make up the majority of the soils consumed at geophagy sites in southeastern Peru. In the current study, we found that birds chose soils with significantly less very thick sand particles (>1 mm) and possibly less thick sand particles (0.5–1.0 mm). These are the only particles in the size range reported as useful for grinding purposes (Best & Gionfriddo 1991). It is of note that the percentage of these large sand grains was relatively small in all soils we tested (x = 10.6% for unused soils and 3.4% for used), suggesting that parrots and other

TABLE 4. *Geochemistry for used soils at avian geophagy sites in southeastern Peru. Raw* P*-values were calculated using* t*-tests and then these* P*-values were corrected using a stepwise Bonferroni correction for 13 tests.*

Sample	Bird use	Total CEC (meq/100g)	Exchangeable cations (ppm)				
			Ca^{2+}	Mg^{2+}	K^{+}	Na^{+}	$A13^{+} + H^{+}$
5	1	14.56	383	518	66	206	21
5	1	12.32	537	466	63	252	21
6	1	16.8	144	423	106	238	505
7	1	13.12	130	542	47	204	225
7	1	18.24	136	782	70	334	55
9	1	17.6	156	615	285	284	505
4	0	14.4	114	441	70	46	542
8a	0	17	134	334	137	37	743
8b	0	13.28	224	536	137	25	360
8c	0	20.96	126	332	109	30	986
$\bar{x}_{used}$	1	15.44	248	558	106	253	222
SD_{used}	1	2.46	172	128	90	50	232
$\bar{x}_{unused}$	0	16.41	150	411	113	34	658
SD_{unused}	0	3.41	50	98	31	9	269
P_{raw}		0.64	0.23	0.09	0.86	<0.0001	0.03
$P_{corrected}$		0.98	0.85	0.61	0.86	0.001	0.27

geophagous birds at our site may be highly sensitive to these particles. Avoidance of sand may be advantageous as the large and resistant sand particles have comparatively little surface area for the adsorption of dietary toxins and should release few useable minerals. Among mammals, ingestion of sandy soil has been found to lead to excessive tooth wear (Kruelen 1985). Parrots have beaks that grow continuously throughout their lifetimes, so beak wear among these birds may be much less important than tooth wear. Mammalian studies have shown that large amounts of sand sometimes accumulate in the digestive tract. In extreme cases, this can be fatal (review in Kreulen 1985). Volant birds, like all those studied here, have many weight-reducing adaptations. While it is unknown if sand is retained by these species, if it were to accumulate in the gut, it would provide strong selective pressure against consuming soils with large sand grains.

ADSORPTION OF DIETARY TOXINS.—We found that birds chose soils with significantly more silt but did not choose soils with higher clay content or higher CEC. Previous work in Peru found the opposite trends despite the fact that they were studying a nearly identical suite of species at locations only 50 and 250 km away (Gilardi *et al.* 1999). Both Gilardi *et al.*'s (1999) work and this study looked at clay content and CEC, characteristics that correlate with toxin adsorption. If the correlation between the measured variables and toxin adsorption are not perfect, it could lead to erroneous conclusions regarding the reasons for avian consumption of clay. Evidence for this is scanty but can be found in both the bird and mammal literature. In New Guinea, birds consumed soils with high silt (48%), low clay (13%), and low CEC (11 meq/100g), but these soils had toxin adsorption capacities equal to or greater than the Peruvian soils with high clay (50 and 80%) and high CEC (21–33 meq/100g; Diamond *et al.* 1999, Gilardi *et al.* 1999). African termite mound soils and forest floor soils have been analyzed and the predicted positive relationship between percent clay and adsorption of toxins was found for only one of the four toxins examined (Mahaney *et al.* 1999). We are currently conducting analyses to directly compare used and unused soils for their ability to adsorb dietary toxins. This should help clarify the role of toxin adsorption in soil choice among this suite of avian species.

MINERAL SUPPLEMENTATION.—The significantly higher amounts of exchangeable sodium ions in consumed soils suggest that birds are choosing soils based on sodium content. The trend toward higher total salinity for consumed soils provides additional evidence that salts are driving the selection of soils by these birds. To put the salinity values found here in perspective, values of 1 or greater are usually found in arid zone soils in which evaporation exceeds precipitation (Sposito 1989). In addition, in agricultural systems a soil is classified as "saline" if the salinity value is greater than 4. By these criteria, four of the six consumed soils qualify as "typical of arid zones" and two of these almost qualify as saline.

TABLE 4. *Extended.*

Electrolytic conductivity or salinity (dS/m)	Nutrients (ppm)					
	Cu	Zn	Mn	Fe	Available *P*	pH
0.47	0.6	2.1	3.2	14.9	5.4	5.9
1.24	0.4	2.4	1	29.9	13.8	6.3
3.85	2.2	13.9	35.3	55.7	4.2	4.1
3.31	0.6	4.7	66.2	61.8	5.3	4.2
0.57	0.5	3.4	18	50.2	9.2	5.1
0.974	0.9	5.2	31.9	74.3	5.1	4.5
0.019	0.6	4.2	10.6	34.5	3.5	4.3
0.034	0.9	4.5	14.8	127.8	4.6	4.3
0.21	1	3.3	46.1	64.4	6.3	4.4
0.056	1.3	5	8.8	73.7	4.7	4.2
1.74	0.87	5.28	25.93	47.80	7.17	5.02
1.47	0.67	4.40	24.27	21.77	3.68	0.92
0.08	0.95	4.25	20.08	75.10	4.78	4.30
0.09	0.29	0.71	17.53	38.91	1.15	0.08
0.04	0.80	0.59	0.67	0.27	0.19	0.11
0.36	0.96	0.99	0.96	0.84	0.81	0.66

The diets of Scarlet Macaws and Red-and-green Macaws in southeastern Peru contain *ca* 38 and 42 ppm sodium, respectively (Gilardi 1996). The mean concentration of exchangeable Na^+ in the soils consumed in this study was 253 ppm. The exchangeable sodium in the samples was all bioavailable because clays only weakly bond Na^+ ions, and in the highly acid environment of the gut, the Na^+ would be almost instantaneously exchanged for H^+, making the sodium available for uptake (Tan 1996). This shows that the parrots are consuming soils with at least eight times more sodium than their diets. The samples undoubtedly contained additional amounts of water-soluble sodium that were not measured in this study.

The importance of exchangeable sodium in this system goes beyond the simple release of sodium in the gut. Clays with higher concentrations of exchangeable Na^+ tend to become "dispersed." This means that the soil structure collapses and the soil becomes very dense and plastic when wet and very hard when dry (Tan 1996). The difference in texture is clearly noticeable in the field (D. Brightsmith, pers. obs.) and should be noticeable to birds as well. These dense clay soils are also nearly impermeable to water and almost impenetrable to roots (Tan 1996). This may explain how these ancient soils maintain concentrations of soluble salts similar to those from arid environments in an area with over 2.8 m of rain per year.

The suggestion that vertebrates consume soil to obtain sodium is hardly novel, as sodium supplementation is the most common explanation for geophagy among vertebrates (reviewed in Klaus & Schmid 1998). Gilardi *et al.* (1999) could not rule out sodium supplementation as a contributing factor in parrot geophagy but their data showed only a weak preference for soils with higher sodium concentrations. One reason for this finding may be that both used and unused samples from their three Manu sites had sodium concentrations 11–47 times greater than the average parrot diet. As geophagy may simultaneously satisfy multiple physiological needs, soil choice by vertebrates may be influenced by multiple criteria (Kruelen 1985). Therefore, at sites with uniformly high sodium concentrations like Manu, birds' soil selection decisions may be based on other variables such as clay content or cation exchange capacity.

Soil selection among geophagous species is obviously nonrandom. This trend holds regardless of the taxon and location in question (Oates 1978, Knezevich 1988, Mahaney *et al.* 1999, this study). Experimental evidence has shown that soils are capable of adsorbing biologically relevant quantities of toxins *in vitro* and that soil consumption by parrots does reduce the absorption of toxins *in vivo* (Gilardi *et al.* 1999). Our study did not find evidence that the parrots are choosing soils with greater CEC or clay content, the characteristics that correlate with the capacity to adsorb toxins. Instead, we found that birds chose soils with higher concentrations of sodium. These two findings are not mutually exclusive but instead suggest that there may be a set of conditional rules for soil selection. In situations in which sodium concentrations are variable, the birds appear to choose soils that are highest in sodium (this study). In areas in which sodium concentrations are uniformly high, birds may choose the soils that have the largest ability to adsorb dietary toxins (Gilardi *et al.* 1999).

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LITERATURE CITED

BEST, L. B., AND G. P. GIONFRIDDO. 1991. Characterization of grit use by cornfield birds. Wilson Bull. 103: 68–82.
BRIGHTSMITH, D. Effects of weather on avian geophagy in Tambopata, Peru. Wilson Bull. In press.
BURCHILL, S., M. H. B. HAYES, AND D. J. GREENLAND. 1981. Adsorption. *In* D. J. Greenland and M. H. B. Hayes (Eds.). The chemistry of soil processes, pp. 221–400. John Wiley and Sons,New York, New York.
BURGER, J., AND M. GOCHFELD. Parrot behavior at a Rio Manu (Peru) clay lick: Temporal patterns, associations, and antipredator responses. Acta Ethol. In press.
DAYKIN, P. W. 1960. Veterinary applied pharmacology and therapeutics. Bailliére, Tindall and Cox, London, England.
DIAMOND, J., K. D. BISHOP, AND J. D. GILARDI. 1999. Geophagy in New Guinea birds. Ibis 141: 181–193.
EMMONS, L. H., AND N. M. STARK. 1979. Elemental composition of a natural mineral lick in Amazonia. Biotropica 11: 311–313.
GIBBONS, J. D. 1985. Nonparametric methods for quantitative analysis. American Sciences, Columbus, Ohio.
GILARDI, J. D. 1996. Ecology of parrots in the Peruvian Amazon: Habitat use, nutrition, and geophagy. Ph.D. dissertation. University of California at Davis, Davis, California.
———, S. S. DUFFEY, C. A. MUNN, AND L. A. TELL. 1999. Biochemical functions of geophagy in parrots: Detoxification of dietary toxins and cytoprotective effects. J. Chem. Ecol. 25: 897–922.
———, AND C. A. MUNN. 1998. Patterns of activity, flocking and habitat use in parrots of the Peruvian Amazon. Condor 100: 641–653.
HOLDRIDGE, L. R. 1967. Life zone ecology, revised edition. Tropical Science Center, San Jose, Costa Rica.
JONES, R. L., AND H. C. HANSON. 1985. Mineral licks, geophagy, and biogeochemistry of North American ungulates. Iowa State University Press, Ames, Iowa.
KLAUS, G., AND B. SCHMID. 1998. Geophagy at natural licks and mammal ecology: A review. Mammalia 62: 481–497.
KNEZEVICH, M. 1998. Geophagy as a therapeutic mediator of endoparasitism in a free-ranging group of rhesus macaques (*Macaca mulatta*). Am. J. Primatol. 44: 71–82.
KREULEN, D. A. 1985. Lick use by large herbivores: A review of benefits and banes of soil consumption. Mammal Rev. 15: 107–123.
———, AND T. JAEGER. 1984. The significance of soil ingestion in the utilization of arid rangelands by large herbivores, with special reference to natural licks on the Kalahari pans. *In* F. M. C. Gilchrist and R. I. Mackie (Eds.). Herbivore nutrition in the subtropics and tropics, pp. 202–221. Science Press,Johannesburgh, South Africa.
KRISHNAMANI, R., AND W. C. MAHANEY. 2000. Geophagy among primates: Adaptive significance and ecological consequences. Anim. Behav. 59: 899–915.
MAHANEY, W. C., S. AUFREITER, AND R. G. V. HANCOCK. 1995. Mountain gorilla geophagy: A possible seasonal behavior for dealing with the effects of dietary changes. Int. J. Primatol. 16: 475–488.
———, R. G. V. HANCOCK, S. AUFREITER, AND M. A. HUFFMAN. 1996. Geochemistry and clay mineralogy of termite mound soil and the role of geophagy in chimpanzees of the Mahale Mountains, Tanzania. Primates 37: 121–134.
———, A. STAMBOLIC, M. KNEZEVICH, R. G. V. HANCOCK, S. AUFREITER, K. SANMUGADAS, M. J. KESSLER, AND M. D. GRYNPAS. 1995. Geophagy amongst rhesus macaques on Cayo Santiago, Puerto Rico. Primates 36: 323–333.
———, J. ZIPPIN, M. W. MILNER, K. SANMUGADAS, R. G. V. HANCOCK, S. AUFREITER, S. CAMPBELL, M. A. HUFFMAN, M. WINK, D. MALLOCH, AND V. KALM. 1999. Chemistry, mineralogy and microbiology of termite mound soil eaten by the chimpanzees of the Mahale Mountains, western Tanzania. J. Trop. Ecol. 15: 565–588.
OATES, J. F. 1978. Water–plant and soil consumption by guereza monkeys *Colobus guereza*: A relationship with minerals and toxins in the diet? Biotropica 10: 241–253.
PEARSON, D. L., AND J. A. DERR. 1986. Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. Biotropica 18: 244–256.
SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry, 3rd edition. W. H. Freeman and Company, New York, New York.
SPOSITO, G. 1989. The chemistry of soils. Oxford University Press, New York, New York.
TAN, K. H. 1996. Soil sampling, preparation, and analysis. Marcel Dekker, New York, New York.

VERMEER, D. E., AND R. R. J. FERRELL. 1985. Nigerian geophagical clay: A traditional antidiarrheal pharmaceutical. Science 227: 634–636.

WILEY, A. S., AND S. H. KATZ. 1998. Geophagy in pregnancy: A test of a hypothesis. Curr. Anthropol. 39: 532–545.

WINK, M., A. HOFER, M. BILFINGER, E. ENGLERT, M. MARTIN, AND D. SCHNEIDER. 1993. Geese and dietary allelochemicals—Food palatability and geophagy. Chemoecology 4: 93–107.