

BIOCHEMICAL FUNCTIONS OF GEOPHAGY IN PARROTS:
DETOXIFICATION OF DIETARY TOXINS AND
CYTOPROTECTIVE EFFECTS

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Abstract—This study tests hypotheses on the biochemical functions of geophagy in parrots: mechanical enhancement of digestion, acid buffering capacity, mineral supplementation, adsorption of dietary toxins, and gastrointestinal cytoprotection. Parrots showed clear preferences for specific soil horizons. Comparisons of preferred and nonpreferred soils from several sites suggest that soils have little ability to enhance grinding and no measurable ability to buffer gastric pH. Soils offered insignificant mineral supplementation since most minerals occurred at similar levels in samples regardless of preference, and the minerals were generally more plentiful in the birds' diets. Sodium was available in moderate levels at some sites (>1000 ppm), but was well below sodium detection thresholds of parrots. X-ray diffraction, cation exchange capacity, and in vitro adsorptive trials showed that the preferred soils are capable of exchanging substantial quantities of cations and are capable of adsorbing low-molecular-weight secondary compounds. In captive *Amazona* parrots, orally administered clay reduced the bioavailability of the alkaloid quinidine by roughly 60%, demonstrating that in vivo adsorption of potentially

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toxic compounds may be a biologically important function of geophagy. Labeled clay remained in the lower gastrointestinal tract of captive parrots for >12 hr, which along with high adsorptive capacities, further suggests a potential role in protecting the gastrointestinal lining from various biological and chemical insults. Detoxification and cytoprotection are the most likely functions of geophagy for parrots and herbivores with similar ecologies. Given the variety of chemically defended seeds consumed by these herbivores, geophagy likely protects consumers from dietary toxins, allowing increased diet breadth and/or enhancing digestibility.

Key Words—Parrot, macaw, geophagy, clay, mineral, detoxification, secondary compounds, dietary ecology, cytoprotection.

INTRODUCTION

The consumption of soil (geophagy) is widespread among vertebrates, particularly herbivores, and is perhaps best known in ungulates' visiting salt-licks (Jones and Hanson 1985). Geophagy is also common in a variety of nonhuman primates (Izawa, 1993; Mahaney et al., 1996), indigenous and modern human cultures (Laufer, 1930; Cooper, 1957; Hunter, 1973; Johns, 1986; Abrahams and Parsons, 1996). Soil-eating has also been documented in koalas (Smith, 1979), reptiles (Sokol, 1971; Marlow and Tollestrup, 1982), and in many seed-eating birds (Pendergast and Boag, 1970; Munn, 1992; Pryce, 1994; Gionfriddo and Best, 1995). Exactly what drives animals and humans to eat soil remains unclear, but the answers might yield insight into the interactions of plant chemistry and vertebrate physiology, as well as shedding light on the origins of self-medication in humans and other vertebrates.

Although one clay lick used by birds and mammals in Peru has been known for some time (Emmons and Stark, 1979; Terborgh, 1983), recent work has found that geophagy is not only geographically widespread in South America, but also occurs in a variety of herbivores and omnivores (C. Munn unpublished data). Reports of parrot geophagy in the Neotropics have now been reported from Mexico, Peru, Bolivia, and Brazil, and the behavior has been observed in many parrots, cracids, pigeons and doves, monkeys, tapirs, and peccaries (Heyman and Hartman, 1991; Munn et al., in preparation; E. Enkerlin, personal communication, P. Roth, personal communication). Similar aggregations of parrots and other herbivorous birds at clay licks have recently been described in Irian Jaya (Diamond et al., 1999), and Grey Louries in Botswana (*Corythaixoides concolor*) (Pryce, 1994). As this behavior is often overlooked, it is expected that new observations will continue to be made and support the notion that avian geophagy is widespread and has evolved several times independently.

Many hypotheses have been proposed to explain geophagy, the best known being: (1) mechanical enhancement of digestive grinding by large particles (grit)

(cf. Best and Gionfriddo, 1991); (2) supplementation of nutrition by release of minerals (Jones and Hanson, 1985; Kreulen, 1985; Hunter, 1993); (3) buffering gastrointestinal pH (Oates, 1978); (4) reduction of toxicity of food by adsorption of plant toxins to clay (Hladik and Gueguen, 1974; Johns, 1990; Johns and Duquette, 1991); and (5) enhancement of the ability of the gastrointestinal tract to protect itself from chemical insult (cytoprotection) by induction and alteration of mucous secretion (Rateau et al., 1982; Kreulen, 1985; Vermeer and Ferrell, 1985; Mahaney et al., 1996). Thus, there are several possible, nonexclusive functions of geophagy in vertebrates.

Given the number of known clay-licks in Peru, and our growing knowledge of the ecology of the birds visiting these sites (Emmons and Stark, 1979; Gilardi and Munn, 1998), this area presented a unique opportunity to conduct an in-depth study of the phenomenon of geophagy, and to test directly these hypotheses on the functions of soil-eating in parrots. We conclude that mechanical enhancement of digestion, buffering of the gastrointestinal tract, and mineral supplementation are unlikely to be the primary cause of geophagy. Rather, geophagy may provide substantial alimentary detoxification of charged secondary compounds and may protect the gut lining from various chemical challenges. For herbivores that consume chemically well-defended foods, soil-eating would thus allow increased diet breadth and/or enhance digestibility of these otherwise toxic resources.

METHODS AND MATERIALS

Sample Collection. We collected soil samples from clay-licks in Manu National Park (11°57'S; 71°17'W) in August 1992 and 1993 and in the Tambopata-Candamo Reserved Zone (13°10'S; 69°30'W) in February 1994. At each site, birds and/or mammals show a clear preference for particular soils, which we noted either by direct observation of the animals or the bill/dental impressions left in the soil. In Manu, this horizon ran for hundreds of meters along the river bank, whereas in Tambopata, the exposed cliff is much higher (≈ 30 m) and the soil horizons less well-defined. At this site, birds consume soil from some patches on the cliff face more than others. At all sites, we collected samples from both the preferred and nonpreferred areas; weighed, dried, and gently ground the samples to a coarse powder; and stored them for all subsequent analyses.

Particle Size and Cation Exchange. We determined clay, silt, and sand fractions of the soil samples using standard methods (sand 2 mm–50 μ m, silt 50–2 μ m, and clay <0.2 μ m) (Gee and Bauder, 1986). Briefly, we dispersed the samples in dilute aqueous sodium hexametaphosphate, passed them through a sieve to remove the sand, resuspended the clay and silt, and sampled the suspension at a fixed time and depth to determine clay content. We dried these fractions

and determined silt content by subtraction. We determined the cation exchange capacity for clays from all licks using a barium method in the DANR laboratory at UC Davis (Janitsky, 1986) and present the results in units of milliequivalents per 100 g.

Mineral Release. We analyzed all samples for mineral release using two extracts, one approximates the extractive conditions of a bird's digestive fluid and a second is exhaustively extractive and provides an estimate of total mineral content. These are referred to hereafter as available and total mineral content, respectively. To estimate available minerals, we added 1 g powdered soil to 15 ml aqueous HCl at pH 2.0, agitated the mixture at 38°C for 1 hr, and then centrifuged it (cf. Hunter and De Kleine, 1984). To estimate total minerals, we added 1 g of powdered soil to 0.5 ml concentrated HNO₃ and 2 ml 30% H₂O₂ in a Teflon vessel and heated it under pressure in a microwave oven (5 min at 40% power, 8 min at 90% power) (CEM Corp. MDS 2000). We diluted these extracts to 15 ml with H₂O, left them to settle, and later analyzed an aliquot of all extracts using inductively coupled plasma optical emission spectroscopy (Thermo Jarrell Ash Atomscan 25) for the following elements: Li, Na, Mg, P, S, K, Ca, Cr, Mn, Fe, Co, Cu, Zn, Se, Mo (for use of ICP on soils, see Wang et al., 1989). We converted raw results to milligrams per kilogram of dry weight using three-point standard curves based on reference solutions for the appropriate element (Fisher Scientific).

From preliminary analyses, we found that minor changes in the ratio of extract solution to soil had a marked effect on the quantity of minerals released on a per gram of soil basis. To determine this relationship, we analyzed a series of samples varying the extract-soil ratio, tested for eight elements (Na, K, Mg, Ca, Fe, S, P, Zn), and present the results in terms of the quantity of mineral released per gram soil as a function of extract-soil.

For particle size, cation exchange capacity (CEC), and mineral content, we compared mean values of preferred soils with those of nonpreferred samples. In the few cases where the preferred values were either higher or lower than nonpreferred values, we compared means using a planned comparison analysis of variance.

Buffering Capacity. We determined the buffering capacity of soils by adding incremental amounts of HCl to soil or antacids in aqueous suspension under constant agitation (Watts, 1994). We added 7-g samples of soil or prescribed doses of over-the-counter antacids to 30 ml distilled H₂O and agitated this ≥10 min. We then added sequentially 2-ml aliquots of HCl (1 M) and recorded the pH after stabilization.

Clay Mineralogy. We analyzed soils from three sites in Manu and the main Tambopata lick for clay mineralogy using standard X-ray diffraction methods (Whittig and Allardice, 1986). Briefly, a small sample of the clay fraction is placed on a pair of quartz plates and each is saturated with different salts. The

crystalline structures of different clay types react differently to a series of chemical and/or heat treatments. We present the results for each plate with the subsequent analyses to aid in identification of or loss of peaks that are diagnostic of specific clay minerals. Although we analyzed several samples from each site, we present data only from Manu since the mineralogy of all Peruvian samples was similar.

In Vitro Adsorption. We determined the adsorption isotherms of soils for two compounds, the polyphenolic gallotannin (Fluka) and the alkaloid quinine (Aldrich), in order to estimate the affinity of these chemicals for soils in a simulated gastric environment. We suspended 1 g of soil in 100 ml of a solution mimicking avian gastric fluid (0.1 N NaCl, pH 2.0 HCl) (Hunter and De Kleine, 1984) and drew off 5-ml aliquots during agitation, transferring them to 15-ml centrifuge tubes. We added varied concentrations of these model compounds to these seven tubes, agitated the samples for 30 min at 38°C, and then centrifuged them at 16,000g for 2 min. We assayed aliquots of the parent compound on a spectrophotometer (Schimadzu) by comparison with standard colorimetric curves using gallotannin (270 nm) and quinine (346.3 nm). Adsorption on clays via cation exchange can be modeled with a Langmuir adsorption isotherm, which provides results in the form of an adsorptive maximum and estimates the quantity of compound a clay will adsorb when saturated (Heimenz, 1986).

Brine Shrimp Bioassay. To test whether soils can reduce the toxicity of parrot foods, we extracted seven of the most toxic seeds in macaw diets (Gilardi and Munn, in preparation) and exposed the extracts to a realistic quantity of soil in a simulated gastric environment. We then compared the toxicity of soil-exposed extracts to controls using a brine shrimp bioassay (Solis et al., 1993). We extracted 1 g of plant material in 20 ml 100% methanol for 24 hr, split these extracts into two portions, and dried them in vacuo. To each dried extract and to two standards (quinidine and digitonin), we then added 10 ml simulated gastric fluid to each (pH 2 HCl, 0.1 N NaCl), and added 250 mg dry soil to one and nothing to the other (control). After agitating them at ≈40°C for 30 min, we titrated them to pH ≈7 with 0.1 M NaOH, and centrifuged at them at 4000g for 10 min. Using a 12-well tissue culture plate (Falcon), we added 0, 20, and 200 μl and 1 ml of extract in triplicate, and artificial seawater (InstaOcean) to make 5 ml total. We then added 10–30 brine shrimp nauplii to each well and counted live and dead shrimp at 24 h and determined the LD₅₀ using probit analysis (Polo Software).

In Vivo Detoxification. To test detoxification in vivo, we dosed eight orange-winged Amazons (*Amazona amazonica*) with weight-specific quantities of the alkaloid quinidine sulfate (150 mg/kg, Aldrich). Although it would have been preferable to use quinine because of its biological relevance and because we used that compound in the in vitro work, we selected the stereoisomer of quinine, quinidine, as our model alkaloid because it is far less toxic to verte-

brates and the available assay methods are more sensitive. For our purposes in testing the in vivo detoxification mechanism, we assume that absorption by the parrot and adsorption by the clay of this model compound were sufficiently representative of a low-molecular-weight alkaloid to be of value. We simultaneously treated half the birds with 4 ml H₂O, and half with 4 ml clay suspension using preferred Peruvian soils (≈ 0.5 g/ml), reversing the water and clay treatments on the same individual birds 14 days later. We administered the clay/water/drug with a stainless-steel feeding tube modified with a short section of plastic tubing on the tip, which held a gel capsule containing the quinidine (size 5 capsules, Chemical and Pharmaceutical Industry, Ramsey, New Jersey). We sampled blood (0.5 cc/draw) at 1, 2, and 3 hr after dosing from either the jugular or the median ulnar vein using 1-cc tuberculin syringes, and stored them in heparinized blood collection tubes (Microtainer, Becton Dickinson & Co., Franklin Lakes, New Jersey). We centrifuged these samples at 150g for 5 min to pellet the red blood cells, and assayed the plasma using a TDx fluorescence polarization immunoassay with reagents for quinidine (Abbott Inc., Abbott Park, Illinois) (Ronald, 1984). We determined circulating drug levels by comparison with a nonlinear standard curve determined from quinidine in *A. amazonica* blood. We analyzed treatment differences using repeated measures analysis of variance (BMDP 2V) (Dixon, 1992).

Soil Passage Rate. To estimate the distribution and transit time of a dose of clay in the gastrointestinal tract of captive parrots, we gavaged a blue-fronted Amazon (*Amazona aestiva*) with 6–8 cc of iodinated contrast fluid (Isovue-200, Bracco Diagnostics, Princeton, New Jersey), and another with iodine-saturated clay (6–8 cc). We fasted both birds for 1 hr before initial dosing and returned them to ad libitum food 4 hr later. Following administration of clay or contrast agent, we took lateral abdominal radiographs at 30 min and at 1.5, 4, 8, 12, and 24 hr.

RESULTS

Particle Size and Cation Exchange. All soil samples contained substantial quantities of clay; preferred soils contained significantly more than nonpreferred sites (50% vs. 35% respectively; Table 1). The elevated clay levels in the preferred sites translates to decreased sand content in these samples, and silt levels were nearly equivalent among the three sample types. These high clay contents correlated well with the relatively high cation exchange capacities (CECs) ($R^2 = 0.235$, $P = 0.047$; Figure 1), and preferred soils had significantly higher CECs than non-preferred samples ($P = 0.019$; Table 1).

Mineral Release. There were marked differences between the two extracts used, the total extract yielding higher values for a given mineral than the avail-

TABLE 1. PARTICLE SIZE (%), CATION EXCHANGE CAPACITY (meq/100 mg), AND AVAILABLE MINERALS (mg/kg) AT PERUVIAN GEOPHAGY SITES^a

Site	Sample ^b	Clay	Silt	Sand	CEC	Ca	Co	Cr	Cu	Fe	K	Li	Mg	Mn	Mo	Na	P	S	Se	Zn
Near	above	13.3	20.8	65.9	11.7	318	bd1	0.35	0.09	4.85	13.7	0.12	376	6.26	0.02	469	0.05	0.88	5.25	1.37
	prefer	47.9	51.3	0.78	30.5	280	0.07	0.21	0.20	3.19	13.6	0.33	388	3.06	bd1	1565	0.48	0.97	bd1	0.71
	below	40.6	52.5	6.84	30.5	408	0.00	0.32	0.06	4.02	11.1	0.35	491	10.7	bd1	1499	0.20	0.93	bd1	2.84
Main	above	52.6	43.4	4.06	20.0	757	nd	nd	nd	6.12	14.1	nd	592	nd	nd	415	0.10	0.43	nd	2.49
	prefer	55.6	42.1	2.32	33.0	309	0.07	0.40	0.04	4.15	9.07	0.39	452	8.78	bd1	1749	0.07	0.08	bd1	1.11
	below	27.8	43.3	29.0	20.5	303	0.15	0.35	0.06	8.99	28.8	0.34	499	11.6	bd1	1598	0.72	12.14	bd1	3.40
Arma	above	25.1	46.7	28.2	17.0	341	0.48	0.21	0.29	6.89	22.6	0.16	387	15.8	bd1	457	6.89	6.72	bd1	2.94
	prefer	44.5	41.0	14.5	27.5	379	0.17	0.25	0.26	4.66	23.7	0.32	381	10.2	bd1	969	0.22	0.73	bd1	2.49
	below	40.3	47.6	12.1	18.5	275	0.36	0.19	0.24	4.33	28.5	0.26	284	15.2	bd1	685	0.15	0.20	bd1	4.01
Tamb ^c	above	37.5	59.3	3.20	15.3	881	1.33	0.27	0.64	113.4	271.9	0.34	726	86.6	0.00	117	104.0	3.43	0.00	21.2
	prefer	81.7	17.3	1.02	20.8	610	0.44	0.06	0.82	73.1	356.4	0.47	824	122	0.00	380	0.45	0.56	0.00	3.12
	below	38.0	48.9	13.0	13.5	317	0.55	0.04	0.56	111.1	196.3	0.18	465	77.4	0.00	75.4	0.41	0.32	1.35	5.24
Mean	above	32.1	42.5	25.3	16.0	574	0.60	0.28	0.34	32.8	80.6	0.20	520	36.2	0.01	365	27.8	2.87	1.75	6.99
prefer	57.4	37.9	4.64	28.0	395	0.19	0.23	0.33	21.3	100.7	0.38	511	35.9	0.00	1166	0.30	0.58	0.00	1.86	
below	36.7	48.1	15.2	20.8	326	0.26	0.22	0.23	32.1	66.2	0.28	435	28.8	0.00	964	0.37	3.40	0.34	3.87	
P =		0.026		0.195	0.019						0.745	0.030				0.176				
Minerals from plant resources (see text)						4738	bd12	bd12	8.43	62.42	16784	bd12	2911	62.13	bd12	36.71	3611	2088	bd12	27.8

^aNear: a small lick = 100m downstream of the "main" lick along the Manu River. Main: the central lick along the Manu river 71°25'30" W, 11°50' S; = 1 hr upstream of Cocha Cashu Biological Station. Arma: a small lick on a tributary off the Manu that is visited primarily by *Ara macaco*. Tamb: ; nd: no data; bd1: below detectable levels; bd12: most samples below detectable levels.

^bCollected 1 m above, below, or at the preferred soil horizon.

^cMeans of three subsamples.

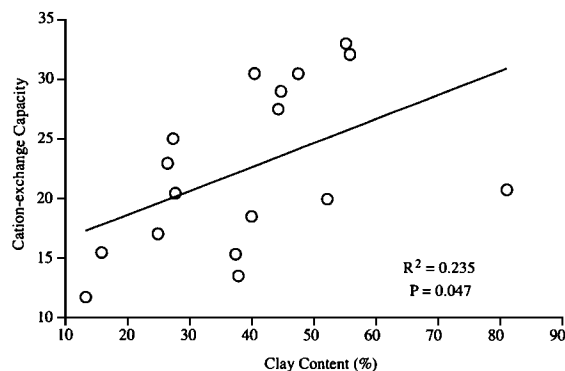


FIG. 1. The relationship of clay content with cation-exchange capacity in soils from geophagy sites in southeastern Peru.

able extract (Table 2). Viewing this difference as extraction efficiency, three elements were relatively available (sodium, calcium, and sulfur), while the others were <15% available. The large difference in iron (<1% available) suggests that the microwave/acid process degrades the crystalline lattice of the clay, releasing large amounts of iron. Within the available extracts, the ratio of clay to water had a profound effect on the minerals released (Figure 2). As the amount of clay was increased in a given volume of water, the amount of minerals released on a per-gram-of-soil basis decreased sharply.

All soils released substantial quantities of some minerals and virtually none of some others (Table 1). Only potassium, lithium, and sodium were released in greater quantities in comparing preferred vs. nonpreferred samples, and only the content of Li was significantly different.

Buffering Capacity. Preferred soils from Manu and Tambopata showed virtually no ability to buffer pH; pH values for the clay suspensions stabilized between 3 and 6 orders of magnitude lower than over-the-counter antacids and were indistinguishable from distilled water (Figure 3). For instance, the soils stabilized at pH 1–1.5 and the antacids between pH 4 and 6.5.

Clay Mineralogy. X-ray analysis of the clays shows that all the Peruvian clays contained smectites, kaolin, and mica (Figure 4). The Manu samples were predominantly smectite, and the Tambopata samples showed greater proportions of kaolin and mica. The smectites are well known for having high surface areas and high CECs, whereas mica and kaolin are intermediate in these properties. Thus, the cation exchange results concur with the clay mineralogy findings in that the Manu clays were both high in smectites and had similarly high CECs. In contrast, the Tambopata samples had little smectite, and despite the higher clay content, had lower CECs.

TABLE 2. DIFFERENCES IN MINERALS RELEASED BY PERUVIAN SOILS EXTRACTED BY MICROWAVE/ACID (MA) vs. SIMULATED GASTRIC CONDITIONS (GC)

Sample and extract	Parts per million									
	Na	K	Ca	S	P	Mg	Fe ^a	Zn		
MC05										
GC	1,320	13.9	714	0.550	0.048	589	6.82	0.681		
MA	1,280	954	1,850	0.806	284	7,310	21,500	91.2		
% Δ	-2.96	98.5	61.4	31.8	100	91.9	100.0	99.3		
MC08										
GC	969	23.7	379	0.727	0.217	381	4.66	2.49		
MA	881	722	779	1.38	384	3,090	21,500	69.1		
% Δ	-10.0	96.7	51.3	47.2	99.9	87.7	100.0	96.4		
MC10										
GC	1,570	13.6	280	0.97	0.484	388	3.19	0.711		
MA	149	949	934	5.75	152	4,630	21,600	64.7		
% Δ	-4.89	98.6	70.0	83.2	99.7	91.6	100.0	98.9		
T1A										
GC	123	299	850	2.75	85.6	736	115.3	19.0		
MA	174	1,371	1,210	4.27	468	3,990	21,500	145		
% Δ	29.3	78.2	30.0	35.6	81.7	81.6	99.5	86.9		

TABLE 2. CONTINUED

Sample and extract	Parts per million									
	Na	K	Ca	S	P	Mg	Fe ^a	Zn		
T4P										
GC	332	345	573	0.642	0.595	812	32.9	4.32		
MA	360	2,010	1,260	0.643	154	4,690	21,500	95.4		
% Δ	7.60	82.8	54.5	0.249	99.6	82.7	99.8	95.5		
T8B										
GC	63.0	183	279	0.323	0.595	407	94.0	4.99		
MA	88.2	1,110	255	1.06	311	1,930	21,500	68.6		
% Δ	28.6	83.6	-9.69	69.6	99.8	78.9	99.6	92.7		
Chaco										
GC	647	374	2,195	136	382	749	189.7	11.6		
MA	964	2,920	6,460	368	686	9,570	12,600	130		
% Δ	32.9	87.2	66.0	63.0	44.2	92.2	98.5	91.1		
Extraction efficiency (%)	88.5	10.6	53.8	52.8	10.7	13.4	0.386	5.61		

^a Microwave/acid extraction for Fe was clearly saturated at this dilution; these figures should therefore be interpreted as minimum values. M samples from Manu, T samples from Tambopata, and Chaco is a soil sold on the streets in Cusco, Peru for gastric irritation, included here for comparison.

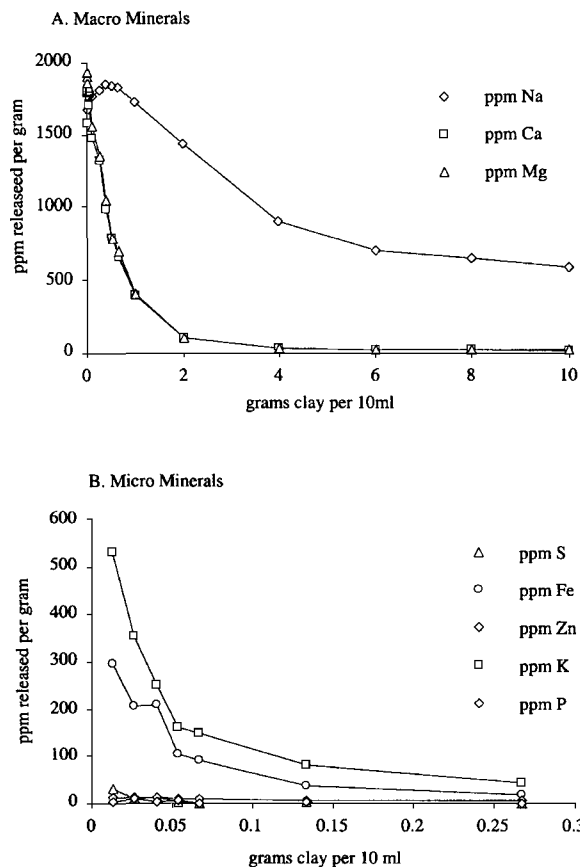


FIG. 2. Minerals released from soils as a function of concentration in solution.

In Vitro Adsorption. These generally high CECs for preferred soils (≈ 28 meq/100 ml) were correlated with the soils' abilities to adsorb secondary compounds. For both classes of organic compounds tested *in vitro*, preferred soils from both Tambopata and Manu showed adsorptive maxima greater than pure kaolin and less than pure bentonite (Figure 5). The adsorptive maxima figures suggest that the preferred soils can adsorb up to 90–125 mg quinine and 6–8 mg tannic acid per gram of ingested soil in simulated gastric conditions.

Brine Shrimp Bioassay. For the plant foods tested, exposure to soil in a simulated gastric environment caused a greater than threefold reduction in toxicity as measured by LD₅₀ in brine shrimp (Figure 6). Soil caused a twofold reduction in the toxicity of the quinidine but had no measurable effect on the

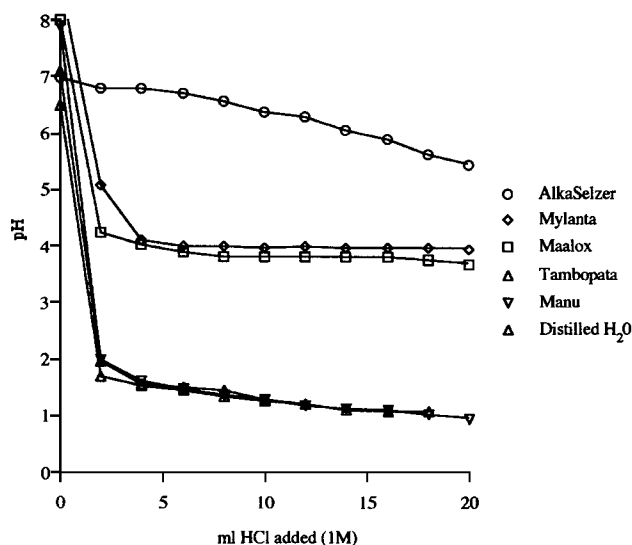


FIG. 3. Buffering capacities of Peruvian soils compared with over-the-counter antacids.

saponin digitonin. Given that the alkaloid is positively charged at pH 2, and the saponin is not, the detoxification is likely occurring via cation exchange.

In Vivo Detoxification. Circulating quinidine levels in birds dosed with clay were reduced by $\approx 60\%$ compared to birds dosed with water during the first 3 hr after ingestion ($P < 0.001$, Figure 7). Peak levels of the drug were reduced from ≈ 1.5 to $\approx 0.6 \mu\text{g/ml}$. Parrots required a very high drug dose to attain detectable levels; 150 mg/kg quidine produced circulating levels of $\approx 1.5 \mu\text{g/ml}$. In contrast, a 3–4 mg/kg dose in humans produces levels of 2–5 $\mu\text{g/ml}$ (Goodman et al., 1990).

Soil Passage Rate. Clay was present in the crop, proventriculus, and gizzard at 30 min after administration and was clearly present in the lower gastrointestinal tract 12 h later (Figure 8a). No clay was visible at 24 h. Pure contrast agent behaved in much the same way, but most was cleared more rapidly, being present only in the cloacal area at 8.5 hr (Figure 8b). Two caveats are worth mentioning. Since birds and mammals eat dry clay, a crop full of lumps of clay is likely to take hours to hydrate and be passed from the muscular stomach to the lower gastrointestinal tract. Moreover, from preliminary testing, the iodine-saturated clay was much less radiodense than pure contrast agent; thus, only large quantities were visible. More natural dosing, more effective labeling, or more sensitive detection would all likely reveal still longer-term presence of clay in the gastrointestinal tract.

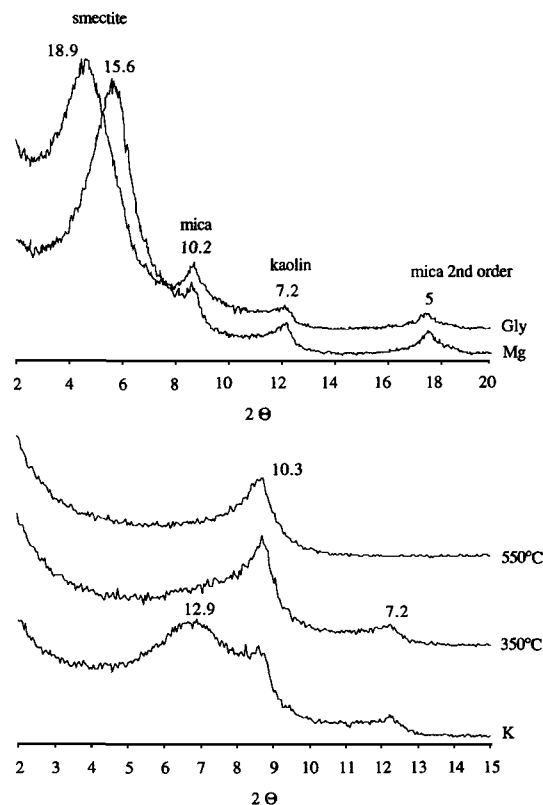


FIG. 4. Clay mineralogy of Manu soil. The top two curves illustrate the spectrum of the sample saturated with magnesium and subsequently with glycerol. The bottom three curves show the potassium saturated curve and subsequent heat treatments of that sample. Peaks occur at differing incident angles (2θ) of the radiation source and correspond to the abundance of various clay minerals with different crystalline structure (indicated by D-space values (\AA) above each peak). Under different chemical or thermal treatments, the crystalline structures of the different clay families change and facilitate the identification of the minerals present.

DISCUSSION

Geophagy is a multifaceted phenomenon, as evidenced by the diversity of animals that exhibit this behavior in a variety of ecological settings. In this investigation we address the question of geophagy in parrots and test several hypotheses on the causes of soil-eating in vertebrates: grit for mechanical enhancement of digestion, mineral supplementation of a deficient diet, acid buffering, adsorp-

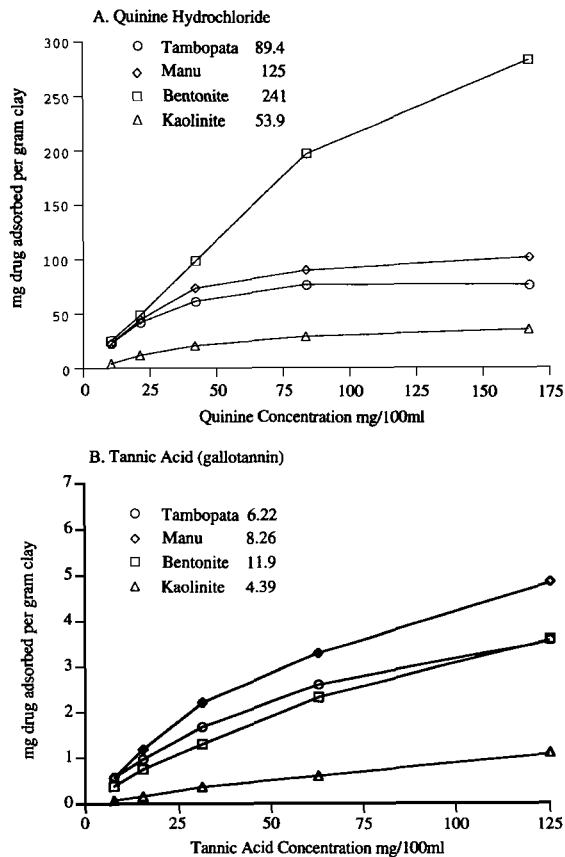


FIG. 5. Langmuir adsorption isotherms of quinine and tannic acid on Peruvian soils and clay standards in a simulated gastric environment; legends show sample identity and the adsorptive maximum (mg/g).

tion of dietary toxins, and gastrointestinal cytoprotection from chemical insults. Our analysis of soils from clay licks in Peru and experiments with captive parrots permitted us to address the validity of the above hypotheses; a brief discussion of each follows.

Mechanical Enhancement of Digestion. The best understood form of avian geophagy is the consumption of grit to enhance the mechanical grinding action of the muscular stomach. Many species of birds collect grit, particularly finches, geese, woodpeckers, corvids, and pipits (McIlhenny, 1932; Kilham, 1960; MacRoberts and MacRoberts, 1976; Verbeek, 1995). Best and Gionfriddo (1991) found that the mean grit size in 22 bird species foraging in cornfields varied

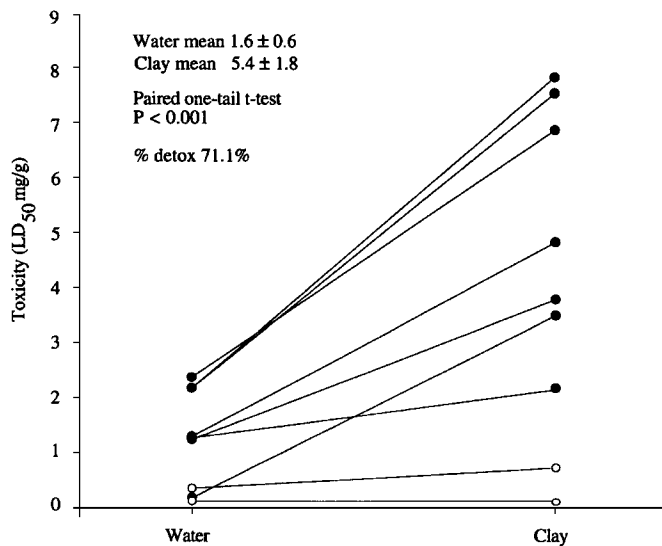


FIG. 6. Detoxification of seed samples by clay using a brine shrimp bioassay (means \pm 2 SE). Sample identification from top to bottom on the clay data are unripe seeds of *Cedrela odorata*, *Hevea guianensis*, *Couratari guianensis*, *Spondias mombin*, whole ripe fruit of *Sapium marmieri*, *Annona* sp., unripe seeds of *Qualea* sp., and the hollow circles are standards of quinidine, digitonin.

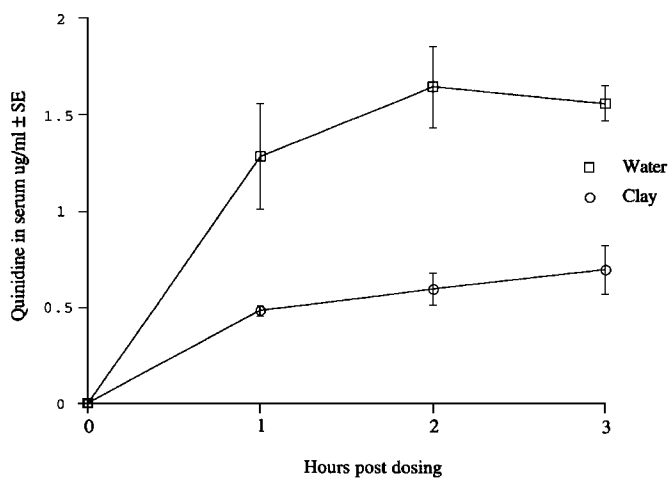


FIG. 7. Effect of clay ingestion on the bioavailability of quinidine in orange-winged Amazon parrots (*Amazona amazonica*).

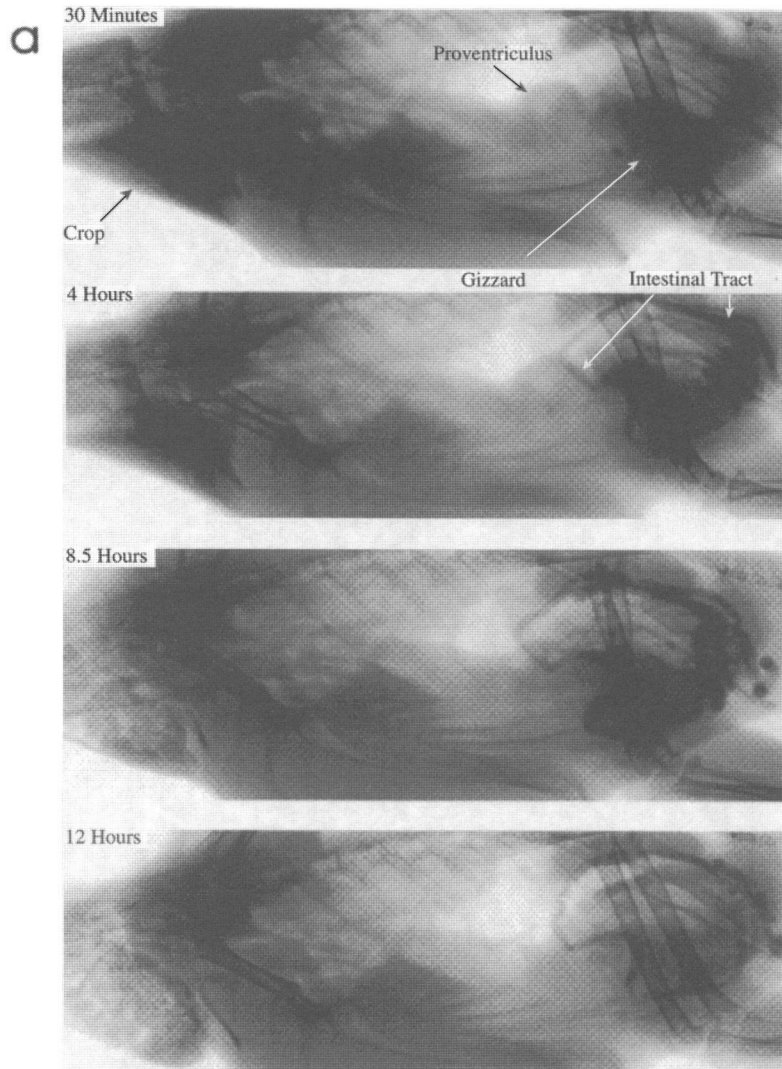


FIG. 8. Radiographs showing the distribution of labeled clay (a) and contrast agent alone (b) moving through the gastrointestinal tract of a blue-fronted Amazon parrot (*Amazona aestiva*).

from 0.5 to 3.5 mm and was directly correlated with body size. In contrast, we found that preferred soils of parrots in Peru were generally smooth in texture with a sand content mean of <5%, which strongly argues that birds do not eat soil to enhance the mechanics of digestion. Rather, the parrots choose fine-grained soils

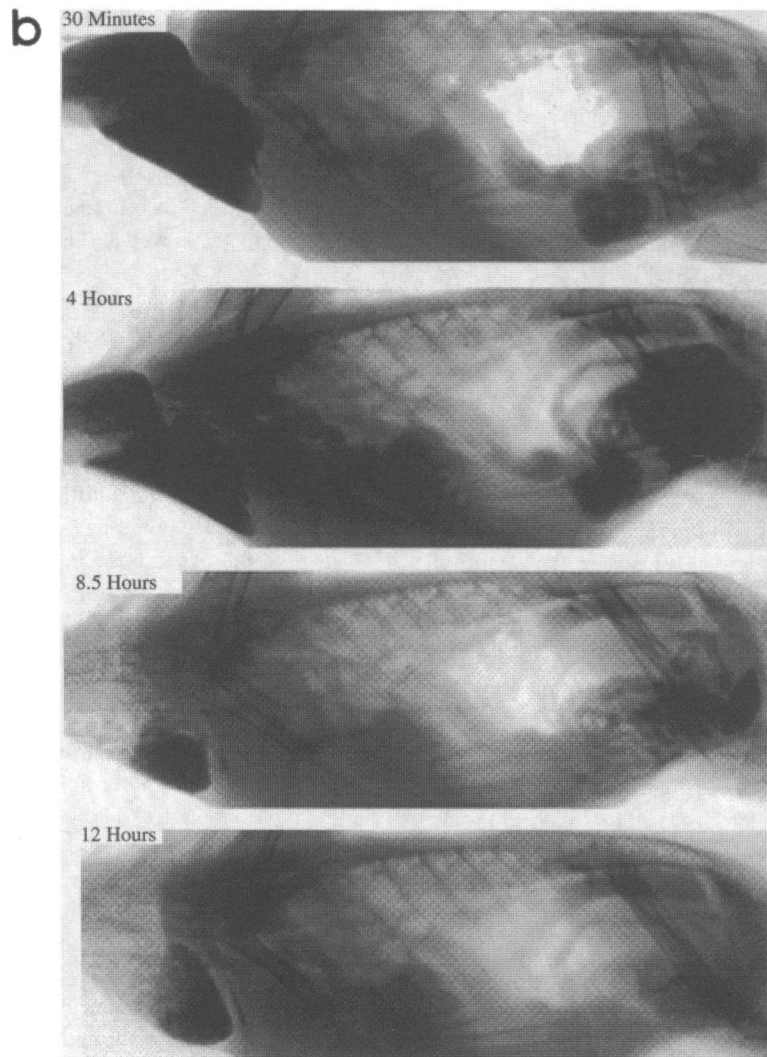


FIG. 8. CONTINUED.

with high clay content and correspondingly high cation exchange capacity (CEC) and presumably can adequately masticate hard food items with their powerful and dexterous bills. Hence, geophagy in parrots invites alternative hypotheses on its function based on the structure and potential function of the clay itself.

Mineral Supplementation. Clays, as crystalline minerals, have very high

surface areas and considerable potential to release minerals. Most reports of clay-eating in ungulates have concluded that animals consume soil for mineral supplementation of an otherwise deficient diet (cf. Jones and Hanson, 1985). Outside the scientific community, this assumption has led many to call geophagy sites salt-licks in English, collpas or salitrales in Spanish, and barrieros in Portuguese. A number of studies have looked at minerals present in soils from geophagy sites, and although the results vary among sites, sodium, calcium, and magnesium are among the most common minerals found (reviewed by Jones and Hanson, 1985).

There are three complicating issues, however, that many of these studies do not address: (1) total vs. available minerals, (2) mineral content of the diet, and (3) the effect of the ratio of gastric fluids to soil on the quantity of minerals released. First several studies in addition to ours suggest that not all minerals present in a soil sample are available and that a simulated gastric environment is a more meaningful way to determine what is available than the determination of "total minerals" (Hunter and De Kleine, 1984; Jones and Hanson, 1985). Second the availability of minerals in the animals' normal diets is frequently not considered, and in some cases exceeds the quantity of a given mineral(s) available in the soil. For instance, without the knowledge of minerals available in parrot diets, it might appear that these Peruvian soils contain biologically important and perhaps supplemental quantities of calcium, magnesium, iron, manganese, and sodium (Table 1). However, all but sodium are considerably more abundant in the animals' food resources than what is available in the soil. Third the ratio of the clay to extracting solution is important *in vitro* but is a difficult parameter to estimate *in vivo*. For instance, our *in vitro* results show that a bird consuming 5 g of soil might extract anywhere from 60 to 7500 μg of calcium, depending on the ratio of soil to gastric fluid as the soil passes through the gastrointestinal tract (Figure 2).

These considerations aside, much is known about geophagy in vertebrates and clearly minerals cannot be discounted altogether. There are several studies demonstrating attraction to minerals in ungulates, rabbits, and even butterflies (Blair-West et al., 1968; Arms et al., 1974; Jones and Hanson, 1985). From our data, we can rule out all the minerals except sodium as the primary cause of geophagy, based on the preferred/nonpreferred comparison, by evaluating the minerals in the birds' diets, or both. Although not significantly more available in the preferred soils, sodium is generally more available in the Peruvian soils than in the plant tissues they consume. In comparison with ungulate licks in North America, two of the preferred soils would be greater than Jones and Hanson's criteria for a lick "high in extractable sodium" (5 meq/100 ml \approx 1150 ppm, 1985, p. 97), and two would be less than this figure.

However, five lines of evidence suggest that there is more to parrot geophagy than attraction to sodium. First, the sites vary widely in the quantity of available sodium. Some of the soils eaten by parrots in Tambopata contain

very little sodium, less than that in some tap water. This suggests that these birds are attracted to soil even if it contains little sodium. Second, we have found evidence that macaws in Tambopata feed on insect larvae (*Hermetia*: Stratiomyidae; Gilardi and Munn, unpublished data). Insect-eating by parrots has been observed in a variety of species in the Neotropics and in Australia (McInnes and Carne, 1978; Roth, 1984; Wyndham and Cannon, 1985; Sazima, 1989; Sick, 1993; Martuscelli, 1995) and presumably provides a source of protein, lipid, potassium, and sodium. By enhancing their sodium intake through insect foraging, parrots could avoid the huge congregations of birds that attract predators at the clay lick (Robinson, 1994; Munn, unpublished data), as well as the metabolic cost of returning from the clay lick with a full crop of soil having no caloric content. Third, we have offered these Peruvian soils to three parrot genera in captivity (*Amazona*, *Pionus*, *Trichoglossus*), and all consume it readily despite the fact that their commercial diets contain more sodium than any of the soils (>2000 ppm; Gilardi unpublished data). Fourth, experiments with budgerigars (*Melopsittacus undulatus*) and other seed-eating birds have shown that, while these birds avidly consume salt, they do not detect it until the concentration is greater than 3000 ppm, which is more than twice the highest value for these soils (Cade, 1964). Fifth, in ungulates where the evidence is strongest for mineral attraction, feeding trials have demonstrated increased growth rates of cattle and lambs when clay is added to a balanced diet and further increases in growth rates when the clay is available ad libitum (Burkitt, 1969; Mendel, 1971; Huntington et al., 1977). These observations suggest that the clay plays a role in digestion other than, or perhaps in addition to, release of minerals.

Buffering Capacity. Although the possibility that soils may buffer the pH of portions of the gastrointestinal tract has been suggested (Oates, 1978), the Peruvian soils show essentially no potential to alter pH. Additional testing of this mechanism in vivo may reveal some activity of the clay that our simple system fails to detect.

Adsorption of Dietary Toxins. Given the clay content of the Peruvian soils, the types of clays present, and the ability of clays to exchange cations, geophagy may provide the vertebrate consumer with two types of advantages: attenuation of toxicity by adsorption of toxins, and gastrointestinal cytoprotection from chemical insults to the gut lining. Several studies of geophagy in primates and humans (Hladick and Gueguen, 1974; Mahaney et al., 1996) have suggested that soils might adsorb dietary toxins, but this function of geophagy in primates remains to be tested in vivo. In humans, clay has been demonstrated to adsorb secondary compounds prior to consumption in the process of preparing acorns and semidomesticated potatoes (Johns, 1986; Johns and Duquette, 1991). Adsorption of, or protection from, secondary compounds would be particularly beneficial to macaws and other parrots that eat foods that are often quite toxic and contain high levels of phenolics (Gilardi and Munn, unpublished data).

Our in vitro adsorption trials show that detoxification via this mechanism is dependent on chemical identity; the soils were able to adsorb large quantities of the alkaloid quinine and relatively little of the polyphenolic tannic acid. Since polyphenolic content can be quite high in parrot diets ($\approx 5\%$ dry weight), the quantities of clay required to significantly reduce toxicity would be many times the weight of the birds' daily food requirements. However, for charged compounds such as alkaloids, which typically occur at much lower levels ($<1\%$ dry wt), and which have greater affinity for clays (≈ 100 mg adsorbed/g, Figure 5), consumption of several grams of soil per day could adsorb biologically significant quantities of the toxin. The clays also significantly reduced the toxicity of seeds that these birds normally consume, further supporting the possible role of clays in dietary detoxification.

Perhaps most importantly, our work with captive parrots demonstrates that geophagy can substantially reduce the bioavailability of a readily adsorbed alkaloid (quinidine) in a controlled experiment. In concert, these results strongly support the proposed function of geophagy as a means of detoxification of dietary toxins. Further tests of this mechanism might use a diet spiked with an easily monitored toxin and would ideally determine if animals can facultatively respond to dietary toxins by voluntarily increasing soil consumption. Such behavioral responses are well known in rats and are perhaps the clearest indication that some vertebrates respond to ingested poisons and nausea by eating soil (Mitchell et al., 1976; Takeda et al., 1993).

If geophagy does play a role in dietary detoxification, the benefits for parrots and other soil-eating vertebrates would be multiple. Geophagy would allow the bird or mammal to consume previously unexploitable resources and/or increased quantities of seeds and fruits that would otherwise cause illness or death. Furthermore, by reducing the exposure of the consumer to toxins, geophagy would reduce the costs of constitutive and inducible enzymatic detoxification (Berenbaum and Zangerl, 1994). Parrots are able to consume nutritionally rich but highly toxic resources during the dry season when food is limiting to other frugivores (Terborgh, 1986; Gilardi and Munn, unpublished data). Thus, by facilitating the expansion of the diet, geophagy may extend the distribution and/or enhance the local abundance of parrots and other animals. Similar benefits have been attributed to the consumption of charcoal by Zanzibar red colobus monkeys (*Procolobs kirkii*), which occur at elevated densities where this behavior occurs (Struhsaker, 1997).

Gastrointestinal Cytoprotection. Geophagy may serve yet another function resulting from the interaction of some clay types with the gut lining and the induction of a cytoprotective effect. This effect has been demonstrated in rats, rabbits, dogs, and humans and is particularly well studied in research on anti-diarrheal medications (Rateau et al., 1982; More et al., 1987; Grandjean et al., 1992; Vivatvakin et al., 1992; Gardiner et al., 1993). Although the mechanism

of this interaction is poorly understood, the presence of clay in the gut increases mucus secretion by goblet cells and prevents mucolysis through increased protein cross-linking. The clay thereby enhances the ability of the mucus barrier to protect the gut lining from various chemical insults (Droy-Lefaix et al., 1985; Leonard et al., 1994). Clay also remains in the gut bound to the mucus layer, where it may continue to adsorb various toxins making the two functions, cytoprotection and adsorption, mutually compatible (Brouillard and Rateau, 1989; Gardiner et al., 1993; Leonard et al., 1994). Our findings on the passage rate of clays in captive parrots indicate that large amounts of clay were present in the gastrointestinal tract for at least 12 h after consumption, suggesting that relatively long-term exposure of the gastrointestinal mucosa occurs in parrots.

Recent studies have demonstrated that high surface area clays such as smectite and attapulgite are effective at inducing these cytoprotective effects and alleviating the symptoms of diarrhea (Leber, 1988; Lexomboon et al., 1994). As a result, the active ingredient of some antidiarrheal medications has been changed to these clay types from the historic kaolin-pectin formulation (Dukes, 1990). Soils from many geophagy sites are kaolin-rich (Vermeer and Ferrell, 1985; Mahaney et al., 1996), but it remains unclear whether these low-surface-area clays can induce cytoprotection. The Peruvian soils we tested contained moderate to high surface area clays, suggesting that consumption of these soils is likely to generate the cytoprotective effects induced by modern clay-based antidiarrheal medications.

Polyphenolics are known to attack and erode the lining of the gut, i.e., tanning the proteins in the mucus or on the mucosal surface, causing the types of damage that clay treatment can prevent (Mitjavila et al., 1977; Freeland et al., 1985; Mole and Waterman, 1986; Gee and Johnson, 1988; Ortiz et al., 1994). Although parrots generally do not exhibit the symptom of diarrhea (Lumeij, 1994), animals suffering the acute effects of large quantities of tannin-rich plants are often diagnosed with diarrhea and/or gastric lesions (Weisman and Thompson, 1984; Holliman, 1985; Hwang et al., 1991). Given that these parrots consume a diet that is high in phenolics, they may be protected from the corrosive effects of these compounds, but in this case, the mechanism involves the induction of a cytoprotective effect in the lining of the gastrointestinal tract. How this cytoprotective mechanism might relate to cation-exchange detoxification remains a question for future study, but there is no obvious theoretical reason why they might not function simultaneously.

In summary, analyses of geophagy soils and experiments on captive parrots strongly reject the grit and pH-buffering hypotheses, and although minerals are released, our data suggest that minerals are unlikely to be the primary cause of geophagy in parrots. From the *in vitro* adsorption trials, the effects on the toxicity of parrot food items, and the reduction of bioavailability of quinidine in captive birds, we conclude that geophagy can function to detoxify dietary toxins

for vertebrate herbivores. The persistence of clay in the gastrointestinal tract and the types of clay present in geophagy soils further suggest the possibility that cytoprotection of the gastrointestinal tract may also be an important function of geophagy. Since detoxification is likely to occur in the lumen of the gut and the gastrointestinal mucosa is roughly similar among vertebrates (Fawcett, 1994), these two functions, dietary detoxification and cytoprotection, may well be universally applicable to all soil-eating animals including humans, nonhuman primates, ungulates, and other herbivores. Because of their structures, however, soils can, and likely do, perform a variety of functions for vertebrate consumers. Given the complexities of plant chemistry, gastrointestinal physiology, and animal ecology, the causes of this phenomenon are likely to be multifactorial.

We propose three ecological adaptations that enable parrots to cope with toxic resources. First, a defining characteristic of the Psittaciformes is the exceptionally large, powerful, and manipulative bill. Macaws in particular are capable of opening the hardest of seeds, delicately peeling away chemically defended seed coats, and consuming the high-quality seed (Gilardi and Munn, unpublished data). Such handling of foods is common in herbivores, but is particularly well known in humans, where processing raw foods by peeling, leaching, boiling, baking, etc., is often a form of detoxification (cf., Stahl, 1984; Johns, 1990). Second, although exposure to household toxins often causes morbidity and mortality in captive parrots (Dumonceaux and Harrison, 1994), wild parrots frequently consume seeds that are toxic to humans, suggesting that parrots are capable of effective inducible enzymatic detoxification (Acedo, 1992; Munn, 1988; Gilardi and Munn, unpublished data; Norconk et al., 1997). Our finding that captive amazons required 50 times the human dose of quinidine to attain similar circulating levels of the drug supports the hypothesis that parrots avoid absorbing ingested toxins, detoxify them rapidly, or both. Finally, widespread and frequent geophagy of clay-rich soils may adsorb significant quantities of dietary toxins and prevent gastric erosion, thus facilitating consumption of otherwise poisonous foods.

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