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Geophagy in birds of Crater Mountain Wildlife Management Area, Papua New Guinea

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Abstract

Numerous New Guinea birds, mostly psittaciforms and columbiforms, have been recorded feeding on soil. This study documents geophagy in the Crater Mountain Wildlife Management Area (CMWMA) in the Eastern Highlands of Papua New Guinea. We present the first documented case of geophagy in the palm cockatoo *Probosciger aterrimus* and in up to 11 other species. Soil from the site where geophagy by palm cockatoos was recorded was highly weathered and acidic, with a mixture of kaolin, gibbsite, goethite and illite in the clay fraction. Analyses may support the hypothesis that soil is ingested to counterbalance the effects of toxic compounds in fruit. We suggest that the accessibility of the site (an exposed bank), rather than the nature of the soil itself, prompted its use by birds. At another site, a blue-coloured soil on which cassowaries fed was rich in vivianite (an iron phosphate) and contained an iron-rich smectite, and some kaolin and mica in the clay fraction. Why cassowaries feed on this particular soil is unclear, but they may obtain trace elements from it, or take advantage of its high iron or phosphorus content. Obtaining other elements, in particular calcium and sodium, may also be important. Alternatively, there may simply be an attraction to its blue colour, which also attracted the interest of local people and folklore. Birds were also reported to drink salt water within the CMWMA. Taken together, there may be quite different reasons for ingestion of minerals/soils among as many as 23 bird species from five families.

Introduction

Geophagy in psittaciforms is well recorded where large flocks of parrots visit 'clay' licks in the neotropics to ingest soil (Munn, 1994; Gilardi & Munn, 1998; Brightsmith & Aramburú, 2004). Records of avian geophagy from other regions are reported, yet few involve detailed studies (Pryce, 1994; Cooper, 2000; May, 2001; Gilardi, 2003; Low, 2003; Symes & Marsden, 2003). Various hypotheses for geophagy in birds have been proposed, each supported by the respective context in which it occurs (Diamond, Bishop & Gilardi, 1999). One reason is to neutralize toxic and/or digestion-inhibiting plant secondary compounds contained in many tropical fruits and seeds (Diamond *et al*., 1999; Gilardi *et al*., 1999). Essential minerals and elements are also probably obtained (March & Sadleir, 1975; Jones & Hanson, 1985; Diamond *et al*., 1999; Sanders & Jarvis, 2000). However, the number of well-documented cases of avian geophagy are few and from a limited number of locations and taxa. Avian geophagy could be more common than literature records suggest and is a topic with various unanswered questions.

While conducting a 7-month project on the effects of anthropogenic forest modification on bird communities in Papua New Guinea (PNG), local landowners (LOs) reported a traditional knowledge of locations where geophagy occurs. This presented the opportunity to investigate geophagy among new taxa in a previously unstudied region.

Study area and methods

Field observations

The study was undertaken in the Crater Mountain Wildlife Management Area (CMWMA) (2700 km^2) situated on the borders of the Eastern Highlands and Chimbu Provinces, PNG, from mid-April to late October 2002 (Fig. 1; see also Igag & Murphy, 2002). The mean annual rainfall is 6000–8000 mm and habitats visited ranged from lowland tropical forest to hill forest between 400 and 1000 m a.s.l. (Mack & Wright, 1996; Wright *et al*., 1997; Weiblen, 1998).

This region is populated by the Pawaiia people who are semi-nomadic cultivators (mostly sago) and hunters, with extensive traditional knowledge about wildlife (Toft, 1983). While conducting other studies in the area, communications with the local people revealed much about avian geophagy. One LO reported a site where he had observed palm cockatoos *Probosciger aterrimus* feeding on soil. The site

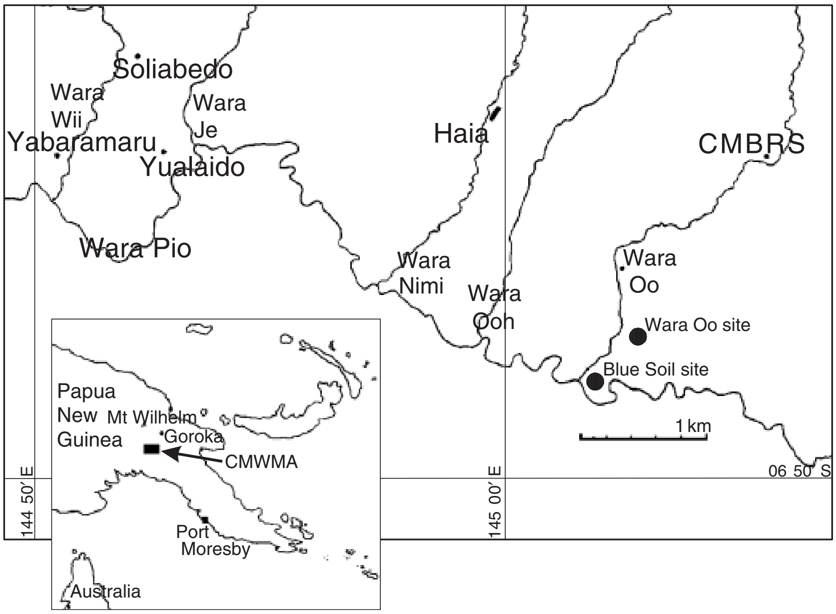

Figure 1 General region of the study within the Crater Mountain Wildlife Management Area (CMWMA) showing settlements and large rivers. The Wara Pio flows from east to west (CMBRS, Crater Mountain Biological Research Station).

(06°46′41.5″S, 145°02′31.8″E; 610 m a.s.l.) was situated *c.* 3 km south of the Wara Oo settlement, and hereafter is referred to as the Wara Oo site. This site was briefly visited in May 2002. In late September two camera-traps (CamTrakker$^{\mathrm{TM}}$, Watkinsville, GA, USA) were set up, attached to long poles over the site, on a bank that was inaccessible from below owing to a steep slope. During the 6 days that they were set, they were checked daily and positions were altered once. A soil sample was collected from the site where the palm cockatoos were seen feeding.

At Soliabedo, west of Wara Oo, a geophagy site was reported by a local Pawaiian, but was not visited. This particular informant was an elderly male with an evident knowledge of local fauna and flora. Determining the species present was carried out by avoiding leading questions (those that gave a yes/no answer) and allowing the informant to scrutinize the images himself. Further debate with other male members of the tribe occurred. In translated and pidgin conference, C. T. S. attempted to determine species observed visiting the site.

Another informant indicated that he knew of a site where dwarf cassowaries *Casuarius bennetti* fed on blue soil near the confluence of the Oo and Pio Rivers (henceforth referred to as the Blue Soil site). A soil sample was brought to C. T. S. Additional records of geophagy in the region were collected from informants, although no other sites were visited. Before this study, numerous species were recorded visiting a saltwater seep at Wara Sera, near the Crater Mountain Biological Research Station (CMBRS), and are also noted (S. Oppel, pers. obs.).

Soil analysis

The moist and dry colours of each soil sample were determined using Munsell colour charts (Munsell Color, 1966). The soil samples were air-dried and gently ground to pass a 2 mm sieve. The particle size distribution of the two soils was determined by the pipette method (Gee & Bauder, 1986). Clay ($<2\,\mu$m) and silt (2–50 μm) fractions were determined after settling according to Stokes' law and the fine (0.05–0.25 mm), medium (0.25–0.50 mm) and coarse (0.50–2.00 mm) sand fractions were determined by dry sieving. Total major elements were measured by X-ray fluorescence spectrometry (XRF) and minor and trace elements by inductively coupled plasma-mass spectrometry (ICP-MS). Phosphorus was measured colorimetrically on a Varian Cary 1E UV–Visible spectrophotometer after extraction with ammonium bicarbonate (AMBIC, Mulgrave, Victoria, Australia) according to The Non-Affiliated Soil Analysis Working Group (1990). pH was measured in distilled water and 1 M KCl using a Radiometer PHM210 pH meter (Copenhagen, Denmark) with a standard glass electrode. A soil:solution ratio of 1:2.5 was used (10 g soil:25 ml solution), and left to stand for about 45 min with occasional stirring using a glass rod. Exchangeable Ca and Mg were measured by atomic absorption spectrophotometry, and Na and K by flame emission (Varian SpectraAA-200) after extraction with 1 M ammonium acetate (pH 7.0) (Carter, 1993), using centrifugation instead of filtering to ensure complete exchange of the cations by ammonium. Extractable acidity was determined in 1 M KCl and measured by titration with 0.1 M NaOH using phenolphthalein as indicator (The Non-Affiliated Soil Analysis Working Group, 1990). Effective cation exchange capacity (ECEC) was calculated as the sum of the exchangeable bases plus acidity. Clay mineralogy was investigated by X-ray diffraction (XRD) using oriented samples of the $<2\,\mu$m fraction following saturation of separate sub-samples with magnesium or potassium. The Mg-saturated preparations were examined air-dry, and after exposure to an atmosphere of ethylene glycol and glycerol. The K-saturated samples were examined air-dry and after heating to 550 °C

(Bühmann, Fey & de Villiers, 1985). All analyses were carried out on a Philips PW1050 diffractometer (Eindhoven, The Netherlands) at 1° min^{-1} with a scanning step of 0.02° from 3 to 40°2Θ using monochromated CoKα radiation. Data were captured by a Sietronics 122D automated microprocessor (Canberra, ACT, Australia) attached to the diffractometer and the diffraction traces were then qualitatively analysed.

Results

Avian geophagy

Twenty-five pigeon and 27 parrot species have been recorded in the CMWMA (Mack & Wright 1996; A. L. Mack & C. T. Symes, pers. obs.). This study considers only those recorded by Mack & Wright (1996) and S. J. Marsden & C. T. Symes (in press; unpubl. data) because they were recorded in the elevational range of this study (Table 1). Fourteen (61%) pigeon species and six (30%) parrot species were recorded or known to practice geophagy, or to drink salt water (Table 1). Magnificent bird of paradise *Cicinnurus magnificus* was also recorded at the Wara Sera saltwater site (S. Oppel, pers. obs.). Geophagy was also recorded/suspected in dwarf cassowary, Blyth's hornbill *Rhyticeros plicatus* and grey crow *Corvus tristis*. However, in each case, the numbers of birds were not recorded.

Wara Oo site

The Wara Oo geophagy site comprised two to four small cleared areas on an almost vertical bank. The slope was south facing, with the exposed bank just below the highest part of a hill. Sections of the bank, *c.* 8 m vertical in height, were devoid of vegetation and showed signs of recent disturbance. At least two specific perches on the bank were observed onto which the cameras were focused. The surrounding area on the bank was covered in mosses, ferns and sparse vegetation. Above the slope pristine forest grew to the edge, with some trees leaning over the edge. The slope fell steeply into the valley below, making it accessible only from above.

Palm cockatoos and Blyth's hornbills were observed in the canopy nearby and immediate vicinity of the site. On the slope below the site, emergent trees and snags provided perches for birds before visiting the geophagy site. On one occasion, two palm cockatoos were flushed from the bank. A primary flight feather from a Blyth's hornbill was collected from below the site by an LO and brought to C. T. S. The palm cockatoo was the only species confirmed, by photographic evidence, to practice geophagy.

Soliabedo site

At a site near Soliabedo (*c.* 25 km to the west of the Wara Oo site), numerous psittaciform and columbiform species, as well as grey crow, were reputed to feed on soil (Table 1; LO, pers. comm.). This site was described as a clearing on a gentle slope in the forest. Birds were reported to visit the site throughout the day, but only in drier weather when the soil became exposed. All species indicated were identified by a Pawaiian informant in a field guide (Beehler, Pratt & Zimmerman, 1986) and are given in Table 1.

Both informants and interviewers vary greatly in reliability, and asking informants to identify birds on the basis of colour plates in a field guide is a method prone to error. The Soliabedo informant mentioned five species of *Ptilinopus* pigeon, suggesting a possible error in identification within this genus. For example, *P. perlatus* and *P. ornatus* are very similar, and because New Guineans identify most species by characteristics other than the colour patterns illustrated in field guides, suspecting errors on their behalf is warranted. However, the informant identified only one species in the plates that was unlikely to occur in the area, suggesting a certain degree of skill at using plates for recognizing species. Another younger guide who assisted in identifying species during transects proved competent at identifying species from call and visually. We therefore accept likely error with the identification of congenerics, and note that although the list is accurate it is not definitive.

In a separate study, LOs identified taxa killed by hunters, using field guides, and had errors of $<5\%$ of 695 specimens including 264 birds of 86 species. In all cases misidentifications were made of similar congeneric allopatric species (A. L. Mack & P. West, unpubl. data).

The record of *C. tristis* given by the Soliabedo informant was given independently of that given by the Wara Oo informant.

Blue Soil site

Descriptions of the Blue Soil site were obscure, yet it was determined that cassowaries and other birds visited the site. Other sites were reported to exist but were not often found as the blue soil became visible only at certain times of the year (LO, pers. comm.). Reports were that local hunters used this soil as a 'lure' for hunting cassowaries. It is also fed to hunting dogs as it reputedly makes them 'invisible'.

Saltwater sites

Three sites were reported by local informants, where numerous bird species, mostly of parrots and pigeons, regularly drank salt water (Table 1). These sites were described as gently flowing streams on steep slopes. Until salt became available via trading stations at colonial settlements, the Pawaiia used these sites to procure salt (LO, pers. comm.). Species that reputedly visit these sites included sulphur-crested cockatoos *Cacatua galerita*, rainbow lorikeets *Trichoglossus haematodus* and dusky lories *Pseudeos fuscata* among others (LO, pers. comm.). At the CMBRS, 10 species of pigeon and magnificent bird of paradise were observed visiting a saltwater seep to drink water (S. Oppel, pers. obs.; Table 1).

Table 1 Bird species recorded in the Crater Mountain Wildlife Management Area (CMWMA) showing (1) status of species at Crater Mountain Biological Research Station (CMBRS) (R, rare; U, uncommon; C, common; A, abundant; t, transient; p, permanent resident), (2) mass of birds, (3) feeding guilds indicated by fr, frugivore; gr, graminivore; ne, nectarivore; ins, insectivore and (4) species in which geophagy has been observed [species noted by local landowners (LOs) as visitors to geophagy sites in the CMWMA (sol, Soliabedo site; wo, Wara Oo site; sw, saltwater site recorded by LOs; ws, recorded at CMBRS Wara Sera saltwater site (S. Oppel, pers. obs.), DBG, Diamond *et al.* (1999); question mark indicates suspected geophagist]. Taxonomy and order follow Beehler *et al.* (1986)

Scientific name	Common name	Status	Mass (g)	Feeding guild[g,h]	Geophagy recorded
Columbidae					
Columba vitiensis	White-throated pigeon	Rt	345–511[d]	fr/gr	—
Macropygia amboinensis	Brown cuckoo-dove	Ap	142–155[c,d]	fr/gr	sol, sw, ws, DBG
Macropygia nigrirostris	Black-billed cuckoo-dove	Cp	66–104[b]	fr/gr	sol, ws
Reinwardtoena reinwardtii	Great cuckoo-dove	Cp	208–305[b,d]	fr/gr	sol, sw, ws
Chalcophaps stephani	Stephan's ground-dove	R[a]	118–126[b,d]	gr	sol
Henicophaps albifrons	New Guinea bronzewing	Rt	247[b,d]	fr	sol
Gallicolumba rufigula	Cinnamon ground-dove	Up	121–140[b,d]	gr	—
Gallicolumba jobiensis	White-bibbed ground-dove	Rt	126–158[b]	fr/gr	—
Otidiphaps nobilis	Pheasant pigeon	Cp	500[b]	fr/ins	—
Ptilinopus magnificus	Wompoo fruit-dove	Rt	250–500[d]	fr	sol, sw
Ptilinopus perlatus	Pink-spotted fruit-dove	Cp	240–257[b,d]	fr	sol?, ws
Ptilinopus ornatus	Ornate fruit-dove	Cp	163–165[b,d]	fr	sol?, ws
Ptilinopus superbus	Superb fruit-dove	Cp	80–145[b,d]	fr	ws
Ptilinopus coronulatus	Coroneted fruit-dove	Rt	69–77[b,d]	fr	—
Ptilinopus pulchellus	Beautiful fruit-dove	Ap	68–76[b,d]	fr	sol, sw, ws
Ptilinopus rivoli	White-breasted fruit-dove	Ct	135–162[b]	fr	—
Ptilinopus iozonus	Orange-bellied fruit-dove	R[a]	105–112[b,d]	fr	—
Ptilinopus nanas	Dwarf fruit-dove	R[a]	47–49[b,d]	fr	sol, ws
Ducula rufigaster	Purple-tailed imperial pigeon	Up	414–582[b,d]	fr	sol
Ducula chalconota	Rufescent imperial pigeon	Up(t?)	613[b]	fr	—
Ducula pinon	Pinon imperial pigeon	Rt	783–802[b,c,d]	fr	sol, ws, DBG
Ducula zoeae	Zoe imperial pigeon	Ap	575–592[b,d]	fr	sol, sw, ws
Gymnophaps albertisii	Papuan mountain pigeon	At	254–259[b,c,d]	fr	DBG?
Psittacidae					
Pseudeos fuscata	Dusky lory	At(p?)	117–192[d,e]	fr/ne	sw
Trichoglossus haematodus	Rainbow lorikeet	Ap	122–141[c,d]	ne/gr	sw, DBG
Trichoglossus goldiei	Goldie's lorikeet	At	45–61[d,e]	ne/fr	—
Lorius lory	Western black-capped lory	Ap	172–260[d,f]	ne/fr	—
Charmosyna multistriata	Streaked lorikeet	Ut	—	ne/fr	—
Charmosyna placentis	Red-flanked lorikeet	Ap	25–48[d,e]	ne	—
Charmosyna pulchella	Little red lorikeet	Ut	24–35[d,e]	ne	—
Charmosyna wilhelminae	Pygmy lorikeet	Rt	—	ne	—
Probosciger aterrimus	Palm cockatoo	Cp	550–1200[c,e,f]	fr	wo, DBG?
Cacatua galerita	Sulphur-crested cockatoo	Cp	727–1012[c,d,e]	gr/fr	sw, DBG
Micropsitta pusio	Buff-faced pygmy-parrot	Rt	10–15[d,e,f]	ins/gr	—
Cyclopsitta gulielmiterti	Orange-breasted fig-parrot	Ap	27–34[d,e,f]	fr/gr	—
Cyclopsitta diophthalma	Double-eyed fig-parrot	Ut	25–56[e]	fr	—
Psittaculirostris desmarestii	Large fig-parrot	Up	108–126[e]	fr	—
Geoffroyus geoffroyi	Red-cheeked parrot	C[a]	130–180[d,e]	fr/gr	—
Geoffroyus simplex	Blue-collared parrot	Ct	161–195[d,e,f]	fr	—
Eclectus roratus	Eclectus parrot	Cp	355–615[c,d,e]	fr	DBG
Psittrichas fulgidus	Vulturine parrot	Cp	690–865[c,e,f]	fr	DBG
Alisterus chloropterus	Papuan king parrot	Up	138–190[d,e]	fr/gr	—
Loriculus aurantiifrons	Papuan hanging parrot	Rt	13–16[e,f]	ne	—
Bucerotidae					
Rhyticeros plicatus	Blyth's hornbill	Cp	1784–1827[b,c]	fr	wo?, DBG
Corvidae					
Corvus tristis	Grey crow	Cp	635–681[b,c]	fr/ins	wo, DBG

Status, after Mack & Wright (1996);
[a]species not recorded in altitudinal range at CMBRS by Mack & Wright (1996), but recorded by C. T. Symes & S. J. Marsden (unpubl. data) in the CMWMA; Mass; [b]Baptista, Trail & Horblitt (1997); [c]Diamond *et al.* (1999); [d]Bell (1978); [e]Rowley & Collar (1997); [f]Forshaw (1989); Feeding guild; [g]Bell (1978); [h]Beehler *et al.* (1986).

Table 2 Particle size distribution (%) of the Wara Oo and Blue Soil samples

Site	Clay[a] (<0.002 mm)	Silt (0.002–0.05 mm)	Sand (0.05–2 mm)	Coarse sand (2–0.5 mm)	Medium sand (0.5–0.25 mm)	Fine sand (0.25–0.05 mm)
Wara Oo	35.36	42.04	22.60	2.26	4.36	15.98
Blue Soil	27.65	49.50	22.85	1.07	0.86	20.92
New Guinea[b]	13	48	39	—	—	—
Peru geophagy[b]	38	49	13	—	—	—
Peru control[b]	82	17	1	—	—	—
Peru geophagy[c]	35.7	47.1	17.2	3.4	1.7	12.1
Peru control[c]	40.4	28.6	31.1	10.6	2.9	17.6

[a] The clay value of 0.2 μm referred to in Diamond *et al.* (1999) is likely a misprint, and should read 2 μm (0.002 mm) as indicated above.

[b] Results from Diamond *et al.* (1999) are given for comparison.

[c] Results from Brightsmith & Aramburú (2004) are given for comparison.

Table 3 Major elements as per cent oxide (in whole sample) in the Wara Oo and Blue Soil samples

Element as oxide	Wara Oo		Blue Soil	
	%	ppm	%	ppm
SiO_2	52.03	243 204	45.39	212 166
Al_2O_3	29.80	157 701	13.02	68 902
Fe_2O_3	14.21	99 385	25.26	176 668
MnO	0.05	387	0.15	1162
MgO	0.70	4220	1.02	6150
CaO	0.13	930	0.47	3360
Na_2O	0.21	1560	0.32	2370
K_2O	1.10	9130	1.44	11 950
TiO_2	1.72	10 310	0.57	3417
P_2O_5	0.23	1004	11.18	48 790
Loss on ignition (%)	18.28		28.94	

Elements as ppm for comparative purposes.

Note: conversion of per cent oxide to ppm (element) calculated as follows: e.g. MgO, molecular mass of MgO = 40.305 (Mg = 24.305, O = 16); therefore, 60.3% is Mg. Wara Oo soil contains 0.70% MgO; therefore, 0.422% Mg (60.30% of 0.70). Multiply % by 10 000 to convert to ppm.

Table 4 Phosphorus, trace and minor elements (in whole sample) in the Wara Oo and Blue Soil samples

Element	Wara Oo (mg kg^{-1})	Blue Soil (mg kg^{-1})
Phosphorus (P)	967.85	45815.21
Scandium (Sc)	3.22	12.15
Vanadium (V)	277.42	123.90
Chromium (Cr)	114.25	68.81
Cobalt (Co)	19.93	26.18
Nickel (Ni)	86.61	41.70
Copper (Cu)	59.35	28.72
Zinc (Zn)	17.03	51.21
Arsenic (As)	2.99	22.37
Rubidium (Rb)	9.54	34.28
Strontium (Sr)	5.43	56.19
Yttrium (Y)	0.98	21.55
Zirconium (Zr)	182.76	93.13
Niobium (Nb)	11.31	6.04
Antimony (Sb)	0.46	0.39
Barium (Ba)	41.53	108.21
Lanthanum (La)	1.28	16.47
Cerium (Ce)	5.39	39.84
Praseodymium (Pr)	0.28	4.51
Neodymium (Nd)	0.89	18.02
Samarium (Sm)	0.22	4.02
Europium (Eu)	0.06	0.97
Gadolinium (Gd)	0.22	3.98
Terbium (Tb)	0.03	0.62
Dysprosium (Dy)	0.20	3.49
Holmium (Ho)	0.04	0.73
Erbium (Er)	0.13	1.93
Thulium (Tm)	0.02	0.30
Ytterbium (Yb)	0.17	1.86
Lutetium (Lu)	0.03	0.28
Hafnium (Hf)	5.17	2.65
Tantalum (Ta)	0.79	0.45
Tungsten (W)	1.49	1.15
Lead (Pb)	17.83	13.40
Thorium (Th)	0.71	5.04
Uranium (U)	1.93	1.72

Soil characteristics

Colour

The colour of the sample from Wara Oo was 5YR 6/6 (reddish yellow; wet) and 2.5YR 4/8 (dark red; dry). The Blue Soil sample was 2.5PB 3/4; wet, and 2.5PB 3/4; dry. [See Symes & Marsden (2003) for an image of the Wara Oo soil sample.]

Particle size

The results of the soil particle size distribution are given in Table 2 and include results from Diamond *et al.* (1999) and Brightsmith & Aramburú (2004) for comparison.

Soil elemental composition

The results of the XRF and ICP-MS analyses are given in Tables 3 and 4, respectively. Table 3 reports total elemental composition and thus includes elements locked in minerals (and are therefore larger than the exchangeable fraction reported in Table 6). These are unlikely to be made available

Table 5 Approximate percentages of the main minerals present within the $<2\,\mu m$ clay fraction of the Wara Oo and Blue Soil samples as estimated from XRF and XRD data (amounts of vivianite and iron-rich smectite given as ranges due to uncertainty in the assumptions used)

Mineral	Wara Oo	Blue Soil
Goethite	15	—
Gibbsite	10	—
Mica/illite	10	14
Quartz	7	10
Hydroxy-interlayered vermiculite	8	—
Kaolin	50	14
Vivianite	—	30–40[a]
Plagioclase feldspar	—	5
Iron-rich smectite	—	20–30[b]

[a] Amount calculated from the P content (XRF and ICP-MS) is about 38%; this may be an overestimate.

[b] Amount calculated is 20%; this may be an underestimate.

XRF, X-ray fluorescence spectrometry; XRD, X-ray diffraction; ICP-MS, inductively coupled plasma-mass spectrometry.

to birds unless the minerals are able to be completely dissolved in the gut.

Clay mineralogy

The estimated proportions of the minerals present are given in Table 5. These values were determined from the XRD patterns of the clay fractions of the two soils based on a number of assumptions (Fig. 2).

Chemical properties

The AMBIC P, pH, exchangeable bases (reported as $\mathrm{cmol_c\,kg^{-1}}$), extractable acidity and ECEC of the two soils are given in Table 6. These detailed analyses of soil are provided for comparative purposes and further research on the topic of geophagy.

Discussion

Avian geophagy has been recorded in many species in the tropical and sub-tropical regions (Munn, 1994; Pryce, 1994; Gilardi & Munn, 1998; Diamond *et al.*, 1999; Cooper, 2000; May, 2001; Gilardi, 2003; Low, 2003; Symes & Marsden, 2003; Brightsmith & Aramburú, 2004). In the neotropics, large numbers of birds (predominantly parrots) have been recorded visiting 'clay licks', and at Tambopata Reserve in Peru at least 28 species (17 parrots) are known to eat soil (Munn, 1994; Gilardi & Munn, 1998; Brightsmith & Aramburú, 2004). We suggest that geophagy is a common phenomenon among large frugivores at CMWMA and other sites in New Guinea. The rarity and/or reclusive nature of larger species may explain why they are not yet recorded as geophagists. Large ground-feeding columbids (e.g. *Otidiphaps nobilis* and *Goura* spp.) may not visit traditional geophagy sites because their terrestrial habit and smaller home ranges might limit them to consuming soil at scattered sites in the forest interior. The likelihood of encountering a regular geophagy site may be less probable and only likely to occur should one lie in a certain individual's territory. Crop content analysis and further observations may indicate that soil is ingested by such species.

The highly leached nature of the Wara Oo sample and its very high acid saturation value of 86% [calculated as the proportion of the ECEC occupied by acidity; Wara Oo soil $= (16.94/19.66) \times 100$; see Table 6] indicate that the soil is not eaten for its nutritional value. The relatively high proportion of kaolin and illite may support the hypothesis that palm cockatoos and other species feed on this soil to

Figure 2 X-ray diffraction (XRD) patterns of the clays from the (a) Wara Oo and (b) Blue Soil samples. The minerals that mainly correspond to the peak *d*-spacings are also indicated in Table 5, summarized as follows: (a) Wara Oo: 1.442 nm (hydroxy-interlayered vermiculite); 1.005 and 0.501 nm (illite); 0.734 and 0.358 nm (kaolin) (latter peak not indicated in (a)); 0.485 and 0.437 nm (gibbsite); 0.417 nm (goethite); 0.426 and 0.334 nm (quartz); 0.352 nm (anatase); 0.269 nm (hematite); and (b) Blue Soil: 1.693 and 1.406 nm (smectite); 1.001 and 0.501 nm (dioctahedral mica/illite); 0.712 and 0.355 nm (kaolin); 0.673 and 0.490 nm (vivianite); 0.473 and 0.448 nm (phyllosilicate minerals); 0.426 and 0.334 nm (quartz); 0.352 nm (anatase); 0.320 nm (plagioclase feldspar). Mg, magnesium saturated; K, potassium saturated; AD, air dry; EG, ethylene glycol; GLY, glycerol; 550 °C, heated to 550 °C. The estimated clay mineralogy of the two samples (Table 5) was obtained from the XRD patterns of the two clays, and was based on the following assumptions: (1) Wara Oo sample: All the Fe indicated by XRF is present as goethite (FeOOH), indicated by the strong 0.417 nm reflection (a), because no clear haematite was observed by XRD. All the K is present as illite (the 1.005 and 0.501 nm reflections on XRD and the absence of any feldspar). Approximate amounts of gibbsite and quartz were estimated directly from the XRD patterns by comparison with standard minerals and the remaining SiO_2 and Al_2O_3 were allocated to kaolin. The remaining reflections shown in (a) represent hydroxy-interlayered vermiculite, anatase (TiO_2) and haematite (as a result of the heating of goethite). (2) Blue Soil sample: All the P measured by XRF occurs as clay-size vivianite ($Fe_3(PO_4)_2 \cdot 8H_2O$) and the excess Fe is present within the smectite mineral observed on XRD (b), because no other iron-containing minerals were present. The former assumption may have resulted in an overestimate of the amount of vivianite in the clay fraction (Table 5) given the small height of the peaks at 0.673 and 0.490 nm (b), unless the vivianite is present as ultra-fine particles or coatings. The amounts of quartz and plagioclase feldspar were estimated directly from the XRD patterns by comparison with standard minerals. All the K measured by XRF was assumed to be in the dioctahedral mica as evidenced by the XRD patterns. These assumptions allow an approximate structural formula for the smectite to be calculated (assuming that all tetrahedral sites are occupied by Si), i.e. $(Si_8)(Al_{1.49}\,Fe_{1.95}\,Mn_{0.04}\,Mg_{0.52})(O_{20}(OH)_4)$. This mineral has an interlayer charge of -0.56 and it is probable that this would be balanced by some of the Ca, Na or K. Such a formula is similar to those given by Brigatti (1983) for a number of iron-rich smectites. The excess SiO_2 and Al_2O_3 were then assumed to be in kaolin (b). These assumptions probably underestimate the amount of iron-rich smectite and overestimate the amount of mica (Table 5). The remaining peaks indicated in (b) represent the phyllosilicate clay minerals (0.473 and 0.448 nm) and anatase (0.352 nm).

counteract the effects of toxic or digestion-inhibiting secondary compounds in fruit and seeds. Palm cockatoos are specialist feeders and are able to access the endocarp of seeds that are difficult to open (e.g. *Cerbera*, *Terminalia* spp.) (Forshaw, 1989; Mack & Wright, 1996). It is believed that ingestion of soil might assist digestion because components in the soil bind with or interfere with the detrimental actions of the secondary compounds produced by plants to inhibit predation by animals (e.g. Waterman & McKey, 1989; Diamond *et al.*, 1999; Gilardi *et al.*, 1999). All the species observed consuming soil ingest fruits, nectar/pollen or seeds that generally contain secondary compounds. The clay contents of the soils in this study compare favourably with geophagy soils in South America (Diamond *et al.*,

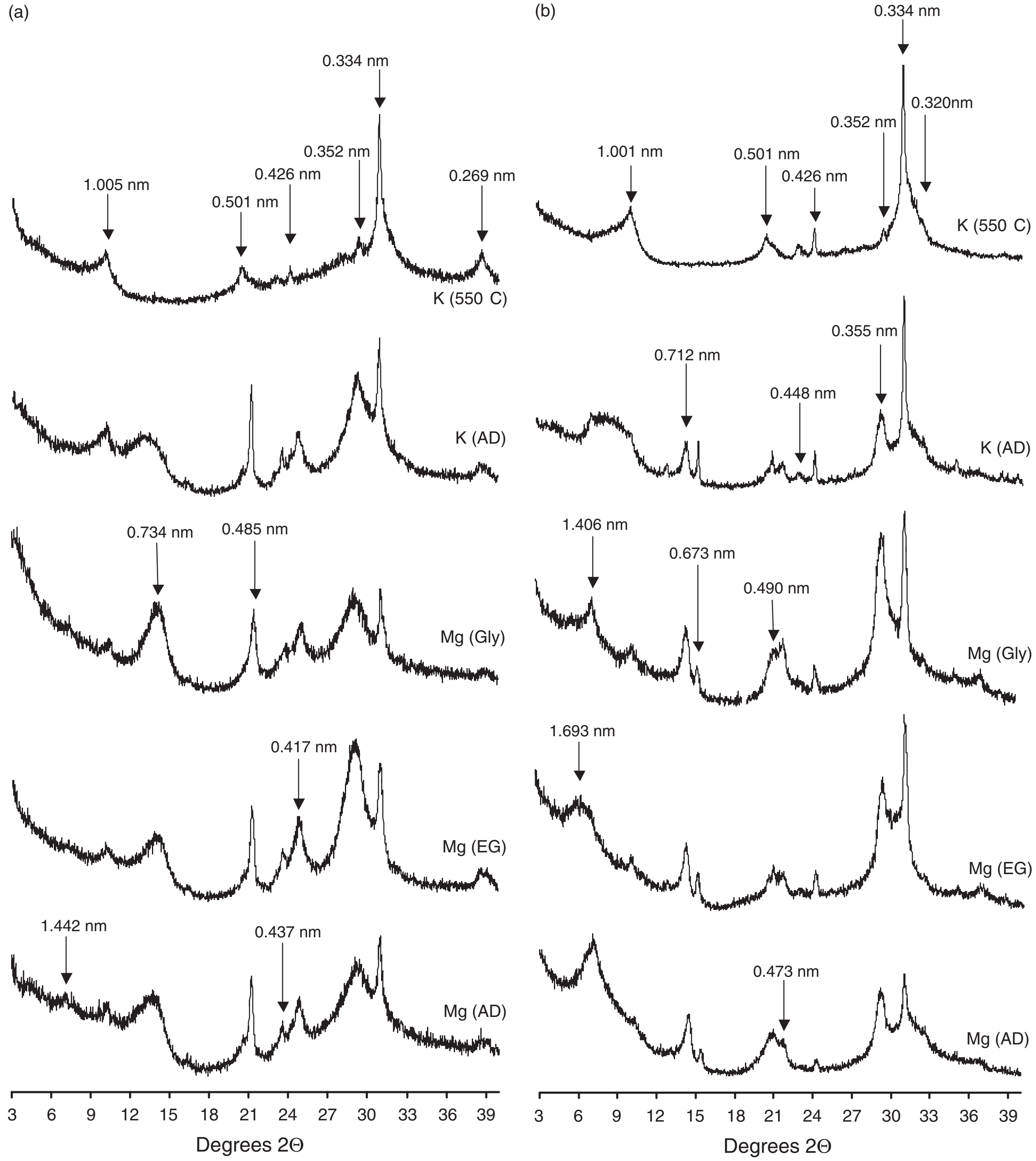

Table 6 Some chemical properties of the Wara Oo and Blue Soil samples

				Ca	Mg	Na	K	Acidity	ECEC
Site	P (mg kg^{-1})	pH (KCl)	pH (H_2O)	(cmol$_c$ kg^{-1}; ppm values in parentheses)					
Wara Oo	0.00	3.92	5.44	0.38 (76.15)	1.00 (121.53)	1.11 (255.19)	0.23 (89.93)	16.94 (170.74)	19.66
Blue Soil	484	3.94	4.20	8.60 (1723.35)	1.02 (123.96)	1.46 (335.65)	0.46 (179.85)	4.55 (45.86)	16.09

Note: 1 cmol Na = (22.99/100) g, so 1.11 cmol$_c$ kg^{-1} = 0.2552 g kg^{-1} = 255.19 mg kg^{-1} (ppm), for Ca and Mg the molar mass is halved as these are divalent ions; cmol$_c$ kg^{-1} values (SI units) equivalent to meq 100 g^{-1}.
ECEC, effective cation exchange capacity.

1999; Brightsmith & Aramburú, 2004) (see Table 2), and soils eaten by African olive pigeons *Columba arquatrix* where the clay content was 26–29% ($n = 3$) (C. Downs, unpubl. data). In addition the moderate ECEC values (Wara Oo 19.66 cmol$_c$ kg^{-1} and Blue Soil 16.09 cmol$_c$ kg^{-1}) in this study (Table 6) suggest a toxin adsorption function (as long as the toxins are cationic), as suggested by Diamond *et al.* (1999). However, these values are not dissimilar to unused soils reported by Brightsmith & Aramburú (2004).

The dwarf cassowary *C. bennetti* (25 kg) is suspected to eat soil (Diamond *et al*., 1999; A. L. Mack, pers. obs.), and observations by local LOs in the CMWMA indicate that it does so. On Mount Missim, a site known well by the local tribespeople, it was observed that cassowaries eat 'graun' (ground) (A. L. Mack, pers. obs.). The site was at an undercut and cassowary footprints were clearly visible in the soil (A. L. Mack, pers. obs.). The Blue Soil analysed in this study is highly unusual inasmuch as it has a strong blue coloration, and it contains vivianite. It is unlikely that vivianite is the source from which blue pigment or colouring is sequestered for the vivid wattles of cassowaries. The mineral is soluble in acid and thus probably altered in the digestive tract. Cassowaries do eat stones and feed on a number of blue-coloured fruit (Wright, 1998). If they have a strong search pattern image for blue, then it is likely they are simply attracted to a blue colour. However, in food colour preference tests with two captive cassowaries, no particular preference for blue shades was observed (Wright, 1998). Cassowaries have a rapid gut transit rate. Their diet in CMWMA is more than 91% fruit in all months (Wright, 1998, 2005). Often fruits pass through the gastrointestinal tract partly or even apparently undigested (Wright, 1998). The Blue Soil is relatively rich in rare earth elements (Table 4) (compared with the soil at Wara Oo), and this may suggest that they seek micronutrients from this rare soil type. Alternatively, it is plausible that the high P content and perhaps the high Fe (Table 3) is an attraction. In addition, the comparatively high Ca content suggests it is a source of this element (Table 6). Alternative sources of Ca may be important for birds, especially during egg-laying periods (Tordoff, 2001).

Our information on the use of saltwater sites is important in the light of recent findings by Brightsmith & Aramburú (2004). They suggest that the most likely reason for soil selection is its sodium content, indicating that further work is in progress to investigate the use of soil for the adsorption of dietary toxins (Brightsmith & Aramburú, 2004). The Wara Oo soil sodium content (255.19 ppm; see Table 6) compares favourably with that of geophagy soils in South America (253 ± 49.8 ppm), thus supporting the hypothesis presented there (Brightsmith & Aramburú, 2004). The Blue Soil site (335.65 ppm) exceeds these values, adding further support to the hypothesis that the soil is a sodium source for birds.

Independent observations at Wara Sera of similar species recorded drinking at saltwater sites (S. Oppel, pers. obs.) give credibility to the hypothesis that eating soil and drinking salt water may serve similar functions, i.e. provide important salts to frugivores. The observations of the magnificent bird of paradise, an understorey frugivore, drinking salt water, begs further questions as to the function of this behaviour. It is suggested that any further study of geophagy includes a study of saltwater drinking sites, and available elements in food eaten by geophagists.

Many species recorded eating soil by Diamond *et al.* (1999) were also those known or suspected to do so in CMWMA. Most were parrots or pigeons, but also include New Guinea's only hornbill species – almost all are frugivores or seed predators. Our understanding of frugivore physiology is insufficient to determine the true reasons for geophagy in each individual species or at each site. Within the CMWMA, we recorded probably a number of different reasons for geophagy/saltwater consumption. Others have indicated that a combination of hypotheses to explain avian geophagy may be supported at any one time and under different circumstances (Diamond *et al*., 1999; Gilardi *et al*., 1999; Brightsmith & Aramburú, 2004). The very different composition of the Wara Oo and Blue Soil sample suggests strongly that the reasons for their use should be different, although accessing a source of particular elements (e.g. in each soil the magnesium contents are similar; Table 6) is highly suggestive.

At Wara Oo, it is suggested that site accessibility may determine its use, although control samples to support this interpretation are lacking. Areas of exposed soil may not be rare within most tropical forests, but such areas re-vegetate quickly, whereas others may not be accessed safely by large canopy frugivores. Some sites, however, may be accessible for longer periods and maintained to a degree through continuous use by animals. Chewed exposed roots and vegetation was observed at Wara Oo and re-vegetation at this site may have been hindered to a certain degree. The importance of these 'traditional' sites needs to be assessed as their availability may influence frugivore ecology and even population levels. Likewise, the impact of tropical forest alterations such as logging, and the local extinction of some frugivore species through, for example hunting, may also influence the ecology of geophagy sites and the birds that use them. We suggest the importance of maintaining the integrity of these multi-functional sites in allowing unhindered accessibility for important frugivore seed dispersers.

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