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Nutritional Content of the Diets of Free-living Scarlet Macaw Chicks in Southeastern Peru

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Abstract: To provide novel information on psittacine diets, we analyzed the texture, crude protein, crude fat, Ca, P (total), Mg, K, Na, S, Cu, Fe, and Zn concentrations of crop contents from 10 free-living scarlet macaw (*Ara macao*) chicks from lowland forests of southeastern Peru. We compared our results with nutrient concentrations of known wild parrot foods and published psittacine dietary recommendations to highlight similarities and differences and suggest future avenues of research. The diets were much coarser textured than those recommended for hand feeding. Soil in the diet provided an important source of Na, but Na levels were still lower than all recommendations. Concentrations of protein, Zn, K, Cu, and P (total) were near to or within the range of recommendations for captive psittacine birds. Fat, Ca, and Mg concentrations were greater in crop contents than in the average food plants and greater than published recommendations. The Na:K ratios were only one-twentieth of those recommended for young poultry. Future analyses should investigate the bioavailability of Fe, Ca, and Zn in these diets and the effects of varying concentrations of fat, Na, Ca, Mg, and Na:K ratio on psittacine growth and development.

Key words: crop contents, fat, free-ranging parrots, minerals, protein, nutrition, avian, scarlet macaw, *Ara macao*

Introduction

The importance of diet to overall health of birds cannot be overstated. Despite this, the nutritional requirements of long-lived companion parrots remain poorly understood. As a result, nutritional deficiencies are among the most common health problems faced by captive parrots today.[1–3] Most published recommendations for psittacine nutrition come from studies of domestic poultry, supplemented by work on captive budgerigars (*Melopsittacus undulatus*) and cockatiels (*Nymphicus hollandicus*).[4–7] However, poultry and parrots are not closely related and differ both developmentally and ecologically. Budgerigars and cockatiels are small ground-foraging, grass seed–eating birds from dry areas, which differ in lifestyle and diet from the large parrots from moist environments, which feed on tree fruits, seeds, and flowers.[8,9] Therefore, it is unlikely that available data adequately model the dietary requirements of most parrots.[10] Many formulated diets are available for psittacine birds, but these vary in their nutrient composition, and many pet owners continue to feed nutritionally inadequate, seed-based diets.[11–13] In parrots, growth rates vary among hand-fed chicks, parent-raised captive chicks, and parent-raised free-living chicks.[14–16] Although these differences could be caused by a mix of factors (eg, feeding frequency, gut bacteria, etc), they likely relate to differences in the nutrient contents of the diets.

To provide novel information on psittacine diets, we examined the nutrient composition of crop contents collected from free-living scarlet macaw (*Ara macao*) chicks from Tambopata Research Center in the lowland forests of south-

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eastern Peru. Here, parrots and macaws consume a mixture of seeds, fruit, flowers, tree bark,[17] and soil from river edge "clay licks."[18–20] The consumption of soil (geophagy), has been studied extensively for decades and is usually attributed to the animal's search for minerals, which are otherwise deficient in their diets. Sodium is the most commonly cited reason for geophagy.[21–25] However, geophagy might also protect animals from dietary toxins,[20,26–28] treat ionic imbalance,[22,29] stabilize gut pH,[27,30] reduce intestinal parasitism,[31] and reduce diarrhea.[32] Although avian use of grit for grinding seeds has been known for decades,[33–35] recent studies find most parrots avoid soil with large particles (grit) and prefer soils with fine particles, which are useless as grinding aids.[20,36–38] These recent studies suggest that sodium supplementation could be driving parrot geophagy.[19,36,39] However, experimental evidence shows that geophagy soils also bind dietary toxins.[20] The parrots also feed soil to their chicks.

In this study, we compared the nutrient levels of the crop contents from nestling scarlet macaws with average nutrient composition of known psittacine foods from the area. Additionally, we analyzed the nutritional importance of soil to the chicks and compared nutrient composition of crop contents with published recommendations and diets for captive psittacine birds. Although the nutrition of free-living animals is not always optimal, the analyses presented provide new information regarding psittacine nutrition and allow comparison of potentially important differences among free-living and captive diets to direct future research.

Materials and Methods

Study site

This study was conducted at the Tambopata Research Center (13°08′S, 69°36′W; 250 m in elevation) in the Tambopata National Reserve (274 690 ha) near the border of the Bahuaja-Sonene National Park (1 091 416 ha). The center is located in a small (<1 ha) clearing surrounded by a mix of mature floodplain forest, riparian successional forest, *Mauritia flexuosa* (Arecaceae) palm swamps, upland forest, and bamboo.[40,41] The forest is classified as tropical moist forest.[42,43] The site is adjacent to a 500-m-long, 30-m-high riverbank clay lick, where up to 1700 macaws and parrots gather daily, resulting in high parrot densities in the area.[18]

Sample collection and processing

We sampled crop contents from 10 chicks in 7 different nests of free-living scarlet macaws. The nests were located in PVC nest boxes hung 15–22 m above the ground in tall trees within 1 km of the Tambopata Research Center. We accessed the chicks by climbing to the nests with the use of single-rope techniques and mechanical ascenders.[44] We climbed the nests every 1–2 days around hatching to determine hatch dates of each chick in the study. Starting at an average age of 28 days (SD = 10 days, n = 10 chicks), chicks were sampled approximately once every 10 days until age 60 days (SD = 19 days, n = 10). At these ages, the parents are the sole source of food and water for these chicks. The chicks do not fledge until age 83–90 days, but after about 60 days, chicks rarely had enough food in the crop to allow sample collection. From January–March 2005, we collected a total of 48 samples of crop contents by the protocol of Enkerlin-Hoeflich et al.[45] Briefly, a 20-cm-long plastic tube was moistened with rainwater and inserted down the esophagus and into the crop. Outside tube diameter was 1 cm for chicks ≤20 days and 1.5 cm for chicks >20 days. Smaller tube diameters were not used because the particles in the sample were too big to enter the tube. The contents of the crop were massaged and pushed up into the tube, the top of the tube was covered with the thumb, and the tube was removed and placed in a Whirl-pak® bag. After sampling, each chick was immediately returned to the nest. These samples were placed in refrigeration at 4°C within 30 minutes of collection. Each sample was weighed and divided into its visually distinct constituents (wood/tree bark, seeds, pulp, insect larvae, etc). Each fraction was weighed, and one of the largest particles of each type was measured for length (longest dimension) and width (longest dimension perpendicular to length). The sample was also scored for the presence or absence of soil. Because soil was usually present as a sticky film of clay-rich mud that could not be separated from the other items in the sample, soil was not separated and weighed. It is probable that some of the water from the sample leaked out of the sampling tube as the tube was removed from the crop. This likely resulted in an underestimate of percent moisture in the sample. After each fraction was weighed, the entire sample was recombined for drying and subsequent nutritional analysis. Samples were stored at 4°C for 3.02 ± 2.16 days, (minimum [min] = 1 day, maximum [max] = 8 days, n = 48 samples) before drying.

Sample analyses

All crop and food samples collected at TRC were weighed fresh and dried to a constant weight in an oven at approximately 55°C. Samples were then stored for up to 3 months in airtight containers with desiccant before analysis. Samples ranged from 0.2 to 5.5 g dry weight (1.55 ± 0.88 g). Because of the small quantity of each sample, 13 samples were analyzed independently, and the remaining 35 were combined into 17 composite samples. Composite samples were created by combining samples from chicks in the same nest collected on the same day (n = 9 composite samples, average chick age difference = 3.0 ± 0.0 days) and samples from chicks from different nests (n = 8, average age difference = 5.3 ± 1.6 days, range 3–7 days).

Laboratory analyses were performed at the Palmer Research Center at the University of Alaska, Palmer, AK. Crude protein was calculated by the Dumas method in a LECO CHN-1000 analyzer (LECO Corporation, St Joseph, MI, USA) for carbon, hydrogen, and nitrogen. Crude fat was calculated by the ether extraction method.[46] Percent moisture was calculated as the difference between the fresh weight and the weight at the time of analysis. We determined the concentrations of calcium (Ca), potassium (K), phosphorus (P), magnesium (Mg), iron (Fe), sodium (Na), zinc (Zn), copper (Cu), and sulphur (S) by boiling 0.25 g of each sample in 20 ml of 5:3 nitric acid : perchloric acid until most of the liquid was gone, then mixing the contents with deionized water and reading the concentrations of each nutrient with ICP mass spectrometry.[47] All data are presented on a dry matter basis.

Food resources

We compiled published information on the protein, fat, Ca, Fe, K, Mg, Na, Zn, P, and Cu concentrations of food items consumed by macaws and parrots in southeastern Peru, including 73 plant parts from 50 species from Gilardi[17] and 22 plant parts from 15 species from Brightsmith et al[19] and Brightsmith (D. J. B., unpublished data, 2003). For all data, the plant parts were dried and analyzed for nutrient content following procedures described by Gilardi.[17] These data on parrot food nutritional contents are presented to show the range of available mineral concentrations in food resources for comparison to the crop contents. They are not weighted by frequency with which birds use each plant resource. The data are presented on a dry matter basis as mean ± SD and sample size (number of distinct plant parts).

Soil data

We compiled information on available Ca, Fe, K, Mg, Na, Zn, P, and Cu concentrations in soils consumed by psittacine birds in southeastern Peru.[19,20,36,48] These values represent available concentrations estimated by an extraction designed to mimic vertebrate gastric fluid.[20] Total available nutrients in the geophagy soils were estimated by using the efficiency of the gastric extractions compared with the total mineral content as calculated by Gilardi et al.[20] These extraction efficiencies were then used along with the average available mineral concentrations to estimate the total available mineral concentrations in geophagy soils in southeastern Peru.

Published diets and recommendations

We compiled nutritional information from published psittacine diets and dietary recommendations for comparison with our results. Values are presented as concentrations based on total dry matter. Values from the National Research Council[49] were converted from "as fed" values to dry matter values by dividing by 0.9, assuming that feedstuffs used in poultry diets contain an average of 90% dry matter.[12] To calculate average values for commercially available macaw diets, the data from Werquin et al[13] were converted from "as fed" to proportion of dry matter by using the percent moisture reported by each food manufacturer on their Web site.[50–54] These were averaged as dry matter nutritional values for all products recommended for 1) adult macaw maintenance and 2) macaw breeding. The recommendations were taken from the manufacturers' Web sites.[50–54]

Data analysis

The distributions of all variables were examined for normality by quantile-quantile plots, frequency histograms, chi-square goodness of fit statistics, and Shapiro-Wilks W statistic with StatGraphics Centurion XV (StatPoint Technologies Inc, 2005, Warrenton, VA, USA). To determine whether nutrient concentrations differed between samples with and without soil, we used Student's *t* tests for normally distributed variables and Wilcoxon signed rank tests for nonnormally distributed variables.[55,56] We tested the relationship between chick age and sample composition (percent moisture, largest particle

Table 1. Nutrient levels (mean, SD, minimum, maximum) of crop contents from free-living scarlet macaw chicks at Tambopata Research Center, January–March 2005. The samples were collected from 10 chicks aged 13–77 days. Values presented below are for all samples analyzed, including those both with and without soil. The sample size varies because many of the samples were not large enough to analyze for all nutrients. All values are presented on a dry matter basis.

	Mean	SD	Min	Max	n
Fat (%)	28.6	8.6	13.7	47.3	24
Protein (%)	23.5	5.6	9.6	31.0	30
Ca (%)	1.40	0.61	0.57	2.99	29
P (%)	0.48	0.13	0.16	0.69	29
Mg (%)	0.36	0.08	0.22	0.58	29
Na (%)	0.024	0.031	0.003	0.154	30
K (%)	0.73	0.22	0.48	1.60	29
Ca:P	3.2	1.5	0.9	8.7	29
Na:K	0.029	0.025	0.005	0.096	29
Cu (ppm)	15	5	9	28	29
Fe (ppm)	2457	5281	60	23 340	29
Zn (ppm)	44	13	27	78	29
S (%)	0.18	0.05	0.09	0.29	29

length, presence of soil, and nutrient concentrations) by univariate linear regression for normally distributed variables and Spearman's rank correlation for nonnormally distributed variables. Nutrient values are presented as mean ± SD (sample size). Nutrient levels for crop contents, available food plants, and available soil nutrients were compared by 1-way analysis of variance and multiple range tests for normally distributed variables, and Kruskal-Wallace and Mood's median test with 95% confidence intervals around the medians for nonparametric variables with StatGraphics Centurion XV. Nutrient levels in crop samples were compared with each recommendation by Student's *t* tests for normally distributed variables and Wilcoxon signed rank tests for nonnormally distributed variables.

Results

Crop samples from free-living scarlet macaw chicks contained seeds, wood/bark, soil, fruit pulp, insect larvae, and unknown items. The samples contained 53.5% ± 12.5% moisture (n = 28 samples). The percentage of moisture in the samples decreased significantly with increasing age of chicks (linear regression: $r^2 = .37$, n = 28, $P < .001$). Soil was present in 19% of samples (n = 48), but its weight could not be accurately determined because it adhered to the other particles in the sample and could not be easily separated without altering the chemical composition of the sample. The samples contained protein (23%) and fat (29%) (on a total dry matter basis), and none of these values varied significantly with chick age ($P > .05$ for all; Table 1). Protein, fat, P, and S were significantly lower in samples containing soil, whereas K, Fe, Na, and Zn were significantly higher in samples containing soil ($P < .05$ for all; Table 2). Only Ca, Mg, and Cu did not differ between samples with and without soil ($P > .05$ for all; Table 2). We found no relationship between chick age and the presence or absence of soil, suggesting that adults did not give more soil to younger chicks (linear regression: $r^2 = .04$, n = 46, $P = .15$). However, Na concentration decreased significantly as chicks aged (Spearman rank correlation: $r = -.7$, n = 30, $P < .001$). K and Mg concentrations in samples also decreased significantly with increasing age of chicks (linear regression: K%, $r^2 = .34$, $P = .001$; Mg%, $r^2 = .22$, $P = .01$). The Ca:P ratio of the samples averaged 3.21 ± 1.51 and decreased with increasing chick age (Spearman rank correlation: $r = -.44$, n = 29, $P = .02$; Fig 1).

The largest food particles in each sample averaged 9.0 ± 3.9 mm × 4.5 ± 2.2 mm (n = 73 particles from 31 different crop contents, 2.4 ± 1.2 particles measured per sample). The size did not vary significantly with chick age (linear regression, $R^2 = .032$, $F_{1,29} = .97$, $P = .33$).

The concentrations of Na, Ca, P, Mg, Fe, Zn, Cu, protein, and fat were significantly greater in crop contents than in food plants ($P < .001$; Tables 3–5). However, crop contents had significantly less K than the average food plant ($P < .001$; Table 3). The concentrations of Ca, P, K, Mg, Fe, Zn, and Cu in crop contents were significantly greater than in geophagy soils ($P <$

Table 2. Nutrient concentrations of crop contents from scarlet macaw chicks from southeastern Peru. Values for samples with visually evident soil and those without are shown separately. Data are presented as mean ± SD (sample size). The *P* values were calculated with Student's *t* test for normally distributed values and Wilcoxon's signed rank test for nonnormally distributed values.

	Without soil	With soil	*P* value
Moisture (%)	55 ± 14 (22)	53 ± 11 (7)[a]	>.05
Protein (%)	26 ± 4 (22)	18 ± 6 (8)[b]	<.01
Fat (%)	31 ± 8 (18)	21 ± 6 (6)[a]	<.01
Ca (%)	1.50 ± 0.64 (21)	1.20 ± 0.50 (8)[a]	>.05
P (%)	0.52 ± 0.10 (21)	0.35 ± 0.14 (8)[a]	<.001
Mg (%)	0.35 ± 0.09 (21)	0.37 ± 0.07 (8)[a]	>.05
Na (%)	0.012 ± 0.970 (22)	0.057 ± 0.046 (8)[b]	<.001
K (%)	0.66 ± 0.12 (21)	0.93 ± 0.31 (8)[a]	<.01
Ca:P	2.9 ± 1.1 (21)	3.9 ± 2.2 (8)[a]	>.05
Na:K	0.018 ± 0.013 (21)	0.055 ± 0.029 (8)[b]	<.001
Fe (ppm)	236 ± 240 (21)	8286 ± 7601 (8)[b]	<.001
Cu (ppm)	15 ± 6 (21)	15 ± 4 (8)[b]	>.05
Zn (ppm)	42 ± 12 (21)	51 ± 13 (8)[b]	<.05
S (%)	0.19 ± 0.04 (21)	0.14 ± 0.04 (8)[a]	<.01

[a] Student's *t* test.
[b] Wilcoxon signed rank test.

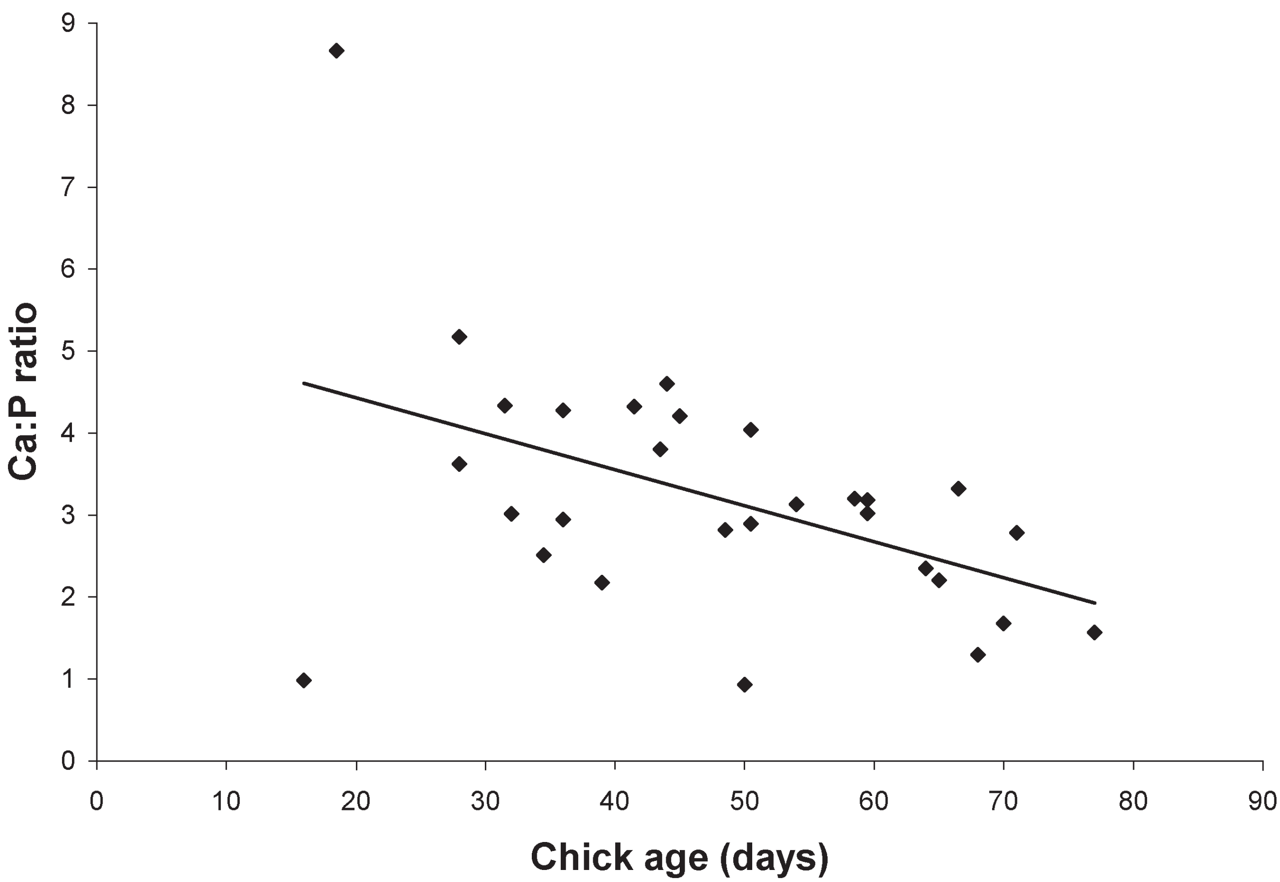

Figure 1. Change in Ca:P ratio of crop contents from 10 free-ranging scarlet macaw chicks from the lowlands of Peru. The decline in Ca:P ratio with age is statistically significant (Spearman rank correlation: $r = -.44$, n = 29, $P = .02$).

Table 3. Macronutrient concentrations in crop contents of free-living scarlet macaw chicks and in food plants and soils consumed by psittacine birds in southeastern Peru. Food plant and soil available nutrient concentrations are taken from published sources[17,19,20,36,48] and reported on a dry matter basis. "Soil total" is an estimate of the total nutrients contained in geophagy soils, calculated with extraction efficiencies reported by Gilardi et al.[20] Data are presented as mean ± SD (sample size), with minimum–maximum.[a]

	Ca (%)	P (%)	Mg (%)
Crop	1.40 ± 0.61 A (29) 0.57–2.99	0.48 ± 0.13 A (29) 0.16–0.69	0.36 ± 0.08 A (29) 0.22–0.58
Food plants	0.52 ± 0.75 B (90) 0.02–4.27	0.36 ± 0.31 B (90) 0.05–1.68	0.28 ± 0.21 B (90) 0.01–1.04
Soil available	0.04 ± 0.04 C (36) 0.005–1.06	0.002 ± 0.002 C (7) 0.001–0.005	0.046 ± 0.046 C (36) 0.002–0.086
P value	<.001	<.001	<.001
Soil total (approx.)	0.074	0.001	0.35

[a] Means in the same column with different letters are significantly different ($P < .05$) according to the Kruskal-Wallis rank sum test.

Table 4. Micronutrient concentrations in crop contents of free-living scarlet macaw chicks, food plants, and soils consumed by psittacine birds in southeastern Peru. Available nutrient concentrations of food plants and soils are taken from published sources[17,19,20,36,48] and reported on a dry matter basis. "Soil total" is an estimate of the total nutrients contained in geophagy soils, calculated with the extraction efficiencies reported by Gilardi et al.[20] Data are presented as mean ± SD (sample size), with minimum–maximum.[a]

	Cu (ppm)	Fe (ppm)	Zn (ppm)
Crop	15 ± 5 A (29) 9–28	2457 ± 240 A (21) 60–23340	44 ± 13 A (29) 27–78
Food plants	11 ± 7 B (50) 2–35	66 ± 48 B (90) 6–309	29 ± 24 B (90) 4–117
Soil available	0.6 ± 0.6 C (33) 0.1–1.8	81 ± 63 B (19) 3–214	3 ± 2 C (36) 0.7–11.1
P value	<.001	<.001	<.001
Soil total (approx.)	NA	22 000	59

Abbreviation: NA, not available because extraction efficiencies were not reported.
[a] Means in the same column with different letters are significantly different ($P < .05$) according to the Kruskal-Wallis rank sum test.

Table 5. Nutrient concentrations of crop contents from scarlet macaw chicks and food plants consumed by psittacine birds in southeastern Peru. Food plant nutrient concentrations are from published sources[17,19] and reported as percent dry matter. Data are presented as mean ± SD (sample size), with minimum–maximum. Data were analyzed by the Wilcoxon rank sum test.

	Protein (%)	Fat (%)
Crop	23 ± 5 (30) 10–31	28 ± 8 (24) 14–47
Food plants	15 ± 10 (85) 3–36	14 ± 17 (79) 0–69
P value	<.001	<.001

.001 for all; Tables 3, 4). However, crop contents had significantly less Na than geophagy soils ($P <$ .001; Table 3).

Protein levels in crop contents were significantly greater than the published recommendations for adult maintenance diets but were not significantly different from the published breeder and hand-feeding diets (see *P* values in Table 6[57,58]). Fat levels in the crop contents were significantly greater than all published adult maintenance, breeding, and hand-feeding diets and recommendations ($P < .001$ for all diets; Table 6). The Ca and Mg levels were significantly higher than those in nearly all published diets, and Na levels were significantly lower (Table 7). The K levels in crop contents were greater than or statistically indistinguishable from those in published diets and recommendations (Table 7). The P concentrations

Table 3. Extended.

Na (%)	K (%)
0.024 ± 0.031 A (30)	0.73 ± 0.22 A (29)
0.003–1.540	0.48–1.60
0.004 ± 0.003 B (89)	1.7 ± 1.6 B (90)
0.000–0.017	0.3–13.6
0.11 ± 0.05 C (36)	0.009 ± 0.007 C (36)
0.038–1.890	0.001–0.036
<.001	<.001
0.12	0.084

were significantly higher than some recommendations and diets and significantly lower than others (Table 7). The Zn levels in crop contents were less than or statistically indistinguishable from levels in published diets and recommendations (Table 8). The Fe levels were much higher than all published diets and recommendations (Table 8), but this is probably because of artifact of analysis (see "Discussion" section). When only samples without soil were included, Fe levels were similar to or higher than most published diets (Table 8). The Cu concentrations were significantly higher than some recommendations and diets and significantly lower than others (Table 8).

Discussion

Crop contents from free-living scarlet macaw chicks contained predominantly seeds with smaller amounts of wood and fruit pulp and the occasional insect larvae. This was similar to the findings of previous studies of 2 free-living scarlet macaw chicks in Belize[63] and 4 in Peru.[17]

Texture

The largest food particles in the crops of young scarlet macaws (nearly 10 × 5 mm) were much larger than expected, especially since nearly all samples contained items difficult to digest (eg, wood). The coarse texture of the food samples stands in stark contrast to the readily digested, finely ground commercial formulas sold for hand feeding young psittacine birds.[61] Even studies of diet texture versus digestibility in adult parrots used diets with most particles <1 mm in size, nearly an order of magnitude smaller than the wild diets we found.[64] Crop stasis has been reported in captive psittacine chicks fed finely ground diets[16,65] and the diet texture might be partially to blame for this phenomenon (S. Hoppes, oral communication, 2008). However,

Table 6. Protein and fat levels of free-living scarlet macaw chick crop contents compared with diets and dietary recommendations from the literature. For commercially available diets, average values are presented, and the number in parentheses is the number of commercial diets used to calculate the average. All values are presented on a dry matter basis. Standard deviations and sample sizes for the crop contents are presented in Table 1.

Taxon	Diet	Type[a]	Protein (%)	Fat (%)	Reference
Poultry[b]	0–6 wk	Rec.	20.0	—[c]	49
Parrot	Maintenance (min)	Rec.	6.0–7.0*	—	57
Parrot	Maintenance	Rec.	10.0–15.0*	4.0–5.0*	7,59,60
Macaw	Maintenance	Diet	8.8*	15.0*	58
Macaw	Maintenance	Diets (15)	17.3*	8.5*	13
Parrot	Maintenance/breeding	Diet	24.0	—	12
Macaw	Breeder	Diets (8)	20.4	12.3*	13
Parrot	Breeder	Rec.	15.0–22.0	10.0–15.0*	59
Parrot	Hand feeding	Rec.	22.0	—	7
Parrot	Hand feeding	Diet	25.8	5.2*	61
Parrot	Hand feeding	Diets (11)	21.7	11.3*	16
Macaw	Hand feeding	Diet	23.8	21.4*	62
Scarlet macaw	Wild chicks	Crop contents	23.5[d]	28.6[e]	This study

[a] Rec. indicates published dietary recommendations; Diet, published diets; Diets (no.), commercially available diets.
[b] Leghorn-type chickens.
[c] —, Not available.
[d] Variable not normally distributed; statistical comparisons by Wilcoxon signed rank test.
[e] Variable normally distributed; statistical comparisons by Student's t test.
* Significantly different at $P < .001$.

Table 7. Macromineral levels of free-living scarlet macaw chick crop contents compared with diets and dietary recommendations from the literature. P is the total phosphorus content of the sample. For commercially available diets, average values are presented, and the number in parentheses is the number of commercial diets used to calculate the average. All values are presented on a dry matter basis. Standard deviations and sample sizes for the crop contents are presented in Table 1. For each nutrient, we tested significant differences between the values from the crop samples and each individual recommendation is noted.

Taxon	Diet	Type[a]	Ca (%)	P (%)	Mg (%)	Na (%)	K (%)	Ref.
Poultry[b]	0–6 wk	Rec.	1.0***	0.44**	0.07***	0.17***	0.28***	49
Parrot	Maintenance	Rec.	0.50***	0.40**	0.06***	0.15***	0.40***	7,60
Parrot	Maintenance	Rec.	0.30–0.70***	0.30–0.70	0.15***	0.20***	0.70	59
Macaw	Maintenance	Diet	0.44***	0.15***	—[c]	—	—	58
Macaw	Maintenance	Diets (11)	0.80***	0.58*	—	0.15***	—	13
Parrot	Maintenance/ breeding	Diet	1.10**	0.80***	0.15***	0.20***	0.70	12
Parrot	Breeder	Rec.	0.70–1.20*	0.50–0.80	—	—	—	7,59
Macaw	Breeder	Diets (7)	0.92*	0.61*	—	0.17***	—	13
Parrot	Hand feeding	Diet	0.47***	0.62***	—	—	—	62
Parrot	Hand feeding	Diet	0.99–1.10**	0.45	—	—	—	61
Parrot	Hand feeding	Diets (11)	0.93*	0.47	0.13***	0.20***	0.53**	16
Scarlet Macaw	Wild chicks	Crop contents	1.40[d]	0.48[d]	0.36[d]	0.02[e]	0.73[d]	This study

[a] Rec. indicates published dietary recommendations; Diet, published diets; Diets (no.), commercially available diets.
[b] Leghorn-type chickens.
[c] —, Not available.
[d] Variable was normally distributed; statistical comparisons were done by Student's *t* test.
[e] Variable was not normally distributed; statistical comparisons were done by the Wilcoxon signed rank test.
* Crop sample values differed significantly from the recommendation at $P < .05$.
** Crop sample values differed significantly from the recommendation at $P < .01$.
*** Crop sample values differed significantly from the recommendation at $P < .001$.

anecdotal accounts suggest that raising captive psittacine chicks on coarse-texture diets results in blockages of the digestive tract. As a result, we do not recommend using coarser texture diets until more research has been conducted. It is unclear what repercussions this difference in texture and digestibility could have on the growth and development of the psittacine digestive tract, but the larger particles might slow down passage rate and increase nutrient absorption. If studies from

Table 8. Micronutrient levels of free-living scarlet macaw chick crop contents compared with diets and dietary recommendations from the literature. For commercially available diets, average values are presented, and the number in parentheses is the number of commercial diets used to calculate the average. All values are presented on a dry matter basis. Standard deviations and sample sizes for the crop contents are presented in Table 1.

Taxon	Diet	Type[a]	Fe (ppm)	Zn (ppm)	Cu (ppm)	Ref.
Poultry[b]	0–6 wk	Rec.	80**	40	5***	49
Parrot	Maintenance	Rec.	80**	50**	8***	7,60
Parrot	Maintenance	Rec.	100*	40–50	4–12**	59
Parrot	Maintenance/breeding	Diet	150	120***	20***	12
Parrot	Breeder	Rec.	100*	50–80**	—[c]	59
Parrot	Hand feeding	Diets (11)	176	114***	20***	16
Scarlet macaw	Wild chicks	Crop contents	236[d,e]	44[e]	15[e]	This study

[a] Rec. indicates published dietary recommendations; Diet, published diets; Diets (no.), commercially available diets.
[b] Leghorn-type chickens.
[c] —, Not available.
[d] The value here represents only the crop contents without soil (see text).
[e] Variable was not normally distributed; statistical comparisons done by the Wilcoxon signed rank test.
* $P < .05$.
** $P < .01$.
*** $P < .001$.

poultry are any indication,[64] parrot chicks raised on "wild-textured" diets should develop a more muscular digestive system than birds raised on powdered diets. Gut musculature could be important, especially for parrots being raised for release into the wild, which need to digest natural foods efficiently.

Moisture

Moisture content averaged 54% in the samples collected and decreased significantly as the chick aged. The percent moisture in the crop contents is lower than that recommended for psittacine hand-fed diets (79% moisture).[61] However, the way in which samples were collected and processed probably led to our underestimating the moisture content by an unknown amount (see "Methods" section). Thus, the absolute value presented here should be taken only as a minimum. In addition, the fine-textured diets normally used in hand-feeding congeal into a gelatinous solid when mixed with insufficient water,[16,61] so water levels between powdered and coarse-textured diets might not be comparable.

Nutrient levels and comparison with recommendations

The scarlet macaw chick crop contents contained protein levels higher than those recommended for parrot maintenance diets but equivalent to those of growing chickens and parrot breeder and hand-feeding diets (Table 6). The crop contents contained about 50% more protein than the average food analyzed in southeastern Peru. Future studies should examine whether adults are choosing higher protein foodstuffs for their chicks or whether, on average, the foods available during the breeding season have higher protein content. The percent protein of the crop contents and foodstuffs presented here are estimated with the use of standard nutritional analyses that use total nitrogen content as a surrogate measure for protein content. If these samples contain significant amounts of inorganic or other nonprotein nitrogen sources, the reported protein values could be overestimated. Additional research is underway to determine what percentage of the diet is composed of amino acids and what amino acids might be potentially limiting chick growth and feather development.

Published dietary fat levels for parrots vary from 5% to more than 20%, even among hand-feeding diets, suggesting that there is no consensus on appropriate dietary fat levels for raising parrots (Table 6). Some breeders freely acknowledge the need to adjust fat content for each species by trial and error. Despite this great variability, the fat levels in the crop contents (29%) were significantly higher than even the highest published values. As with protein, the crop contents contained higher fat levels than the average food plants, suggesting that adults are choosing foods with the highest fat levels to feed their young. High-fat diets are advantageous for raising poultry in hot climates because fats (unlike carbohydrates) are absorbed passively from the gut and thus generate less metabolic heat per unit energy absorbed.[66] However, whether the drive to lessen metabolic heat is favoring high-fat diets in tropical macaws is unknown. Higher caloric density is known to increase weight gain in birds,[67] so the high fat levels might contribute to the higher growth rates recorded for parent-raised versus hand-raised psittacine birds.[14–16] Alternatively, needs for essential fatty acids or specific fatty acid profiles could be driving the high fat content of the crop samples found here. Feeding trials with parrot chicks on diets with varying fat content and fatty acid profiles are needed.

Calcium levels in published breeding and hand-feeding diets were usually higher than those for adult maintenance diets, but some hand-feeding formulas had concentrations of Ca as low as maintenance diets (Table 7). Calcium levels ranged from 0.47% to 1.1% for published hand-feeding diets (Table 7), whereas Wolf and Kamphues[16] reported a range of 0.35%–1.1% in commercial hand-feeding formulas they analyzed. These ranges show the lack of consensus on appropriate levels of Ca for raising psittacine chicks. The crop contents contained more Ca than all the published diets. The calcium concentration in the crop contents was nearly 3 times more than the average food plant, suggesting that the adults might be seeking out foods high in Ca.

Our findings contrast with the interpretations of Wolf and Kamphues,[16] who cautioned that commercial hand-feeding formulas with 0.93% Ca were excessively high in Ca compared with the requirements for cockatiels and lovebirds (*Agapornis* species). The Ca levels determined in our study also exceeded those found to reduce growth of young poultry.[68] However, some evidence suggests that the amount of Ca that is bioavailable in the crop contents might be much lower than what is shown here: 1) Ca absorption in high-fat diets is reduced as Ca gets tied up in fatty acid "soaps"[69,70]; 2) only about 50% of the calcium in soil could be available to vertebrates[20] (Table 3); and 3) nonionic forms of Ca, including Ca bound to oxalates and phytates, are common in plant tissue and are not nutritionally available.[71] In addition, Ca is absorbed by the body both passively and actively (mediated by vitamin D). Because birds do not effectively use plant-produced vitamin D_2 and because vitamin D_3 is synthesized on exposure to UVB rays,[59,71,72] macaw chicks raised in nest cavities with little exposure to sunlight would have little vitamin D for use in active Ca absorption. As a result, dietary Ca requirements for altricial chicks could be higher than for precocial species like poultry fed a diet with readily available Ca and ample exposure to UVB. The actual amount of Ca absorbed could be significantly less than what is reported here (Table 1).

Phosphorus recommendations for psittacine diets ranged from a low of 0.15% to 0.80%, showing a lack of consensus in the literature and suggesting that psittacine birds can tolerate a wide range of dietary P. The P levels in the crop contents fell well within the range of dietary recommendations (Table 7). However, much of this P is likely bound up as phytate or is otherwise unavailable, in that 17 studies in poultry found that only about 40% of the P from plant sources was nutritionally available.[73]

Evaluation of the Ca:P ratio in the diet is important because excess P can inhibit the uptake of calcium and result in bone growth abnormalities, especially in growing animals.[68,70,71] To a lesser extent, surplus Ca reduces P uptake.[70,73] The observed Ca:P ratio in the crop contents analyzed here (3.2:1) exceeded the range of 1:1 to 2:1 recommended for psittacine birds and other vertebrates.[59] It even exceeds the ratio considered "tolerable" by some authors (0.5:1 to 2.5:1).[60,74] However, although this ratio is high, it is not unprecedented, in that laying hens in production facilities receive diets with Ca:P of up to 12:1.[49] As the macaw chicks aged, the Ca content decreased slightly, whereas P increased slightly. The result was a decline in the Ca:P ratio from about 4:1 at age 30 days to about 2:1 at age 75 days (Fig. 1). The drop in the Ca:P ratio with age contrasts with the dietary recommendations for most birds, which either increase with age (bobwhite, ducks, and leghorn chickens) or remain approximately the same (turkeys and geese).[49] Only in the recommendations for pheasants does the Ca:P ratio drop with age, and these recommendations are likely because high-Ca diets cause developmental problems and high mortality among pheasant chicks.[75]

Magnesium recommendations for parrots range from 0.067% to 0.15%, and the concentrations in the crop contents were more than 2 times greater than even these highest recommendations (Table 7). The crop content Mg concentrations were less than the maximum tolerable limit for nonlaying poultry (0.50%).[68] The Mg concentrations in the crop contents is higher than the average for the available food plants, suggesting that adult macaws could be choosing to feed foods with higher Mg concentrations. In general, Mg from plant sources is highly available, with 95% availability in 10 studies of galliform birds[76] The biological processes influencing bioavailability and absorption of Mg are complex, and although they have been little studied in birds, in mammals these processes apparently involve dietary levels of Na, Ca, P, and vitamin D.[77] In ruminants, diets low in Na reduce Mg absorption.[76] The macaw crop contents were low in Na, yet the importance of Na to Mg absorption in birds is unknown.

Published recommendations for Na do not vary greatly for macaws and chickens (range 0.15%–0.20%; Table 7). In fact, recommendations for captive mammals (rodents, nonhuman primates, and rabbits) and birds (Galliformes) span this same range, except for pigs (0.10%) and rats (0.05%).[70,78] Given this general consensus, it is unusual that about 35% of the commercial diets reviewed by Werquin et al[13] contain less than half of the recommended concentration of Na. Few experimental studies have been conducted on Na requirements, but Na levels of 0.10% and 0.048% resulted in reduced growth rates in poultry[79] and rats,[80] respectively. Among wildlife, minimum Na dietary concentrations have not been studied directly but have been estimated as 0.006% for prairie voles (*Microtus ochrogaster*), 0.008% for mountain hares (*Lepus timidus*), and 0.03% for white-tailed deer (*Odocoileus virginianus*).[70]

At only 0.024%, the Na levels in the crop contents were far below all the recommendations for captive vertebrate diets but within the range reported for the mammalian wildlife mentioned above. The Na levels of crop contents were nearly 7 times the values in the average food, suggesting that the adults actively seek out Na sources, like the soil from the clay lick (see the "Contributions of Soil" section below). Sodium deficiency can result in dehydration and slow growth.[69] Extensive work on chick growth has found no evidence of chronic slow growth at this site,[15] and studies of dehydration are underway. Future investigations should address whether Na limits chick growth or other population parameters and explore whether these species can tolerate lower Na levels than previously thought.

Published K levels for psittacine diets vary greatly (0.44%–0.70%), with values for parrots being higher than those for young chickens (Table 7). The crop contents we analyzed were nearly equal to these highest recommended values. Of note, the crop contents contained much less K than the average food available to free-living macaws in this area (Table 3). High levels of K can inhibit uptake of Na,[70,81] which is potentially the most limiting nutrient in the birds' diets at this site. In addition, the relative quantity of Na and K in the diet is an important determinant of growth for young chickens, and Na:K ratios for poultry chicks should range from 0.5 to 1.8.[82] The crop contents we analyzed had a Na:K ratio of 0.028 ± 0.025, about one-twentieth the recommended value for young chickens. However, the available food plants had even more skewed Na:K ratios: 0.0033 ± 0.0039 ($n = 89$), or $<1\%$ of the minimum recommended for young chickens.[82] As a result, it appears that the adults' behavior of seeking out supplemental Na sources (eg, the clay lick) and using food plants with lower K results in an 8-fold increase in the Na:K ratio in the diets of the chicks. Future investigation should examine whether adult macaws specifically choose foods with lower K levels to avoid mineral imbalances and the ecological, nutritional, and developmental repercussions of these skewed Na:K ratios.

In general, nutrient requirements should decrease as the chick ages because the level of growth proportional to body weight declines with age and digestive efficiency increases.[62,83] The concentrations of most of the nutrients in the crop contents showed no significant change with time. However, concentrations of 3 of the principal cations declined significantly from age 30 days to age 75 days: Na declined from 0.030% to 0.004% (an 87% reduction), K declined from 0.87% to 0.52% (a 41% reduction), and Mg declined from 0.40% to 0.29% (a 27% reduction). Although we do not know how the nutrient composition of the available food plants changed during this time, the main source of Na, the clay lick soil, was equally available throughout the period. This suggests that the parents are adjusting diets on the basis of their chicks' requirements. After the first few days of life, diets recommended for raising young psittacine birds do not change as the chicks age.[61,62,84] Among other birds, feeding recommendations show no universal trends for the few birds studied to date: recommended Na concentration declines for turkeys but not leghorn chickens, ducks, pheasants, or bobwhites; Mg recommendations decline for chickens but not turkeys; and K recommendations decline in turkeys but not leghorn chickens.[49]

Iron concentrations in the crop contents averaged nearly 2500 ppm, about 20 times greater than the recommended values and 5 times greater than the maximum tolerable level set for poultry.[68] However, this value is a gross overestimate of the amount of available Fe in the samples. Crop contents with soil contained about 35 times more Fe than samples without soil, suggesting that soil was the principal source of Fe in this study. However, only about 0.2% of the more than 12 000 ppm Fe in Peruvian soils consumed by birds might be available to vertebrates (Table 4).[20] Therefore, we presented only the Fe contents of the samples without soil for comparison with published nutritional recommendations. Even so, the Fe levels we found averaged 236 ppm: 175% greater than the adult maintenance diets, 76% greater than the breeding and hand-feeding diet recommendations, but less than the reported maximum Fe tolerance for poultry of 500 ppm.[68] The Fe levels in the crop contents apparently without soil averaged more than 3 times the value in the average food plant. This suggests that some Fe samples scored as "without soil" could have contained soil that was not visible at the time of processing. Further investigations are needed to quantify the levels of available Fe in the crop contents and what levels are optimal for growing psittacine chicks.

The recommended Cu levels are about 20 ppm for parrot chicks and range from 4 to 12 ppm for adult maintenance diets. However levels of up to 200 ppm result in increased growth for poultry, presumably because of the antibacterial properties of Cu.[85] The Cu levels in the scarlet macaw crop contents were slightly lower than the recommendations for hand feeding and higher than recommendations for maintenance diets. If the poultry model is valid for Cu, the current levels are unlikely to be detrimental, but higher levels could increase growth.[86]

Zinc levels found in the crop contents were similar to the recommendations for growing chickens and parrot maintenance diets but average about half of what is recommended for breeding and hand-feeding diets. Some of the Zn in these samples is from the soil, and only about 5% of the soil Zn is predicted to be available to the birds.[20] In addition, Zn deficiency can be exacerbated by high Ca levels.[69,87] Taken together, these birds could be getting less Zn than currently recommended.

Contributions of soil

In our study, samples that contained soil differed greatly from those that did not. Crude protein and crude fat were lower (Figure 1) in samples with soil, suggesting that soil is providing sufficient nutritional benefits to offset this reduction in protein and fat. Samples containing soil were higher in Zn, Fe, K, and Na. The samples with soil had about 34 times more Fe and about 25% more Zn than those without soil. This is not surprising because soils have more total Fe and Zn than the food plants (Table 4). However, about 99.8% of the Fe and 95% of the Zn contained in geophagy soils are considered unavailable during normal vertebrate digestion.[20] Also, our methods (boiling the samples in acid) undoubtedly released minerals from the soil that would not have been available to the birds. Further studies of the bioavailability of Fe in soils and parrot foods are needed. The finding of more K in crop contents with soil remains enigmatic because soil contains 2 orders of magnitude less K than the average plant resources (Table 3). The lower quantity of P and S in samples with soil is not surprising because soils consumed by parrots in southeastern Peru are known to have low concentrations of these nutrients compared with the foods the birds consume (Table 3).[20] Because the amount of P in samples without soil is similar to the dietary recommendations, the reduction in P is not likely of much nutritional consequence.

The samples with soil had more than 3 times more Na than those without. This was expected because soils consumed by birds have much higher Na content than their foods (Table 3).[19,20] Analyses suggest that nearly 90% of the Na in clay lick soils is available to vertebrates.[20] On average, vertebrates need about 9 mg/kg per day of Na.[70] This suggests that a 500-g chick would need to consume about 19 g of food (dry weight) per day to fulfill its sodium requirement, assuming the food contains 0.024% Na as in the average crop content sample evaluated. However, a chick would need to consume 36 g of food without soil (according to the average crop content sample without soil with 0.012% Na) or 129 g of food plants (0.0035% Na on average) per day to meet their Na requirements. For comparison, hand feeding recommendations suggest feeding about 40 g (dry weight) per day for 500-g macaw chicks,[61] and adult captive macaws consume only about 30 g of food per day (dry weight; D. J. B., unpublished data). Samples with soil also had a Na:K ratio more than 3 times greater than those without. These findings support the contention that sodium could be driving clay lick use[36,39] and suggest that clay lick soil is an important source of sodium for scarlet macaw chicks that could help prevent mineral imbalances in these birds.

The concentrations of protein, Zn, K, Cu, and P (total) were near to or within the range of recommendations for captive psittacine birds, suggesting that current recommendations are likely adequate for these nutrients. However, fat, Ca, and Mg concentrations were greater in crop contents than in the average food plants and greater than published recommendations, suggesting that future research should investigate how variations in these nutrients affect the growth and development of large psittacine birds. The low levels of Na and low Na:K ratios suggest that these wild birds might be facing Na limitation and that the need for supplemental Na could be driving clay lick use at this site.

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