

Diet and Geophagy Across a Western Amazonian Parrot Assemblage

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ABSTRACT

We identified species- and community-level dietary characteristics for a species-rich Amazonian parrot assemblage to determine relationships among dietary metrics and use of geophagy sites. Previous studies suggest that soil is consumed at geophagy sites in this region mainly to supplement dietary sodium. We accumulated 1400 feeding records for 16 parrot species over 2 yr and found that seeds, flowers, and fruit pulp featured prominently in diets, while bark, insects, and lichen were consumed in small quantities. Food availability across 1819 trees was measured, and we found that flower availability was highest in the dry season and fruit production peaked in the wet season, but that phenology patterns of the 20 most commonly foraged plant species suggest no serious food bottlenecks. Partitioning of available food resources among the 13 most commonly encountered parrots is suggested by an ordination analysis (DCA), which placed the large macaws (*Ara*) with the *Amazona* parrots at the ‘primary forest’ end of a dietary resource axis and four smaller species at the ‘successional forest’ end of the axis. Parrot species associated with successional forest also consumed less plant species overall. Furthermore, these parrot species consuming successional forest resources had higher claylick visitation rates than those consuming primary forest resources suggesting they derive the greatest benefits from soil consumption.

Abstract in Spanish is available in the online version of this article.

Key words: *Bertbolletia*; dietary niche; *Euterpe*; keystone species; mineral lick; Peru; Phenology.

INTRODUCTION

INFORMATION ON DIET AND FOOD AVAILABILITY IS IMPORTANT TO UNDERSTAND SPECIES’ NICHES AND HABITS, such as the consumption of soil (geophagy). Geophagy appears to be particularly important for parrots in southeastern Peru where hundreds of individuals of over 20 species regularly consume soil from riverside claylicks (Brightsmith 2004, Lee *et al.* 2010, Brightsmith & Villalobos 2011). The drive to consume soil is not equal among the region’s parrots as some common species are rarely seen on claylicks and not all claylicks are used by all species (Lee 2010). To date, it remains unknown what drives these differences, but studies have not looked for links between diet and propensity to use claylicks. A species’ dietary breadth and foraging niche have many implications for community assembly (Ackermann & Doebeli 2004) and species coexistence (Brandl *et al.* 1994, Marsden & Whiffin 2003), and may also explain differential patterns of clay consumption by parrot species.

Geophagy in the Amazon has been documented for a range of herbivores including bats (Bravo *et al.* 2008) and several monkeys (Ferrari *et al.* 2008). Ingestion of intrinsically low-sodium plant tissue is often insufficient to meet nutritional requirements (Aumann & Emlen 1965) and parrots preferentially consume soil high in sodium (Powell *et al.* 2009). However, plants consumed by macaws do not contain more sodium than those not consumed (Gilardi & Toft 2012). It has been demonstrated that the soil parrots consume can adsorb dietary toxins associated with a seed-rich diet (Gilardi *et al.* 1999) leading to the hypothesis that soil is consumed to bind poisonous and/or bitter-tasting secondary compounds (Diamond *et al.* 1999). This theory suggests that species consuming a greater proportion of highly toxic foods (like seeds) would consume more soil than species which consume traditionally less toxic foods like flowers and fruits. Soil consumption could also be increased during times of food bottlenecks when less toxic foods are unavailable.

Despite its importance, there is little published on dietary relationships for the great majority of Amazonian parrot communities (but see Marsden & Whiffin 2003). Most Neotropical parrots consume seeds (Higgins 1979, Gilardi 1996, Renton 2006) and at least some fruit (Galetti 1997). Many also eat flowers and

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nectar (Cotton 2001, Ragusa-Netto 2007). To a lesser degree, they also consume insect larvae (Renton 2006), termites (Sazima 1989), tree bark/wood (Renton 2006), and leaves (Kristosch & Marcondes-Machado 2001). In general, Neotropical parrots are considered adaptable, changing their diet according to seasonal availability of food as well as adapting to novel foods in modified environments (e.g., Matuzak *et al.* 2008). However, the decline of some parrot species has been linked to the decline of keystone plant resources (Berg *et al.* 2007) suggesting that conservation of at least some parrots may require conservation of important foods.

In most tropical ecosystems variations in plant community phenology patterns provide alternating periods of food abundance and scarcity for herbivores (van Schaik *et al.* 1993). Wet tropical forests with seasonal rainfall typically show high fruit and seed abundance at the beginning of the wet season, and flowering concentrated during the dry season (Janzen 1967). Phenology patterns can differ between flooded and *terra firme* forests (Haugaaen & Peres 2005), and plant community composition and associated food resources also depend on the forest age structure and successional stage (Robinson & Terborgh 1997). The few species that produce fruit and seed during quiescent periods, like *Ficus* figs, are usually considered keystone species and help support a variety of important vertebrate populations (e.g., Shanahan *et al.* 2001).

In this study, we document food resource use and availability for a species-rich Amazonian parrot assemblage in southeastern Peru. We identify key plant resources for this community and examine phenological data for potential food bottlenecks to determine if soil is consumed in the absence of preferred food items. To test the theory that geophagy offers protection from dietary toxins, we hypothesize that parrots consuming a greater proportion of seed and unripe fruit would consume soil more than those consuming a greater proportion of flowers and ripe fruit.

METHODS

STUDY SITES.—Study sites were located in the Department of Madre de Dios in southeastern Peru (Fig. S1). Parrot surveys were conducted within the Tambopata National Reserve and associated buffer zone (274,690-ha and 186,450-ha respectively), in lowland Amazon rain forest of southeastern Peru. Of the three dominant Amazonian ecological systems of Peru and adjacent Bolivia: sub-andean, floodplain, and *terra firme* (Josse *et al.* 2007), only the later two are present in the study area (*terra firme* 85%, floodplain 12% for Madre-de-Dios and Beni departments). *Terra firme* is found on uplifted Holocene and Pleistocene alluvial terraces (Räsänen 1993) and tends to be nutrient poor in comparison to floodplain forests (Kalliola *et al.* 1993). Late successional stage floodplain forests (*sensu* Robinson & Terborgh 1997, hereon referred to as floodplain forest) are dominated by large trees e.g., *Ceiba* and *Dipteryx* spp. and are associated with the floodplains of the larger rivers. Early stage successional forest (successional forest) dominated by *Gynerium sagittatum* or the fast growing trees

Ochroma pyramidale and *Cecropia* spp. includes both young floodplain forest occurring on recent deposits associated with meandering watercourses and fallow agricultural allotments, and accounts for 2.6 percent of the study area. The altitudinal range was between 195 and 350 m asl. Temperature ranges between 10°C and 38°C and rainfall between 1600 and 2400 mm, falling mostly in the rainy season between November and April (Räsänen 1993, Brightsmith 2004).

Foraging studies were based from the tourist lodges Posada Amazonas (Posada, 12°48'06" S, 69°18'05" W), Refugio Amazonas (Refugio, 12°52'25" S, 69°24'40" W), and Tambopata Research Center (TRC, 13°08'05" S, 69°36'40" W). Claylick use by parrots was monitored at one claylick on the Las Piedras River and five claylicks located on or in close proximity to the Tambopata River (Fig. S1).

FORAGING RECORDS.—Standardized foraging transects were conducted along 12 routes of 2 km length from January 2008 to December 2009 at Refugio, Posada, and TRC. Transects were conducted between 0600 and 1100 h and from 1500 to 1800 h. For any time parrots were encountered foraging, the following information was recorded: parrot species, species of plant (or other food type) and the part of the plant consumed. As there were few encounters with foraging birds (0.2 groups/km), additional foraging records were taken on an opportunistic basis whenever feeding birds were observed from a sample area covered by over 45 km of trails through all forest types. To characterize the foraging habitats used by each species, we recorded the habitat association of each encounter (successional, mature floodplain [including *Mauritia* palm swamps] or mature *terra firme*). Species which fed predominantly on successional forest species (> 40%) are classified for the remainder of the article as successional species. To determine dietary species richness for parrot species from observed foraging encounters, we estimated the number of potential dietary items using species richness estimators. We chose the JACK1 estimator from EstimateS (Colwell 2006) as this has been found to be an accurate predictor of species richness (González-Oreja *et al.* 2010). To indicate the degree of uncertainty with predicted species richness, we also report the Abundance-based Coverage Estimator (ACE; Chao & Lee 1992).

DIETARY AND CLAYLICK USAGE METRICS.—A detrended correspondence analysis (DCA) was used to identify community-level patterns of consumption of individual plant parts of different plant species across the parrot community (*sensu* Cornelis *et al.* 1999). We included the following plant parts: flowers, leaves, pulp, whole fruit, and seed. For species with small seeds e.g., *Cecropia* and *Ficus*, we recorded the dietary part as whole fruit. We omitted three parrot species from our analyses for which we had < 14 feeding records. We performed DCA in the PAST software (Hammer *et al.* 2001). We retained scores for each of the 13 commonly recorded parrot species on the first two ordination axes. Proportional data were arcsine transformed prior to inclusion in the DCA.

For each parrot species, nine diet metrics were calculated as follows: (1 & 2) scores on DCA axes 1 & 2; (3) proportion of plant parts consumed that consisted of seed components; (4) proportion of fruit pulp; (5) proportion of flowers; (6) proportion of whole fruits; (7) proportion of non-ripe items; (8) proportion of rare food items: each forage species was classified as either rare (<5 per ha in the phenology plots) or common (>5 per ha) following Walker (2007); (9) dietary specialization: Levin's standardized niche breadth index (Levin 1968) in which values close to 0 indicate dietary specialization and a value close to 1 indicates a broad diet.

An index of claylick use was calculated for each species based on the monitoring protocol described in Brightsmith (2004). Birds on the clay surface were counted at 5-min intervals at six claylicks (Fig. S1) from January 2006 to July 2009. We took the mean of the highest daily counts from the six claylicks as an indication of the minimum number of individuals of each species using claylicks in the area. This value is sensitive to local population density of the parrot species (a rare species that feeds on clay frequently may be indistinguishable from a common species that feeds rarely), so we divided it by the population estimates for an area with a 10-km radius (species densities from Lee & Marsden [2012] * π * 100). This represents a relative proportion of each local population using the claylicks.

For each species, we created a measure of seasonal use of claylicks as the average value of the mean daily claylick use for the 3 mo with the least claylick use, divided by that of the 3 mo with the most claylick use. Values close to 1 represent little seasonality, while values close to 0 represent marked seasonal patterns of clay consumption.

We examined whether there was autocorrelation between dietary similarity and phylogenetic relatedness using Mantel tests (Sokal & Rohlf 1995). Dietary similarity between pairs of parrot species was taken as the difference between their scores on a given DCA axis. Phylogeny across genera was taken from Figure 1 of Wright *et al.* (2008), and for the four species within the genus *Ara*, the phylogeny of Oliveira–Marques (2006). Phylogenetic relatedness was taken as the number of nodes along the phylogenetic tree from a species' position to the other species' position (a species pair in the same genus scored one and the *Ara* species could score up to three). We used Spearman's rank correlation analysis to examine relationships between the population density of parrot species and the proportion of rare food items in their diet, the number of plant species consumed (dietary richness), and dietary specialization (Levin's index). We also used Spearman's analysis to examine correlations among the dietary measures, and between dietary measures and claylick use.

WOODY PLANT ABUNDANCE AND PHENOLOGY.—A total of 3266 trees with dbh >10 cm were marked in 30 plots of 10 m × 100–200 m (5-ha total). Plots were located in *terra firme* forest (9), floodplain forest (16) and successional (5) forest at Refugio, Posada and TRC. These trees were used to calculate relative abundance of woody tree species. The 1819 trees located in floodplain and *terra firme* forest at Posada and Refugio were

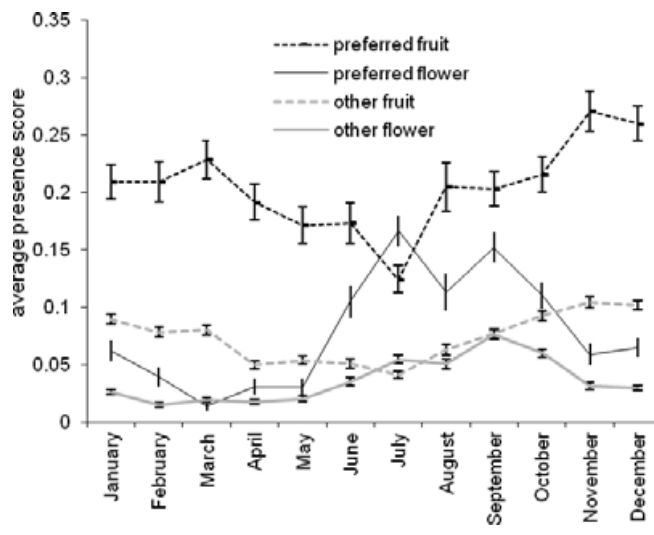


FIGURE 1. Phenological patterns for trees in plots at Refugio and Posada: the mean \pm SE proportion of 1216 marked trees with fruit or flower per month for the period 2006–2009. Preferred fruit and flowers represent the patterns of the 20 species upon which parrot species were recorded foraging most frequently.

monitored on a monthly basis for the presence of fruit and flower from January 2006 to December 2009, but did not include plots in successional forest. Of the 1819 trees, 603 were never registered with fruit or flower, so phenological patterns were based on the remaining 1214 trees (30,051 observations). Monitoring was not possible for all plots every month, so results from all years are combined for the presentation of seasonal phenological patterns, recognizing this may mask annual variation. Botanical classification follows Brako and Zarucchi (1993) and APG (2003).

We recorded fruit and flower presence as proportions of individuals of each species fruiting or flowering per month. Combined flowering and fruiting rates in the wet vs. dry seasons, as well as for preferred forage species (those that featured most regularly in parrot species diet) vs. other tree species, were treated as repeated measures of the same phenology plots and tested with Wilcoxon signed ranks tests. Mann–Whitney *U*-tests were used to compare overall fruit availability between seasons and between floodplain and *terra firme* forests; and to compare the 20 most common plant species in phenology plots to those selected for in parrot diets. For the most common plants in plots and those preferred in parrot diets, we also examined whether the proportions of trees fruiting and flowering in each month of the year were related using a Spearman's rank correlation analysis.

RESULTS

PARROT DIETS.—Standardized searches for foraging parrots were conducted on 758 occasions covering 1468 km. Altogether, including opportunistic encounters, we recorded 1469 foraging groups of 16 parrot species (Table S1 for all foraging

encounters). Of these, 291 were multiple records from the same tree and these repeats were excluded leaving 1178 independent observations in the analyses. *Amazona farinosa* was encountered most often (196 events), followed by *Pionites leucogaster* (190) and *Ara macao* (178), while Blue-headed Macaw *Primolius couloni*, Dusky-billed Parrotlet *Forpus modestus*, and Red-bellied Macaw *Orthopsittaca manilata* were recorded on three or fewer occasions.

Diets in terms of plant species and plant parts consumed varied greatly among parrot species. Seeds (including seed parts e.g., endosperm and embryo) were the most commonly recorded dietary items (38% of $N = 918$), followed by fruit pulp (27%), flower parts (21%), and whole fruit (14%). Seeds formed the largest proportion of plant parts consumed by eight parrot species including all large macaws and short-tailed parrots (Table 1). Unripe items were most common in the diet of the three large macaws (mean = $63 \pm 7\%$).

Leaves, bark, and insects accounted for 2 percent of foraging bouts. Six parrot species were recorded feeding on termites

Nasutitermes corniger (Isoptera: Termitidae: Nasutitermitinae). *Pionites leucogaster* was observed feeding on ants (*Crematogaster* sp.). *Pyrrhura rupicola* was observed feeding on unidentified insect larvae in leaf galls. Six parrot species were recorded feeding, on 13 occasions, on bark or dead wood of various tree species. *Ara ararauna* and *Ara chloropterus* were observed feeding on the lichen *Marchantia* (Marchantiaceae) on the bark of the emergent tree *Bertholletia excelsa*.

Dietary niche breadth varied from 0.24 for *Brotogeris cyanopectera* to 0.6 for *Amazona ochrocephala* and most parrot species showed relatively narrow dietary niche breadths (for ten species Levin's < 0.5), indicating that use tended to be concentrated on only a few of the available resources.

PHENOLOGY AND KEYSTONE PLANTS.—The forests under study showed broad seasonal variation in fruiting and flowering patterns. A peak in flowering in September preceded the peak period in fruit availability from October to March (Fig. 1). A greater

TABLE 1. Dietary metrics, claylick use and supporting information for 13 parrot species from southeastern Peru. *Wt*—Body weight (g); *Dens*—density (inds./km²); *Flower*, *Pulp*, *Seed*, and *Whole* are the proportions of flowers, fruit pulp, seed, and entire fruits in the diet; *Unripe*—the proportion of dietary items which were unripe seeds or unripe fruits; and *Rare*—proportion of dietary items which were from rare plant species (< 5 per ha); *Levin*—Levin's dietary breadth; *Claylick*—index of claylick use based on abundance in the forest vs. abundance at the claylick (see Methods for calculation); *Season*—the ratio of the 3 mo of low claylick use to the 3 mo of high claylick use; *Enc*—the total number of independent foraging encounters and *Spp* is the total number of plant species upon which a parrot was observed to feed. *Jack1* and *ACE* are the results of dietary species richness estimators, *Jack1* being the JACK1 estimator ± standard deviation, and *ACE* is the Abundance-based Coverage Estimator.

	Wt	Dens	Flower	Seed	Pulp	Whole	Unripe	Rare	Levin	Claylick	Season	Enc	Spp	Jack1	ACE
<i>Ara ararauna</i> , Blue-and-yellow Macaw	1,125	0.37	0.10	0.63	0.21	0.03	0.74	0.75	0.32	0.5	0.22	57	18	52 ± 5.2	62 ± 6.9
<i>Ara macao</i> , Scarlet Macaw	1,015	1.74	0.08	0.57	0.24	0.07	0.62	0.49	0.49	0.6	0.08	178	45	99 ± 7.8	103 ± 6.7
<i>Ara chloropterus</i> , Red-and-green Macaw	1,214	2.17	0.06	0.53	0.25	0.11	0.61	0.69	0.33	1.4	0.09	137	34	80 ± 6.9	84 ± 6.6
<i>Ara severus</i> , Chestnut-fronted Macaw	343	0.18	0.54	0.28	0.15	0.02	0.41	0.71	0.27	32.9	0.20	47	19	37 ± 4.3	55 ± 6.7
<i>Aratinga leucophthalma</i> , White-eyed Parakeet	155	0.96	0.54	0.28	0.18	0.00	0.76	0.41	0.44	9.9	0.03	41	11	26 ± 2.5	36 ± 6.4
<i>Aratinga weddellii</i> , Dusky-headed Parakeet	108	0.66	0.48	0.32	0.03	0.08	0.10	0.41	0.51	28.1	0.77	39	10	22 ± 1.9	29 ± 3.7
<i>Pyrrhura rupicola</i> , Rock Parakeet	75	8.09	0.18	0.26	0.39	0.13	0.42	0.38	0.37	0.7	0.24	103	30	82 ± 7	112 ± 13
<i>Brotogeris cyanopectera</i> , Cobalt-winged Parakeet	56	11.6	0.41	0.18	0.11	0.29	0.23	0.55	0.24	5.4	0.09	99	29	62 ± 5.5	69 ± 6.6
<i>Pionites leucogaster</i> , White-bellied Parrot	158	11.0	0.24	0.34	0.31	0.11	0.45	0.45	0.27	0.3	0.05	190	44	100 ± 7	117 ± 11
<i>Pyrrhura barrabandi</i> , Orange-checked Parrot	140	1.00	0.13	0.64	0.16	0.06	0.53	0.26	0.36	4.0	0.27	15	5	19 ± 2.1	40 ± 10
<i>Pionus menstruus</i> , Blue-headed Parrot	251	2.84	0.03	0.47	0.32	0.16	0.37	0.32	0.55	2.4	0.17	46	20	58 ± 5.3	133 ± 13
<i>Amazona ochrocephala</i> , Yellow-crowned Parrot	440	1.03	0.04	0.35	0.33	0.20	0.58	0.36	0.60	9.7	0.14	9	7	27 ± 1.2	105 ± 6.0
<i>Amazona farinosa</i> , Mealy Parrot	626	14.7	0.03	0.55	0.32	0.09	0.46	0.39	0.44	1.8	0.08	196	40	278 ± 21	346 ± 13

proportion of trees had flowers in the dry season (dry: 0.1, 0.07–0.2; wet: 0.08, 0.07–0.13; $t = 14.4$, $P < 0.001$), while more trees had fruit in the wet season (dry: 0.13, 0.1–0.2; wet: 0.15, 0.08–0.3; $Z = 9.6$, $P < 0.001$). Flowering and fruiting patterns of the 20 preferred forage species (Table S2 and S3) were positively correlated with the broader phenology patterns at the monthly level (flower: $r_s = 0.80$, $P = 0.02$, $N = 12$; fruit: $r_s = 0.85$, $P = 0.001$, $N = 12$). Preferred forage items were available during all months; the month with the lowest number of preferred forage species available was April with 11 fruit or flower species available (Table S3). This coincides generally with a low period of claylick use by parrots.

Of 3266 trees within plots, 3111 (95%) were identified to species level and included 442 species belonging to 226 genera and 71 families. The 20 most common plant species accounting for 40 percent of all marked trees are displayed in Table S2. Eight of the 20 most common tree species were not recorded as being consumed by parrots. Parrots fed on 26 percent of species and 37 percent of plant genera represented in the plots.

Feeding encounters were recorded on 49 families, 129 genera, and 204 species of plants. The most commonly consumed items were seeds or pulp of the palm *Euterpe precatoria* (Arecaceae) (10% of all foraging records); consumed by all the 13 common parrot species as well as *Primolius couloni*. Flowers of *Ocroma pyramidale* were consumed by ten parrot species, but only rarely by the large parrots. Brazil nut trees *Bertholletia excelsa* (Lecythidaceae) were used by nine parrot species, but there was a notable difference in the parts eaten: large macaws ate young seeds and parrots ate flowers. The Lecythidaceae family was generally important for the large macaws, while Fabaceae (especially *Inga* spp.), Arecaceae, and Moraceae were important for the entire parrot family. Very few foraging events were recorded for the area's most common palm *Iriartea deltoidea*.

DIETARY AND HABITAT METRICS.—Proximity on the DCA axes indicates association, and for axis 1 of the DCA the plant parts with high scores are associated with floodplain forest, but mostly with successional forest (Fig. 2; Table S4 for ordination scores). These include *Caryocar pallidum* and *Chorisia insignis* (mature floodplain trees) and the fruits of several *Ficus* species, while the majority of the rest are successional species, including the seeds and pulp of the lianas *Cayaponia macrocalyx* and *Fevillea amazonica*, flowers of *Ocroma pyramidale*, *Erythrina poeppigiana*, *Erythrina ulei*, and fruit of *Cecropia sciadophylla*. A group of five parrot species had diets associated with these types of plants: the small macaw *Ara severus* and four parakeet species *Aratinga leucophthalma*, *Aratinga weddellii*, *Pyrrhura rupicola*, and *Brotogeris cyanopectera*. These species were all encountered most often foraging in successional forest types (>40%). The lower values on axis 1 were dominated by seeds including large primary forest trees of either floodplain forest such as *Swartzia cardiosperma* and *Dipteryx micrantha*, or terra firme e.g., *Enterolobium barnebyanum*, *Anthodiscus klugii*, *Otoba glycyarpa*, *Jacaranda copaia*, *Parkia nitida*, and *Eschweilera* spp. Parrot species with similarly low values on DCA axis 1 were the three large *Ara* macaws and the two *Amazona* species. Although *Amazona*

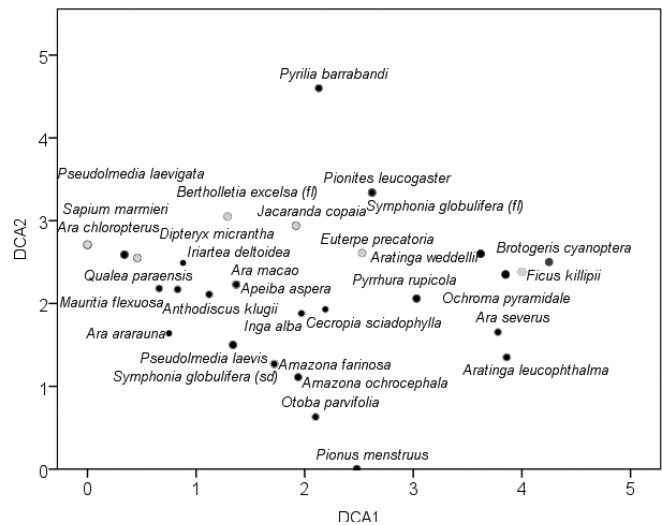


FIGURE 2. Centroids for each parrot species (black circles) and preferred forage species (open circles) on DCA axis 1 (eigenvalue = 0.67, high scores associated with successional forest food plants) and axis 2 (eigenvalue = 0.41).

ochrocephala and *A. farinosa* have similar dietary values, *A. ochrocephala* is associated more with successional forest. High values on DCA axis 2 were associated with *Pourouma* spp., *Sloanea guianensis*, and *Heisteria acuminata*—all trees associated with terra firme. This axis separated the diets of the three medium-sized short-tailed parrot species (*Pyrrhura barrabandi*, *Pionetes leucogaster* with high values and *Pionus menstruus* with a lower value).

Predicted dietary plant species richness as determined by species richness estimators was lowest for four parrot species which fed predominantly on successional plant species (*Aratinga weddellii*, *A. leucophthalma*, *Amazona ochrocephala*, and *Ara severus*) as well as *P. barrabandi* associated with terra firme forest. Predicted dietary species richness values were highest for the species with the highest number of foraging encounters ($r_s = +0.95$, $P < 0.01$, $N = 13$).

Scores on DCA axis 1 were positively correlated with flower consumption ($r_s = +0.63$, $P = 0.02$, $N = 13$; Table 2) and negatively with fruit pulp consumption ($r_s = -0.63$, $P = 0.02$, $N = 13$) indicating separation of diet based on the consumption of successional forest flowers. Fruit pulp consumption was also negatively correlated with scores on DCA axis 2 ($r_s = -0.61$, $P = 0.02$, $N = 13$). Relative proportions of plant components consumed are indicated in Fig. 3.

There was no significant relationship between phylogenetic similarity of parrot species and the similarity of their dietary positions on DCA axes (axis 1: $r = +0.10$, $P = 0.15$, $N = 13$; axis 2: $r_s = +0.04$, $P = 0.26$, $N = 13$). There were no significant correlations between population density for parrot species and the proportion of rare food items in their diets ($r_s = -0.27$, $P = 0.38$, $N = 13$), the richness of their diet ($r_s = -0.22$, $P = 0.48$, $N = 13$), or Levin's index of dietary specialization ($r_s = -0.07$, $P = 0.81$, $N = 13$).

TABLE 2. Matrix of Spearman's rank correlation coefficients between dietary and claylick usage across 13 species of parrot from southeastern Peru. Bold values indicate $P < 0.05$. DCA 1 and DCA 2 are axes 1 and 2 of the DCA. Seasonality indicates claylick seasonality. Terra Firme, Successional, and Floodplain indicate parrot species foraging affiliations. See Table 1 for other variable names.

	DCA1	DCA2	Flower	Seed	Pulp	Whole	Unripe	Rare	Levin	Jack1	ACE	FP	Succ	TF	Seasonality
Claylick	0.59	-0.20	0.43	-0.35	-0.45	-0.30	-0.34	-0.15	0.20	-0.69	-0.58	-0.39	0.64	-0.35	0.24
Seasonality	0.02	0.16	0.15	0.06	-0.26	-0.02	-0.42	-0.19	0.09	-0.53	-0.27	-0.67	0.44	-0.04	
Terra Firme (TF)	-0.68	0.06	-0.76	0.63	0.44	0.18	0.23	-0.33	0.12	0.17	0.52	-0.23	-0.68		
Successional	0.74	0.02	0.82	-0.62	-0.52	-0.14	-0.33	0.12	-0.14	-0.63	-0.68	-0.47			
Floodplain (FP)	-0.20	-0.26	-0.23	0.07	0.29	-0.14	0.44	0.18	0.09	0.54	0.29				
ACE	-0.46	-0.37	-0.77	0.20	0.90	0.47	0.01	-0.29	0.21	0.73					
Jack1	-0.30	-0.03	-0.43	-0.04	0.51	0.51	0.01	0.22	-0.21						
Levin	-0.22	-0.52	-0.38	0.13	0.45	-0.02	0.08	-0.63							
Rare	-0.07	0.19	0.29	0.00	-0.40	-0.23	0.17								
Unripe	-0.54	-0.12	-0.26	0.60	0.16	-0.57									
Whole	0.14	-0.01	-0.21	-0.51	0.40										
Pulp	-0.41	-0.57	-0.74	0.14											
Seed	-0.84	0.03	-0.59												
Flower	0.76	0.42													
DCA2	0.03														

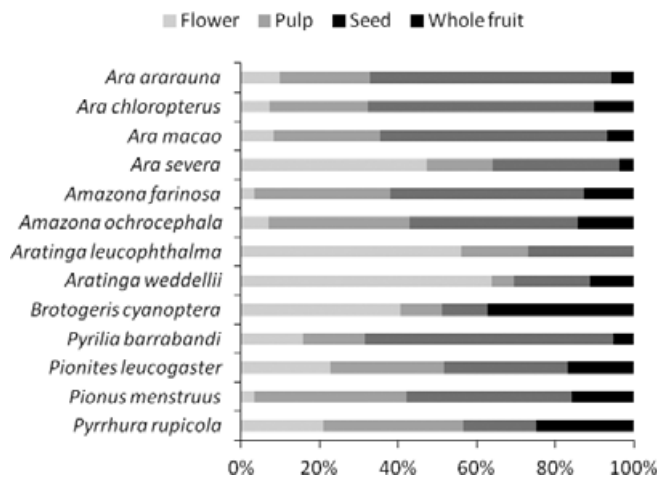


FIGURE 3. Proportions of all items for seed, flower, fruit pulp, or whole fruits consumed by the 13 common parrot species of the study area.

CORRELATIONS WITH CLAYLICK USE.—Observations were made at claylicks on 1140 d (228 ± 95 d across the six claylicks). All parrots for which foraging bouts were recorded were also observed on at least one of the claylicks. Of the 13 species most frequently encountered foraging (Table 1), five species were observed at all claylicks: *Ara severa*, *Amazona farinosa*, *Pionus menstruus*, *Pyrilia barrabandi*, and *Aratinga weddellii*, while *Ara ararauna* was observed at only one. While most species displayed seasonality in their patterns of claylick use, there was no clear trend linking seasonality to habitat use, with the successional forest species presenting

both highest seasonality (*A. leucophthalma* 0.02) and the lowest seasonality (*A. weddellii* 0.77). Relative to their densities, claylick use was highest for successional forest species *Ara severa*, *Aratinga weddellii*, and *Aratinga leucophthalma* and lowest for primary forest species *Pionites leucogaster*, *Ara ararauna*, and *Ara macao* (Table 1). Predicted dietary richness was negatively correlated with claylick use (Jack1: $r_s = -0.70$, $P = 0.01$; ACE: $r_s = -0.58$, $P = 0.04$, $N = 13$). There was no correlation between claylick use and plant part ripeness ($r_s = -0.34$, $P = 0.25$, $N = 13$), or the proportion of seeds consumed ($r_s = -0.35$, $P = 0.25$, $N = 13$). Claylick use was significantly positively correlated with scores on DCA axis 1 ($r_s = +0.59$, $P = 0.03$, $N = 13$) and successional forest ($r_s = +0.64$, $P = 0.02$, $N = 13$), indicating that it was parrot species consuming successional forest-type flowers and fruits that had higher claylick visitation rates than those consuming primary forest seeds.

DISCUSSION

COMMUNITY DIETARY RELATIONSHIPS.—There were clear patterns of niche differentiation based on the diets of the 13 common parrot species. Niche separation at the dietary level appears to be driven by: (1) species' ability to consume large or unripe seeds; (2) preference for flowers; and (3) habitat foraging preference. The primary axis of dietary variability across the assemblage ordinated species largely according to their use of habitats—large macaws and *Amazona* parrots appeared at the 'primary forest' end of this axis. The diets of the small macaw *A. severa* and the three parakeets *A. weddellii*, *A. leucophthalma*, and *B. cyanoptera* were associated with the flowers and fruits of successional

habitats, including *Ochroma pyramidale*, *Inga alba*, *Acacia lorentensis*, and *Cecropia* spp.

Observed dietary species richness for the parrots of the primary forest types was high and predicted species richness was potentially over 100 plant types for six parrot species. The lower dietary species richness we found for parrot species of successional forests was expected, as successional forests have much lower plant species richness when compared to mature floodplain and *terra firme* forest (Corlett 1995).

PARROT DIETS IN A PLANT SPECIES-RICH ENVIRONMENT.—In our study, parrots fed on 26 percent of the over 400 species of trees in the phenology plots, and on many other species of trees, plants, and lianas. Extensive botanical studies in nearby Manu National Park have recorded over 1000 species of tree (Pitman *et al.* 2002). The predicted dietary species richness for the parrot community (median = 66, range 19 to 346) while high is realistic given the very high levels of botanical richness at our sites. Our study used a blanket approach in marking and recording phenology patterns for all species of trees in phenology plots based on observations from MPNV and Munn (1988) that parrots (specifically macaws) were catholic in their diet and likely to feed on almost any species. Our results suggest instead that this parrot community likely consumes large numbers of plant species over the long term (as indicated by the predicted species richness), but that most foraging focuses on a relatively small suite of preferred plant species, and that individual parrot species specialize on subsets of this suite of plants.

PLANT PHENOLOGY, BOTTLENECKS, AND KEYSTONE PLANT SPECIES.—The forests in this study displayed phenological patterns consistent with those expected for tropical rain forests with a clear dry and wet season: flowering peaked in the dry season and fruiting peaked in the early wet season. From a parrot food perspective, lower fruit availability in the dry season is offset by increased flower (and thus nectar) availability. This may account for the generally high proportion of flowers consumed across this parrot assemblage. A similar pattern was found in southern Pantanal, Brazil (Ragusa-Netto & Fecchio 2006) where parrots also make extensive use of nectar during the dry season in gallery forest when fruit availability is limited. However, flowers at our site are unlikely to be simply ‘starvation’ food. Instead it appears that their consumption is likely an adaptation by certain parrots to exploit these abundant resources as many of the smaller parrots and parakeets breed during the dry season when flower availability is at its peak (Brightsmith 2005). In contrast, the larger macaws and parrots breed in the wet season when fruit and seed abundance peaks.

Despite an incomplete dataset for successional habitats, phenology patterns of preferred forage species revealed no apparent food bottleneck for the plants monitored in floodplain and *terra firme* forests, with >10 preferred forage species available throughout the year in the older forest types. This suggests that soil consumption is not a direct effect of food shortages.

We have identified the relatively common palm *Enterpe precatia* and the *terra firme* tree *Bertholletia excelsa* as the plant species

most preferred by the parrot community as a whole and a potential keystone species for this system. *Ficus* species have been identified as keystone species for primates in the region (Terborgh 1983) and for tropical frugivores generally (Shanahan *et al.* 2001, Walker 2007), but they were relatively unimportant for the parrots in our study. The large emergent tree *Dipteryx micrantha* and the palm *Mauritia flexuosa* have been identified as keystone nesting resources (Brightsmith 2005) that are also featured in the diets of several macaws. Both of these species are targeted for commercial reasons, *D. micrantha* by the wood-floor and charcoal industries (Putzel *et al.* 2011), and *M. flexuosa* for their fruit crop (Vásquez & Gentry 1989). Our work reinforces the importance of conserving both of these species to help maintain the integrity of these parrot communities.

DIETS AND CLAYLICK USE.—The parrot species which fed most heavily on the flowers and fruits of successional habitats, had the highest claylick use indices and there was no indication that species that foraged mainly on seeds or unripe fruit consumed more soil. As flowers and ripe fruits are predicted to contain fewer plant secondary metabolites compared to seeds and unripe fruits (Coley & Barone 1996), our findings do not support the hypothesis that dietary toxins drive geophagy in this parrot assemblage (Gilardi *et al.* 1999). All other available research suggests sodium is the driver for geophagy among this group of parrots (Brightsmith & Munoz-Najar 2004, Powell *et al.* 2009, Brightsmith *et al.* 2010). The presence of documented claylicks together with their associated parrot species richness increases with distance from the eastern coastline of South America and associated sodium deposition rate (Lee *et al.* 2010). Dudley *et al.* (2012) propose that the diverse vertebrate visitors to the well-known claylicks of the western Amazon have a common goal of sodium supplementation in a region deprived of salt. This sodium shortage influences many levels of the ecosystem from nutrient cycling (Kaspari *et al.* 2009) to animal movements (Tobler *et al.* 2009).

There is a strong correlation between breeding season and bird activity at claylicks, and macaws are known to feed clay to their chicks (Brightsmith *et al.* 2010). However, the degree to which other parrots feed clay to their chicks has not been quantified. At this time, it is difficult to determine how the general nutritional need for sodium from clays and the seasonal need to feed soil to the chicks interact to produce the annual patterns of lick use seen in the region.

Ongoing anthropogenic activities (hunting, mining, habitat conversion, etc.) may deprive species of the opportunity to consume soil from many traditional geophagy sites in the near future. The potential impacts of reducing geophagy should be investigated, as it is unknown how survival and reproduction may change should parrots be deprived of the opportunity to consume soil.

Our results suggest parrot species predominantly associated with successional forests (generally widespread species of low conservation concern) consume more soil. This implies that these have the most to gain by consumption of supplemental sodium. However, this hypothesis needs to be tested and the causes for this finding determined. Given the broad range of plant species

consumed and habitats used by this parrot community, maintaining this species-rich community of parrots will require the conservation of the full range of forest habitats and associated food resources together with the sites where soil is consumed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Plant species and plant parts consumed by 16 parrot species of Madre-de-Dios department, Peru.*

TABLE S2. *The 20 most common trees in phenology plots in relation to species on which parrots were most commonly observed feeding.*

TABLE S3. *The phenology patterns for 20 preferred forage species.*

TABLE S4. *Ordination scores for plant species and plant parts, as well as parrot species.*

FIGURE S1. A map of the study area showing survey sites and claylick locations in relation to major forest types.

LITERATURE CITED

- ACKERMANN, M., AND M. DOEBELI. 2004. Evolution of niche width and adaptive diversification. *Evolution* 58: 2599–2612.
- APG. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399–436.
- AUMANN, G. D., AND J. T. EMLEN. 1965. Relation of population density to sodium availability and sodium selection by microtine rodents. *Nature* 208: 198–199.
- BERG, K. S., J. SOCOLA, AND R. R. ANGEL. 2007. Great Green Macaws and the annual cycle of their food plants in Ecuador. *J. Field Ornithol.* 78: 1–10.
- BRAKQ, L., AND J. L. ZARUCCHI (Eds.). 1993. Catalogue of the flowering plants and gymnosperms of Peru. Missouri Botanical Garden, St. Louis, Missouri.
- BRANDL, R., A. KRISTIN, AND B. LEISLER. 1994. Dietary niche breadth in a local community of passerine birds: An analysis using phylogenetic contrasts. *Oecologia* 98: 109–116.
- BRAVO, A., K. E. HARMS, R. D. STEVENS, AND L. H. EMMONS. 2008. Collpas: Activity hotspots for frugivorous bats (Phyllostomidae) in the Peruvian Amazon. *Biotropica* 40: 203–210.
- BRIGHTSMITH, D. J. 2004. Effects of weather on parrot geophagy in Tambopata, Peru. *Wilson Bull.* 116: 134–145.
- BRIGHTSMITH, D. J. 2005. Parrot nesting in southeastern Peru: Seasonal patterns and keystone trees. *Wilson Bull.* 117: 296–305.
- BRIGHTSMITH, D. J., D. MCDONALD, D. MATSAFUJI, AND C. A. BAILEY. 2010. Nutritional content of the diets of free-living Scarlet Macaw chicks in southeastern Peru. *J. Avian Med. Surg.* 24: 9–23.
- BRIGHTSMITH, D. J., AND R. A. MUNOZ-NAJAR. 2004. Avian geophagy and soil characteristics in southeastern Peru. *Biotropica* 36: 534–543.
- BRIGHTSMITH, D. J., AND E. M. VILLALOBOS. 2011. Parrot behavior at a Peruvian clay lick. *Wilson J. Ornithol.* 123: 595–602.
- CHAO, A., AND S. M. LEE. 1992. Estimating the number of classes via sample coverage. *J. Am. Stat. Assoc.* 87: 210–217.
- COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27: 305–335.
- COLWELL, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8. <http://purl.oclc.org/estimates>
- CORLETT, R. T. 1995. Tropical secondary forests. *Prog. Phys. Geogr.* 19: 159–172.
- CORNELIS, J., J. CASAER, AND M. HERMY. 1999. Impact of season, habitat and research techniques on diet composition of roe deer (*Capreolus capreolus*): A review. *J. Zool.* 248: 195–207.
- COTTON, P. A. 2001. The behavior and interactions of birds visiting *Erythrina fusca* flowers in the Colombian Amazon. *Biotropica* 33: 662–669.
- DIAMOND, J., K. D. BISHOP, AND J. D. GILARDI. 1999. Geophagy in New Guinea birds. *Ibis* 141: 181–193.
- DUDLEY, R., M. KASPARI, AND S. P. YANOVIAK. 2012. Lust for Salt in the Western Amazon. *Biotropica* 44: 6–9.
- FERRARI, S. F., L. M. VEIGA, AND B. URBANI. 2008. Geophagy in New World monkeys (Platyrrhini): Ecological and geographic patterns. *Folia Primatol.* 79: 402–415.
- GALETTI, M. 1997. Seasonal abundance and feeding ecology of parrots and parakeets in a lowland Atlantic forest of Brazil. *Ararajuba* 5: 115–126.
- GILARDI, J. D. 1996. Ecology of parrots in the Peruvian Amazon: Habitat use, nutrition and geophagy. PhD Dissertation. University of California, Davis.
- GILARDI, J. D., S. S. DUFFEY, C. A. MUNN, AND L. A. TELL. 1999. Biochemical functions of geophagy in parrots: Detoxification of dietary toxins and cytoprotective effects. *J. Chem. Ecol.* 25: 897–922.
- GILARDI, J. D. AND C. A. TOFT. 2012. Parrots Eat Nutritious Foods despite Toxins. *PLoS ONE* 7: e38293.
- GONZÁLEZ-OREJA, J. A., C. GARBISU, S. MENDARTE, A. IBARRA, AND I. ALBIZU. 2010. Assessing the performance of nonparametric estimators of species richness in meadows. *Biodivers. Conserv.* 19: 1417–1436.
- HAMMER, Ø., D. A. T. HARPER, AND P. D. RYAN. 2001. PAST: Paleontological Statistics Software Package for education and data analysis. *Palaeontol. Electron.* 4: 9.
- HAUGAASEN, T., AND C. A. PERES. 2005. Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica* 37: 620–630.
- HIGGINS, H. L. 1979. Intensity of seed predation on *Brosimum utile* by Mealy Parrots (*Amazona farinosa*). *Biotropica* 11: 80.
- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within dry season in Central America. *Evolution* 21: 620–637.
- JOSSE, C., G. NAVARRO, F. ENCARNACIÓN, A. TOVAR, P. COMER, W. FERREIRA, F. RODRÍGUEZ, J. SAITO, J. SANJURJO, J. DYSON, E. RUBIN DE CELIS, R. ZÁRATE, J. CHANG, M. AHUITE, C. VARGAS, F. PAREDES, W. CASTRO, J. MACO, AND F. REÁTEGUI. 2007. Ecological systems of the Amazon Basin of Peru and Bolivia. Classification and mapping. NatureServe, Arlington, Virginia.
- KALLIOLA, R., A. LINNA, M. PUHAKKA, J. SALO, AND M. RÄSÄNEN. 1993. Mineral nutrients in fluvial sediments from the Peruvian Amazon. *Catena* 20: 333–349.
- KASPARI, M., S. P. YANOVIAK, R. DUDLEY, M. YUAN, AND N. A. CLAY. 2009. Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. *Proc. Natl Acad. Sci. USA* 46: 19405–19409.
- KRISTOSCH, G. C., AND L. O. MARCONDES-MACHADO. 2001. Diet and feeding behavior of the Reddish-bellied parakeet (*Pyrrhura frontalis*) in an Araucaria forest in southeastern Brazil. *Ornithol. Neotrop.* 12: 215–223.
- LEE, A. T. K. 2010. Parrot claylicks: Distribution, patterns of use and ecological correlates from a parrot assemblage in southeastern Peru. PhD Dissertation. Manchester Metropolitan University, Manchester.

- LEE, A. T. K., S. KUMAR, D. J. BRIGHTSMITH, AND S. J. MARSDEN. 2010. Parrot claylick distribution in South America: Do patterns of 'where' help answer the question 'why'? *Ecography* 33: 503–513.
- LEE, A. T. K., AND S. J. MARSDEN. 2012. The influence of habitat, season, and detectability on abundance estimates across an Amazonian parrot assemblage. *Biotropica* 44: 537–544.
- LEVIN, R. 1968. *Evolution in changing environments*. Princeton University, Princeton, New Jersey.
- MARSDEN, S. J., AND M. WHIFFIN. 2003. The relationship between population density, habitat position and habitat breadth within a Neotropical forest bird community. *Ecography* 26: 385–392.
- MATUZAK, G. D., B. BEZY, AND D. J. BRIGHTSMITH. 2008. Foraging ecology of parrots in a modified landscape: Seasonal trends and introduced species. *Wilson J. Ornithol.* 120: 353–365.
- MUNN, C. A. 1988. Macaw biology in Manu National Park, Peru. *Parrotletter* 1: 18–21.
- OLIVEIRA-MARQUES, A. R. 2006. Molecular phylogeny of species from Genus *Ara* (Psittaciformes, Aves). Master's Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo.
- PITMAN, N. C. A., J. W. TERBORGH, M. R. SILMAN, P. N. VARGAS, D. A. NEILL, C. E. CERON, W. A. PALACIOS, AND M. AULESTIA. 2002. A comparison of tree species diversity in two upper Amazonian forests. *Ecology* 83: 3210–3224.
- POWELL, L. L., T. U. POWELL, G. V. N. POWELL, AND D. J. BRIGHTSMITH. 2009. Parrots take it with a grain of salt: Available sodium content may drive collpa (clay lick) selection in southeastern Peru. *Biotropica* 41: 279–282.
- PUTZEL, L., C. M. PETERS, AND M. ROMO. 2011. Post-logging regeneration and recruitment of shihuahuaco (*Dipteryx* spp.) in Peruvian Amazonia: Implications for management. *For. Ecol. Manage.* 261: 1099–1105.
- RAGUSA-NETTO, J., AND A. FECCHIO. 2006. Plant food resources and the diet of a parrot community in a gallery forest of the southern Pantanal (Brazil). *Braz. J. Biol.* 66: 1021–1032.
- RAGUSA-NETTO, J. 2007. Nectar, fleshy fruits and the abundance of parrots at a gallery forest in the southern Pantanal (Brazil). *Stud. Neotrop. Fauna Environ.* 42: 93–99.
- RÄSÄNEN, M. 1993. La geohistoria y geología de la Amazonía Peruana. In R. Kalliola, M. Puhakka, and W. Danjoy (Eds.). *Amazonía Peruana: Vegetación húmeda tropical en el llano subandino*, pp. 43–67. Paut and Onern, Jyväskylä, Finland.
- RENTON, K. 2006. Diet of adult and nestling Scarlet Macaws in southwest Belize, Central America. *Biotropica* 38: 280–283.
- ROBINSON, S. K., AND J. TERBORGH. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. *Ornithol. Monogr.* 48: 641–672.
- SAZIMA, I. 1989. Peach-fronted parakeet feeding on winged termites. *Wilson Bull.* 101: 656.
- van SCHAIK, C. P., J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353–377.
- SHANAHAN, M., S. SO, S. G. COMPTON, AND R. CORLETT. 2001. Fig-eating by vertebrate frugivores: A global review. *Biol. Rev.* 76: 529–572.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. 3rd edn. Freeman, New York.
- TERBORGH, J. 1983. *Five new world primates—A study in comparative ecology*. Princeton University Press, Princeton.
- TOBLER, M. W., S. E. CARRILLO-PERCASTEGUIA, AND G. POWELL. 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. *J. Trop. Ecol.* 25: 261–270.
- VÁSQUEZ, R., AND A. H. GENTRY. 1989. Use and misuse of forest-harvested fruits in the Iquitos area. *Conserv. Biol.* 3: 350–361.
- WALKER, J. S. 2007. Dietary specialization and fruit availability among frugivorous birds on Sulawesi. *Ibis* 149: 345–356.
- WRIGHT, T. F., E. E. SCHIRTZINGER, T. MATSUMOTO, J. R. EBERHARD, G. R. GRAVES, J. J. SANCHEZ, S. CAPELLI, H. MUELLER, J. SCHARPEGGE, G. K. CHAMBERS, AND R. C. FLEISCHER. 2008. A multilocus molecular phylogeny of the parrots (Psittaciformes): Support for a Gondwanan origin during the Cretaceous. *Mol. Biol. Evol.* 25: 2141–2156.