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Dietary relationships in relation to 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. We accumulated 1400 feeding records for 16 parrot species over two years 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 in floodplain and terra firme forests 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 twenty 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.

Keywords: *Bertholletia*; dietary niche; *Euterpe*; keystone species; mineral lick; Peru; phenology

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 is 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 has 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 monkey species (Ferreira *et al.* 2008). Dietary 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, macaws do not appear to make dietary selections based on mineral content (Gilardi & Toft 2012) while 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 in some cases soil is consumed to bind poisonous and/or bitter-tasting secondary compounds (Diamond *et al.* 1999).

Species richness in the western Amazon is the highest in the world for many taxa including birds (Haffer 1990, Rahbek & Graves 2001) making this area ideal for studies of the relationship between diets and community structure. The parrot family (Psittacidae) has many

species of conservation concern due to overharvesting in the wild and loss of nesting resources (Snyder *et al.* 2000). Despite its importance, there is little published on dietary relationships for the great majority of Amazonian parrot communities (but see Marsden & Whiffen 2003). Most Neotropical parrots consume seeds (Higgins 1979, Gilardi 1996, Renton 2006) and at least some fruit (Galetti 1997). Many also eat flowers and nectar (Cotton 2001, Raguso-Netto 2007). To a lesser degree, they also consume insect larvae (Renton 2006), termites (Sazima 1989), tree bark/wood (Renton 2006, Brightsmith *et al.* 2010) 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 (Haugaasen & Peres 2005) and plant community composition and associated food resources also depend on the forest age structure or successional stage (Robinson & Terborgh 1997). Tropical herbivores respond to scarcity in various ways, including diet switching, seasonal breeding, and movements (*e.g.* Wermundsen 1997, Poulin *et al.* 1992, Peres 1994, Renton 2001, Bjork 2004). 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. We expect parrots consuming seed and unripe fruit items to consume soil more than those consuming other dietary items.

METHODS

STUDY SITES.—Study sites were located in the Department of Madre de Dios in southeastern Peru (Fig. 1). Parrot surveys were conducted within the Tambopata National Reserve and associated buffer zone (274,690 ha and 186,450 ha respectively), in lowland Amazon rainforest of southeastern Peru. Of the three dominant Amazonian ecological systems of Peru and Boliva 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 includes uplifted Holocene and Pleistocene alluvial terraces (Räsänen 1993), and tend to be nutrient poor in comparison to floodplain forests (Kalliola 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 below terra firme terraces. 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 water courses and fallow agricultural allotments, and accounts for 2.6% of the study area. The altitudinal range was between 195 and 350 m asl. Temperature ranges between 10ºC and 38ºC 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. 1).

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. All transects at Posada and TRC were within 5 km of known parrot claylicks. All sampling at Refugio was conducted 5-10 km from any known macaw claylick, although one transect passed <200 m from a mammal claylick known to be visited by two species of parakeet. Transects were conducted between 0600 and 1100 h and from 1500 to 1800 h. During transects, as well as for any other time parrots were encountered foraging, the following information was recorded: parrot species, number of individuals of each 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, as well as a tower and observation points over the canopy that allowed for close observation of the birds. In order 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. In order 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. If the plant part consumed could not be ascertained with confidence, then that record was omitted, as were records of parrots eating insects. For species with small seeds e.g. *Cecropia* and *Ficus* we recorded the dietary part as whole fruit. We omitted parrot species from our analyses for which we had < 14 feeding records (N = 13 species). We performed DCA in the PAST software (Hammer *et al.* 2001). We retained scores for each of the thirteen commonly recorded parrot species on the first two ordination axes (eigenvalues of 0.67 and 0.41 for axes 1 and 2 respectively). Proportional data were arcsine transformed prior to inclusion in the DCA.

For each parrot species, nine diet metrics describing dietary composition, breadth and seasonality were calculated as follows: (1 & 2) scores on DCA axes 1 & 2; (3) Proportion of

plant parts consumed that consisted of seeds: this includes all seed components *e.g.* embryo and endosperm; (4) Proportion of fruit pulp; (5) Proportion of flowers; (6) Proportion of whole fruits; (7) Proportion of food items consumed classified as non-ripe; (8) Proportion of rare food items: each forage species was classified as either rare (<5 per ha or not recorded in the phenology plots) or common (>5 per ha in the plots) following Walker (2007); (9) Dietary specialisation: Levin's standardised 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 five minute intervals at six claylicks (Fig. 1) from January 2006 to July 2009 (see Lee (2010) for additional details). 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, multiplied by 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. This was calculated as the average value of the mean daily claylick use for the three months with the least claylick use, divided by that of the three months 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 (axes 1 and 2 analysed separately). Phylogeny was taken from Fig. 1 of Wright *et al.* (2008). Phylogenetic relatedness was taken as the number of nodes along the phylogenetic tree from a species' genus position to the other species' genus position. Species in the same genus were scored zero. 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 specialisation (Levin's index). We also used Spearman's analysis to examine correlations among the dietary measures (see above), and between dietary measures and claylick use.

WOODY PLANT ABUNDANCE AND PHENOLOGY.—A total of 3266 trees with dbh >10cm were marked in 30 plots of 10m × 100-200m (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 and not necessarily placed along foraging transects. The 1819 trees located in floodplain and terra firme forest at Posada and Refugio were monitored on a monthly basis for the presence of fruit and flower from January 2006 to December 2009, but did not include plots in early stage successional forest. Each tree was scored for presence or absence of fruit or flowers. There were 47,398 visits to trees during the course of the survey, however 603 of the 1819 trees (33%) were never registered with fruit or flower, so phenological patterns were based on the remaining 1214 trees (30,051 observations). We consider fruit presence regardless of state of ripeness as state of ripeness was often mixed or

could not be registered with certainty for all species. Monitoring was not possible for all plots every month, so results from all years are combined for the presentation of seasonal phenological patterns, recognising this may mask annual variation. Trees were identified by MPNV in 2008. Botanical classification follows Brako & 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 versus dry seasons, as well as preferred forage species (those that featured most regularly in parrot species diet) versus other tree species, were treated as repeated measures of the same phenology plots and tested with Wilcoxon signed ranks tests, for which we present mean ± standard deviation for proportions of fruiting or flowering trees. Mann-Whitney U-tests were used to compare overall fruit availability between seasons and between floodplain and terra firme forests; and to compare the twenty 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 was 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 1151 independent observations in the analyses. *Amazona farinosa* were 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 ± 7%), while ripe fruits were more common than unripe fruit for the small *Ara severus* and the rest of the parrot assemblage (mean = 58 ± 12%). In only four species did flowers contribute more than one-third of foraging records (Table 1).

Leaves, bark and insects accounted for the remaining 2% of foraging bouts, although these activities may be more cryptic than feeding on large fruits and thus under recorded. Six parrot species on seven occasions were recorded feeding on termites *Nasutitermes corniger* (Isoptera: Termitidae: Nasutitermitinae). *Pionites leucogaster* was observed feeding on ants (*Crematogaster* sp.) on one occasion. *Pyrrhura rupicola* was twice 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 cyanoptera* 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. 2). A greater 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 twenty preferred forage species (Table 2; Table 4) 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 4).

Of 3266 trees within the quadrats 3111 (95%) were identified to species level and included 442 species belonging to 226 genera and 71 families. Parrots fed on 26% of species that could be identified to species level and 37% of plant genera represented in the plots. The 20 most common plant species accounting for 40% of all 3266 marked trees are displayed in Table 2. Eight of the twenty most common tree species were not recorded as being consumed by parrots, while twenty-seven families and 143 genera in plots recorded no foraging events. Feeding encounters were recorded on 49 families, 129 genera and 204 species of plants including eight families and 36 genera not recorded in plots.

The most commonly consumed items were seeds or pulp of the palm *Euterpe precatoria* Arecaceae (10% of all foraging records). Fruits of the palm *Euterpe precatoria* were consumed

by all the 13 common parrot species as well as *Primolius couloni.* Flowers of *Ochroma pyramidale* was consumed by ten parrot species, but only very rarely by the large macaws and short-tailed 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 early stage successional forest (Fig. 3; Table S2 for plant species 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 *Ochroma 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, Pyrhurra rupicola* and *Brotogeris cyanoptera.* 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 glycicarpa, 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 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 plant parts such as the pulp and seed of *Pourouma* spp., the fruits of *Sloanea guianensis* and seeds of *Heisteria acuminata* – all trees associated with terra firme. This axis also separated the diets of the three medium-sized short-tailed parrot species (*Pyrilia barrabandi, Pionetes leucogaster* with high values and *Pionus menstruus* with a lower value).

Predicted dietary plant species richness as determined by species richness estimators Jack1 and ACE was lowest for four parrot species which fed predominantly on successional plant species (*Aratinga weddellii, A. leucophthalma, Amazona ochrocephala* and *Ara severa*) 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 3) and negatively correlated with fruit pulp consumption ($r_s = -0.63$, $P = 0.02$, $N = 13$) indicating separation of diet based on the consumption of early successional flowers. Fruit pulp consumption was also negatively correlated with scores on DCA axis 2 ($r_s = -0.61$, $P = 0.02$, $N = 13$) indicating a partitioning of diets among some parrot species based on amount of fruit pulp consumed. Relative proportions of plant components consumed are indicated in Fig. 4.

There was no significant relationship between phylogenetic similarity of parrot species and the similarity of their dietary positions on DCA axis 1 (Mantel test: $r_s = +0.02$, $P = 0.30$, $N = 13$) or DCA axis 2 (Mantel test: $r_s = -0.01$, $P = 0.37$, $N = 13$). 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 specialisation (r_s = -0.07, P = 0.81, N = 13).

CORRELATIONS WITH CLAYLICK USE: Observations were made at claylicks on 1140 days (228 ± 95 days 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 severus, Amazona farinosa, Pionus menstruus, Pyrilia barrabandi, Aratinga weddellii. Ara ararauna* was observed at only one claylick. While all species displayed marked seasonality in their pattern 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 severus, 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 plant part ripeness and claylick use (r_s = -0.34, P = 0.25, N = 13), or between the proportion of seeds consumed and claylick use (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, all of which also consumed soil. Niche separation at the dietary level appears to be driven by 1) species' ability to consume large or unripe seeds, 2) preference for flowers components, 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 with trees such as *Brosimum utile* and *Caryocar pallidum*. While macaw species shared a large proportion of dietary items associated with primary forest, in general the degree of phylogenetic relatedness of parrot species was not significantly correlated with dietary similarity. The diets of the small macaw *A. severus* 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 loretensis* 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, Jacqueman *et al.* 2001).

PARROT DIETS IN A PLANT SPECIES RICH ENVIRONMENT.—In our study, parrots fed on 26% 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 this 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 small 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 rainforests 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 since 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 multiple 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 *Euterpe precatoria* 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, featuring only in *B. cyanoptera* and *P. rupicola* diets. 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 the large 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 (Vasquez & 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. Since flowers and fruits are predicted to contain fewer plant secondary metabolites compared to seeds (Coley & Barone 1996), our findings do not support the hypothesis that dietary toxins from a seed rich diet drive geophagy in this parrot assemblage. All other available research suggests sodium as being the

driver for regular 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 events (Lee *et al.* 2010). Dudley *et al.* (2012) propose that the diverse vertebrate visitors to the well-known mineral licks of the western Amazon have a common goal of sodium supplementation in a region deprived geographically 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, and at this stage it is difficult to separate a general need for clay from a dietary perspective from those seasonal patterns which are displayed among the parrot species, which may be linked to the habit of feeding clay to chicks.

Whether ongoing anthropogenic activities (hunting, uncontrolled tourism, land transformation) will deprive species of the chance to visit soil needs to be investigated at the physiological or reproductive output level, as it is unknown how dietary or reproductive patterns 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 least conservation concern) consume more soil, implying greater levels of sodium starvation. This hypothesis needs to be more rigorously tested in the future. However, we suspect 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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Table 1. *Dietary metrics, claylick use and supporting information for thirteen parrot species from southeastern Peru. Wt – Body weight (g); Dens – density (inds. km^{-2}); 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 versus abundance at the claylick (see Methods for calculation); Season – the ratio of the three months of low claylick use to the three months 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
Ara ararauna, 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
Ara macao, 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
Ara chloropterus, 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
Ara severus, 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
Aratinga leucophthalma, 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
Aratinga weddellii, 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
Pyrrhura rupicola, 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
Brotogeris cyanoptera, 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
Pionites leucogaster, 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
Pyrilia barrabandi, Orange-cheeked 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
Pionus menstruus, 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
Amazona ochrocephala, 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
Amazona farinosa, 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

Table 2. *The twenty most common tree trees in phenology plots in relation to species on which parrots were most commonly observed feeding. Forage species not recorded in phenology plots are represented by `-`.*

Most common trees	# (*N* = 3263)	diet rank	Most common in diet	# (*N* = 1178)	Abundance rank
Iriartea deltoidea	317	12	*Euterpe precatoria*	132	2
Euterpe precatoria	141	1	*Bertholletia excelsa*	95	212
Socrotea exorrhiza	123	-	*Ochroma pyramidale*	87	-
Pourouma minor	83	6	*Inga alba*	63	85
Pseudolmedia laevis	76	7	*Symphonia globulifera*	47	66
Mauritia flexuosa	67	19	*Pourouma minor*	32	4
Otoba parvifolia	57	10	*Pseudolmedia laevis*	30	5
Hevea brasiliensis	36	95	*Sapium marmieri*	30	42
Triplaris americana	35	-	*Dipteryx micrantha*	29	98
Astrocaryum murumuru	31	-	*Otoba parvifolia*	28	7
Erythrina ulei	31	24	*Jacaranda copaia*	26	100
Mabea maynensis	31	-	*Iriartea deltoidea*	25	1
Senefeldera inclinata	30	-	*Erythrina poeppigiana*	23	152
Leonia glycycarpa	29	-	*Cecropia sciadophylla*	22	69
Oenocarpus bataua	29	59	*Ficus killipii*	22	382
Sorocea pileata	25	202	*Pseudolmedia laevigata*	21	53
Hirtella lightioides	24	-	*Qualea paraensis*	16	-
Pourouma mollis	24	86	*Mauritia flexuosa*	15	6
Tachigali polyphylla	23	34	*Anthodiscus klugii*	14	144
Virola calophylla	22	-	*Apeiba aspera*	14	48

Table 3. *Matrix of Spearman's rank correlation coefficients between dietary and claylick usage across thirteen 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														

Table 4. *The phenology patterns (mean±standard deviation fruit or flower presence) for twenty preferred forage species from Table 2, separated by plant part consumed by parrots: fruit (any seed, pulp or other fruiting body) and flower (including nectar). 'Parrots' is the sum of all parrot species observed feeding on any species. Fruit and Flower availability are counts of the presence of preferred forage species available to parrots for any given month. Blank lines represent preferred species for which we have no phenology data.*

Preferred forage fruit	parrots	January	February	March	April	May	June	July	August	September	October	November	December
Anthodiscus klugii	6	0.3±0.48	0.33±0.51	0.71±0.48	0.62±0.51	0.44±0.52	0.4±0.54	0.44±0.52	0.2±0.44	0.5±0.52	0.12±0.35	0.2±0.44	0.11±0.33
Apeiba aspera	6	0	0	0	0	0.1±0.31	0.33±0.5	0.46±0.51	0	0.15±0.37	0.18±0.4	0.4±0.51	0.05±0.24
Bertholletia excelsa	8	0.6±0.51	0.2±0.44	0.57±0.53	0.57±0.53	0.28±0.48	0.66±0.51	0.37±0.51	0.6±0.54	0.44±0.52	0.77±0.44	0.6±0.54	0.62±0.51
Cecropia sciadophylla	6	0.09±0.3	0.33±0.48	0.62±0.49	0.75±0.44	0.51±0.5	0.52±0.51	0.52±0.51	0.75±0.44	0.36±0.49	0.16±0.37	0.16±0.38	0.06±0.25
Dipteryx micrantha	8	0	0	0.09±0.3	0	0.21±0.42	0.3±0.48	0.16±0.38	0.12±0.35	0	0.06±0.25	0.07±0.27	0
Euterpe precatoria	14	0.41±0.49	0.32±0.46	0.35±0.48	0.2±0.4	0.12±0.33	0.01±0.1	0.03±0.18	0.2±0.4	0.31±0.46	0.32±0.46	0.46±0.5	0.49±0.5
Ficus killipii	4	0	0	0	0	0	0	0	0	0.5±0.7	0	0.5±0.7	0
Inga alba	9	0	0	0	0	0	0	0.08±0.28	0	0	0.18±0.4	0.11±0.33	0.07±0.27
Iriartea deltoidea	8	0.2±0.4	0.25±0.43	0.24±0.43	0.26±0.44	0.26±0.44	0.28±0.45	0.21±0.41	0.28±0.45	0.21±0.4	0.24±0.42	0.3±0.46	0.25±0.43
Jacaranda copaia	3	0.41±0.51	0.33±0.51	0.44±0.52	0.33±0.5	0	0.11±0.33	0	0.16±0.4	0	0	0	0
Mauritia flexuosa	4												
Ochroma pyramidale	2												
Otoba parvifolia	5	0.12±0.35	0	0	0	0	0	0	0	0	0.28±0.48	0.14±0.37	0.45±0.52
Pourouma minor	7	0.05±0.22	0.08±0.28	0.06±0.25	0	0.02±0.17	0.08±0.27	0.07±0.26	0.02±0.16	0.05±0.22	0.06±0.25	0.07±0.26	0.08±0.28
Pseudolmedia laevigata	6	0.12±0.35	0	0	0	0	0	0	0	0	0	0	0
Pseudolmedia laevis	7	0.04±0.2	0.04±0.2	0.04±0.19	0.01±0.11	0	0	0	0.04±0.2	0.11±0.32	0.12±0.33	0.04±0.2	0.08±0.27
Qualea paraensis	4	0	0	0	0	0	0	0	0	0	0	0	0.33±0.57
Sapium marmieri	5	0	0	0	0	0	0	0	0	0	0.33±0.57	0	0
Symphonia globulifera	3	0.11±0.33	0	0	0	0	0	0.09±0.3	0	0	0	0	0
Fruit availability		**11**	**8**	**9**	**7**	**8**	**9**	**10**	**9**	**9**	**12**	**12**	**11**
Preferred forage flowers													
Bertholletia excelsa	4	0.6±0.51	0.2±0.44	0	0	0.14±0.37	0.16±0.4	0.12±0.35	0	0.33±0.5	0	0.6±0.54	0.37±0.51
Cecropia sciadophylla	4	0.16±0.37	0.26±0.45	0.04±0.2	0.08±0.28	0.03±0.17	0.08±0.28	0	0	0	0.03±0.17	0	0
Dipteryx micrantha	3	0.13±0.35	0	0.09±0.3	0	0	0	0	0	0	0	0	0.13±0.35
Erythrina poeppigiana	6												
Euterpe precatoria	1	0.05±0.22	0.07	0	0.02±0.15	0.02±0.17	0.34±0.47	0.42±0.49	0.22±0.42	0.32±0.47	0.22±0.41	0.06±0.24	0.03±0.19
Iriartea deltoidea	3	0.06±0.25	0.07±0.25	0.01±0.11	0.04±0.19	0.02±0.15	0.02±0.15	0.07±0.25	0.1±0.3	0.1±0.3	0.09±0.28	0.08±0.27	0.11±0.32
Mauritia flexuosa	2												
Ochroma pyramidale	11												
Pseudolmedia laevis	1	0.03±0.18	0	0.02±0.16	0	0.01±0.12	0.09±0.29	0.05±0.23	0.04±0.2	0.11±0.32	0.08±0.27	0.01±0.11	0.01±0.13
Symphonia globulifera	8	0	0.25±0.46	0	0.25±0.46	0	0.25±0.5	0.18±0.4	0	0	0	0.1±0.31	0
Flower availability		**6**	**4**	**4**	**4**	**5**	**6**	**5**	**3**	**4**	**4**	**5**	**5**

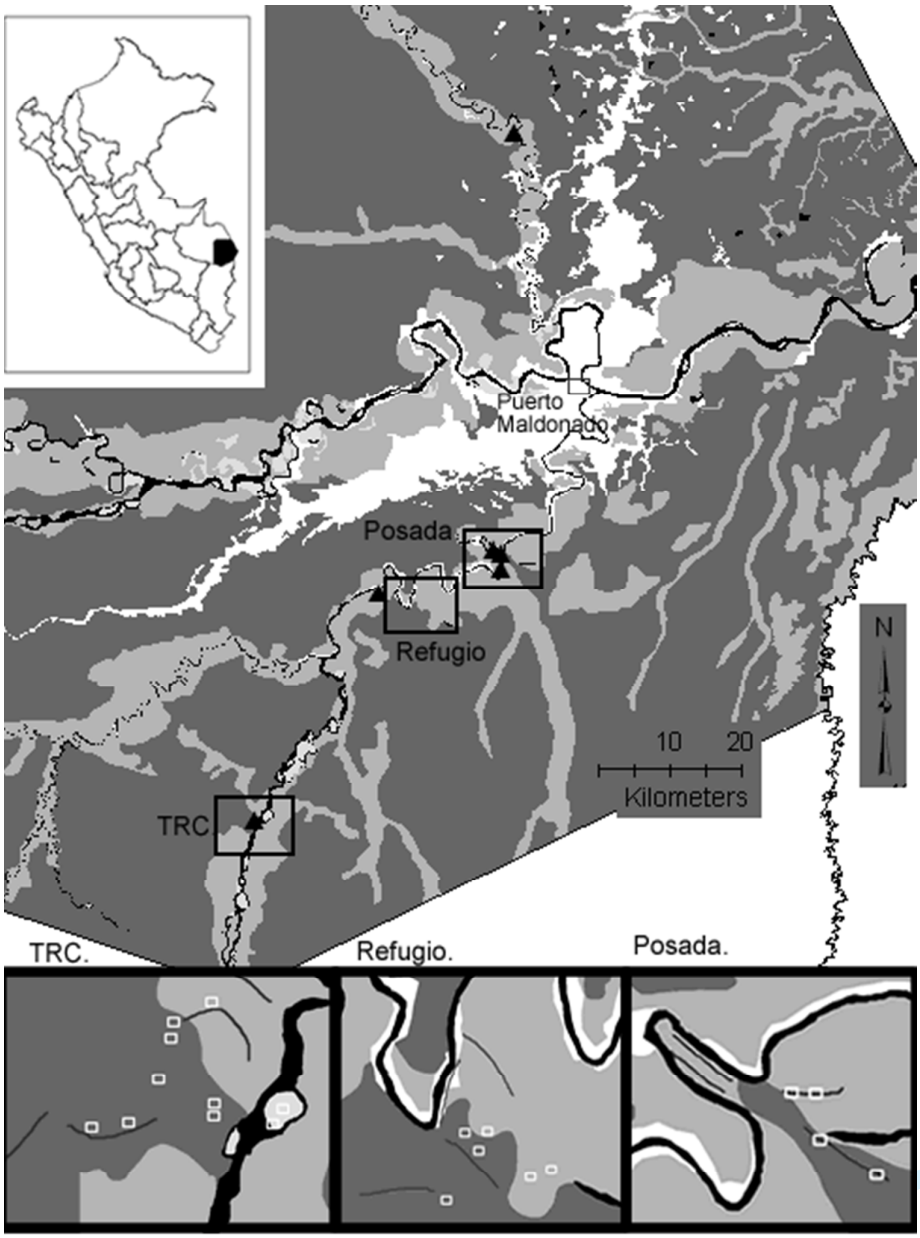
FIGURES

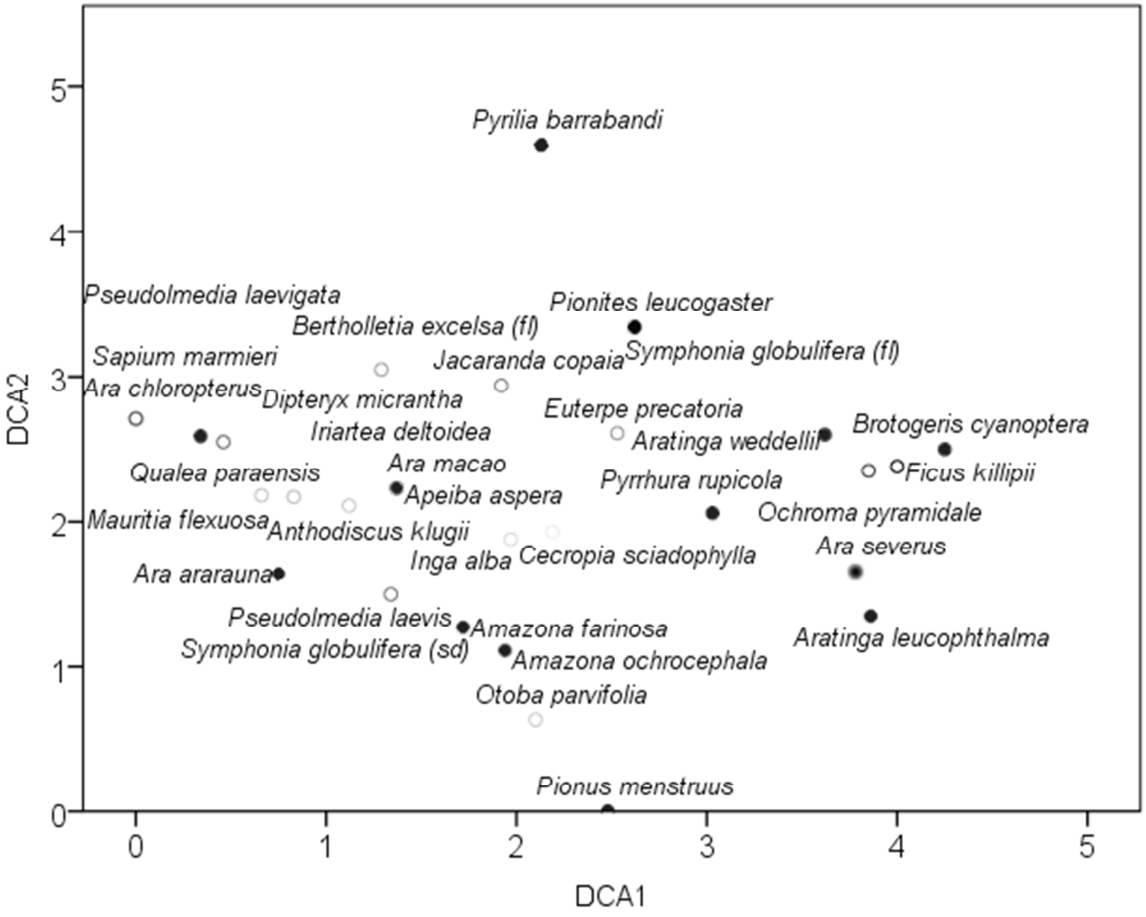
Figure 1: A map of the study area showing survey sites and claylick locations (black triangles) in relation to major forest types. Puerto Maldonado is the largest town (pop. c 50 000). White forest is anthropogenically modified habitat, lightest grey represents successional forests, medium grey areas are floodplain forest, while the dark grey forest away from the rivers tends to be terra firme. Inset maps: foraging transect routes are thin grey lines; phenology plot locations are white rectangles.

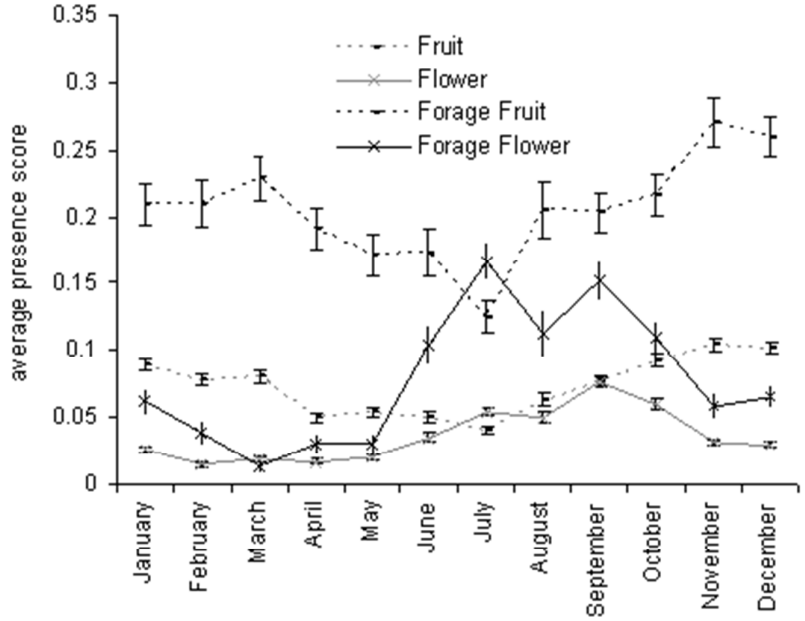
Figure 2: Phenological patterns for trees in plots at Refugio and Posada: the mean ± SE proportion of 1214 marked trees with fruit or flower per month for the period 2006-2009.

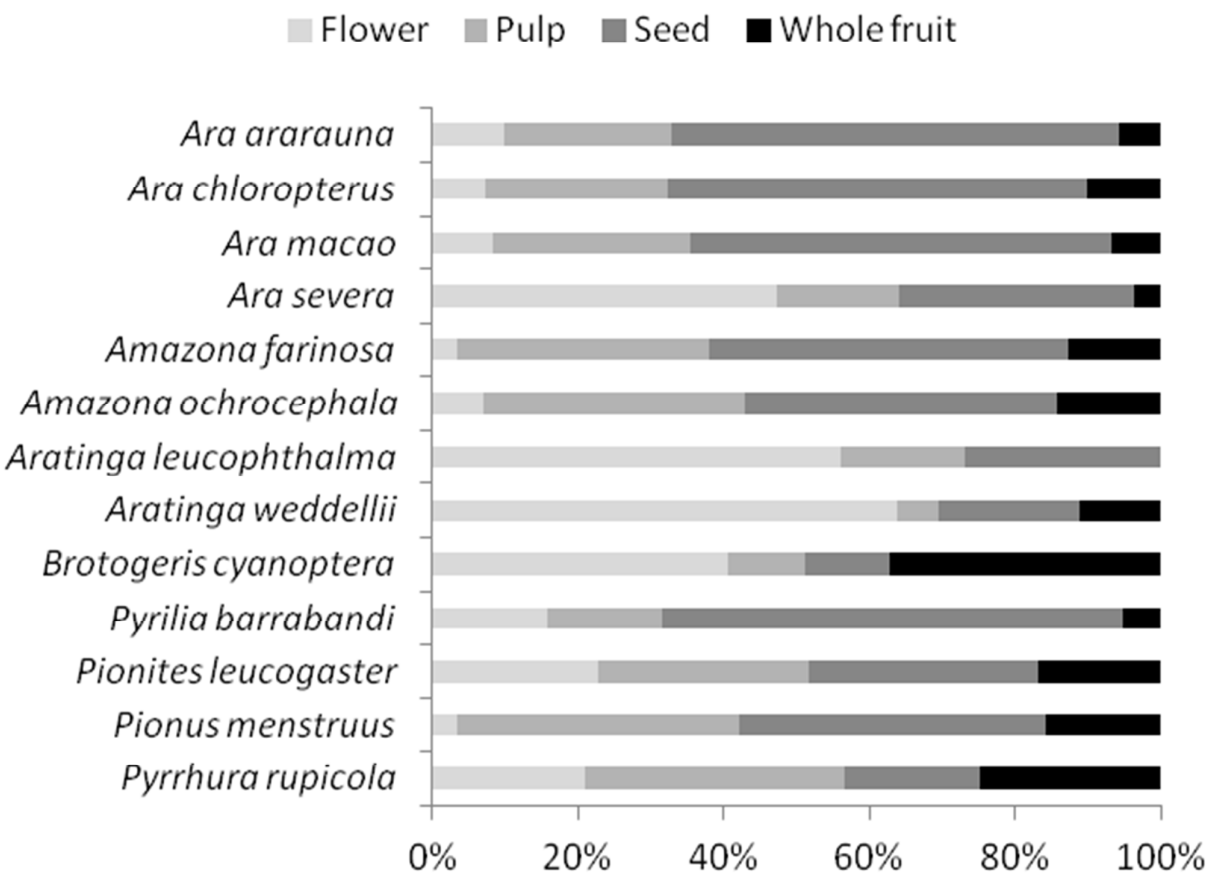
Figure 3: Centroids for each parrot species (black circles) and preferred forage species (open circles) on DCA axis 1 (eigenvalue = 0.67, high scores associated with successional forest food plants) and axis 2 (eigenvalue = 0.41).

Figure 4: Proportions of all items for seed, flower, fruit pulp or whole fruits consumed by the thirteen common parrot species of the study area.




Pyrilia barrabandi
Pseudolmedia laevigata
Pionites leucogaster
Bertholletia excelsa (fl)
Sapium marmieri
Jacaranda copaia
Symphonia globulifera (fl)
Ara chloropterus
Dipteryx micrantha
Euterpe precatoria
Brotogeris cyanoptera
Iriartea deltoidea
Aratinga weddelli
Qualea paraensis
Ara macao
Ficus killipii
Pyrrhura rupicola
Apeiba aspera
Mauritia flexuosa
Anthodiscus klugii
Ochroma pyramidale
Inga alba
Cecropia sciadophylla
Ara severus
Ara ararauna
Pseudolmedia laevis
Amazona farinosa
Aratinga leucophthalma
Symphonia globulifera (sd)
Amazona ochrocephala
Otoba parvifolia
Pionus menstruus
DCA2
DCA1
0
1
2
3
4
5


Fruit
Flower
Forage Fruit
Forage Flower
average presence score
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
January
February
March
April
May
June
July
August
September
October
November
December



Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Anacardiaceae																		
Astronium graveolens	Pulp	3								3								
	Seed	1								1								
Tapirira obtusa	Pulp	8			1					6						1		
Annonaceae																		
	Pulp	1						1										
	Wholefruit	1								1								
Guatteria Oxandra xylopioides	Seed	1								1								
	Flower	1														1		
	Leaves	1																1
	Pulp	1																1
	Seed	8								1						5		2
	Unknown	1																1
	Wholefruit	1															1	
Apocynaceae																		
Aspidosperma megalocarpon muell	Seed	4								4								
Rauwolfia Tabernaemontana heterophylla	Flower	1														1		
	Seed	2								2								
	Unknown	1								1								
Tabernaemontana stenotachya	Seed	1								1								
Arecaceae																		
Euterpe precatoria	Flower	1									1							
	Pulp	96	2	3	14	3		1	1	10	4	2	4		1	33	5	13
	Seed	24			4					2		4			1	9	1	3
	Unknown	2		1	1													
	Wholefruit	9		1						2						4		2
Iriartea deltoidea	Flower	13											1			4		8
	Pulp	5		1						1			1				1	1

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
	Unknown	4	1	1	1											1		
	Wholefruit	3		1									2					
Mauritia flexuosa	Flower	2								1								1
	Pulp	13	3	4	5					1								
Oenocarpus bataua	Pulp	3			2											1		
	Unknown	2	1		1													
	Wholefruit	1		1														
Oenocarpus mapora	Seed	2								1					1			
	Unknown	1		1														
Socratea exorrhiza	Flower	1													1			
	Leaves	1	1															
	Wholefruit	1	1															
Bignoniaceae																		
Arrabidaea	Seed	2														2		
Jacaranda copaia	Pulp	5		3	1													1
	Seed	20		13	6													1
	Unknown	1		1														
Mansoa	Pulp	1														1		
Sparattosperma leucanthum	Flower	1		1														
Bixaceae																		
Bixa urucurana	Seed	1			1													
Bombacaceae																		
	Seed	1											1					
Chorisia insignis	Seed	6											6					
Huberodendron swieteniodes	Pulp	1		1														
	Seed	1	1															
	Wholefruit	1											1					
Ochroma pyramidale	Flower	84	1	1	2	16				1	7	9	31		1	1		14

Plant / Food item name	Part consu-med	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
	Pulp	3											2					1
Boraginaceae																		
Cordia ucayalina	Seed	2			2													
	Unknown	1			1													
Bromeliaceae																		
Aechmea angustifolia	Seed	2																2
Streptocalyx	Wholefruit	1																1
Burseraceae																		
Protium	Pulp	1																1
Protium amazonicum	Seed	1								1								
	Wholefruit	1		1														
Protium aracouchini	Seed	2								2								
	Wholefruit	1								1								
Protium neglectum	Pulp	1								1								
Protium rhynchophyllium	Seed	2								2								
Protium sagotianum	Pulp	1											1					
Trattinickia rhoifolia var. Lancifolia	Seed	3			3													
Caryocaraceae																		
Anthodiscus klugii	Pulp	1																1
	Seed	4		1	2					1								
	Wholefruit	9	1	2	4			1		1								
Caryocar amygdaliforme	Seed	1		1														
	Unknown	1			1													
Caryocar glabrum	Seed	1		1														
Caryocar pallidum	Seed	1											1					

Plant / Food item name	Part consu-med	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Clusiaceae																		
Chrysoclamys ulei	Seed	13			1											11		1
	Unknown	1														1		
Clusia	Pulp	1											1					
	Seed	4														4		
Moronobea coccinea	Flower	1											1					
Symphonia globulifera	Flower	43	5		6	1				4		3	5			17		1
	Pulp	1														1		
	Seed	3			1					1						1		
Tovomita stylosa	Seed	2														2		
Combretaceae																		
Combretum fruticosum	Flower	1										1						
Combretum laxum	Leaves	1											1					
Combretum sp	Seed	1														1		
Terminalia oblonga	Seed	6			1					2		1				1		1
	Unknown	1			1													
Cucurbitaceae																		
Cayaponia macrocalyx	Pulp	4				4												
	Seed	4				4												
Fevillea amazonica	Seed	2				2												
Ebenaceae																		
Diospyros poeppigii	Pulp	1									1							
	Seed	3			2					1								
	Unknown	1			1													
Elaeocarpaceae																		
Sloanea fragrans	Seed	1		1														
Sloanea guianensis	Seed	4								4								
	Wholefruit	7								7								

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Euphorbiaceae																		
	Seed	1				1												
Alchornea triplinervis	Seed	1														1		
Croton lechleri	Flower	1																1
	Seed	2			2													
Dalechampia stipulacea	Seed	1		1														
Drypetes gentryi	Pulp	2								1							1	
	Seed	2		1	1													
Hevea brasiliensis	Seed	3	2	1														
Sapium glandulosum	Pulp	1																1
	Seed	1								1								
Sapium ixiamasense	Seed	1								1								
	Unknown	3			1					1								1
	Wholefruit	1								1								
Sapium marmieri	Pulp	1								1								
	Seed	28			12	4				9						2		1
	Unknown	1			1													
Fabaceae																		
Abarema laeta	Seed	1															1	
Acacia loretensis	Flower	3			3													
	Leaves	2		1	1													
	Other	1				1												
	Seed	7			2	2				2							1	
Apuleia leiocarpa	Flower	2														1	1	
	Seed	3								3								
Barbebydendron riedelii	Flower	2			1	1												
Caesalpinia apuleia	Insect	1		1														
Cedrelinga cateniformis	Seed	2								1							1	
	Wholefr	2														2		

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Copaifera	Seed	1			1													
Dialium guianense	Pulp	1								1								
	Seed	7			2					2	3							
Dipteryx micrantha	Flower	3								1			1					1
	Insect	1																1
	Leaves	4		2	1			1										
	Other	3		1	1					1								
	Pulp	11	1	6	2					2								
	Seed	4		3	1													
	Unknown	2		1												1		
	Wholefruit	1															1	
Enterolobium	Seed	1		1														
Enterolobium barnebyanum	Pulp	1								1								
	Seed	5								1							4	
Enterolobium cyclocarpum	Seed	2	1	1														
Erythrina	Flower	7			1	1					1	1	2			1		
Erythrina poeppigiana	Flower	23	1		1	3					9	7	2					
Erythrina ulei	Flower	12			1	2		1			5	2	1					
	Other	1			1													
	Seed	1			1													
Hymenaea courbaril	Seed	2								2								
Hymenaea oblongifolia	Seed	8		1						6						1		
	Unknown	1								1								
	Wholefruit	2		1	1													
Inga	Flower	1		1														
	Other	1										1						
	Pulp	2			1												1	
	Seed	7	2		1						1	1					2	
	Wholefruit	6		1						1						2	1	1
Inga acreana	Pulp	1		1														

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Inga alba	Other	1															1	
	Pulp	42	1	1	2			1		10	1					8	8	10
	Seed	14		2	2					3						3	3	1
	Unknown	1															1	
	Wholefruit	5		1						1						1	1	1
Inga chartacea	Leaves	1		1														
	Wholefruit	2				1	1											
Inga cinnamomea	Pulp	1														1		
Inga coriacea	Seed	3															3	
Inga edulis	Pulp	8		1		1				2						1	2	1
	Seed	1															1	
	Unknown	1			1													
	Wholefruit	1			1													
Inga punctata	Pulp	4			2					2								
	Seed	5			4					1								
	Unknown	2				1											1	
Inga semialata	Pulp	1		1														
Machaerium	Seed	1										1						
Parkia	Seed	2		2														
Parkia nitida	Seed	2	1		1													
Parkia velutina	Seed	5	4		1													
Pterocarpus rohrii	Flower	2														1	1	
Schizolobium parahybum	Seed	4		4														
	Unknown	1			1													
Schwartzia	Seed	1	1															
Swartzia	Pulp	1														1		
	Seed	6	4	2														
Swartzia cardiosperma	Seed	2								2								
Tachigali polyphylla	Seed	10						2		7							1	
	Unknown	1								1								

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Tachigali vasquezi	Pulp	1									1							
	Seed	1								1								
Zygia corombosa	Seed	1															1	
Flacourtiaceae																		
Casearia decandra	Pulp	7			1					6								
	Seed	5			5													
	Unknown	2			2													
Laetia procera	Pulp	2								1					1			
	Seed	5			1											3		1
	Wholefruit	1								1								
Hugoniaceae																		
Roucheria punctata	Seed	1									1							
Icacinaceae																		
Leretia cordata	Pulp	1																1
Lauraceae																		
Ocotea cernua	Seed	2		2														
Lecythidaceae																		
Bertholletia excelsa	Flower	17		8	1										1	7		
	Other	4		2	1											1		
	Pulp	9	2	3	1	1							1					1
	Seed	61	24	23	10					2						2		
	Unknown	2	1	1														
	Wholefruit	2		2														
Cariniana decandra	Flower	1								1								
	Seed	5	1	1	3													
Cariniana estrellensis	Unknown	1															1	
Cariniana guianensis	Flower	4														4		
Couratari guianensis	Flower	6											1			4		
	Seed	3		2	1													

Plant / Food item name	Part consu-med	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Eschweilera coriacea	Seed	2		1	1													
	Unknown	2			2													
Eschweilera tesmanni	Seed	13	1	5	6					1								
Loganiaceae																		
Strychnos asperula	Seed	1						1										
	Unknown	2			1								1					
Loranthaceae																		
Psittacanthus	Flower	1														1		
	Pulp	1											1					
Malpighiaceae																		
Byrsonima	Unknown	1			1													
Byrsonima arthropoda	Unknown	1								1								
Byrsonima poeppigii	Pulp	4		2	1											1		
	Seed	4		1	1			1								1		
	Wholefruit	3		1	1											1		
Mascagnia platyrachis	Seed	4			1	1					1						1	
Malvaceae																		
	Seed	1											1					
Apeiba aspera	Pulp	4	1	1	1												1	
	Seed	9		4	1											3		1
	Wholefruit	1			1													
Ceiba pentandra	Flower	1														1		
	Seed	1											1					
Ceiba samauma	Wholefruit	1				1												
Quararibea ochrocalyx	Seed	6		4	2													
Marcgraviaceae																		
Norantea guianensis	Flower	3				1							1			1		
Marchantiacea																		

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Marchantia	Other	2	1	1														
Melastomataceae																		
Miconia	Wholefruit	1														1		
Miconia barbeyana	Flower	1														1		
	Seed	1																1
Meliaceae																		
Cedrela odorata	Seed	1			1													
Guarea guidonia	Seed	1														1		
	Unknown	1														1		
	Wholefruit	1										1						
Guarea pubescens	Seed	2		1												1		
Trichilia pleeana	Unknown	1								1								
Menispermaceae																		
Anomospermum boliviana	Pulp	3														1	1	1
	Seed	1			1													
Anomospermum grandifolium	Pulp	1		1														
Borismene japurensis	Unknown	1								1								
Moraceae																		
Brosimum	Leaves	1																1
Brosimum acutifolium	Pulp	4														2		2
	Seed	3								2								1
	Unknown	1								1								
Brosimum alicastrum	Pulp	8								3			2			1		2
Brosimum guianense	Pulp	1								1								
	Seed	1								1								
Brosimum lactescens	Pulp	2								1								1

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
	Seed	1								1								
	Wholefruit	1								1								
Castilla ulei	Pulp	3	1							2								
	Seed	1			1													
	Wholefruit	2			1												1	
Clarisia racemosa	Pulp	1								1								
	Seed	1								1								
Ficus	Wholefruit	6								1			3					2
Ficus caballina	Wholefruit	3											2					1
Ficus coerulescens	Wholefruit	3											2					1
Ficus guianensis	Wholefruit	1											1					
Ficus insipida	Wholefruit	6														4		2
Ficus killipii	Wholefruit	22											18			1	1	2
Ficus mathewsi	Wholefruit	6						1										5
Ficus maxima	Wholefruit	5										2				3		
Ficus paraensis	Wholefruit	6														6		
Ficus perforata	Wholefruit	3											3					
Ficus pertusa	Other	1			1													
	Wholefruit	8			1								6			1		
Ficus schultsi	Wholefruit	4										1	1			1		1
Ficus sphenophylla	Wholefruit	1														1		
Ficus trigona	Wholefruit	2								1						1		
Helianthostylis acuminata	Pulp	1													1			
Helicostylis tomentosa	Wholefruit	1								1								
Pseudolmedia	Pulp	1																1
	Seed	1											1					

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
	Unknown	1										1						
	Wholefruit	4		1									1			1	1	
Pseudolmedia laevigata	Pulp	13		1	7					3						1		1
	Seed	8								5						2	1	
Pseudolmedia laevis	Flower	1		1														
	Pulp	13		2				1		7							1	2
	Seed	9		1						4			1			1		2
	Wholefruit	7		2						4							1	
Pseudolmedia macrophylla	Pulp	6		2	2					1								1
	Seed	5			1					4								
	Unknown	2								1							1	
Pseudolmedia rigida	Pulp	1								1								
Sorocea pileata	Seed	1			1													
Myristicaceae																		
Otoba	Seed	1								1								
Otoba glycicarpa	Pulp	2														2		
	Unknown	1									1							
Otoba parvifolia	Pulp	9	3	1	4					1								
	Seed	17	1	1	7					8								
	Wholefruit	2								1							1	
Myrtaceae																		
Psidium guajava	Seed	2				2												
Ochnaceae																		
Ouratea	Flower	1														1		
	Seed	1														1		
Olacaceae																		
Heisteria acuminata	Seed	1								1								
Opiliciaceae																		
Agonandra	Other	1			1													

Plant / Food item name	Part consu-med	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Poaceae																		
Guadua	Leaves	3			2	1												
	Shoot	1			1													
Rubiaceae																		
Calycophyllum spruceanum	Flower	2														1		1
Hilla ulei	Leaves	1			1													
Rutaceae																		
Zanthoxylum huberi	Seed	2																2
Zanthoxylum tambopatense	Seed	5									1		1			1	1	1
Sapindaceae																		
Sapindus saponaria	Seed	1																1
Sapotaceae																		
Chrysophyllum argentium	Flower	1											1					
Ecclinusa guianense	Wholefruit	2														2		
Ecclinusa lanceolata	Pulp	5	1							2						2		
	Seed	2								1							1	
Guatteria acutissima	Unknown	1								1								
Pouteria	Flower	1														1		
	Pulp	2								1						1		
	Seed	4								2						1	1	
Pouteria macrophylla	Pulp	1								1								
	Seed	2			1			1										
Pouteria paridy	Wholefruit	1								1								
Pouteria procera	Pulp	2								1						1		
	Seed	4								2						2		
Pouteria trilocularis	Pulp	2								1						1		
	Seed	3								1					1	1		
	Unknown	1								1								
Sterculiaceae																		
Byttneria	Seed	1			1													

Plant / Food item name	Part consumed	Total	*Ara ararauna*	*Ara chloropterus*	*Ara macao*	*Ara severus*	*Orthopsittaca manilata*	*Amazona ochrocephala*	*Primolius couloni*	*Amazona farinosa*	*Aratinga leucophthalma*	*Aratinga weddellii*	*Brotogeris cyanoptera*	*Forpus modestus*	*Pyrilia barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	*Pyrrhura rupicola*
Byttneria pescapriifolia	Pulp	1		1														
	Seed	3			3													
	Unknown	1		1														
	Wholefruit	1			1													
Guazuma ulmifolia	Seed	1				1												
Guazuma.	Seed	1					1											
Pterygota amazonica	Insect	1															1	
Sterculia rugosa	Seed	1			1													
Sterculia tessmannii	Seed	1								1								
Theobroma	Seed	1								1								
Termites	Insect	3										1	2					
Ulmaceae																		
Celtis	Seed	1														1		
Celtis iguanaea	Seed	1									1							
Celtis iguanaea	Seed	2									2							
Trema micrantha	Flower	1											1					
	Seed	1											1					
	Wholefruit	3																3
Urticaceae																		
Cecropia	Wholefruit	1											1					
Cecropia sciadophylla	Wholefruit	22	2		1					4			2	1		4		8
Cecropia tesmanni	Wholefruit	3											1					2
Coussapoa trinervia	Wholefruit	2														2		
Pourouma	Other	1			1													
	Pulp	1			1													
Pourouma cecropiifolia	Pulp	2		1	1													
	Seed	4													1	3		
	Unknown	1														1		
	Wholefr	1			1													

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Pourouma cucura	Seed	1														1		
Pourouma guianensis	Pulp	7		3	2					1						1		
Pourouma minor	Pulp	13		2				1		7						2		1
	Seed	15		2	2					2					6	1		2
	Unknown	1			1													
	Wholefruit	3		2											1			
Pourouma mollis	Pulp	1			1													
	Seed	3													2	1		
Pourouma palmata	Pulp	2	1													1		
Vochysiaceae																		
Qualea grandiflora	Flower	1														1		
	Seed	8		5	2											1		
Qualea paraensis	Seed	16		7	2			1		6								
		146	7	18	22	5		1		25	4	3	12		1	23	6	13
		8	6	3	4	6	2	5	1	4	2	9	5	1	9	1	3	7