



## FORAGING ECOLOGY OF PSITTACINES IN THE TAMBOPATA NATIONAL RESERVE, PERU

Daphne Matsufuji<sup>1</sup>, Martha Williams<sup>1</sup>, Carlos Reynel<sup>1</sup>, Karina Quinteros<sup>1</sup>, Paola Martínez<sup>2</sup>, Donald J. Brightsmith<sup>3</sup><sup>1</sup> Universidad Nacional Agraria La Molina, Av. La Molina s/n, La Molina, Lima, Perú.<sup>2</sup> Asociación Bosques Perú, Ca Pérez de Tudela N°289, Lima 15107, Perú.<sup>3</sup> Department of Veterinary Pathobiology, Texas A&M University, TAMU 4467, College Station, Texas 77843-4467, USA.

E-mail: Daphne Matsufuji · dmatsufuji@gmail.com

**Abstract** · Between May 2004 and April 2005, we observed 15 species of psittacines foraging along transects and during fortuitous encounters in the Tambopata National Reserve, Peru. Psittacines fed on 84 plant species from 62 genera and 30 families. We report 51 plant species as new food sources for psittacines in southeastern Peru. The greatest foraging activity took place from 06:00 h to 07:00 h. The most consumed plant parts were seeds (41% of 469 foraging encounters), followed by pulp (15%), whole fruits (13%), flowers (12%), arils (10%), leaves (1.5%), bark (0.6%), floral buds (0.4%), and fruit juice (0.4%). We found no difference between ripe and unripe seed consumption (48% and 47%, respectively), but other fruit parts were eaten mostly ripe (more than 67%).

**Resumen · Ecología del forrajeo de psitácidos en la Reserva Nacional Tambopata, Perú**

Entre mayo de 2004 y abril de 2005 observamos 15 especies de psitácidos forrajeando a lo largo de transectos y durante encuentros fortuitos en la Reserva Nacional Tambopata, Perú. Los psitácidos se alimentaron de 84 especies de plantas de 62 géneros y 30 familias. Reportamos 51 especies de plantas como nuevas fuentes de alimento para psitácidos en el sureste del Perú. La mayor actividad de forrajeo se registró desde las 06:00 h hasta las 07:00 h. Las partes más consumidas fueron semillas (41% de 469 encuentros de forrajeo), seguidas por pulpa (15%), frutos completos (13%), flores (12%), arilos (10%), hojas (1,5%), corteza (0,6%), botones florales (0,4%) y jugo de las frutas (0,4%). No encontramos diferencias entre el consumo de semillas maduras e inmaduras (48% y 47%, respectivamente), pero las otras partes de los frutos fueron consumidas principalmente maduras (más del 67%).

**Key words:** Amazon · Diet · Macaws · Parrots · Rainforest

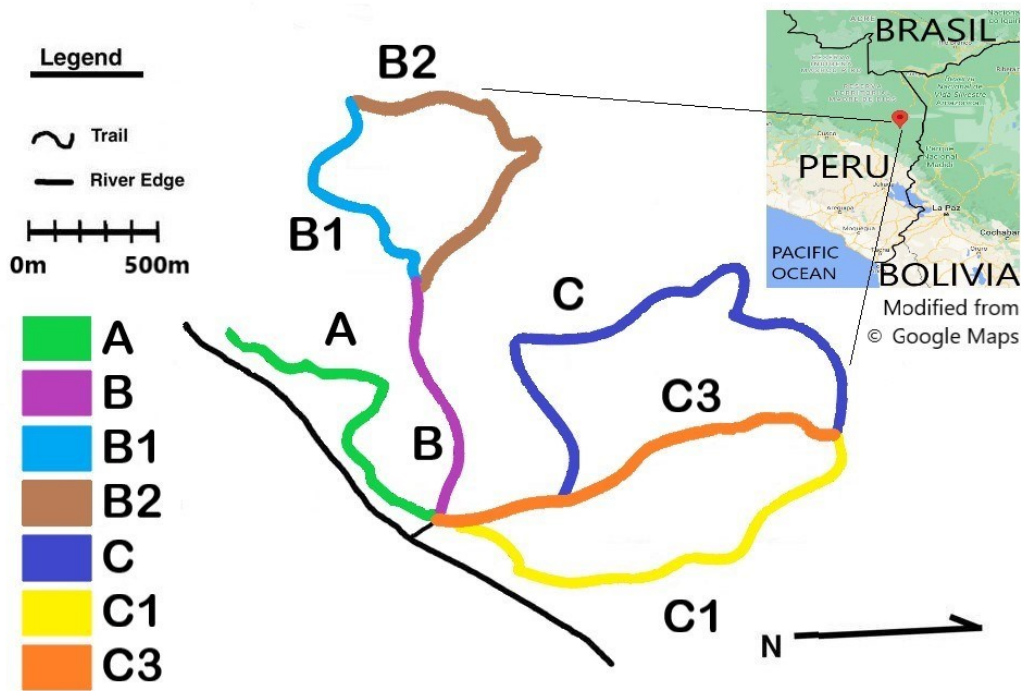
## INTRODUCTION

Birds in the family Psittacidae include some of the most threatened species in the world, with 17% endangered or extinct, 15% vulnerable, 14% near threatened, and just 54% in least concern (IUCN 2021). The causes of this situation appear to be manifold and mainly of anthropogenic origin (Berkunski et al. 2017), such as loss of habitat due to agriculture and logging, hunting, illegal pet trade, and invasive alien species (Olah et al. 2016). Although psittacines have been held in captivity for many decades in zoos and other animal holding facilities (Young et al. 2012), their diets in captivity bear little resemblance to the foods they rely on in the wild (Toft & Wright 2015).

The Amazonian lowlands are globally recognized for the abundance of psittacine species, offering great opportunities to study the biology and ecology of these Neotropical birds (Gilardi 1996). We conducted our study in the Tambopata National Reserve, Peru, an area known to hold 19 species of psittacines (Brightsmith 2004). Few plant species fruit and flower year-round, meaning that food availability and abundance vary greatly throughout the year (Martínez-Sovero et al. in press). Diets and variation in annual food supply are known to have broad impacts on the natural history of most species, including psittacines (Tang & Bennett 2010, Lee et al. 2014, Brightsmith et al. 2018). In southeastern Peru, the variation in diet among species and across seasons has large impacts on the breeding season, clay lick use, habitat use, and seasonal movements (Brightsmith 2005, Vigo et al. 2011, Lee et al. 2014, Brightsmith et al. 2018, 2021). During seasonal food shortages, psittacines are known to switch diets, switch habitats, and even make long distance seasonal migrations (Renton 2001, McReynolds 2012, Brightsmith et al. 2021). In many cases these movements can take the birds away from their breeding sites and outside of protected areas, with potential consequences for their conservation (Bjork 2004, Brightsmith et al. 2021). Understanding the diet composition and, consequently, the distribution and availability of their food sources, benefits the conservation of psittacine

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**Figure 1.** Map of the seven scheduled transects at Tambopata Research Center, Peru. May 2004 – April 2005.

species and their habitats (Vaughan et al. 2006). Hence, knowledge of the foraging resources used is vital for understanding the drivers behind seasonal variations in food supply and many aspects of psittacine natural history.

With this study, we want to complement the lists of plants on which wild parrots feed in southeastern Peru, in addition to learning more about the foraging ecology of these birds.

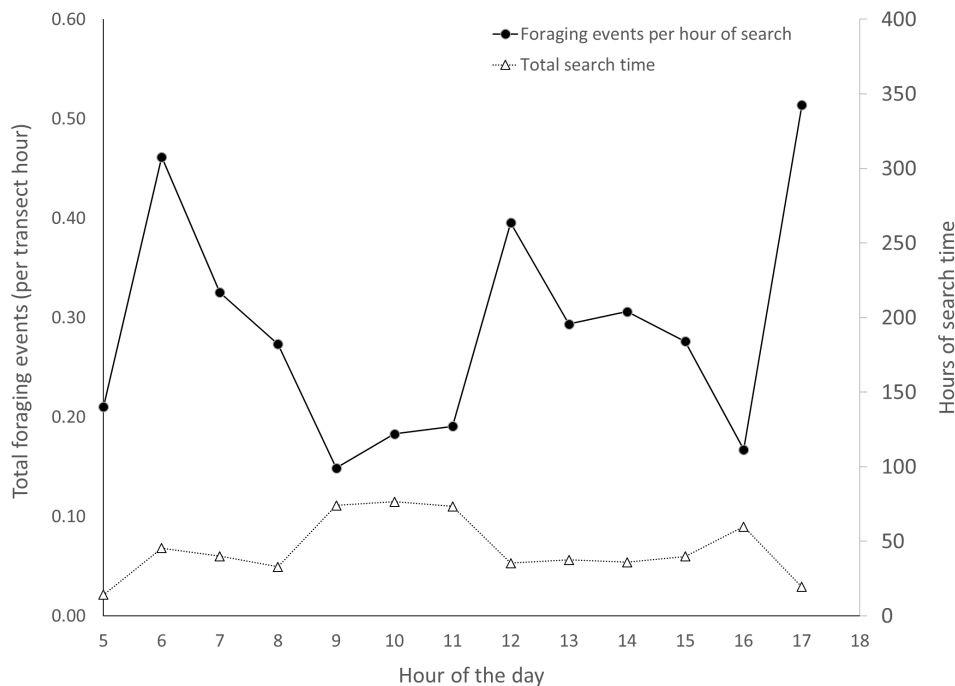
## METHODS

**Study site.** The study was conducted in the trail system surrounding the Tambopata Research Center (TRC, 13°07'36"S, 69°36'54"W). TRC is located in the Tambopata National Reserve (274,690 ha), near the border of the Bahuaja Sonene National Park (1,091.416 ha), in the Madre de Dios department in southeastern Peru. The elevation is 250 m a.s.l., with an annual precipitation of 3,200 mm (Brightsmith 2004). The rainy season spans from October to March and the dry season from April to September (Brightsmith et al. 2018).

The study area was characterized by the presence of palm swamps (*Mauritia flexuosa*), floodplain forest, successional forests, and *terra-firme* forests (Phillips et al. 2003). Griscom et al. (2007) also identified bamboo patches of *Guadua* spp. This diversity of habitats offers a great assortment of potential food items for psittacines. The site contains a riverbank clay lick used as a supplemental sodium source (Brightsmith et al. 2018) by 17 species of psittacines: *Ara macao*, *Ara chloropterus*, *Ara ararauna*, *Primolius couloni*, *Ara severus*, *Orthopsittaca manilatus*, *Amazona farinosa*, *Amazona ochrocephala*, *Pionus menstruus*, *Pionites leucogaster*, *Pyrilia barrabandi*, *Psittacara leucophthalmus*, *Aratinga weddellii*, *Brotogeris cyanopectera*, *Forpus modestus*, *Nanopsittaca dachilleae*, and *Brotogeris sanctithomae* (Brightsmith 2004). Two other psittacine species, *Pyrrhura rupicola* and *Touit huetii* have been reported for the study

site, but have not been seen using the clay lick (Brightsmith 2005), totaling 19 species of psittacines in the area.

**Data collection.** Our research project was conducted between May 2004 and April 2005. We collected data in three different ways: scheduled transects (Figure 1), extra random transects, and fortuitous foraging events. The scheduled transects were established to provide a minimum of data with the same characteristics, while the extra transects covered the same scheduled transects, but at random time slots and mixing different transects or part of them. The extra transects were established to increase the data collection according to the time availability of the researchers. For scheduled transects, we followed seven different fixed transects passing through palm swamps, floodplain forest, successional forests, *terra-firme* forests, and some bamboo patches. Each scheduled transect was, in average, 1.457 km in length (SD = 0.62 km) and 0.1 km wide (0.05 km to the sides). The total area covered by the seven scheduled transects was 1.02 km<sup>2</sup> (10.2 km of transects long and 0.1 km of transects wide). We walked one scheduled transect almost every day, covering all seven scheduled transects approximately each week, and we had different times of daylight hours to start them (05:30–07:14, 07:15–08:59, 09:00–10:44, 10:45–12:29, 12:30–14:14, 14:15–15:59, and 16:00–17:44 h). The time slot for each scheduled transect changed weekly, completing all the time slots for each scheduled transect every seven weeks. Some scheduled transects were not completed due to weather or other logistical issues. Scheduled transects took on average 59 minutes to complete (SD = 14 min, N = 320 transects). The extra transects were about 1.7 km in length (SD = 1.04 km) and 0.1 km wide (0.05 km to the sides), and were visited about five times a week. The average time to complete the extra transects was 65 minutes (SD = 32 min, N = 269 transects). Finally, any fortuitous observation of a feeding psittacine was recorded.



**Figure 2.** Daily variation in psittacine foraging activity at Tambopata Research Center, Peru. May 2004 – April 2005. Foraging events differed by hour of the day ( $P = 0.018$ ).

Fortuitous observations occurred while in route to different locations around TRC to conduct other research activities, usually between 05:00 h and 18:30 h.

To locate foraging psittacines, we walked slowly along the transects (approximately 26 m/min) while listening for vocalizations of macaws, parrots and parakeets, and for objects falling from trees. When we found foraging psittacines, we used 10 x 42 binoculars to conduct observations. For each foraging event we recorded the psittacine species, number of individuals for each species, plant species, consumed part (flower, seed, aril of the seed, leaf, pulp, bark, fruit juice, or whole fruit), ripeness stage of the fruit (ripe or unripe), date, time, and location. We also collected samples of fruit and leaves to facilitate identification. Photos of samples and dried samples were compared to the reference collection of the Herbarium of the Faculty of Forestry at the Universidad Nacional Agraria La Molina in Lima, Peru, to confirm identification.

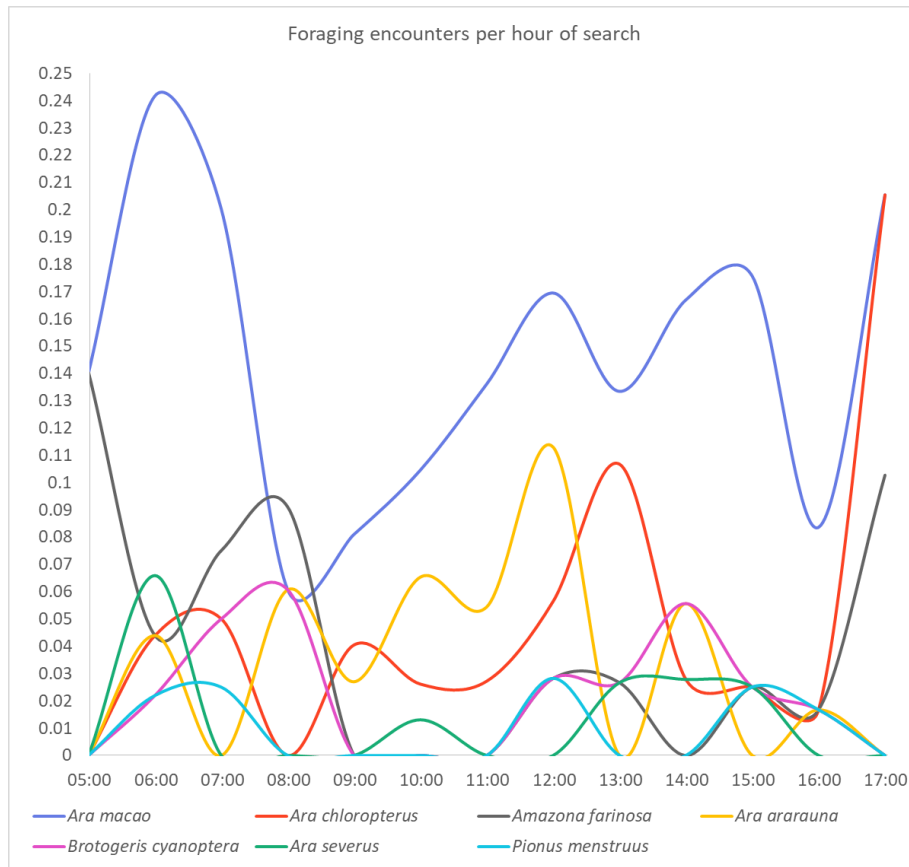
Data was treated in different ways. For “Daily variation in foraging events” and the “Ripeness stage,” only a single event was considered, even if two or more species of psittacines were found feeding on the same plant species. For “Plant species per psittacine species,” “Plant parts consumed,” and “Proportions of all plant parts consumed by psittacine species” we separated the foraging events per species (i.e., if more than two species were feeding on the same plant species at the same time, we recorded one event for each species). To distinguish one from the other, the former will be hereafter referred to as “events” and the latter as “encounters”. We defined a foraging encounter as an event per psittacine species. Finally, when a species was found feeding on two or more plant species at the same time, the foraging events were recorded separately as if they were independent events.

**Data analysis.** To determine daily foraging variation, we tal-

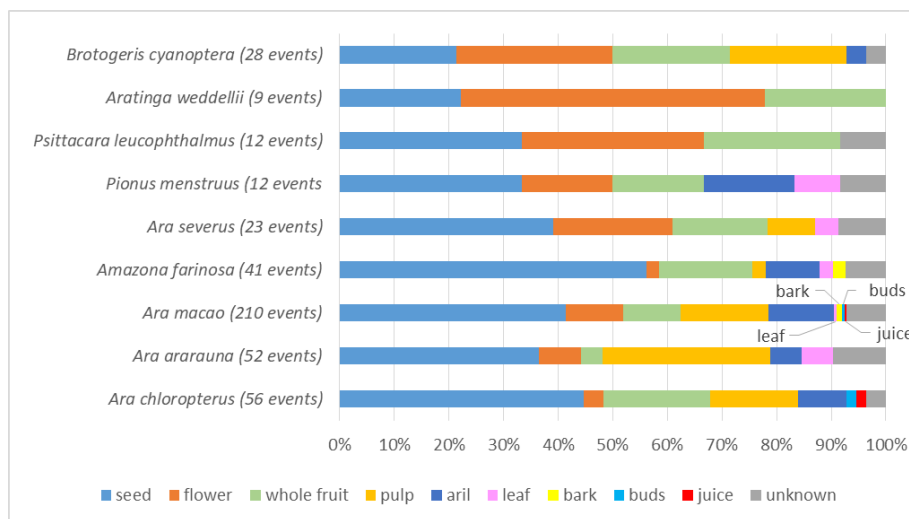
lied the total number of foraging events detected during transects during each hour of the day (e.g., all events detected between 06:00 and 06:59 h, all detected between 07:00 and 07:59 h, etc., across all transects). We then used the effort (i.e., the total time we conducted transects during each hour of the day) to calculate the expected number of foraging events for each hour of the day. We then compared the observed number of foraging events to the expected number using a chi-squared goodness of fit test. To determine if consumption of fruit ripeness stages differed between seasons, we compiled data for all foraging observations (from scheduled transects, extra transects, and fortuitous events) for which plant ripeness was known, and used a contingency table with a Pearson chi-square test to compare data from the wet and dry seasons. A similar chi-square test was conducted to determine if consumption of different plant parts varied between the wet and dry seasons. All statistical analyses were conducted using JMP Pro v. 15.2.1. (SAS Institute 2019). We compared whether diet composition varied with psittacine body masses. Body mass data used in the analysis was obtained from Dunning (2007).

## RESULTS

We recorded 15 psittacine species (*A. macao*, *A. chloropterus*, *A. ararauna*, *P. couloni*, *A. severus*, *O. manilatus*, *A. farinosa*, *A. ochrocephala*, *P. menstruus*, *P. leucogaster*, *P. barribandi*, *P. leucophthalmus*, *A. weddellii*, *B. cyanoptera*, *P. rupicola*) in 416 foraging events, of which 152 were during 589 scheduled transects and extra transects. 264 additional events were fortuitous encounters. The 589 scheduled and extra transects corresponded to 613 hours and 938 km. We identified 84 plant species from 62 genera in 30 families that were consumed by at least one psittacine species. Of the 416 foraging events, 375 involved only a single psittacine species, 29 events had two species involved, and 12 events had three



**Figure 3.** Daily variation in foraging encounters of seven psittacine species at Tambopata Research Center, Peru. May 2004 – April 2005. Hours of search time is the number of hours invested in each one-hour time lapse of the day. Foraging encounters per hour of search are the number of events per psittacine species in each one-hour time lapse of the day divided by the number of hours of transects walked during that hour.



**Figure 4.** Proportions of plant parts consumed by psittacine species at Tambopata Research Center, May 2004 - April 2005. Species are arranged by size order, smallest first. Numbers in parentheses show the total number of foraging encounters.

species involved, for a total of 469 foraging encounters.

**Plant species per psittacine species.** Of the 84 plant species found (Table 1), just 10 of them accounted for 50% of the foraging events for all the psittacine species combined. These species were: *Sapium marmieri* (8.27%), *Otoba parvifolia* (7.49%), *Mauritia flexuosa* (6.72%), *Erythrina poeppigiana* (6.46%), *Couratari macrosperma* (5.17%), *Caryocar amygdaliforme* (4.13%), *Apuleia leiocarpa* (3.88%), *Socratea exorrhiza* (3.10%), *Byrsonima putumayensis* (2.58%), and *Ochroma pyramidale* (2.33%). 22 plant species were consumed by three or more psittacine species, 18 plant species were eaten

by two psittacine species and 44 plant species by one psittacine species.

*A. macao* consumed the most plant species (48 species), followed by *A. chloropterus* (25 species), *A. ararauna* and *A. farinosa* (21 species each), *B. cyanoptera* (16 species), *A. severus* (10 species), *P. menstruus* (9 species), *A. weddellii* (6 species), *P. leucogaster* and *P. leucophthalmus* (4 species each), *P. couloni*, *A. ochrocephala* and *P. barrabandi* (2 species each), and *P. rupicola* and *O. manilatus* (1 species each).

**Daily variation in foraging events.** Foraging activity varied significantly with time of day ( $\chi^2 = 24.3$ ,  $df = 12$ ,  $P = 0.018$ ).

**Table 1.** Plant families and plant species consumed by 15 psittacine species in the Tambopata region of southeastern Peru.

Family/Species	<i>Amazona farinosa</i>	<i>Amazona ochrocephala</i>	<i>Ara ararauna</i>	<i>Ara chloropterus</i>	<i>Ara macao</i>	<i>Ara severus</i>	<i>Aratinga weddellii</i>	<i>Brotheria cyanoptera</i>	<i>Orthopsittaca manilatus</i>	<i>Pionites leucogaster</i>	<i>Pionus Menstruus</i>	<i>Primolius couloni</i>	<i>Psittacara leucophthalmus</i>	<i>Pyrrhura barrabandi</i>	<i>Pyrrhura rupicola</i>
Anacardiaceae															
<i>Spondias mombin</i>					X										
<i>Spondias venulosa</i>					X										
Annonaceae															
<i>Oxandra cf. xylopioides</i>				X											
Apocynaceae															
<i>Himantanthus sucuba</i>	X				X										
<i>Tabernaemontana heterophylla</i>	X			X						X					
Arecaceae															
<i>Euterpe precatoria</i>				X	X										
<i>Iriartea deltoidea</i>			X	X				X							
<i>Mauritia flexuosa</i>			X	X	X				X						
<i>Socratea exorrhiza</i>			X		X		X								
Bignoniaceae															
<i>Tanaecium pyramidatum</i>				X											
Boraginaceae															
<i>Cordia lomato-loba</i>	X						X	X							X
Burseraceae															
<i>Protium cf. amazonicum</i>	X				X										
Caryocaraceae															
<i>Caryocar amygdaliforme</i>				X	X										
Cecropiaceae															
<i>Cecropia sciadophylla</i>			X		X		X								
<i>Pourouma guianensis</i>					X										
Clusiaceae															
<i>Symphonia globulifera</i>					X			X							
Combretaceae															
<i>Terminalia amazonia</i>	X										X				
Cucurbitaceae															
<i>Gurania eriantha</i>													X		
Elaeocarpaceae															
<i>Sloanea fragans</i>					X										
Euphorbiaceae															
<i>Croton glandulosum</i>			X	X	X			X							
<i>Hevea guianensis</i>			X												
<i>Hura crepitans</i>				X											
<i>Manihot condensata</i>					X										
<i>Manihot esculenta</i>				X											
<i>Pausandra trianae</i>					X										
<i>Sapium glandulosum</i>	X				X										
<i>Sapium marmieri</i>	X		X		X	X					X	X			
Fabaceae															
<i>Acacia sp.</i>					X										
<i>Apuleia leiocarpa</i>	X		X	X	X	X					X	X			
<i>Dipteryx micrantha</i>			X	X	X										
<i>Erythrina poeppigiana</i>			X	X	X	X	X	X					X		
<i>Erythrina ulei</i>					X										
<i>Hymenaea oblongifolia</i>	X		X	X	X										
<i>Hymenaea parvifolia</i>	X														
<i>Inga acreana</i>	X			X	X						X				
<i>Inga cf. ruiziana</i>				X	X										
<i>Inga edulis</i>											X				
<i>Inga marginata</i>			X	X	X										
<i>Inga sp.(11)</i>					X										
<i>Inga sp.(12)</i>			X												
<i>Mucuna sloanei</i>			X												
<i>Schizolobium parahyba</i>			X												
<i>Swartzia sp.</i>					X										

Daily foraging showed a peak from 06:00 h to 07:00 h, then declined to a mid-morning low (09:00 h to noon). Foraging in the afternoon was variable, with a peak around mid-day, moderate levels in mid-afternoon (13:00 h to 15:00 h), and a drop at 16:00 h followed by a peak at 17:00 h. Reduced sampling effort may have complicated the results for the 05:00 h and 17:00 h times (Figure 2). The peak at 17:00 h was due to *A. macao*, *A. chloropterus* and *A. farinosa*, whereas activity decreased for all the other species (Figure 3).

**Plant parts consumed.** Seeds were the plant part most frequently consumed (41% of 469 foraging encounters from all data sources combined), followed by pulp (15%), whole fruits (13%), flowers (12%), and arils (10%). Lesser amounts of leaves (1.5%), bark (0.6%), floral buds (0.4%), and fruit juice (0.4%) were also consumed (Table 2). Consumption of plant parts varied between the wet and dry season (Pearson Chi-Square Test:  $\chi^2 = 70.6$ ,  $df = 5$ ,  $P < 0.0001$ , Table 2). The most noteworthy differences were the greater consumption of

**Table 1 (continued).** Plant families and plant species consumed by 15 psittacine species in the Tambopata region of southeastern Peru.

Family/Species	<i>Amazona farinosa</i>	<i>Amazona ochrocephala</i>	<i>Ara ararauna</i>	<i>Ara chloropterus</i>	<i>Ara macao</i>	<i>Ara severus</i>	<i>Aratinga weddellii</i>	<i>Brotogeris cyanoptera</i>	<i>Orthopsittaca manilatus</i>	<i>Pionites leucogaster</i>	<i>Pionus menstruus</i>	<i>Prionolus couloni</i>	<i>Psittacara leucophthalmus</i>	<i>Pyrrhura barrabandi</i>	<i>Pyrrhura rupicola</i>
Lecythidaceae															
<i>Cariniana decandra</i>			X												
<i>Couratari macrosperma</i>	X		X	X	X										
<i>Eschweilera coriacea</i>				X	X										
Loranthaceae															
<i>Psittacanthus cucullaris</i>											X				
Malpighiaceae															
<i>Byrsonima crista</i>				X											
<i>Byrsonima putumayensis</i>			X	X	X										
Malvaceae															
<i>Apeiba membranacea</i>			X		X										
<i>Ceiba insignis</i>					X		X	X			X				
<i>Clusia cf. minor</i>										X					
<i>Clusia sp.</i>															
<i>Guazuma ulmifolia</i>											X				
<i>Huberodendrum swietenoides</i>					X										
<i>Ochroma pyramidale</i>		X	X		X			X							
Meliaceae															
<i>Cabralea canjerana</i>										X				X	
<i>Guarea macrophylla</i>								X							
<i>Guarea sp.(4)</i>					X										
Moraceae															
<i>Brosimum utile</i>	X				X										
<i>Ficus coerulescens</i>						X		X							
<i>Ficus guianensis</i>	X							X							
<i>Ficus maxima</i>	X				X										
<i>Ficus sp.(11)</i>								X							
<i>Ficus sp.(5)</i>				X		X		X							
<i>Ficus sp.(8)</i>						X									
<i>Ficus sp.(9)</i>								X							
<i>Ficus trigona</i>								X							
<i>Pseudolmedia laevis</i>	X				X										
Myristicaceae															
<i>Otoba parvifolia</i>	X		X	X	X			X		X					
<i>Virola elongata</i>				X											
Petiveriaceae															
<i>Gallesia integrifolia</i>	X														
Polygonaceae															
<i>Coccoloba peruviana</i>					X										
Quiinaceae															
<i>Quiina amazonica</i>	X														
Rubiaceae															
<i>Randia armata</i>					X										
Rutaceae															
<i>Zanthoxylum tambopatense</i>					X								X		
Sabiaceae															
<i>Meliosma herbertii</i>					X										
Salicaceae															
<i>Salix humboldtiana</i>		X				X					X				
Sapotaceae															
<i>Micrhopolis guyanensis</i>					X										
<i>Pouteria cuspidata</i>					X										
<i>Pouteria guianensis</i>	X														
<i>Pouteria sp.(4)</i>					X										
Unknown															
sp.x8				X	X	X	X	X					X	X	

pulp and arils during the wet season and the greater consumption of flowers during the dry season, even though seeds were the most consumed part during both seasons (Table 2).

*A. macao* was found foraging most often (45% of 469 encounters) and fed on the greatest variety of plant parts: flowers, pulp, seeds, whole fruits, arils, bark, floral buds, fruit juice, and leaves (Figure 4). Our data suggest that the largest psittacines (250 g to 1214 g) consumed mostly seeds of *S. marmieri*, *C. macrosperma*, *B. putumayensis*, *Dipteryx micrantha*, and *Euterpe precatória*. These species were *A. chlo-*

*ropterus* (1214 g body weight; 45% of seed consumption of 56 foraging encounters), *A. ararauna* (1125 g; 37% of 52 encounters), *A. macao* (1015 g; 41% of 210 encounters), *A. farinosa* (626 g; 56% of 41 encounters), *A. severus* (343 g; 39% of 23 encounters), and *P. menstruus* (251 g; 33% of 12 encounters). In contrast, the smaller parakeets consumed greater proportions of flowers such as *E. poeppigiana*, *O. pyramidale*, *Ceiba insignis*, and *Symphonia globulifera*. These smaller parakeets were *A. weddellii* (108 g; 56% of flower consumption of 9 foraging encounters) and *B. cyanoptera* (56 g; 29% of 28 encounters). Leaf consumption was observed only

**Table 2.** Consumption of plant parts by psittacines in the Tambopata region of southeastern Peru. Plant part consumption differed between wet and dry seasons ( $P < 0.0001$ ).<sup>a</sup> Pulp and aril were combined for the statistical analyses.<sup>b</sup> Leaves, bark, flower buds, and juice were combined for the statistical analyses.

Plant part	Combined	Wet season	Dry season
Seeds	39.1%	43.4%	34.5%
Pulp <sup>a</sup>	15.5%	18.9%	12%
Whole fruit	13.3%	9%	18%
Flowers	11.6%	2.3%	21.5%
Aril <sup>a</sup>	10%	18.9%	0.5%
Leaves <sup>b</sup>	1.5%	0.5%	2.5%
Bark <sup>b</sup>	0.7%	0.5%	1%
Flower buds <sup>b</sup>	0.5%	0.9%	0%
Juice <sup>b</sup>	0.5%	0.9%	0%
Unknown	7.3%	4.7%	10%

in the largest species: *A. ararauna* (6% of leaf consumption of 52 foraging encounters), *A. macao* (0.5% of 210 encounters), *A. severus* (4% of 23 encounters), *A. farinosa* (2% of 41 encounters), and *P. menstruus* (8% of 12 encounters). Two species were observed feeding on bark: *A. farinosa* (2% of 41 encounters) and *A. macao* (1% of 210 encounters). *A. macao* and *A. chloropterus* were also observed consuming juice from the fruits of *O. parvifolia* (0.5% of 210 encounters and 2% of 56 encounters, respectively). Individuals were observed holding the fruit with their beaks, throwing their heads back and using their tongues to guide the liquid into their mouths.

**Ripeness stage.** Of the 416 foraging events recorded, seeds were eaten ripe and unripe in approximately equal proportions (48% ripe, 47% unripe of 161 events with seeds). Whole fruits were eaten mostly ripe (67% of 55 events with whole fruits). The pulp was also eaten mostly ripe (81% of 64 events with pulp), as well as the aril (71% of 41 events with aril). Consumption of ripe versus unripe plant parts did not differ between wet and dry seasons (Pearson Chi-Square Test:  $\chi^2 = 0.15$ ,  $df = 1$ ,  $P = 0.7$ ).

## DISCUSSION

Of the 84 plant species recorded in our study, 51 were reported for the first time as psittacine food resources in southeastern Peru. Of these, we documented 30 new food plants species for *A. macao*, 13 new species for *A. farinosa*, 16 new species for *A. chloropterus*, 4 new species for *P. leucogaster*, 10 new species for *A. ararauna*, 1 new species for *P. rupicola*, 9 new species for *B. cyanoptera*, 7 new species for *P. menstruus*, 7 new species for *A. severus*, 5 new species for *A. weddellii*, 2 new species for *P. leucophthalmus*, 2 new species for *A. ochrocephala*, 2 new species for *P. barrabandi*, no new species for *O. manilatus*, and 2 new species for *P. couloni* (Supplementary Table 1). Adding to the findings in Lee et al. (2014) in Tambopata, Gilardi (1996) in Tambopata and Manu, and Munn (1988) in Manu, there are a total of 343 species of plants eaten by psittacines in southeastern Peru.

We observed the greatest foraging activity at around 06:00 h and in the late afternoon at around 17:00 h. Activities that require elevated metabolic rates are usually undertaken when temperatures are relatively mild, so early morning hours provide a relatively cool opportunity for foraging activities (Gilardi 1996). Similar observations were reported by Botero-Delgado et al. (2010) in *Pyrrhura viridicata*, an endemic endangered parakeet from Colombia, with foraging activity peaking between 06:00 h to 08:00 h. Renton and

Salinas Melgoza (2002) also found that the main foraging activity of *Amazona finschi*, an endangered endemic psittacine from Mexico, occurs in the first two or three morning hours, and two hours before going to sleep.

Our study documented several species of psittacines consuming seeds, pulp, flowers, whole fruits, aril, bark, floral buds, fruit juice, and leaves, as shown in previous studies (Roth 1984, Munn 1988, Desenne 1994, Nycander et al. 1995, Gilardi 1996, Ragusa-Netto & Fecchio 2006, Renton 2006, Vaughan et al. 2006, Matuzak et al. 2008, Tubelis 2009, Gilardi & Toft 2012, Peron & Grosset 2013, Lee et al. 2014, Renton et al. 2015, Benavidez et al. 2021). Seeds were the most common item eaten by psittacines, supporting the results by Matuzak et al. (2008) and Lee et al. (2014). Although our study did not focus on other prey items, it is known that psittacines can also feed on adult insects like termites (Lee et al. 2014), larvae (Roth 1984, Brightsmith et al. 2010, Díaz 2012), clay (Abrahams & Parsons 1996, Gilardi et al. 1999, Brightsmith & Aramburú Muñoz-Najar 2004, Mee et al. 2005, Brightsmith et al. 2008, Powell et al. 2009, Lee et al. 2010, Dudley et al. 2011, Lee et al. 2014), seaweeds, and water snails (Roth 1984).

Our results suggest that flowers are eaten more often during the dry season than the rainy season. This agrees with studies by Galetti (1993) and Ragusa-Netto & Fecchio (2006), although we should note that when unable to identify if birds were consuming the whole flower or just the nectar, we would record the event just as flower consumption. The larger psittacines consumed mostly seeds (Figure 4), as in the study by Matuzak et al. (2008) and Gilardi (1996), presumably due to greater energy content. Roth (1984) stated that the type of fruit eaten depends on the size of the bird and the robustness and structure of the beak, and that not always the same part of the same fruit is eaten by different species of psittacines. Instead, smaller psittacines consumed mostly flowers, aril, pulp, and whole fruits (Figure 4). Since flowers are a lesser energy food resource, requiring a large energy investment to harvest, smaller-bodied psittacines may have an advantage when exploiting these resources (Brightsmith 2005). This use of less energy resources may allow these species to breed earlier in the dry season than larger psittacines (Brightsmith 2005). In contrast, species with greater body mass may incur food shortages in the dry season, explaining the wet season breeding of larger psittacines found in Tambopata (Brightsmith 2005), when fruits are abundant (Lee et al. 2014).

We found that seeds were consumed ripe and unripe in similar proportions during the dry and rainy season, whereas other parts of the fruit (fruit juice, pulp, aril, and whole fruit) were consumed mostly ripe, with more than 75% during



both seasons. From an energetic point of view, seeds represent the richest part of the plant, with greater contents of protein and lipids, and less fiber than fruit pulp from the same species of plants (Gilardi & Toft 2012). Psittacines forage on seeds, regardless of their state of ripeness (Munn 1988). By comparison, other parts of the fruit increase greatly in sugar contents when ripe. For vertebrate-dispersed species, mature fruits are expected to be less toxic than immature fruits, and toxicity is expected to decrease more for the pericarp than for the seed from the immature to the mature stage (Beckman 2013). For most groups of birds, the food with greater concentration of toxins is regarded as the less preferred food type (Molokwu et al. 2011). Contrary to what might be expected, psittacines consume seeds that are very toxic to humans and other vertebrates, with a great ability to break and digest them (Gilardi 1996, Gilardi & Toft 2012). Many studies suggest psittacines are mostly seed predators rather than seed dispersers (Kricher 1997). Other studies report that psittacines may play an important role in the availability of fruit and seed production of some tree species (Galetti 1993). Conversely, more recent studies suggest psittacines may act as long-distance seed dispersers (Tella et al. 2015, Blanco et al. 2016), in part because they waste a lot of food while foraging (Blanco et al. 2016). Desenne (1994) argued psittacines may disperse very small seeds or larger seeds when consuming ripe fruits.

Our study illustrates the great diversity of psittacine diets in southeastern Peru. This information should be considered when caring for captive individuals and when developing plans for selective logging, agroforestry, and forest restoration near these birds' natural range areas. These plans should reflect spatial patterns of development and ecological vulnerability, and support the recuperation of fallow lands and secondary forest (Alvarez & Naughton-Treves 2003). While deforestation rates decline globally, they are rising in the western Amazon (Caballero Espejo et al. 2018). Peru is the country with the ninth largest forest area in the world, with 72 million hectares, and it occupies the seventh place among the countries with the greatest number of tree species with more than 4,000 (FAO & UNEP 2020). Roughly 2,848 km<sup>2</sup> of Peru's forests are cut down every year, around 80% of them illegally (Smith & Schwartz 2015). Alvarez and Naughton-Treves (2003) found that the highest rate of clearing in Tambopata was observed along roads during 1986–1991. Not so far from our study site, in 2011, a transoceanic highway that begins in Brazil and crosses Peru to the Pacific Ocean was built. This has led to a human population expansion towards the Amazon and has given access to forests that could not be previously accessed, increasing agriculture, mining and selective logging (Smith & Schwartz 2015). Without proper planning, forests will continue to be damaged, affecting keystone psittacine species that are vital for community stability and diversity (Brightsmith 2005, Diaz-Martin et al. 2014).

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