

FORAGING ECOLOGY OF PARROTS IN A MODIFIED LANDSCAPE: SEASONAL TRENDS AND INTRODUCED SPECIES

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ABSTRACT.—We studied the diet and foraging ecology of a community of six psittacines in western Costa Rica. All had a varied diet with clear seasonal changes in preferred food items, mostly due to changes in plant phenology. There was a significant relationship between parrot mass and food types: larger-bodied parrots consumed more seeds and smaller-bodied parakeets consumed more fruit pulp. Leaves, bark, and lichen were also consumed by most psittacines. Most parrots consumed more plant species in the dry season when food availability was at its peak. Levins' niche breadth showed varying levels of diet specialization among species and, for some species, variation among seasons. There was less similarity in seasonal psittacine diets when compared to overall diets. Scarlet Macaws (*Ara macao*) under study were captive raised and released which may have contributed to their narrow diet breadth as they may have lacked the knowledge or experience to exploit additional food sources. Non-native and cultivated species comprised 76% of the diet of Scarlet Macaws, and averaged 28% for all other species. This suggests that foraging parrots may have increased conflicts with humans as landscapes become increasingly modified. Forest restoration strategies should augment the abundance of food species consumed when overall food supply is at its annual low. Received 20 February 2007. Accepted 4 September 2007.

Knowledge about diets is fundamental for understanding species' niches, roles in communities, and potential impacts on other species (Moegenburg and Levey 2003, French and Smith 2005, Munshi-South and Wilkinson 2006). Knowledge of diet is also needed to design effective conservation and management strategies, and to predict how landscape level changes may affect species (Pitter and Christiansen 1995, Bennett and Owens 1997). Approximately one third of all psittacines are threatened with extinction and with anthropogenic changes, many species have become locally or regionally extinct (Collar 1997). However, in some cases parrot species increase in abundance with landscape conversion and become agricultural pests (Forshaw 1989, Bucher 1992). Overall, the natural history of psittacines is poorly known with little or no information on the diet of over 75% of the recognized species (Collar 1998). This lack of basic diet information poses problems for those who work to understand and con-

serve threatened parrots, mitigate agriculture damage, and understand the impacts of parrots on vegetative communities (Collar 1998, Moegenburg and Levey 2003).

Parrots feed predominantly on seeds, fruit pulp, and flowers along with variable amounts of leaves, bark, nectar, and insects (Forshaw 1989, Sazima 1989, Pizo et al. 1995). Parrots eat ripe and unripe fruits, and many species consume large amounts of immature and mature seeds, making some psittacines effective pre-dispersal seed predators (Desenne 1994, Pizo et al. 1995). Pollination and seed dispersal have rarely been recorded for parrots (Fleming et al. 1985, Cotton 2001) with most parrot feeding leading to some reduction in plant fitness (Galetti 1993, Ragus-Netto 2005). Identifying and conserving key food resources and their habitats may be vital to the long term conservation of some parrot communities.

We conducted a 2-year study on the foraging ecology and diet of a community of six sympatric parrot species in western Costa Rica. Our objectives were to document: (1) the plant species and plant parts consumed by each parrot species, (2) the level of seed predation and frugivory for each species, (3) seasonal diet changes, and (4) key resources used by each psittacine species. We also discuss the importance of introduced and cultivated plant

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species to foraging parrots in view of the changing landscape throughout the Neotropics.

METHODS

Study Area.—This study was conducted on the southern Nicoya Peninsula in the Province of Puntarenas, western Costa Rica. The primary research site was Curú Wildlife Refuge (09° 47' N, 84° 56' W). Curú is a private wildlife refuge and working farm of 1,492 ha with 70% forested habitats, and 30% pastures and plantations (Schutt and Vaughan 1995). Curú is part of the Peninsular Biological Corridor, a loosely connected network of small forested fragments on the southern Nicoya Peninsula (Vaughan et al. 1994). We collected additional data on Tortugas and Negritos islands, ~2 and 5 km, respectively, from Curú in the Nicoya Gulf.

Rainfall totals ~200 cm per annum and is strongly seasonal with a wet season from May to November, and a dry season from December to April (months with <10 cm of precipitation). The average temperature throughout the year is 27.3° C (Vaughan et al. 1994). The site is at the boundary of tropical dry forest, tropical moist forest, and tropical premontane life zones (Tosi 1969), and contains a mosaic of mangroves (*Avicennia*, *Rhizophora*, *Laguncularia*), dry deciduous forest, semi-deciduous forests, mixed coconut (*Cocos*) forest, beaches, evergreen forest, pastures, and plantations of *Tectona grandis* and *Mangifera indica* (Vaughan et al. 1994).

Six psittacine species occur on southern Nicoya Peninsula: Scarlet Macaw (*Ara macao*—900 g), Yellow-naped Amazon (*Amazona auropalliata*—480 g), Red-lored Amazon (*A. autumnalis*—420 g), White-fronted Amazon (*A. albifrons*—230 g), Orange-fronted Parakeet (*Aratinga canicularis*—80 g), and Orange-chinned Parakeet (*Brotogeris jugularis*—65 g) (weights from Stiles and Skutch 1989). Scarlet Macaw is considered an endangered species (Appendix 1 of the Convention on International Trade in Endangered Species [CITES]). The small population of macaws in the project area was established in an area absent of a wild population in 1999 through a reintroduction program. Macaws observed were a group of 9–12 birds that had been released 4 years prior to the onset of our study

(Brightsmith et al. 2005). Yellow-naped Parrot is a threatened species (CITES 2002) and the area contains one of the largest known roosting populations of the species in Costa Rica with a minimum of 300 individuals (Matuzak and Brightsmith 2007).

Parrot Foraging Observations.—We established six transects in areas known to be frequented by parrots to document psittacine diets. Transects averaged 1,000 m in length and were in deciduous and semi-deciduous forests, mixed coconut forest, evergreen (gallery) forest, mixed mangroves, open pastures, and plantations of *T. grandis*, *M. indica*, and mixed citrus (*Citrus* spp.). We established one transect in each habitat type; however, some transects crossed multiple habitat types. Each transect was surveyed a minimum of three times per week. Each habitat and season received the same survey effort throughout the study.

We walked transects in the morning (630–1030 hrs) and early afternoon (1400–1800 hrs) during known parrot foraging peaks (GDM, unpubl. data). Data were collected from August 2003 to July 2005. We also recorded opportunistic observations of parrots foraging at any time of day. The following data were noted whenever parrots were found feeding: date, time, habitat type, species of parrot, number of parrots, species of plant, and plant part consumed. Fruit was considered fruit pulp and not whole fruits. We ascertained whether parrots were consuming fruit pulp, seeds, or both based on evaluating dropped fruits when whole fruits were being consumed. Cultivated tree species include native and non-native trees planted by humans (usually in plantations) for the consumption of fruits and seeds, whereas non-native species refer to any species introduced to Costa Rica from another country and can include ornamentals planted for their flowers. Therefore, some species such as *M. indica* can be native and cultivated for their fruit. The two groups of islands and adjacent areas to Curú were visited sporadically, and foraging observations in these areas were recorded opportunistically. An observation of one or more parrots feeding was recorded as a single feeding bout; however, if a parrot or group of parrots flew to and fed upon another plant of the same or different species, an additional feeding bout was

recorded (Galetti 1993, Wermundsen 1997, Renton 2001).

Statistical Analyses.—The standardized Levins' (1968) niche breadth index was calculated from the number of parrots observed feeding on each plant species consumed. Values close to 0 indicates dietary specialization and a value close to 1 indicates a broad diet (Colwell and Futuyama 1971). We analyzed seasonal changes in diet by comparing the Levins' diet breadth index and number of food plant species consumed between the wet (Jun–Nov) and dry seasons (Dec–May) (Levins 1968; Renton 2001, 2006).

Pearson product-moments and simple linear regression were used to test the relationship between body mass and percent seeds, fruit pulp, flowers, and leaves in the diet using the Data Desk software package (Data Description Inc. 2006). Jaccard similarity coefficients (J), a statistic used to compare the similarity of plant species in the diets between psittacines, were estimated to compare the overall and seasonal diets between the five main parrot species. All data are presented as mean \pm SD. All statistical tests used $\alpha = 0.05$.

RESULTS

Foraging Ecology and Diet.—We recorded 1,159 foraging bouts by six species representing all of the psittacines known from the area: Scarlet Macaw (52%), Yellow-naped Parrot (10%), White-fronted Parrot (9%), Orange-fronted Parakeet (10%), Orange-chinned Parakeet (19%), and Red-lored Parrot (<1%; Tables 1–3). Red-lored Parrots were rare at the site and only observed foraging three times; this species was eliminated from further analysis.

We observed psittacines foraging on 61 plant species from 25 families ($\bar{x} = 31 \pm 2$ plant species and $\bar{x} = 18 \pm 1.3$ plant families per psittacine species, $n = 1,159$ foraging bouts) (Tables 1–3). Twelve plant species were non-native and/or cultivated in Costa Rica (54% of all feeding bouts) (Tables 1–3). The number of feeding bouts per food plant species ranged from 1 to 238 ($\bar{x} = 19 \pm 35$, $n = 1,159$). *Terminalia catappa* (Family: Combretaceae) represented 21% of the foraging bouts. The nine next most common diet species together represented an additional 46% of the total: *Delonix regia*—9% (Family:

Caesalpiniaceae), *Mangifera indica*—6% (Family: Anacardiaceae), *Tectona grandis*—6% (Family: Verbenaceae), *Pithecellobium saman*—5% (Family: Fabaceae), *Cocos nucifera*—5% (Family: Palmae), *Guazuma ulmifolia*—4% (Family: Sterculiaceae), *Elaeis guineensis*—4% (Family: Palmae), *Bombacopsis quinata*—4% (Family: Bombacaceae), and *Spondias mombin*—3% (Family: Anacardiaceae).

Psittacines ate seeds (54%), fruit pulp (24%), flowers (10%), leaves (7%), bark (4%), and lichen (<1%). Excluding Scarlet Macaws, the proportions were fruit pulp (38%), seeds (34%), and flowers (16%). All parrots consumed both ripe and unripe seeds and they fed on both cultivated and non-native species. The parrot community consumed 41 species during the wet season ($n = 572$ foraging bouts, Levins' diet breadth = 0.364) and 50 species during the dry season ($n = 587$ bouts, Levins' diet breadth = 0.205), an 18% increase in the dry season.

Scarlet Macaw.—This species ate 32 food plant species from 15 families ($n = 600$ foraging bouts, Levins' diet breadth = 0.118) (Table 1). *T. catappa* (38%) and *D. regia* (16%) were the most commonly consumed species; both are non-native. The diet was comprised of seeds (73%), fruit pulp (10%), bark (6%), flowers (5%), leaves (5%), and lichen (<1%). Non-native and cultivated plant species represented 76% of macaw foraging bouts. Macaws ate 27 food plant species in the dry season ($n = 262$ foraging bouts, Levins' diet breadth = 0.139) and 18 in the wet season ($n = 338$ foraging bouts, Levins' diet breadth = 0.216), a 33.3% increase in the dry season.

Amazona Parrots.—Yellow-naped Parrots ate 34 food plant species from 21 families ($n = 121$ foraging bouts, Levins' diet breadth = 0.388) (Table 2) and White-fronted Parrots ate 36 food plant species in 21 families ($n = 108$ foraging bouts, Levins' diet breadth = 0.225) (Table 2). The diet of Yellow-naped Parrots was comprised of seeds (61%), fruit pulp (23%), flowers (7%), leaves (7%), bark (<1%), and lichen (<1%) while the diet of White-fronted Parrots was comprised of seeds (37%), fruits (31%), flowers (26%), leaves (5%), and bark (2%). Non-native and cultivated plant species represented 37% of Yel-

TABLE 1. Foraging observations for Scarlet Macaws. Species marked with * are non-native, ** are cultivated, and *** are both non-native and cultivated. Parts eaten are coded as S = seeds, FP = fruit pulp, B = bark, L = leaves, F = flowers, and Li = lichen.

Family/Species	Part eaten	Total # individuals	Feeding bouts	Months
Anacardiaceae				
<i>Anacardium excelsum</i>	S	10	4	Feb–Mar
<i>Spondias mombin</i>	FP,B	66	27	Jul–Sep
<i>Spondias purpurea</i>	FP	2	1	Mar–Apr
<i>Mangifera indica</i> **	FP	10	6	Feb–May
Bignoniaceae				
<i>Tabebuia rosea</i>	F	2	1	Feb–Mar
Bombacaceae				
<i>Ceiba aesculifolia</i>	F,S,B,L	9	5	Feb–Apr
<i>Ceiba pentandra</i>	S,B	4	2	Feb–Apr
<i>Bombacopsis quinata</i>	F,S,B	7	5	Dec–Feb
<i>Ochroma pyramidale</i>	F	12	4	Feb–May
Caesalpiniaceae				
<i>Schizolobium parahybum</i>	S,L,B	9	6	Apr–May
<i>Delonix regia</i> *	F,S,L	206	98	Sep–Dec
<i>Cassia grandis</i>	F,S,B	8	4	Dec
Combretaceae				
<i>Terminalia catappa</i> *	F,S,L	498	230	All year
Lythraceae				
<i>Lagerstroemia speciosa</i> *	S	31	11	Oct–Jan
Meliaceae				
<i>Cedrela odorata</i>	S	2	1	Feb–Mar
<i>Swietenia macrophylla</i>	S	2	1	Jun
Fabaceae				
<i>Pseudosamanea guachapele</i>	F,L,B	23	9	Nov
<i>Lysiloma divaricatum</i>	S	7	3	Jan–Mar
<i>Enterolobium cyclocarpum</i>	B,Li	4	2	Feb–Mar
<i>Inga vera</i>	F,S,L	18	4	Mar–May
<i>Inga</i> sp.	S	5	6	Mar–Apr
<i>Pithecellobium saman</i>	F,S,L,B	56	42	Jan–Mar
Moraceae				
<i>Ficus</i> sp.	F,S,FP	2	1	Oct
Myrtaceae				
<i>Psidium guajava</i> **	F,S,FP,L	19	5	Mar–Apr
Palmae				
<i>Cocos nucifera</i> *	S	92	55	All year
<i>Elaeis guineensis</i> ***	F	30	14	Jul–Sep
Rhizophoraceae				
<i>Rhizophora mangle</i>	B,L	5	4	Sep
Sterculiaceae				
<i>Sterculia apetala</i>	S	2	1	Mar
<i>Guazuma ulmifolia</i>	F	12	7	Dec–Feb
Tiliaceae				
<i>Luehea seemannii</i>	F,S	9	4	Jan–Feb
Verbenaceae				
<i>Tectona grandis</i> ***	S,L	76	31	Sep–Nov
<i>Avicennia germinans</i>	S	6	6	Sep
Total # individuals and bouts		1,244	600	

low-naped Parrot foraging bouts, while non-native and cultivated plant species represented 24.1% of White-fronted Parrot foraging bouts.

Yellow-naped Parrots ate 18 plant species in the wet season ($n = 61$, Levins' diet breadth = 0.373) and 23 in the dry season ($n = 60$, Levins' diet breadth = 0.370), a 21.7% increase in the dry season. White-fronted Parrots ate 22 plant species in the wet season ($n = 44$, Levins' diet breadth = 0.160) and 26 in the dry season ($n = 64$, Levins' diet breadth = 0.417), a 15.4% increase in the dry season.

Parakeets.—Orange-fronted Parakeets ate 24 food plant species in 16 families ($n = 113$ foraging bouts, Levins' diet breadth = 0.551) (Table 3) and Orange-chinned Parakeets ate 30 food plant species in 17 families ($n = 214$ foraging bouts, Levins' diet breadth = 0.244) (Table 3). The diet of Orange-fronted Parakeets was comprised of fruits (47%), seeds (25%), flowers (20%), leaves (6%), and bark (3%) while the diet of Orange-chinned Parakeets was comprised of fruits (47%), seeds (20%), leaves (15%), flowers (14%), and bark (4%). Non-native and cultivated plant species represented 33% of Orange-chinned Parakeets foraging bouts, while non-native and cultivated plant species represented 17% of the foraging bouts of Orange-fronted Parakeets.

Orange-fronted Parakeets ate 14 plant species in the wet season ($n = 39$, Levins' diet breadth = 0.574) and 17 in the dry season ($n = 74$, Levins' diet breadth = 0.580), a 17.6% increase in the dry season. Orange-chinned Parakeets ate 19 plant species in the dry season ($n = 124$, Levins' diet breadth = 0.175) and 23 in the wet season ($n = 90$, Levins' diet breadth = 0.361), a 17.4% decrease in the dry season.

Diet Similarities.—Overall diet overlap was greater (J range 52–71.4) than diet overlap when compared in the dry and wet seasons (J dry range 26.1–57.1, J wet season range 26.3–46.2). The greatest overall similarity in psittacine diets was between Orange-chinned Parakeets and Scarlet Macaws ($J = 71.4$) and Orange-fronted Parakeets ($J = 66.7$), and between both *Amazon* parrots ($J = 65.2$). Seasonally, the greatest similarity in psittacine diets was in the wet season between Orange-chinned Parakeets and White-fronted Parrots ($J = 56$) and Orange-fronted Parakeets ($J = 57.1$), and between White-fronted Parrots and

Orange-fronted Parakeets ($J = 52.4$). In the dry season, the greatest similarity in diets was between Orange-chinned Parakeets and Scarlet Macaws ($J = 46.2$) and White-fronted Parrots ($J = 45$), and between Orange-fronted Parakeets and Scarlet Macaws ($J = 43.5$).

Body Type and Food Type Preference.—There was a significant positive correlation between body mass and percent seeds in the diet ($r = 0.97$, $P = 0.008$), and a significant negative correlation between body mass and percent fruit pulp in the diet ($r = -0.96$, $P = 0.009$, Fig. 1). Body mass did not correlate with either the percent of flowers ($r = -0.71$, $P = 0.179$) or percent of leaf consumption ($r = -0.48$, $P = 0.42$) in the diet of this parrot community.

DISCUSSION

Foraging Ecology and Diet.—The Costa Rican parrot community studied ate predominantly seeds (54% of all foraging observations). This confirms the general characterization of parrots as major seed predators (Desenne 1994, Renton 2001). However, when Scarlet Macaws were excluded, parrots in our study consumed more fruit pulp and flowers than seeds. This was due to the smaller-bodied species consuming more fruit and flowers than seeds, as reported in other parrot communities (Desenne 1994, Pizo et al. 1995).

All parrots in Curú foraged on flowers (5–26% of their diets). This is a larger percentage of flowers than reported by most studies: Renton (2001) found that Lilac-crowned Parrots (*Amazona finschi*) do not consume flowers in Mexico; flowers comprised only 4.1% of the diet of the Pacific Parakeet (*Aratinga strenua*) in Nicaragua (Wermundsen 1997); and flowers were only 2.5% of the diet of Puerto Rican Amazons (*Amazona vittata*) (Snyder et al. 1987). Desenne (1994) and Pizo et al. (1995) documented that flowers comprised 18% of all foraging bouts in two parrot communities, while Galetti (1993) found that flowers comprised 20% of the diet of Scaly-headed Parrots (*Pionus maximiliani*) and Pizo et al. (1995) reported that flowers comprised 25% of the diet of Reddish-bellied Parakeets (*Pyrrhura frontalis*). Flower consumption is important because some psittacines reportedly act as pollinators (Cotton 2001), while many destroy the flowers they eat (Ragusa-Netto 2005;

TABLE 2. Foraging observations for Yellow-naped and White-fronted parrots. Species marked with * are non-native, ** are cultivated, and *** are both non-native and cultivated. Parts eaten are coded as S = seeds, FP = fruit pulp, B = bark, L = leaves, F = flowers, and Li = lichen.

Family/Species	Part eaten	Yellow-naped Parrot		White-fronted Parrot		Months
		# ind.	# bouts	# ind.	# bouts	
Anacardiaceae						
<i>Anacardium excelsum</i>	S	2	1	6	3	Mar–Apr
<i>Spondias mombin</i>	FP	40	6	10	2	Aug–Sep
<i>Mangifera indica</i> **	FPL	15	6	18	8	Mar
<i>Astronium graveolens</i>	S	0	0	2	1	Mar
Annonaceae						
<i>Annona</i> sp.	FP	4	1	0	0	Feb
Bignoniaceae						
<i>Tabebuia rosea</i>	F	4	2	4	2	Feb–Mar
Bombacaceae						
<i>Ceiba pentandra</i>	S,L,B	0	0	4	3	Feb
<i>Bombacopsis quinata</i>	FFPS	33	11	0	0	Feb–Apr
<i>Ochroma pyramidale</i>	F	0	0	2	1	Jan
Boraginaceae						
<i>Cordia alliodora</i>	S,F	2	1	3	2	Feb
Burseraceae						
<i>Bursera simaruba</i>	S	50	8	9	4	Feb–Mar
Caesalpiniaceae						
<i>Schizolobium parahybum</i>	FL	9	4	5	2	Apr–May
<i>Senna reticulata</i>	S	0	0	5	1	Feb
<i>Tamarindus indica</i>	S	0	0	2	1	Feb
Chrysobalanaceae						
<i>Licania platypus</i>	L	2	1	0	0	Jan
Combretaceae						
<i>Terminalia catappa</i> *	S	8	1	17	4	Feb–Mar
<i>Terminalia oblonga</i>	S	2	1	3	1	Feb
<i>Combretum</i> sp.	F	3	2	0	0	Feb
Elaeocarpaceae						
<i>Muntingia calabura</i>	S,FP	12	1	0	0	Jan
Euphorbiaceae						
<i>Sapium glandulosum</i>	S,FP	9	3	10	1	Sep–Oct
Leguminosae						
<i>Erythrina poeppigiana</i>	F	4	2	35	9	Dec–Jan
<i>Erythrina costaricensis</i>	F	5	1	2	1	Jan–Feb
Lorantaceae						
<i>Psittacanthus</i> sp.	S,F	0	0	10	3	Oct–Dec
Meliaceae						
<i>Cedrela odorata</i>	S,FP	29	5	2	1	Feb–Mar
Fabaceae						
<i>Lysiloma divaricatum</i>	S	4	2	4	2	Mar–Apr
<i>Enterolobium cyclocarpum</i>	S,L,B,Li	19	7	5	2	Feb–Apr
<i>Inga</i> sp.	S,F,B	0	0	10	4	Jul
<i>Pithecellobium saman</i>	S,FL	0	0	7	3	Mar
<i>Leucaena leucocephala</i>	S	21	7	5	2	Jun–Sep

TABLE 2. Continued.

Family/Species	Part eaten	Yellow-naped Parrot		White-fronted Parrot		Months
		# ind.	# bouts	# ind.	# bouts	
Moraceae						
<i>Brosimum alicastrum</i>	S,FP	0	0	45	1	Oct
<i>Ficus insipida</i>	S,FP	12	2	19	2	Oct
Myrtaceae						
<i>Psidium guajava</i> **	S,FP	3	1	0	0	Apr
Palmae						
<i>Scheelea rostrata</i>	FP	4	2	0	0	Jun, Sep
<i>Elaeis guineensis</i> ***	FP	0	0	145	8	May–Jun
Rhizophoraceae						
<i>Rhizophora mangle</i>	F	0	0	4	1	Jan
Rubiaceae						
<i>Calycophyllum candidissimum</i>	S	6	1	0	0	Feb
Rutaceae						
<i>Citrus aurantifolia</i> ***	S	10	2	0	0	Oct–Nov
<i>Citrus limeta</i> ***	S	6	2	0	0	Nov
<i>Citrus aurantium</i> ***	S	49	17	17	2	Oct–Dec
<i>Citrus paradise</i> ***	S	2	1	0	0	Nov
<i>Zanthoxylum</i> sp.	S,FP	8	1	2	1	Sep
Sterculiaceae						
<i>Sterculia apetala</i>	S	0	0	2	1	Feb–Mar
<i>Guazuma ulmifolia</i>	S,FP	1	1	23	9	Nov–Jan
Tiliaceae						
<i>Luehea seemannii</i>	S,F	4	1	33	11	Dec–Jan
Verbenaceae						
<i>Tectona grandis</i> ***	S	67	16	15	4	Aug–Nov
<i>Avicennia germinans</i>	S,L	4	1	11	4	Apr–Sep
Unknown Vine sp.	S	0	0	5	1	Feb
Total # individuals and bouts		453	121	501	108	

GDM, unpubl. data). Given that parrots and other flower eaters can destroy the entire flower crop of individual trees (Galetti 1993, Ragusa-Netto 2005), it is important for researchers to be aware of the possible ecological impacts of lowering fitness of these plant species in heavily modified landscapes where tree abundances of some species may have been drastically lowered by habitat clearing.

The relationship between parrot body size and the percentage of seeds or fruit in the diet may be related to nutritional requirements of parrot species. Seeds are generally high in protein (Gilardi 1996) and larger-bodied avian species may require greater amounts of protein for maintenance (Klasing 1998). Smaller-bodied species may require more fruit pulp, which can be high in sugars, as their metab-

olism may require additional energy since they have higher energy needs than larger-bodied species. Therefore, the abundance and ratios of larger-bodied and smaller-bodied parrots in a psittacine community may be a good predictor of what plant species may be required to sustain populations in certain areas.

The small-bodied parakeets and *Amazona* parrots showed the most similarity in overall psittacine diets, suggesting that congeneric and similar-sized species forage on a large subset of the same plant species. The greater similarity in psittacine diets in the wet season as opposed to the dry season could be related to fewer species of trees producing parrot food in the wet season (Matuzak and Brightsmith 2007) making it more likely that psittacines would forage on the same plant species.

TABLE 3. Foraging observations for Orange-fronted and Orange-chinned parakeets. Species marked with * are non-native, ** are cultivated, and *** are both non-native and cultivated. Parts eaten are coded as S = seeds, FP = fruit pulp, B = bark, L = leaves, F = flowers, and Li = lichen.

Family/Species	Part eaten	Orange-fronted Parakeet		Orange-chinned Parakeet		Months
		# ind.	# bouts	# ind.	# bouts	
Anacardiaceae						
<i>Anacardium excelsum</i>	F	0	0	2	1	Feb
<i>Spondias mombin</i>	FP	12	2	21	2	Sep
<i>Spondias purpurea</i>	L	3	1	0	0	Oct
<i>Mangifera indica</i> **	FP	4	1	532	47	May–Aug
Bignoniaceae						
<i>Tabebuia rosea</i>	FL,B	8	4	17	5	Apr, Jun
Bombacaceae						
<i>Ceiba aesculifolia</i>	S,F	0	0	14	8	Jan–Apr
<i>Ceiba pentandra</i>	S,FL,B	0	0	172	11	Feb–Apr
<i>Bombacopsis quinata</i>	S,FL,B	23	5	100	22	Jan–Apr
Caesalpiniaceae						
<i>Schizolobium parahybum</i>	L	0	0	8	1	Jul
<i>Delonix regia</i> *	F	8	1	2	1	Jun
<i>Senna</i> sp.	F	2	1	20	1	Mar
Cecropiaceae						
<i>Cecropia</i> sp.	S,F	0	0	6	2	Jul
Combretaceae						
<i>Terminalia catappa</i> *	F	28	3	0	0	Dec
<i>Terminalia oblonga</i>	S	2	1	0	0	Feb
<i>Laguncularia racemosa</i>	L	0	0	73	8	Feb–May
Euphorbiaceae						
<i>Sapium glandulosum</i>	FP	7	2	15	2	Aug–Oct
Leguminosae						
<i>Gliricidia sepium</i>	S,F	15	7	0	0	Jan–Feb
<i>Erythrina poeppigiana</i>	F	4	1	0	0	Jan
Lorantaceae						
<i>Psittacanthus</i> sp.	S,F	6	2	31	6	Sep–Oct
Meliaceae						
<i>Cedrela odorata</i>	S,FPL,B	34	8	11	2	Sep–Oct
<i>Swietenia macrophylla</i>	S	0	0	4	1	Nov
Fabaceae						
<i>Enterolobium cyclocarpum</i>	L,B	12	1	67	8	Mar–Aug
<i>Inga vera</i>	F	0	0	3	1	Feb
<i>Pithecellobium saman</i>	S,FL	10	2	88	11	Jan–Feb
Moraceae						
<i>Brosimum alicastrum</i>	S,FP	0	0	14	4	Jun
<i>Ficus insipida</i>	S,FP,B	0	0	209	12	May–Jul
Myrtaceae						
<i>Psidium guajava</i> **	S,FP	25	7	60	10	Mar–Apr
Palmae						
<i>Elaeis guineensis</i> ***	FP	18	3	156	19	Jun–Jul
Rutaceae						
<i>Zanthoxylum</i> sp.	S,FP	16	3	16	5	Jun–Aug

TABLE 3. Continued.

Family/Species	Part eaten	Orange-fronted Parakeet		Orange-chinned Parakeet		Months
		# ind.	# bouts	# ind.	# bouts	
Sterculiaceae						
<i>Sterculia apetala</i>	S	22	2	46	7	Jan–Feb
<i>Guazuma ulmifolia</i>	S,FP	115	32	3	2	Dec–Apr
Tiliaceae						
<i>Luehea seemannii</i>	S,F	5	2	4	1	Jan, Jun
Verbenaceae						
<i>Tectona grandis</i> ***	S,F	36	11	15	3	Jun–Sep
Verbenaceae						
<i>Avicennia germinans</i>	S,L	57	11	29	5	Aug–Sep
Unknown Vine sp.	S	0	0	31	6	Jan–Feb
Total # individuals and bouts		472	113	1,869	214	

Smaller parrot species such as those in *Brotogetis* and *Aratinga* often increase in abundance in modified landscapes, as larger parrot species decline (Karubian et al. 2005). Thus, anthropogenic impacts can drastically reduce the ratio of large to small psittacines in a community. Smaller-bodied parrot species may even disperse some smaller-seeded trees (Janzen 1981, Fleming et al. 1985). Plant reproduction and regeneration in modified landscapes could be altered by removing the largest-bodied seed predators, and increasing floral predators and potential dispersers of small seeds.

Diet Specialization and Seasonal Shifts.—The number of plant types consumed by each parrot species ranged from 24 to 36 species from 15 to 21 plant families. The numbers of food items consumed by the two *Amazona* species in Curú are similar to those for other parrot species: Scaly-headed Parrots in Brazil ate 38 plant species from 18 families (Galetti 1993) and Lilac-crowned Parrots in Mexico ate 33 plant species from 14 families (Renton 2001). Orange-fronted Parakeets in Curú foraged on 24 food plant species in 16 families. This is greater than the 15 species from 12 families recorded for the congeneric Pacific Parakeet in Nicaragua (Wermundsen 1997). Scarlet Macaws foraged on 32 food plant species in 15 families in Curú, while studies of wild Scarlet Macaws reported 15, 43, and 52 food species in Belize; Carara, Costa Rica; and Peru, respectively (Gilardi 1996, Renton 2006, Vaughan et al. 2006).

Diet composition of each species of parrot varied seasonally. Four of five parrot species ate more plant species during the dry season than the wet season. This trend corresponds with an increase in the number of food species available, and the percentage of trees bearing seeds and flowers during the dry season (GDM, unpubl. data). The number of food species and trees bearing large quantities of fruit pulp such as *M. indica*, *S. mombin*, *E. guineensis*, *Psidium guajava*, and *Scheelea rostrata* increased during the wet season. The wet season was also when leaves became a larger part of the diet of each species.

Diet breadth among parrots usually increases with increasing food abundance and diversity of available food items (Wermundsen 1997, Renton 2001). This pattern held for only one species in our study, White-fronted Parrot, which had a 260% increase in diet breadth when food availability peaked in the dry season (Matuzak and Brightsmith 2007). The increase in diet breadth of Orange-chinned Parakeets during the wet season could also be related to food abundance, as fruit pulp (the species preferred food part) abundance peaks at this time of year (GDM, unpubl. data). Two other species, Scarlet Macaws and Orange-chinned Parakeets, had more specialized diets during the dry season food peak (36 and 52% reductions in diet breadth, respectively). During the dry season in Belize, Scarlet Macaws have a less specialized diet (Levins' diet breadth = 0.394; Renton 2006) than did Scarlet Macaws in our study (Levins' diet breadth

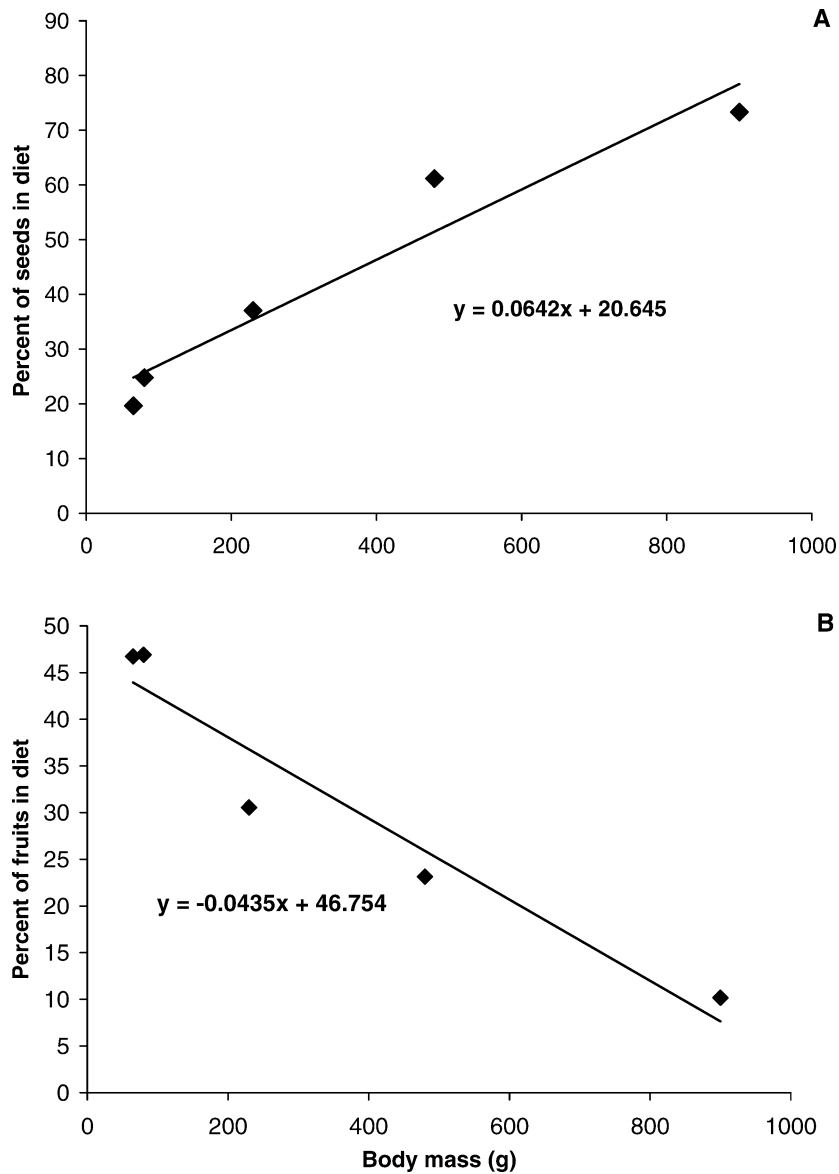


FIG. 1. Body mass versus percent of seeds (A) and fruits (B) in the diets of parrots in Curú Wildlife Refuge on the Nicoya Peninsula of Costa Rica.

= 0.139). In Curú, Scarlet Macaws in the dry season specialize on two food items, *P. saman* and *T. catappa*, both of which produce abundant resources in the dry season and combine for 53% of the macaws' dry season diet. The more specialized diet of macaws in this study may be due to several factors, including less food diversity and availability due to a human modified landscape, a preference for *T. catap-*

pa over other available resources, and/or a lack of knowledge and training to find local resources after their release to the site. The diet breadth of Lilac-crowned Amazons in Mexico was 0.22 in the dry season and 0.55 in the wet season when the number of food species available peaked (Renton 2001). The diet breadth of the two species of *Amazona* parrots in Curú was larger in the dry season

and lower in the wet season when compared to Lilac-crowned Amazons; however, food availability peaked in the dry season in Curú. Yellow-naped Parrots and Orange-fronted Parakeets exhibited no major difference in diet breadth between seasons.

Native versus Non-native Food Plant Species.—Use of non-native food resources by parrots is widespread and important in sustaining some species during times of low food availability (Forshaw 1989, Pitter and Christiansen 1995). Over half of all foraging bouts in our study were on non-native and cultivated tree species; however, when macaws are not included, only 29% of foraging bouts were on non-native and cultivated species. Non-native species consumed included two naturalized species that occur along the coasts of Costa Rica (*C. nucifera* and *T. catappa*), seven species cultivated for fruit (4 species of *Citrus*, *M. indica*, *P. guajava*, and *E. guineensis*), two non-native ornamentals (*D. regia* and *Lagerstroemia speciosa*), and *T. grandis*, a tree planted for timber (Holdridge et al. 1997).

Two species (*C. nucifera* and *T. catappa*) were used mainly by Scarlet Macaws and represented 48% of their diet. Wild populations of macaws at other sites in Costa Rica forage heavily on *T. catappa* as this plant species is highly abundant and is in seed all year along coastal areas and beaches where wild macaws are found. The macaws in Curú exploit a similar range of food resources in similar environments as wild macaws along the central coast of Costa Rica (Vaughan et al. 2006; GDM, unpubl. data).

Citrus trees (lime, lemon, grapefruit, and orange) were an important food resource for Yellow-naped Parrots from November to December, a period of increasing food abundance prior to onset of nesting (Matuzak and Brightsmith 2007). Two species, *E. guineensis* and *T. grandis*, provided important food resources for the entire parrot community. These species were important during declining food availability and low food diversity, April–June and September–October, respectively (Matuzak and Brightsmith 2007).

CONSERVATION IMPLICATIONS

The ability of psittacines to exploit non-native resources may be important for their future survival, not only in Costa Rica, but

across Latin America. The high rates of habitat conversion in Costa Rica over the past several decades have produced millions of hectares dominated by forest fragments, small farms, and plantations (Kleinn et al. 2002). Parrots have greatly expanded their available food base by using introduced and cultivated food plants. As more areas of the Neotropics are converted from native habitats to small farms, persistence of parrots may become linked to their ability to exploit introduced and cultivated species in modified landscapes.

Use of non-native and cultivated species brings psittacines into direct competition with humans, making them a perceived pest of crops (Bucher 1992). Psittacines in many parts of the world are trapped or killed due to real or perceived damage to crops (Bucher 1992). The benefits of feeding on introduced and cultivated species for most psittacines apparently outweigh the mortality inflicted by humans and, as a result, some species become abundant in modified landscapes (Pitter and Christiansen 1995, Moegenburg and Levey 2003). However, for uncommon psittacines with low reproductive rates like macaws or large amazons, conflicts with humans could threaten the species' persistence (Bucher 1992).

Deforestation in Costa Rica has removed up to 60–70% of the nation's original forest cover (Kleinn et al. 2002). In the study area, many hectares are regenerating forest cover as farms and pastures are being abandoned (Kleinn et al. 2002). Targeted restoration of *G. ulmifolia*, *B. quinata*, *S. mombin*, and *L. seemannii* in our study area would be feasible and of great benefit as these native tree species provide key food resources to psittacines. *G. ulmifolia* and *S. mombin* are of special importance since both fruit during the time of lowest overall food availability and may turn out to be keystone species in these dry forest environments. Increasing the abundance of native species should also decrease the dependence of psittacines on introduced and cultivated species, and decrease the potential for negative interactions with humans.

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