

Great Green Macaws and the annual cycle of their food plants in Ecuador

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ABSTRACT. The Great Green Macaw (*Ara ambiguus*) is one of the largest New World parrots and is considered endangered with extinction. Their precarious decline in western Ecuador has been attributed to food scarcity, among other pressures. To understand the effects of food abundance on macaw behavior, phenological patterns of a community of food plants were documented in a dry tropical forest in southwest Ecuador from June 1999 to May 2000. Edible biomass was estimated weekly for 100 trees representing 10 species of macaw food plants. Simultaneously, we conducted a census of macaws. Of the plants studied, little food was produced during nearly 4 consecutive months (February–May). Food availability was unrelated to macaw abundance, but was positively correlated with the amount of time macaws spent in the study area. One plant species (*Cynometra bauhiniifolia*) produced more food than nine other species combined and was responsible for the correlation. Additional study of macaws foraging on *C. bauhiniifolia* and other plant species is needed, with special attention paid to those species with both large crops and large seeds. Although the diet of Great Green Macaws remains poorly known, our study illustrates the potential importance of quantifying differences in food production by plant species consumed by threatened granivores.

SINOPSIS. El guacamayo verde mayor y el ciclo anual de las plantas alimenticias en el Ecuador

El Guacamayo Verde Mayor (*Ara ambiguus*) es un de los loros más grande del Nuevo Mundo y es considerado amenazada on la extinción. Su declinación ha sido abrupta en el Occidente del Ecuador y atribuido a la escasez de alimento, entre otras presiones. Para entender los efectos de la abundancia de comida en relación al comportamiento de los guacamayos, documentamos los patrones fenológicos de un grupo de arboles en un bosque seco tropical en el suroeste del Ecuador entre Junio 1999 y Mayo 2000. Nosotros estimamos la oferta de biomasa comestible cada semana en 100 arboles pertenecentes a 10 diferentes especies. Simultáneamente, un monitoreo de los guacamayos fue realizado. De las plantas que estudiamos, poca comida fue producida durante casi cuatro meses consecutivos. La disponibilidad de alimento no fue relacionada con la abundancia de los guacamayos, pero si fue positivamente correlacionada con el tiempo que los guacamayos pasaron en el sitio. Una especie (*Cynometra bauhiniifolia*) produjo más comida que las otras nueve especies combinadas y fue la responsable de la correlación. Se carece de estudios adicionales de los guacamayos forrajeando la *C. bauhiniifolia* y otras especies de plantas, con atención especial a aquellos especies que combinan cantidades importantes de semillas con un tamaño individual grande. Aunque la dieta de esta población de guacamayos es aun escasamente conocida, nuestro estudio ilustra la importancia potencial de cuantificar la producción de comida de especies consumidas por las granívoras amenazadas.

Key words: *Ara ambigua guayaquilensis*, *Cynometra*, dry tropical forest, Ecuador, granivory, phenology

Because many parrot species depend on seeds (Foreshaw 1978, Janzen 1981, Waltman and Beissinger 1992, Yamashita and Valle 1993, Bonadie and Bacon 2000, Renton 2001), understanding how seed production may explain temporal changes in bird abundance is critical for developing management plans for threatened species (Terborgh 1986, Levey et al. 2002, Moegenburg et al. 2002). Great Green Macaws

(*Ara ambiguus*), one of the largest New World psittacines, are considered endangered with extinction (Stattersfield and Capper 2000, Snyder et al. 2000, Birdlife International 2005). Their threatened status is not surprising given their large body size, long generation time, small clutch size, and habitat specialization (Owens and Bennett 2000). Although human persecution is a direct threat, the ecological processes by which habitat loss affects populations are poorly understood and require additional study (Beissinger 2000). Great Green Macaws occupy a variety of habitats, ranging from humid tropical forest in Central America and Colombia to pluvial and deciduous tropical forests in western Ecuador.

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Previous attempts to document changes in parrot abundance in response to phenological patterns of food plants have often involved estimation of the number of trees with fruit over a period of time, or categorical estimation of the number of fruits present on a sample of trees (Poulin et al. 1992, Bonadie and Bacon 2000, Renton 2001). These methods often assume seed size is similar across plant species, and do not provide a comparable estimate of food availability in other regions (reviewed by Blake et al. 1990). Using these methods, data are efficiently collected and have been important in determining seasonal fluctuations of parrots within a region. However, where differences in seed morphology exist, edible biomass (EBM) estimates rather than number of seeds should explain more of the temporal variation in parrot abundance.

Ideally, studies seeking to link the foraging behavior of wide-ranging birds, such as macaws, with food availability should be conducted over similarly large areas using species where diets are relatively well known. Unfortunately, macaws in southwest Ecuador are poorly known, have small population sizes, and are difficult to observe in the wild. Given their endangered status and the current rate of deforestation, remaining populations could be extirpated before such knowledge is acquired. With this in mind, we concentrated our study on a smaller scale, targeting the only known reproductively viable population, and estimated the available, EBM for 10 species of macaw food plants over a 1-year period. Macaw abundance and time spent in the area were quantified simultaneously to examine the effects of food supply.

The decline in populations of Great Green Macaws in Ecuador has been due, at least in part, to selective and systematic habitat alteration over the last 50 years (Dodson and Gentry 1991, Neill 1997) that has potentially reduced availability of some sources of food and introduced temporal and spatial gaps in their annual cycle of food availability. Identification of peak periods of food availability, and the plant species responsible, is thus an important step in developing an effective conservation strategy for remnant forests and macaws.

METHODS

Study site. Our study was conducted from June 1999 to May 2000 in the Bosque Protec-

tor Cerro Blanco (S 2°07'30", W 80°04'40"), Province of Guayas, Ecuador. This 6000-ha private reserve protects a forest at the southern extreme of a coastal mountain range where the only known nesting attempts by Great Green Macaws in Ecuador have occurred in recent years (López-Lanús 1999, J. Socola, pers. observ.). Three plant community types were present at Cerro Blanco, including Tropical Dry Forest (50–300 m elevation), Moist Tropical Forest (300–400 m elevation), and Riparian Forest (150–350 m elevation). Forests were dominated by old (50–80 yr) second growth deciduous vegetation and ranged from 150 to 350 m elevation. *Cavanillesia platanifolia* (Bombacaceae) was the dominant tree species in a discontinuous canopy reaching 35 m in height. Precise climate data for the study site have not been recorded. The closest weather station with a similar climate was located near sea level 17 km east of our study site. Over a 10-year period, median rainfall was 1050 mm per year, with 99% falling from December to May. Median temperature was 22°C (range = 18.0°–34.4°C; INAMHI 1994).

Food plants. Observations at our study site indicated that macaws fed on the seeds of nine species of trees (López-Lanús 1999, J. Socola unpubl. data). Although we had not observed macaws feeding on a 10th tree species (*Terminalia valverdeae*), we chose to monitor this species based on the morphological characteristics of these seeds and because it was common in the study area. Although food plant densities were not quantified, these 10 species comprised most of the trees in the study area and were the trees we monitored (Table 1).

Edible biomass. Edible parts were determined based on previous observations of macaws feeding (J. Socola, unpubl. data) and anecdotal accounts obtained from local residents (M. Morgan and C. Medina, pers. comm.). Typically, macaws pry open exocarps with their bills and extract and consume only seeds. However, macaws consume the entire fruit of two species (*Cecropia littoralis* and *Vitex gigantea*). Based on these observations, samples of fresh fruits from at least five different trees of each species of macaw food plants were collected to obtain dry weights of edible parts (Table 1). The sample for *Pseudobombax millei* was smaller ($N = 4$) because of their large fruits and small crop number. Edible mass was measured with a balance (Ohaus Model MB200, Pine Brook, NJ) after

Table 1. Characteristics of macaw food plants in Ecuador.^a

Family and species	Mean EBM/ fruit (g)	SD	N	Mean EBM/ tree (g)	DBH (cm)	Peak	Color
Fabaceae							
<i>Centrolobium ochroxylum</i> ^b	0.55	0.4	72	29	66.5	July	Brown
<i>Leucaena trichodes</i>	1.03	0.2	42	335	11.0	Sep	Brown
<i>Cynometra baubiniifolia</i>	15.40	9.4	39	9468	51.9	Jan	Brown
Cochlospermaceae							
<i>Cochlospermum vitifolium</i> ^b	8.85	2.8	30	74	23.7	Oct	Brown
Combretaceae							
<i>Terminalia valverdeae</i> ^b	0.01	*	50	75	100.4	Aug	Brown
Bombacaceae							
<i>Cavanillesia platanifolia</i> ^b	0.92	0.2	45	18	177.5	Nov	Brown
<i>Pseudobombax milleri</i> ^b	42.00	15.5	4	130	45.1	Dec	Green
<i>Ochroma pyramidale</i>	10.40	3.0	15	3	48.7	Oct	Brown
Cecropiaceae							
<i>Cecropia litoralis</i>	5.11	1.8	38	450	20.9	Jan	Green
Verbenaceae							
<i>Vitex gigantea</i> ^b	1.01	0.4	36	25	18.0	Jan	Black

^aEdible biomass (EBM) per fruit was estimated from dry weights of fruits collected from each species. Mean EBM per tree was based on 44 visits to each of 108 trees from 15 July to 15 May 2000. Peak production was the month with the largest number of fruits observed.

^bIndicates species included in the low elevation transect.

*Two compound samples of 25 fruits each were used.

heat drying to a constant mass at 38°C. Edible mass for *T. valverdeae* seeds was determined using two samples of 25 seeds because of their small size (0.01 g).

Plant phenology. Two line transects were located 0.5 and 1.2 km from where we recorded three nesting attempts by macaws from 1997 to 2000 (López-Lanús 1999, unpubl. data; Fig. 1). The area was traversed by creeks with evergreen riparian forest along their banks and flood plains (see Foster [1992] for a more detailed description). Along each transect, we selected the first 10 trees of each species visible from the line (>10 cm DBH, $N = 108$; Table 1). We selected 10 trees of each of nine species, and 18 of *Centrolobium ochroxylum* as part of another study. All trees were identified, geo-referenced, measured (diameter at breast height, or DBH), and labeled with numbered, aluminum tags. Voucher specimens were collected and deposited at the National Herbarium (QCNE; Quito, Ecuador), and duplicates forwarded to the Missouri Botanical Garden (St. Louis, MO). Deciduous food plants dominated the low elevation transect (mean elevation = 169 ± 27 m [SD]). Most evergreen tree species (three of four) were concentrated along the higher elevation transect (mean elevation = 387 ± 32 m [SD]).

Crop estimate. All trees were visited approximately every eight days from 15 July 1999 to 15 May 2000 ($N = 44$ visits), and the amount of available fruit estimated. For 7 of the 10 species, fruits were counted directly. For *T. valverdeae*, fruit availability was based on branches ($N = 8$) removed from three different trees, with fruits counted manually. A standing crop estimate was calculated by multiplying the mean number of fruits per branch by the number of similar-sized fruiting branches on each tree. Fruit availability for *Cynometra baubiniifolia* was sampled by visually selecting one or two branches on each tree and counting the fruits using a telescope. We then extrapolated the mean number of fruits per branch to the number of similar-sized branches on each tree. Finally, fruit availability for *C. litoralis* was estimated by counting with binoculars the number of catkins in a sample of bunches ($N = 40$) and then extrapolating the mean number of catkins per bunch to the number of bunches on each of the trees during each visit.

Because we began selecting trees in June, no systematic observations of the entire community were made until early July. However, fruits were too immature to have been included in our counts during June, so we are confident that little or no food was present. We interpolated fruit

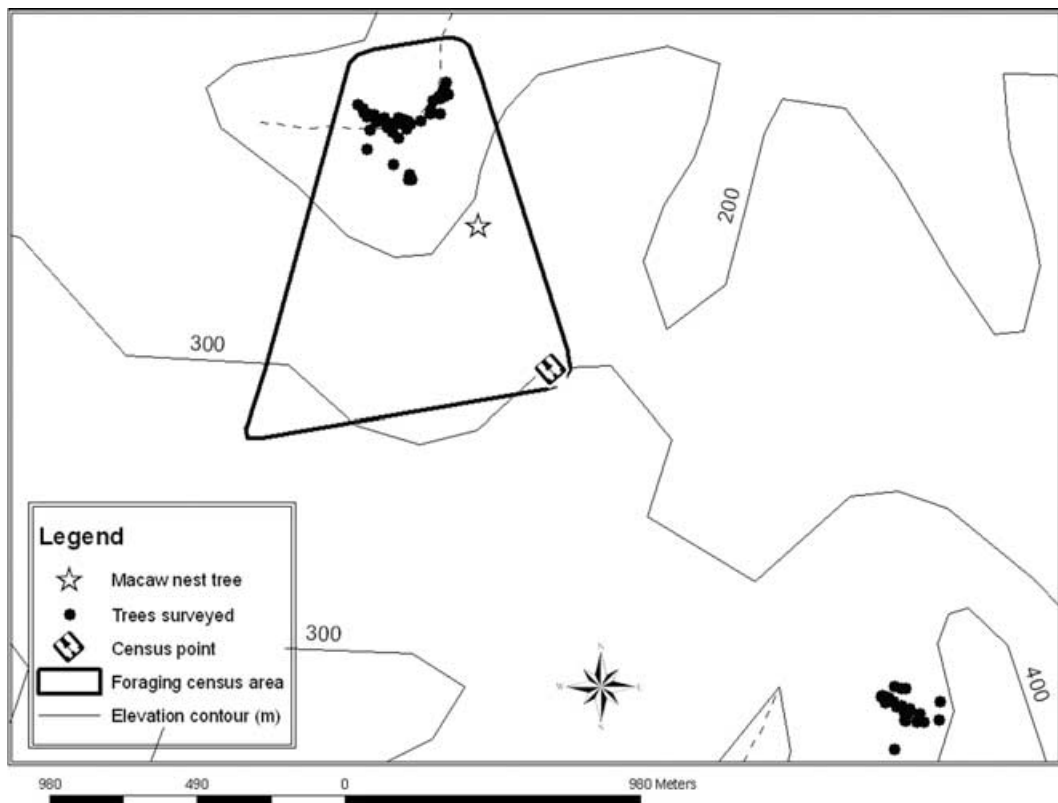


Fig. 1. Map of the study site in the Bosque Protector Cerro Blanco, Guayas Province, Ecuador.

counts of individual trees on 44 occasions when data were missing (1.3% of counts). Trees ($N = 108$) had a mean DBH of 60.6 ± 33.9 [SD] cm. *C. litoralis* was the only dioecious species studied, and 6 of the 10 trees selected were males. The dry season was beginning when we made our first observations in early June 1999 and peaked about six months later in mid December. Heavy showers (> 50 mm) began in mid February and occurred weekly through early May 2000.

Macaw survey and time budget. From June 1999 to May 2000, we conducted a census of macaws three times a week (5 h per census) from a mountain top that provided panoramic views of their habitat (total observation time = 672 h; Fig. 1). The site was selected because of the large area of suitable habitat that could be observed and because macaws had been predictably sighted in the area. Location coordinates were obtained with a handheld GPS at the observation point and at four different locations bordering the valley that included our

field of view. When we mapped coordinates using ArcGIS (v. 8.3, ESRI, Redlands, CA), the resulting pentagon had an area of 73 ha and included the low elevation transect (Fig. 1). A 20–60x spotting scope and binoculars were used when observing macaws. The high elevation plant species were present at the site where macaws were monitored, but at lower densities and distances too far to directly observe macaw foraging (i.e., distant hill tops). We did not feel that results from surveying macaws in the highland transect would have been comparable to data collected from the lowland site, given the limited visibility in the former. Most surveys were conducted between 08:00 and 13:00.

A time budget was generated by noting the number of macaws observed and the combined time they were in view (e.g., two macaws $\times$ 1 h = 2 h). To avoid double counting, abundance estimates were based on maximum flock size per observation period. The area where macaws were observed included a macaw nest that was

active from June to November 1999, and we excluded the time macaws spent at the nest from our time budget analyses. For foraging macaws, we recorded, if possible, food items, quantity consumed, length of time to consumption, and length of time spent in a particular tree with fruit. Their large size, brightly colored plumage and raucous calls, combined with a characteristically open canopy, made macaws generally easy to detect.

Statistical analysis. Repeatability of the maximum crop on each tree was determined from variance components by nesting measurements on each tree within species. Similarly, measurements of EBM of each fruit were also nested within species to estimate repeatability of the food production of each species. The mean weight of dry, edible food per fruit was calculated for each species. These means were then extrapolated to the numbers of fruits appearing on each tree to generate an EBM estimate for each census. Because macaw survey periods varied, the time macaws were present was calculated as total time present/observation period $\times$ the total time present and summed for each month. Using the mean did not alter our main conclusions. Distributions were analyzed for evidence of heteroscedasticity and nonnormality, and log transformations were conducted as needed. To make our results more easily compared to those of future investigators, where age of stands might represent a nonrandom effect, we tested for the effects of size of tree (DBH) on number of fruits, excluding trees that did not reproduce, and predicted that larger trees would produce more fruits. We then included a species $\times$ size interaction in the model to determine whether the intraspecific relationship differed across species. We tested for correlations between variables using the Corr Procedure. General Linear Models (GLM) were used for analysis of variance (ANOVA) and to test for the effects of food availability on the number of macaws present as well as the amount of time macaws were observed during the census. All statistical analyses were performed using the Statistical Analysis System (SAS 2002), and significance was accepted at $\alpha = 0.05$. Values are presented as mean $\pm$ 1 SD.

RESULTS

Fruit morphology. Morphological characteristics of fruits varied considerably (Table 1). The amount of edible food in each fruit was

highly repeatable within species ($F_{9,286} = 86.9$, $r_{\text{food}} = 0.76$, $P < 0.0001$). Although fruits contained an average of 8.5 ± 12.8 g of dry, edible food ($N = 405$ fruits), five tree species produced small seeds with dry, edible matter weighing near or less than 1 g. Fruit exocarps were inconspicuous (brown, green, or black; Table 1, but see Church et al. 1998), but relatively large (5 of 10 species had fruit lengths > 10 cm).

Food availability. The size of crops also varied. The maximum number of fruits on each tree was highly repeatable within species ($F_{9,95} = 8.99$, $r_{\text{fruits}} = 0.90$, $P = 0.0006$). Pooling all species, tree size (DBH) was unrelated to the maximum number of fruits ($N = 74$ trees, $r = 0.03$, $P = 0.13$). However, the model improved considerably when species, DBH, and a species $\times$ DBH interaction were included as predictors of crop size ($r^2 = 0.97$, $F_{17,56} = 91.6$, $P = 0.0001$), with all terms significant and suggesting heterogeneity of slopes across species (Engqvist 2005). The average number of fruits per month peaked in July, then gradually declined (Fig. 2 A). In contrast, average EBM peaked from December to January (Fig. 2 A). EBM was higher during the wet season and the nonbreeding season, but differences were not significant (all $P > 0.11$). Both the number of fruits and EBM were a function of species, month, and a species $\times$ month interaction (Table 2). *C. baubiniifolia* was the main cause of the peak in EBM. Fruit production by this species ($= 9.5 \pm 15.8$ kg, $N = 10$ trees) was almost an order of magnitude greater than for the rest of the community combined ($= 1.0$ kg, $N = 9$ species). The two months with the highest mean estimates of *C. baubiniifolia* were December and January, essentially the same as for all species pooled. No trees exhibited a peak in fruit production from February to May.

Macaw surveys and time budget. Macaws were observed during every month from June 1999 to May 2000 and on 71 different days (65% of census days). Flock size ranged from 1 to 9 individuals and was higher during the nonbreeding period ($F_{1,70} = 16.6$, $P = 0.0001$). The amount of time macaws were observed varied, with an increase at the beginning of the wet season and two periods of marked absence (Fig. 2 B). The longest periods with no observations of macaws were 27-day periods in November 1999 and March 2000. During observations, macaws spent 8.7% of their time foraging. Macaws fed more on seeds than either

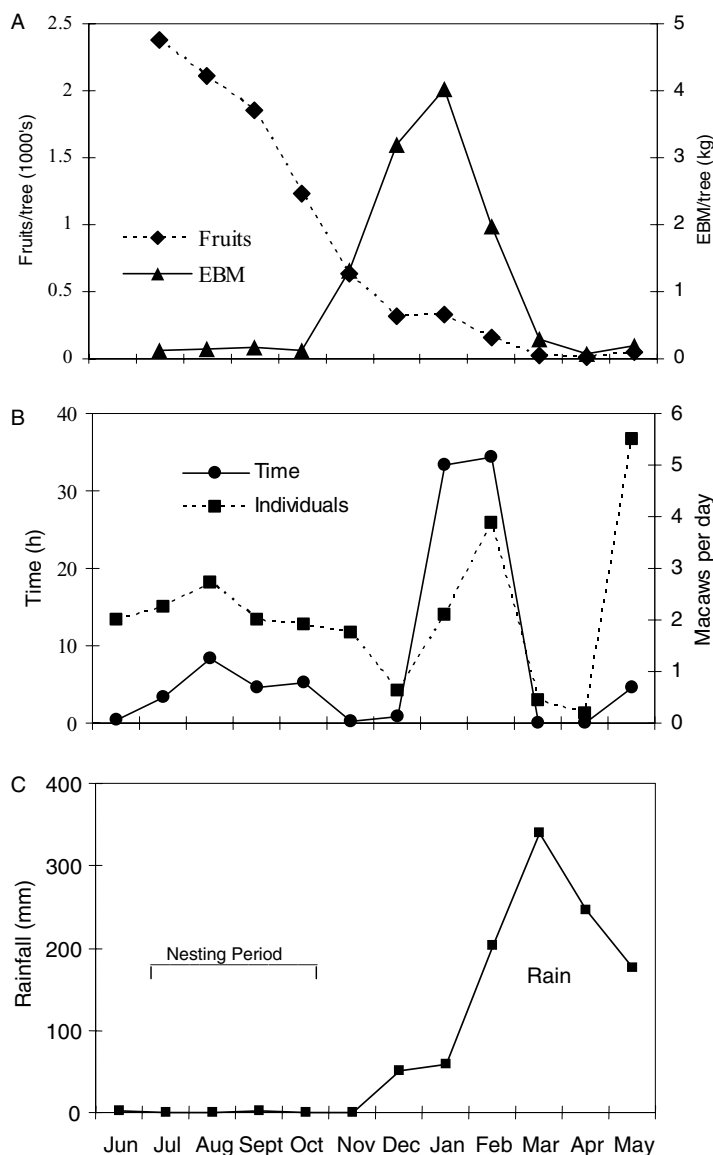


Fig. 2. Relationship between food availability and abundance of Great Green Macaws in Ecuador in 1999–2000. (A) Mean number of fruits per month relative to edible biomass (EBM). (B) Cumulative amount of time macaws spent in the area each month relative to mean abundance per month. (C) The timing and duration of the breeding period was based on three nesting attempts from 1997 to 2000. Rainfall data are from Guayaquil (INAMHI 1999, 2000).

pulp or mesocarps (6 of 10 species). Macaws fed on at least eight species of plants, with most time spent feeding on *C. ochroxylum* (3.5%), *T. valverdeae* (2.5%), and *C. platanifolia* (1.0%) trees. Overall, macaws spent most of their time perching (75.2%), preening (5.5%), and flying (5.1%; Table 3).

Macaw-plant interactions. The time macaws spent in the area each month was positively correlated with mean EBM ($N = 11$, $r = 0.60$, $P = 0.051$). Although marginally nonsignificant, both time in the area and mean EBM increased at the beginning of the wet season (Fig. 2A, B). Although total time

Table 2. Analysis of the fruiting patterns of 10 species of food plants in the diet of Great Green Macaws in southwestern Ecuador based on 44 visits to each tree during 1999–2000.^a

Source	Number of fruits			Edible biomass		
	df	F	P	df	F	P
Species	9	1277	0.0001	9	286	0.0001
Month	10	164	0.0001	10	57	0.0001
Species × Month	80	152	0.0001	80	64	0.0001

^aBoth the number of fruits and amount of edible biomass were a function of species, month, and their interaction (Fruits: $F_{99,3343} = 256.3$, $r^2 = 0.89$, $P = 0.0001$; Biomass: $F_{99,3343} = 83.1$, $r^2 = 0.71$, $P = 0.0001$).

per month was not correlated with macaw abundance ($N = 11$, $r = 0.39$, $P = 0.21$), the correlation became significant when one outlier (May) was removed ($N = 10$, $r = 0.66$, $P = 0.03$). Macaw abundance and EBM were not correlated ($N = 11$, $r = -0.08$, $P = 0.8$).

Given the disproportionate level of food production by *C. baubiniifolia*, we analyzed this species separately. EBM per month for *C. baubiniifolia* was similarly correlated with total time macaws spent in the area per month ($N = 11$, $r = 0.57$, $P = 0.07$), but EBM for the other nine species of trees was not ($N = 11$, $r = -0.14$, $P = 0.68$). Because we

only observed macaws feeding on *T. valverdeae*, *C. ochroxylum*, *Pseudobombax millei*, and *C. platanifolium* (Table 3), we also analyzed the relationship between the total time macaws were observed and EBM of these trees. However, we found no relationship ($N = 11$, $r = -0.38$, $P = 0.25$). Thus, the correlation between EBM and the time macaws spent in the study area was due to the disproportionate contribution of *C. baubiniifolia* to food production.

DISCUSSION

Our results provide a clear description of the fruiting patterns of a conspicuous group

Table 3. Macaw activity budget based on 672 census hours in the Bosque Protector Cerro Blanco, Guayas, Province, Ecuador between June 1999 and May 2000.^a

Activities		Hours	Proportion (%)
Flying		5.60	5.1
Perching		82.07	75.2
Preening		6.00	5.5
Allofeeding		2.87	2.6
Foraging on			
<i>Centrolobium ochroxylum</i>	Fruits	3.82	3.5
<i>Cavanillesia platanifolia</i> ;	Buds	0.03	0.0
	Flowers	0.32	0.3
	Bark	0.22	0.2
	Leaves	0.07	0.1
	Fruits	1.07	1.0
<i>Encyclia</i> sp.	Pseudobulb	0.27	0.2
Unidentified orchid	Pseudobulb	0.15	0.1
<i>Pseudobombax millei</i>	Fruits	0.67	0.6
<i>Terminalia valverdeae</i> ;	Fruits	2.72	2.5
	Flowers	0.05	0.0
<i>Spondius</i> sp.	Fruits	0.08	0.1
Unidentified plant	Fruits	0.12	0.1
Unidentified activity		2.97	2.7%
TOTAL		109.07	100

^aTime dedicated to each activity was weighted by the observation period and the number of macaws present.

of plants in southwest Ecuador during 1 year and help quantify their potential food value to a population of large macaws on the verge of extirpation. In Ecuador, perhaps as few as 100 Great Green Macaws were shared between two isolated populations (Stattersfield and Capper 2000). Although our study was restricted to one small site, we observed flocks with as many as nine individuals that could represent 9% of the population in Ecuador. Deforestation is widespread in western Ecuador and, combined with extreme local endemism, threatens numerous plant taxa (Dodson and Gentry 1991, Neill 1997, Valencia et al. 2000, Myers et al. 2000). The decline (and in one case extinction) of three other large macaws in South America has been attributed, in part, to the declining availability of important food plants (Yamashita and Valle 1993). The precarious decline of the *guayaquilensis* race of the Great Green Macaws, endemic to western Ecuador, has also been attributed to food scarcity due to habitat destruction (Waugh 1995). Our results provide a first step to understanding how temporal changes in local food availability affect macaw seasonal movements and can be used by future investigators to estimate the density of food plants in a broader landscape context and more adequately address the far-ranging nature of large macaws.

Both the size of the crop and the amount of food provided by each fruit were species-specific traits in this plant community and both varied across species. The significant month by species interaction indicates that fruiting phenologies were chronologically staggered over much of our study period. Our results also indicate that these plants provided little food during a 4-month period, suggesting that many food plants used by this macaw population remain unknown and may not be receiving protection. Developing an effective conservation strategy will require information about what the macaws are eating from March to June (and other times), the contribution of those plants to food production, and their protected status.

The size of trees was related to the number of fruits, suggesting that age of stands may also influence food availability. This is predicted by a typical allometric relationship between girth and number of fruits (Greenberg 2000), and suggests that food supply may increase where forests are allowed to regenerate. However, the significant species by size interaction indicates

that food production did not respond equally to girth across species. This is likely explained by an uneven age distribution across plant species due to selective harvesting of valuable timber combined with differential regeneration rates. For example, the number of fruits produced by *C. platanifolia* trees, the species with the largest and perhaps oldest trees, actually declined as size of trees increased (results not shown). *C. platanifolia* were about 1500 times larger than the smallest trees (Table 1), suggesting two age extremes in our study. Those cutting trees in the region may avoid trees like *C. platanifolia* because of its soft wood and hollow trunk and, as a result, this species is abundant in several, otherwise deforested, areas in the Cordillera de Chongon (K.S. Berg, pers. observ.).

Our results support the hypothesis that seasonal movements of macaws are influenced by temporal changes in local food availability. Similarly, Bonadie and Bacon (2000) found that seasonal movements of red-bellied Macaws (*Ara manilata*) were correlated with the fecundity of a small group of tree species during the wet season in Trinidad. Renton (2002) found that different species of macaws were more abundant during the wet season in eastern Peru and suggested that this might be related to food availability. Our results partially support such a relationship; some of the plants that fruited during the wet season yielded more EBM, but several months of the wet season were characterized by a general paucity of food, at least among the plants we studied. In contrast, Karubian et al. (2005) found that several species of macaws were more common during the dry season in eastern Ecuador. Such results suggest that macaws track changes in food availability, but that this ultimately depends on interspecific differences in diet and how food production is organized spatially and temporally, and may only be indirectly related to rainfall patterns.

A disproportionate number of plant species thought to comprise the diet of macaws in this population were small-seeded and wind-dispersed. However, larger parrots might be expected to prefer larger seeds (Bradbury et al. 2001, Brightsmith 2005). Our lack of direct observations of foraging on many of the plant species, despite their conspicuousness in the study area, suggests that many of these trees may be of limited importance in the diet of macaws in our study population. This might underlie

the fact that when the large-seeded crop of *C. baubiniifolia* was removed from the analysis, no relationship between available food and time spent by macaws remained. If increased body size has selected for large seeds in macaw diets, increasing densities of small-seeded species due to deforestation could make it increasingly difficult for macaws to survive in southwest Ecuador.

Although the positive relationship between time spent by macaws and amount of edible food was apparently due to seed production by *C. baubiniifolia* from December to January, this result must be viewed with caution because we had no direct observations of macaws foraging on this species. Because we had few observations of foraging by macaws, we cannot preclude the possibility that macaws foraged disproportionately outside of our field of view or on different species. However, the large ranges of macaws, the proximity of the macaw survey to the high elevation site and the positive correlation we did find, together raise the question as to whether *C. baubiniifolia* might represent a pivotal food source for macaws in southwest Ecuador. The fact that all 10 plant species were present where we monitored macaws, and the asynchrony of fruiting across species lends additional support.

It is thus tempting to conclude that the curious spike in the time macaws spent in our study area 2 months after nesting ended might be attributable to the crop in *C. baubiniifolia*. However, the increase in aggregate time spent during December–January was at least partially explained by larger flocks. Thus, an alternative explanation is that the increase in abundance of macaws we observed during this time was due to the fact that breeding pairs of macaws defend nest sites, but are more gregarious outside of the breeding period (Bonadie and Bacon 2000, Renton 2004). However, macaws spent considerably more time in our study area when *C. baubiniifolia* was in fruit and, as availability declined, we detected no prolonged visits of similarly large flocks of macaws during the non breeding period.

C. baubiniifolia is a large evergreen canopy tree with a range-restricted geographic distribution (D. Neill, pers. comm.) that is limited to humid ridges and riparian habitat in the region, and is dispersed by vertebrates (K. S. Berg, pers. observ.). Because its valuable wood has made it the focus of timber harvesting (Valverde 1991), Cerro Blanco likely represents an impor-

tant refuge for *C. baubiniifolia*. Although its considerable crop of large seeds was correlated with time spent by macaws in our study area, future research should concentrate on obtaining direct observations of macaws foraging on this and other plant species, paying special attention to those with both large crops and large seeds. We recognize that our study did not take into account other potentially critical variables, such as plant species density, seed masting, chemical/nutrient content of seeds, diet switching, and search/handling times. However, our results show that one plant species had the potential to produce more food than nine other species combined and underlines the importance of incorporating EBM estimates into studies that quantify the value of habitat to wildlife.

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LITERATURE CITED

- BEISSINGER, S. R. 2000. Ecological mechanisms of extinction. *Proceedings of the National Academy of Sciences* 97: 11688–11689.
- BIRDLIFE INTERNATIONAL [ONLINE]. 2005. *Ara ambiguus*. In: 2006 IUCN Red List of threatened species. <http://www.iucnredlist.org> (10 January 2007).
- BLAKE, J. G., B. A. LOISELLE, T. C. MOERMOND, D. J. LEVEY, AND J. S. DENSLOW. 1990. Quantifying abundance of fruits for birds in tropical habitats. *Studies in Avian Biology* 13: 73–79.
- BONADIE, W. A., AND P. R. BACON. 2000. Year-round utilisation of fragmented palm forest by Red-bellied Macaws (*Ara manilata*) and Orange-winged Parrots (*Amazona amazonica*) in the Nariva Swamp (Trinidad). *Biological Conservation* 95: 1–5.
- BRADBURY, J. W., K. A. CORTOPASSI, AND J. R. CLEMONS. 2001. Geographic variation in the contact calls of Orange-fronted Parakeets. *Auk* 118: 958–972.
- BRIGHTSMITH, D. J. 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. *Wilson Bulletin* 117: 296–305.

- CHURCH, S. C., A. T. D. BENNETT, I. C. CUTHILL, AND J. C. PARTRIDGE. 1998. Ultraviolet cues affect the foraging behaviour of Blue Tits. *Proceedings of the Royal Society of London B* 265: 1509–1514.
- DODSON, C. H., AND A. H. GENTRY. 1991. Biological extinction in western Ecuador. *Annals of the Missouri Botanical Garden* 78: 273–295.
- ENGQVIST, L. 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour* 70: 967–971.
- FORSYTH, J. M. 1978. *Parrots of the world*. T. F. H. Publications, Neptune, NJ.
- FOSTER, R. B. 1992. Cerro Blanco (moist limestone forest): site description and vegetation. In: *Status of forest remnants of the Cordillera de la Costa and adjacent areas of southwestern Ecuador* (T. A. Parker III and J. L. Carr, eds.), pp. 42–43. RAP Working Papers No. 2, Conservation International, Washington, D. C.
- GREENBERG, C. H. 2000. Individual variation in acorn production by five species of southern Appalachian oaks. *Forest Ecology and Management* 132: 199–210.
- INAMHI. 1994. *Anuario meteorológico*. Instituto Nacional de Meteorología e Hidrología. Quito, Ecuador.
- . 1999. *Boletín meteorológico mensual*. Instituto Nacional de Meteorología e Hidrología. Quito, Ecuador.
- . 2000. *Boletín meteorológico mensual*. Instituto Nacional de Meteorología e Hidrología. Quito, Ecuador.
- JANZEN, D. H. 1981. Seed predation by Orange-chinned Parakeets in Costa Rica. *Auk* 98: 841–844.
- KARUBIAN, J., J. FABARA, D. YUNES, J. P. JORGENSEN, D. ROMO, AND T. B. SMITH. Temporal and spatial patterns of macaw abundance in the Ecuadorian Amazon. *Condor* 107: 617–626.
- LEVEY, D. J., W. R. SILVA, AND M. GALETTI (eds.). 2002. *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International, New York.
- LÓPEZ-LANÚS, B. 1999. The biology of Great Green Macaw *Ara ambigua* in southwest Ecuador. *Pageienkunde* 3: 147–169.
- MOEGENBURG, S. M., AND D. J. LEVEY. 2002. Prospects for conserving biodiversity in Amazonian extractive reserves. *Ecology Letters* 5: 320–324.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DE FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- NEILL, D. A. 1997. Ecuadorian Pacific coast mesic forests. In: *Centres of plant diversity: a guide and strategy for their conservation*, vol. 3 (S. D. Davis, V. H. Heywood, O. Herera-Macbride, J. Villa-lobo, and A. C. Hamilton, eds.), pp. 508–512. IUCN, Cambridge, UK.
- OWENS, I. P. F., AND P. M. BENNETT. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences* 97: 12144–12148.
- POULIN, B., G. LEFEBVRE, AND R. MCNEIL. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73: 2295–2309.
- RENTON, K. 2001. Lilac-crowned Parrot diet and food resource availability: resource tracking by a parrot seed predator. *Condor* 103: 62–69.
- . 2002. Seasonal variation in occurrence of macaws along a rainforest river. *Journal of Field Ornithology* 73: 15–19.
- . 2004. Agonistic interactions of nesting and non-breeding macaws. *Condor* 106: 354–362.
- SAS INSTITUTE. 2002. SAS Online Doc Version 9.1.3 Cary, NC.
- SNYDER, N. P., P. MCGOWAN, J. GILARDI, AND A. GRAJAL. 2000. *Parrots. Status survey and conservation action plan 2000–04*. IUCN, Switzerland, and Cambridge, UK.
- STATTERFIELD, A. J., AND D. R. CAPPER. 2000. *Threatened birds of the world*. Birdlife International, Cambridge, UK.
- TERBORGH, J. 1986. Keystone plant resources in the tropical forest. In: *Conservation biology: the science of scarcity and diversity* (M. E. Soulé, ed.), pp. 330–344. Sinauer, Sunderland, MA.
- DE VALVERDE, F. M. 1991. *Estado actual de la vegetación de la Cordillera del Chongon-Colonche*. Universidad de Guayaquil, Ecuador.
- VALENCIA, R., N. PITMAN, S. LEÓN-YÁNEZ AND P. M. JØRGENSEN. 2000. *Libro rojo de las plantas endémicas del Ecuador*. Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
- WALTMAN, J. R., AND S. R. BEISSINGER. 1992. Breeding behavior of the Green-rumped Parrotlet. *Wilson Bulletin* 104: 65–84.
- WAUGH, D. 1995. Buffon's Macaw in Ecuador: the urgency for conservation action. *Psittascene* 7: 1–5.
- YAMASHITA, C., AND M. P. VALLE. 1993. On the linkage between *Anodorhynchus* macaws, palm nuts, and the extinction of the Glaucous Macaw. *Bulletin of the British Ornithologists' Club* 113: 53–59.