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THE DIET OF THE OILBIRD IN VENEZUELA

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Resumen. El Gúacharo (*Steatornis caripensis*), es un frugívoro Suramericano de hábitos nocturno que anida colonialmente en cuevas ubicadas en regiones selváticas desde Trinidad hasta Perú y Bolivia. Hemos estudiado la dieta de una colonia de Gúacharos al noreste de Venezuela (Caripe, Estado Monagas), desde Julio de 1985 hasta Enero de 1988, haciendo énfasis en la composición de especies de frutas, disponibilidad estacional, contenido energético y nutricional de las pulpas y morfometría de las frutas y semillas. Los Guácharos consumieron las frutas de aproximadamente 32 especies de árboles, de los cuales 19 pertenecieron a la familia Lauraceae, 9 a Palmae, 3 a Burseraceae y 1 Araliaceae. La contribución porcentual de cada una de estas familias a la dieta, estimada mediante la recolección de las semillas regurgitadas por adultos y pichones de la colonia, fue: Lauraceae 43.9 %, Palmae 46.5 %, Burseraceae 9.3 % y Araliaceae 0.4 %. Sin embargo, considerando el porcentaje de pulpa consumida, las lauraceas (47.1 %) fueron mas importantes que las palmas (22.1 %) y las Burseraceas (30.7 %). La mayoría de las especies de Lauraceae mostró un período de fructificación bien definido mientras que las palmas, en contraste, fueron poco estacionales. *Dacryodes trinitensis*, la principal Burseraceae de la dieta, fructificó a intervalos supra-anuales. El período reproductivo de los Guácharos coincidió con el período de máxima disponibilidad de frutas de Lauraceae. Las frutas de los laureles mas importantes de la dieta comenzaron a madurar en Marzo durante el período previo a la postura de los huevos y alcanzaron un máximo desde Abril, cuando comienza la postura de los huevos, hasta Julio, cuando la mayoría de los nidos tienen pichones grandes. Durante la mayor parte de la estación no reproductiva los Guácharos dependieron principalmente de las frutas de palmas. La pulpa de las lauraceas consumidas tiene en promedio, en base a materia seca, en promedio, un alto contenido de lípidos (49.6 %) y de energía (31.8 kJ por g) y un contenido de Nitrógeno de 1.47 %. Las palmas presentaron un menor contenido de lípidos (12.5 %) y de energía (23.2 kJ por g) y un contenido de Nitrógeno de 1.52 %. Las Burseraceae fueron mas ricas en Nitrógeno (2.38 %). Dentro del grupo de frutas consumidas en nuestra zona de estudio, no encontramos ningún patrón que relacionara aquellas características de las frutas que puden ser consideradas como beneficiosas para los pájaros (contenido de energía o de Nitrógeno de las pulpas o su porcentaje de materia seca) y aquellas, como la masa de las semillas, que pueden acarrear un costo a las aves que las consumen. Se discuten las consecuencias de tener una dieta rica en lípidos y en energía relación a los hábitos frugívoros de los Guácharos.

Abstract. The Oilbird (*Steatornis caripensis*) is a nocturnal frugivore that breeds and roosts in caves in forested areas from Trinidad through to Peru and Bolivia. We have studied the diet of a colony of Oilbirds in north-eastern Venezuela (Caripe, Monagas State), from July 1985 to January 1988, emphasizing the species composition of the fruit plants utilized, seasonality of fruit availability, energy content and nutrient composition of the fruit pulp, and fruit and seed dimensions. Oilbirds ate the fruits of 19 species of Lauraceae, 9 of palms, 3 of Burseraceae, and 1 of Araliaceae. The proportions to the diet contributed by each of those families, estimated from collections of seeds regurgitated by Oilbirds in the study colony, were: Lauraceae 43.9 %, Palmae 46.5 %, Burseraceae 9.3 % and Araliaceae 0.4 %. However, when considering proportions of fruit pulp consumed, Lauraceae (47.1 %) were more important that palms (22.1 %) and Burseraceae (30.7 %). Most species of Lauraceae had a clearly defined, but rather prolonged, fruiting season. Palms, in contrast, showed little seasonality. *Dacryodes trinitensis*, the most important Burseraceae eaten, produced fruit at supra-annual intervals. The breeding season of Oilbirds in the study area coincides with the period of maximum Lauraceae fruit availability. The fruits of the most important laurels of the diet begin to ripen in March during the pre-laying period, and peak from April, when egg laying begins, through July, when most nests have well-developed young. During the non-breeding season Oilbirds depended mainly on palms. The pulp of Lauraceae fruit had on average, on a dry matter basis, a very high lipid (49.6 %) and energy content (31.8 kJ per g) and a Nitrogen content of 1.47 %. Palms had a lower lipid (12.5 %) and energy content (23.2 kJ per g) and a Nitrogen content of 1.52 %. Burseraceae had the highest Nitrogen content (2.38 %). Within the set of fruits used by Oilbirds in our study area no simple pattern emerged between fruit characteristics that could be considered rewarding to the birds (such as energy or Nitrogen content of the pulps) and those, such as seed load, that could be considered costly. We discuss the consequences of using a lipid and energy rich diet in relation to frugivory in Oilbirds. *25 September 1994.*

Key words: Oilbird, Steatornis caripensis, *fruits, frugivory, Lauraceae, Burseraceae, Palmae, Neotropics, Venezuela.*

INTRODUCTION

Fruit characteristics such as energy density and nutrient composition of the pulp, seed size or the seed to pulp ratio affect the ecology, behavior, and physiology of birds. For instance, seed size limits the number and kinds of consumers that take fruits (Wheelwright 1985, Lambert 1989) and the ways that seeds are handled by the birds (Levey 1987, Levey & Grajal 1991). Frugivores that feed on succulent, energy dilute fruits typically have brief gut transit times and must consume large quantities of food daily (Karasov & Levey 1990). In contrast, frugivores that feed on lipid-rich fruits retain the food longer and need to process proportionally smaller quantities (Bosque and Parra 1992, Place and Stiles 1992). The length of time that the food is retained in the bird's gut might, in turn, affect the seed deposition pattern (Clench & Mathias 1992). Knowledge of fruit characteristics is essential to fully understand interactions between fruits and frugivores.

The cave dwelling Oilbird (*Steatornis caripensis*) is one of the few bird species that can subsist exclusively on fruit as well as raise their young on them (Snow 1961, 1962). In Trinidad, where Snow (1962) studied the Oilbird's diet extensively, he found that they largely select fruits belonging to only three plant families: Lauraceae, Palmae and Burseraceae. In Venezuela and Ecuador the diet of Oilbirds is less well known but a similar taxonomic composition of food plants has been reported by Tannenbaum & Wrege (1978) and B. K. Snow (1979). Analysis of the pulp of some of those fruits indicates that they have non-succulent pericarps, are rich in fat and have a protein content that Snow (1962) considered to be higher than that of succulent fruits (Snow 1962, White 1974, B. K. Snow 1979).

Nutritional and energetic properties of fruit pulp consumed by Oilbirds are of interest because nestling growth in this species seems to be limited by dietary protein, rather than energy (Snow 1962, White 1974, Ricklefs 1976). Extensive fat deposits that nestlings accumulate before fledging seem to be the consequence of feeding on an energy rich but rather nitrogen poor diet (Foster 1978, Thomas *et al.* 1993).

The Oilbird (body mass c. 415g), the only nocturnal frugivorous bird, is distributed along mountain chains from Trinidad to Perú and Bolivia (Hilty and Brown 1986). Birds nest and roost in the high ledges of caves, orienting by echolocation (Griffin 1953, Suthers & Hector 1985). Nightly they leave their caves to forage for fruits in the surrounding forest. One to three Oilbirds nestlings are attended by both parents and spend 95 to 120 days in the nest. Throughout its growth period they deposit extensive fat reserves becoming approximately 50 % heavier than adults before fledging (Snow 1961, White 1974, Tannenbaum & Wrege 1978, Ramírez 1987).

In this work we document the diet of an Oilbird population in north-eastern Venezuela, emphasizing the species composition of fruiting plants utilized and seasonality of fruit availability, energy density and nutrient composition of the fruit pulp, and fruit and seed dimensions. This information is in turn necessary to improve our knowledge of how Oilbird nestlings grow on a diet of only fruit pulp (see Bosque & Parra 1992, Thomas *et al.* 1993). In addition, knowledge of the Oilbird's diet is useful in the design of protected areas for conservation purposes of this species in Venezuela.

STUDY SITE AND METHODS

The study was conducted at Gúacharo Cave (10° 10'N, 63° 33' W), near the town of Caripe, Estado Monagas, in north-eastern Venezuela. The Guácharo Cave lies in a mountainous massif with elevations fluctuating from 500 m in the valleys to mountain-tops generally below 1800 m, maximum elevation in the area is 2500 m. Rainfall is seasonal with a rainy period between May and November but some rain falls most of the year. Mean annual precipitation is 1200 mm and mean annual temperature is approximately 21° C. Montane forest covers large expanses east of the cave but around its immediate vicinity it is extensively planted with coffee and orange.

The bird population

The cave hosts a breeding population of approximately 10000 Oilbirds (Tannenbaum & Wrege 1978, Bosque & Ramírez 1988). Reproduction is seasonal, most egg laying occurring in the second half of April and May. Eggs are occasionally laid however as early as mid-March and as late as mid-July. Most pairs have nestlings by June and large nestlings occur in nests in July and August. Most fledging occurs before September (Tannenbaum & Wrege 1978, Ramírez 1987).

During the study period (July 1985 to January 1988) most birds migrated from the cave after the breeding seasons of 1985 and 1986. Between November 1985 and February 1986 and again during the same months in 1986—87, less than 300 birds remained in the cave (Bosque & Ramírez 1988). Birds returned to the cave before the following breeding season. In contrast, bird numbers remained high (3000—6000) during the post-breeding season of 1987—88 (pers. observ.).

The Guácharo cave is one of approximately 25 caves with Oilbirds that the Sociedad Venezolana de Espeleología has explored in the region (Bosque 1978, 1986). Extensive movements of birds occur between these caves (Bosque & Ramírez 1988).

Seed traps

Both adult and nestlings Oilbirds swallow fruits whole and regurgitate the seeds in the cave. To determine the fruit species eaten by Oilbirds and their relative abundance in the diet, we placed seed traps made of wire mesh (1.1 x 1.1 m) on the cave floor to collect recently regurgitated seeds from adults and nestlings on ledges above. Five traps were run continuously from 1 July to 15 November 1985. From December 1985 to January 1988 4 nets were run, usually for 3 or 4 days at monthly or bi-monthly intervals. Total trap-days per year were as follows: 705 in 1985, 109 in 1986, 68 in 1987 and 8 in 1988. We did not know the number or stage of the nests that contributed seeds to the seed traps. A reference collection of the seeds was made for species determination.

Phenology

We randomly selected trees for phenological studies from undisturbed forests and plantations up to 30 km from the cave. Trees were individually marked and floral and vegetative samples were collected for species identification (see acknowledgements). Voucher specimens were deposited in the Herbario Nacional (VEN) and in the Universidad Simón Bolívar herbarium in Caracas. Additional voucher specimens of Lauraceae were deposited in the Missouri Botanical Garden and those of palms and Burseraceae in the New York Botanical Garden.

Approximately 10 marked individuals of the more common species but only 2 or 3 of the rarer ones (*Beilschmiedia sulcata*, *Persea rigens*) were visited at approximately monthly or bi-monthly intervals between February 1986 and August 1988. Two additional visits were made in July and August 1990. We recorded fruiting status of marked trees as not in fruit, few mature fruits or heavily fruiting. Flowering was also recorded but it is not reported here. Although our methods provide only a rough estimate of fruit availability they were adequate for our objective of assessing large-scale temporal patterns of fruit abundance. Since Oilbirds forage over vast areas (Snow 1962, Roca & Gutierrez 1991), an accurate estimate of fruit availability that would take into account tree species density would be extremely difficult.

Lauraceae is taxonomically a difficult group and there is some uncertainty in the determination of some of the species. Specifically, Nectandra aff. laurel most likely involves a complex of species (Jens Rohwer, *pers. comm.*). Furthermore, we were not able to secure adequate floral samples of the species reported here as *Trattinickia* sp. and Araliaceae (G. sp.), their tentative identification was based on comparisons of their rather peculiar seeds with those depicted in Snow (1962, his Fig. 3). We did not distinguish between the seeds of *Roystonea regia* and *R. venezuelensis*, seeds belonging to either of those species are indicated as *Roystonea* spp.

Proximate analysis and energy content

We collected fresh, ripe fruits from positively identified trees and kept them frozen in air tight plastic bags until processing. Pulp samples were dried at 55 °C to constant mass to determine water content and then ground for further analysis. Proximate analysis was done according to methods of the American Organization of Analytical Chemists (Horwitz 1984) at the Laboratorio de Producción Animal, Universidad Central de Venezuela in Maracay. Nitrogen was determined by micro-kjeldahl with a Tecator model 1003 and the lipid fraction (crude fat) was extracted with anhydrous ether in a Labconco Goldfisch apparatus. Samples were analyzed in duplicate or until differences between replicates were less than 5 %.

The combustion energy of dry pericarps was measured in a Parr adiabatic calorimeter calibrated with benzoic acid. Combustion energy values were corrected for ash content, heat of combustion of fuse wire (Parr 45C10 nickelchromiun) and acid formation according to the specifications of the manufacturer. Ash (mineral content) was determined by mass change after combustion for 6hr in a muffle furnace at 500 ° C. All ash and calorimetric samples were run in triplicates and coefficient of variation was always less than 3 %. All energy values are ash-free (AFDM).

We also measured Sodium and Calcium content of the fruits of a few species by flame spectophotometry.

Analyses are reported as percent of dry matter.

Fruit and seed dimensions

We measured length and width of 15 to 20 fruits and seeds of each species to the nearest 0.1 mm with vernier calipers. Fruit and seed mass of larger fruits were measured with a balance accurate to 0.1 g, but those weighing less than 5 g on a balance accurate to 0.01 g. We estimated fruit and seed volume by displacement of water volume on graduated cylinders of 1 or 0.1 ml appreciation. Standard Deviations are not available for volume estimates since several fruits, or seeds, were placed together in the same cylinder.

Statistical tests used are indicated in the text.

TABLE 1. Yearly number, percentage of seeds collected and estimated percentage of pulp contributed by each species in Cueva del Guácharo, eastern Venezuela. Data from seed traps between July 1985 and January 1988.

Family/Species				Total seeds(1)		Approx. % of(2)
	1985	1986	1987	Number	%	total pulp mass
LAURACEAE						47.1
Beilschmiedia sulcata	1	0	5			0.1
Nectandra aff. *laurel*	648	417	643			2.0
Nectandra membranacea	472	4034	210	4716	5.4	7.3
Nectandra turbacensis	72	304	569	945	1.1	0.8
Ocotea aff. *austinii*	0	54	18	72	0.1	1.7
Ocotea floribunda	823	29	610	1433	1.6	9.2
Ocotea sp.	0	5	12	17	(**)	0.2
Persea coerulea	6756	2233	5864	14853	16.9	6.1
Persea rigens	29	146	3	178	0.2	1.9
Phoebe cinammomifolia	517	6127	7399	14043	16.0	17.8
Pleurothyrium costanense	16	10	2	28	(**)	
G. sp. 1	0	151	25	176	0.2	
Other Lauracea(3)	272	51	36	359	3.8	
PALMAE				40807	46.5	22.1
Bactris setulosa	1	7	4	12	(**)	0.1
Euterpe precatoria	5634	2273	991	8900	10.1	9.3
Euterpe sp.	165	13	0	178	0.2	
Geonoma densa	9814	1320	8700	19862	22.6	3.5
Jessenia bataua	80	11	15	128	0.1	1.7
Prestoea acuminata	6096	858	3323	10279	11.7	7.5
Prestoea sp.	870	186	329	1385	1.6	
Roystonea spp.	55	1	7	63	0.1	
BURSERACEAE				8156	9.3	30.7
Dacryodes trinitensis	7099	0	557	7656	8.7	30.7
Protium sp.	0	13	322	335	0.4	
Trattinnickia? sp.	140	15	10	165	0.2	
ARALIACEAE				347	0.4	
Gen. sp.	60	0	287	347	0.4	
TOTAL				87844		

(1) Seeds collected during January 1988 (N = 55) are not shown separatly but are included in the total. The symbol "***" indicates less than 0.1 % of total seeds. (2) Percentages of pulp contributed by each species have been calculated considering only those species for which we had data on pulp mass. (3) Includes *Aniba citrifolia* and *Ocotea aff. whitei.*

RESULTS

Seed traps

We collected a total of 87844 seeds (Table 1). Seeds belonged almost exclusively to three plant families: Lauraceae, Palmae and Burseraceae. We found the seeds of 19 species of Lauraceae, of these, 12 were determined to species and one to genus. The remaining 6 species were rather rare in the sample and could not be properly identified. The rest of the diet included 9 species of palms, 3 Burseraceae and 1 Araliaceae, bringing the total fruit species used by Oilbirds in the Caripe area to approximately 32. However, 8 species accounted for 93.3 % of all seeds brought to the cave. Palms were numerically dominant (46.5 % of all seeds) but contributed less pulp (22.1 %) than Burseraceae (30.7 %) and Lauraceae (47.1 %).

Seeds from fruits consumed were brought to the cave in a seasonal pattern (Fig. 1). Seed numbers started to increase around April coinciding with the period of nest building and egg laying, and peaked in June-August when most nests had well grown nestlings. By September, when most nestlings have fledged, seed numbers dropped rapidly. Thereafter, from October through March, few or no seeds were collected during our monthly sampling, during this period there are fewer birds in the cave (*see* Study Site and Methods) and those remaining regurgitate most seeds in the forest before returning to the cave.

Fruiting seasonality

Most species of Lauraceae had a clearly defined, but rather prolonged, fruiting season (Table 2). The only Lauraceae that produced fruits throughout the year was *Ocotea austinii*, which accoun-

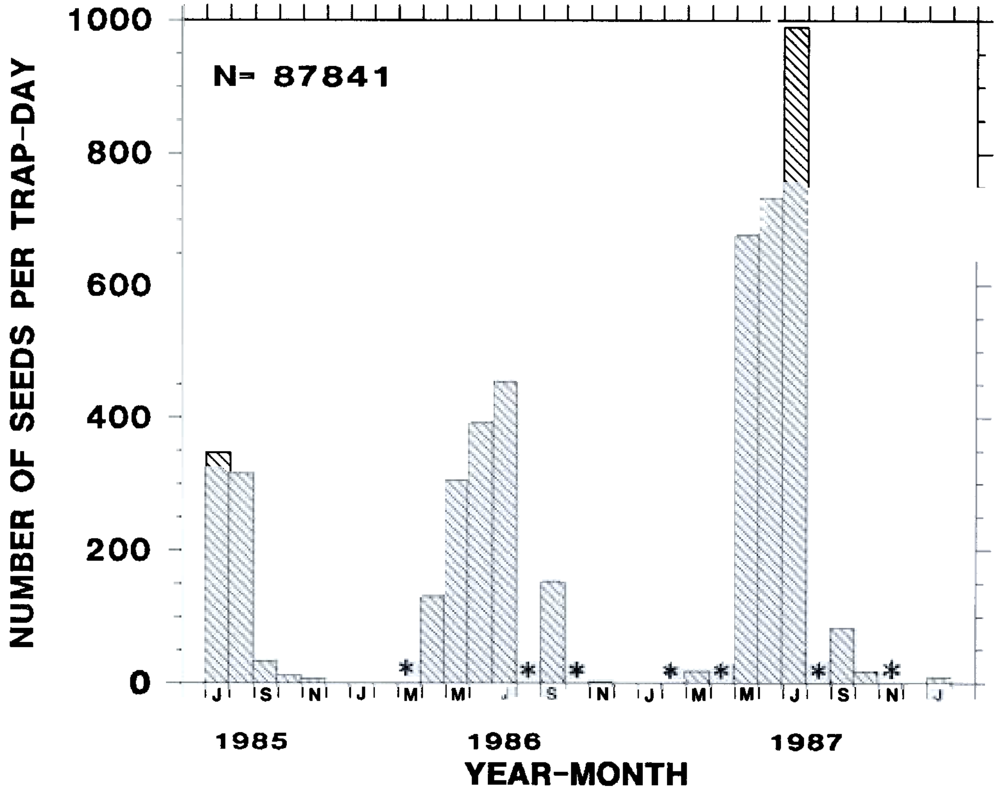

FIG. 1. Monthly average of total number of seeds collected daily in seed traps during the study period in Cueva del Guácharo. The asterisks indicate those months that were not sampled.

ted for only 0.1 % of seeds brought to the cave (Table 1). Number of species of Lauraceae in fruit was greatest between February and July but the species that contributed most pulp to the diet, *Phoebe cinnamomifolia*, *Ocotea floribunda* and *Nectandra membranacea*, had peak fruiting periods in April and May, and *Persea coerulea* in July and August (Table 2). From September onwards, at the end of the breeding season, availability of Lauraceae decreases sharply. The few species that produce some fruit during the non-breeding season are rare in the forest and contribute little to the seed pool.

Most palms, in contrast to laurels, did not have a clearly defined fruiting season (Table 2). Small numbers of individuals in fruit could be found in the forest during any month of the year, but fruit seemed to be less abundant from September to November. The only seasonally fruiting palm was *Bactris setulosa* which has little importance for the Guácharo Cave population but is more important for birds that inhabited less perturbed forest sites (*per. observ.*).

Changes in the composition of seeds brought to the cave by the birds reflected changes in the availability of fruit belonging to different species (Fig. 2). During the early part of the breeding season birds relied more heavily on *Phoebe cinnamomifolia* and *Nectandra membranacea* (in 1986) among the Lauraceae. The end on the fruiting season of those species in August coincides with the fruiting peak of *Persea coerulea* (Table 2) which then becomes the most important laurel of the diet. The more uniform availability of palms throughout the year was also reflected in the birds' diet. Thus, the most important palms, *Geonoma densa*, *Euterpe precatoria* and *Prestoea acuminata* were consumed rather evenly throughout the breeding season (Fig. 2). From the end of the fledging period in late September

TABLE 2. Fruiting periods of species eaten by Oilbirds in the vicinity of Cueva del Guácharo as determined from visits to individually marked plants in the surrounding forest. X indicates main fruiting period; x indicates months of less abundant crop.

Family/Species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
LAURACEAE												
Beilschmiedia sulcata			X									
Nectandra aff. laurel		x	x	x	X							
N. membranacea		x	x	X	X	x	x					
N. turbacensis		X	x			X	X					
Ocotea aff. austinii		x	x	X	X	x	x					
O. floribunda			x	X								
Ocotea sp.			x									
Persea coerulea							X	X				
P. rigens		X	X									
Phoebe cinnamomifolia		x	x	X	X							
Pleurothyrium costanense			x						x			
Number of species in fruit	4	6	10	6	5	6	5	2	5			
PALMAE												
Bactris setulosa					x	X	X					
Euterpe precatoria	x		x		x	x	x	x	x	x	x	
Geonoma densa	x	X	X		x	x	x	X	X	X	x	x
Jessenia bataua(1)	X				x	x	x		x	x	X	X
Prestoea acuminata	x		x	x	X	X	X	x	x	x	x	x
Number of species in fruit	4		3	4	5	5	5	3	4	4	4	3
BURSERACEAE												
Dacryodes trinitensis					X	X	X					
ARALIACEAE												
G. sp.									X			

(1) Individuals of this species were monitored away from the study area at Guatopo National Park, in central Venezuela. Supplementary information was added from examination of seeds brought to the cave by birds.

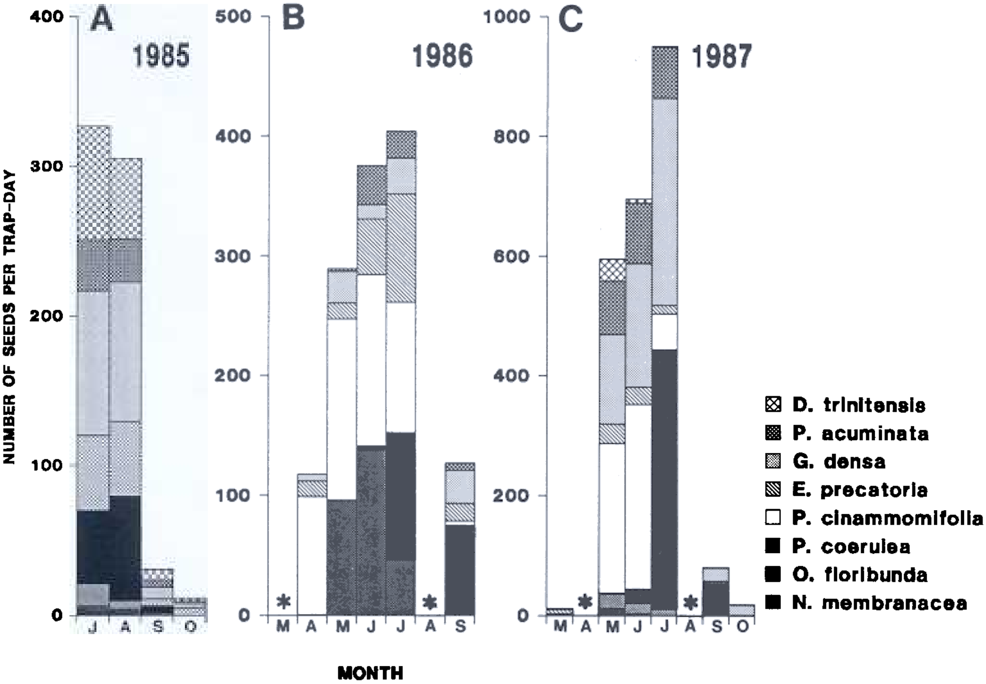

FIG. 2. Monthly average of number of seeds of the most important species collected daily at seed traps during three reproductive seasons at Cueva del Guácharo. The asterisks indicate those months that were not sampled. Note differences in scale among years.

and through most of the non-breeding season until February, search for fresh seeds in the cave indicated that birds rely almost exclusively on palms during this period, very few fresh Lauraceae or Burseraceae seeds could be found then.

Fruit consumption of *Dacryodes trinitensis* (Burseraceae) differed among years. In 1985, birds brought large numbers of seeds to the cave, but the crop apparently failed in 1987 and few seeds were brought. Since Dacryodes seems to fruit at bi-annual intervals (Snow 1962, and *pers. observ.*), no seeds were found in 1986.

Proximate analysis and energy content

The pulp of Lauraceae consumed by Oilbirds in Caripe typically has a high lipid and energy content. Since the water content of the pulp is rather low, energy content per g of fresh pulp is also very high (Table 3). Pulp composition of palms was more variable than those of Lauraceae. Lipid content ranged from a high of 28.3 % in *Bactris setulosa* to a low of 1.1 % (dry mass) in *Prestoea acuminata*. Water content was also highest in *Bactris setulosa* (70.5 %) and lowest in the very dry pulp of *Jessenia bataua* (37.3 %).

Overall, fat content of dry pulp and energy content of dry and fresh Lauraceae pulp were higher than those of palms (Mann-Whitney U-test = 9.51, 8.55 and 7.51; $P = 0.009$, 0.014 and 0.023 respectively). Palms had significantly higher fiber and ash contents (Mann-Whitney U-test = 7.93 and 6.72; $P = 0.019$ and 0.035 respectively). No significant differences existed in the water or nitrogen content of the pulp of palms and laurels. The very high ash (and Sodium) content of *Geonoma densa* is noteworthy. Both Burseraceae and Araliaceae had a watery pulp with a low fat content and energy content but with a rather high nitrogen content.

When all fruits are considered, a significant positive correlation exists between energy content and fat content of the pulp ($r = 0.96$, $N = 15$, $P < 0.001$; Fig. 3). The high coefficient of determination of this linear relationship ($r^2 =$

TABLE 3. Composition and energy content of the pulp of fruits eaten by the Oilbirds of Cueva del Guácharo. Standard Deviations for family averages are given in parenthesis. For comparison, average pulp composition of other fruits are shown at the bottom of the table.

Family/Species	Water (%)	Percent of dry mass						Energy content[1]	
		Nitrogen				Ca++	Na+		
LAURACEAE	57.9(7.4)	1.47(.58)	49.6(12.8)	19.1(4.1)	3.1(0.9)				
Beilschmiedia sulcata	67.6	1.84	33.3	15.1	2.5				
Nectandra aff laurel	57.7	2.54	63.2	20.4	2.7				
N. membranacea	52.9	1.06	67.8	15.5	2.7				
N. turbacensis	50.0	1.76	60.2	19.9	3.3	0.07	0.01		
Ocotea aff. austinii	65.4	0.67	54.8	23.1	5.3				
O. floribunda	61.8	1.71	52.4	18.4	2.7				
Ocotea sp	52.1	0.88	36.0	12.5	2.3				
Persea coerulea	43.7	1.14	46.5	25.4	3.0				
P. rigens	64.6								
Phoebe cinnamomifolia	60.7	1.60	34.0	21.5	3.8	0.08	0.25		
PALMAE	51.4(12.0)	1.52(.82)	12.5(11.2)	38.1(14.8)	7.1(7.6)				
Bactris setulosa	70.5	2.96	28.3	21.4	7.3				
Euterpe precatoria	51.3	1.01	8.0	45.3	1.8				
Geonoma densa	48.5	1.39	5.5	35.4	20.1	0.21	7.70		
Jessenia bataua	37.3	1.04	19.7	29.0	3.1	0.04	0.05		
Prestoea acuminata	49.5	1.20	1.1	59.5	3.2				
BURSERACEAE									
Dacryodes trinitensis	79.4	2.38	2.5	27.5	4.8	0.24	0.10	19.3	
ARALIACEAE									
Gen. sp.	68.0	1.71	3.6	23.1	6.8			21.9	7.0
NEOTROPICAL FRUITS[2]	71.3	1.77 [3]	18.5		5.6				
MEDIAN FOR 29 FAMILIES[4]	79.0	1.48 [3]	5.2						

Ash-free. [2] From Jordano (1992). [3] Calculated from the original data as dry protein/4.4. [4] From Moermond & Denslow (1985).

TABLE 4. Characteristics of fruits and seeds eaten by Oilbirds in the Cueva del Guácharo area. Averages and (standard deviations) were calculated from 15 to 25 fruits or seeds of each species.

Family/Species	fruit					seed			
	color[1]	length (mm)	width[2] (mm)	mass (g)	volume (ml)	length (mm)	width[2] (mm)	mass (g)	volume (ml)
LAURACEAE									
Beilschmiedia sulcata	pu.-bl.	54.2(3.4)	21.1(1.4)	17.9(2.3)	15.9	52.8(3.4)	18.8(1.3)	13.2(1.8)	10.9
Nectandra aff. laurel	bl.-pu.	15.1(2.1)	11.2(1.1)	1.44(.42)	1.31	13.5(1.7)	9.5(1.0)	0.90(0.32)	0.79
N. membranacea	pu.-bl.	12.4(0.7)	10.5(0.5)	1.41(.22)	1.20	9.9(0.7)		0.74(.14)	0.60
N. turbacensis	pu.-bl.	12.9(1.1)	8.6(1.2)	0.77(.18)	0.81	12.1(0.7)	6.3(0.6)	0.41(.09)	0.31
Ocotea aff. austinii	pu.	35.4(1.8)	26.1(1.9)	18.3(2.3)	17.6	33.8(1.6)	19.4(1.4)	8.00(1.0)	7.00
O. floribunda	pu.	21.6(1.2)		6.6(0.9)	4.5	18.3(1.0)		3.85(0.6)	2.9
Ocotea sp.	pu.-bl.	48.4(4.1)	22.9(0.9)	16.9(1.8)		45.4(4.5)	19.8(0.9)	10.9(1.5)	
Persea coerulea	pu.-gr.	7.9(0.5)	10.2(0.5)	0.68(.08)	0.47	6.6(0.5)	8.4(0.9)	0.50(.08)	0.33
P. rigens		32.7(2.3)	21.0(1.5)	12.3(2.0)	10.3	30.8(2.1)	17.0(0.8)	7.63(1.4)	6.67
Phoebe cinnamomifolia	bl.-pu.	16.4(0.8)	8.6(0.5)	1.02(.16)	1.93	14.0(1.4)	6.5(0.4)	0.48(.09)	1.93
PALMAE									
Bactris setulosa	red	19.6(2.7)	18.8(1.0)	5.36(1.69)	5.00	16.2(4.0)	15.6(1.1)	3.03(1.0)	2.66
Euterpe precatoria	pu.	12.0(0.4)		1.14(0.13)	1.24	10.2(0.6)		0.69(.10)	0.76
Geonoma densa	br.-pu.	7.3(0.7)		0.23(0.03)	5.50	6.4(0.5)		0.14(.01)	3.50
Jessenia bataua	pu.-bl.	35.5(1.8)	25.0(1.2)	14.7(2.14)	11.88	31.9(1.7)	22.1(1.3)	8.88(1.32)	8.44
Prestoea acuminata	gr.-bl.	13.0(0.6)		1.27(0.12)	1.05	10.7(0.7)		0.96(.09)	0.80
BURSERACEAE									
Dacryodes trinitensis	gr.	25.2(0.9)	15.9(0.9)	3.23(0.43)	1.48	23.9(0.7)	14.0(0.9)	1.51(0.43)	1.07
ARALIACEAE									
Gen. sp.	gr.	17.7(2.7)	15.1(1.5)	3.12(1.10)	4.00				

[1] bl. = black, pu. = purple, gr. = green, br. = brown. [2] Only lenght is given for those fruits or seeds that are approximately roun

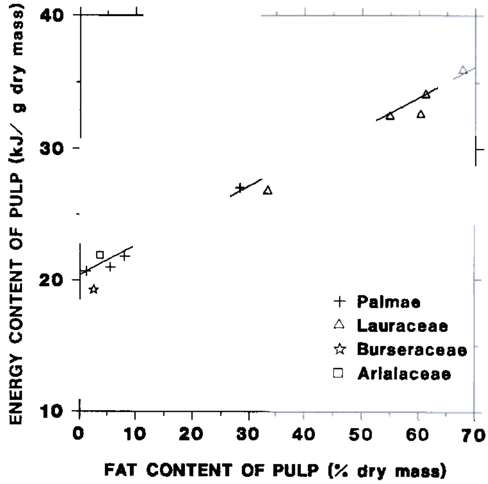

FIG. 3. Relationship between energy and fat content of fruit pulps eaten by Oilbirds of Cueva del Guácharo. The regression equation is $Y = 20.4 + 0.23X$ ($r = 0.96$, $N = 15$, $P < 0.001$).

0.92) indicates that most of the variation in energy content of the pulp can be explained by variations in its fat content.

Although there was no clear relationship between the energy and protein content of pericarps (Fig. 4), it is of interest that none of the fruits consumed by Oilbirds fall in the lower left quadrant, where fruit with a low energy and a low nitrogen content would fall. The distribution of points in the figure suggests that Oilbirds use fruits which have a high energy or a high nitrogen content or those which have both, but that it does not include in its diet species that have neither.

Fruit and seed morphometrics

With the single exception of the unidentified species of Araliaceae, Oilbirds fed on single seeded fruits. Fruit mass (including seed) ranged from 0.23 g (*Geonoma densa*) to 17.9 g (*Beilschmiedia sulcata*). Similarly to fruit consumed by Oilbirds in Trinidad (Snow 1962), most fruit consumed in Caripe were black or purple-brownish (Table 4).

Within the set of fruits used by Oilbirds in our study area no simple pattern emerged between fruit characteristics that could be considered rewarding to the birds and those that could be considered costly (*e.g.*, seed load). We found no significant linear relationship between energy content of dry or fresh pulp and seed mass ($r = 0.04$, $P = 0.88$, $N = 15$; $r = 0.22$, $P = 0.41$, $N = 15$ respectively), water content of pulp and seed mass ($r = 0.14$, $P = 0.60$, $N = 16$), or nitrogen content of pulp and seed mass ($r = 0.22$, $P = 0.43$, $N = 15$). There also was no tendency for the amount of pulp energy per unit of seed mass to increase as seed mass increased ($r = 0.17$, $P = 0.55$, $N = 15$; Fig. 5).

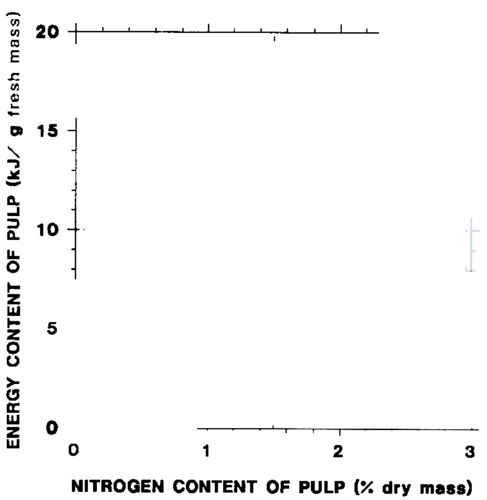

FIG. 4. Scatterplot of energy and nitrogen content of fruit pulps eaten by Oilbirds of Cueva del Guácharo. Note that there no fruits in the lower left quadrant. Symbols as in Fig. 3.

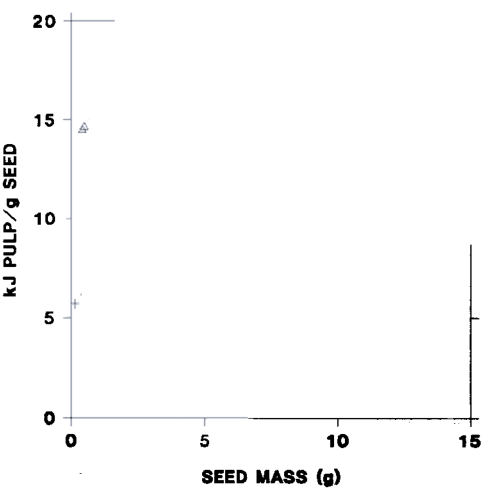

FIG. 5. Scatterplot of the amount of energy available from fruit pulp per unit of seed mass load vs. seed size in fruits eaten by Oilbirds of Cueva del Guácharo. Symbols as in Fig. 3.

DISCUSSION

Species composition and seasonality

The diet of the Oilbird has been examined in Trinidad (Snow 1962), Venezuela (Tannenbaum & Wrege 1978, this study) and Ecuador (B. K. Snow 1979). These studies together indicate that Oilbirds have a relatively narrow diet throughout their range. They eat almost exclusively the fruits of only three plant families: Burseraceae, Lauraceae and Palmae. Furthermore, within any one specific locality only a few species account for the majority of the diet. During our study, as in Trinidad, only 8 species accounted for 93 % of all fruit consumed (our calculations from Table VI in Snow 1962). The highly selective diet, and the fact that Oilbirds rely only on fruit for maintenance as well as for raising their nestlings, make this bird unique in specialization to an exclusive fruit diet.

In the Guácharo Cave, and in many other caves in northern Venezuela breeding is seasonal with a pronounced laying peak around April and May (Tannenbaum & Wrege 1978, Ramírez 1987, *pers. observ.*), corresponding with the availability of Lauraceae fruit. The fruits of the most important laurels of the diet begin to ripen in March during the pre-laying period of Oilbirds, and peak from April, when egg laying begins, through July, when most nests have well-developed young. During August most nests have nestlings that have already reached their peak body mass before undergoing a period of mass recession (Ramírez 1987) when their food demands decrease (Thomas *et al.* 1993). At this time and through September when fledging is over the only important Lauraceae available is *Persea coerulea*. This decline in Lauraceae availability at the end of the breeding season was also noted in the same area in 1976 (Tannenbaum & Wrege 1978). Use of palms is more constant throughout the breeding season and from October through January, during the non-breeding season, Oilbirds rely almost exclusively on them.

Our estimates of fruit availability are very rough since we did not actually quantify fruit production but only recorded the fruiting periods of the species involved (*see* Blake *et al.* 1990 for discussion). In the Caripe area during the non-breeding season Oilbirds might fly more than 100 Km in one direction in a single night from their roosting cave (Roca & Gutierrez 1991), making it extremely difficult to quantify fruit availability over such a huge foraging area. The question remains, do fruiting periods reflect true changes in fruit availability? In our study we believe that peaks of Lauraceae fruit availability roughly coincided with periods when we recorded the fruiting of the most important species of the diet. Conversely, periods of low Lauraceae fruit availability roughly correspond with periods when the most important species of the diet are not fruiting. The close correspondence between the periods when seeds were collected in the seed traps and the fruiting periods of the same species recorded independently in the forest suggest that Oilbirds were closely tracking changes in fruit availability.

In Trinidad, where the environment is less seasonal than in northern Venezuela, Oilbirds have a considerably longer breeding season. Young birds may be in the nest in any month of the year, but there is a marked peak of laying in the months December–May (Snow 1961, 1962). As in Venezuela, the period of greatest Lauraceae abundance occurs in the months April–June when most young are in the nest (Snow 1962).

Among-year differences in the number of seeds collected of some of the plant species, emphasises the importance of long term studies of the resources used by frugivores. Dacryodes trinitenses accounted for the largest percentage of pulp consumed during the 3-year study (30.7 %, Table 2), but was eaten extensively only in 1985. Had the study not included 1985, it could have erroneously concluded that Burseraceae was not an important resource for Oilbirds in Venezuela. Likewise, large among-year differences in the numbers of *Nectandra membranacea* (Fig. 2) were the result of crop failure in 1987 due to insect parasites. Palms also showed large among-year fluctuations. Similar fluctuations were noted for some of the plants in Snow's (1961, 1962) 5 year study.

Fruit morphometrics

Frugivores that swallow fruits whole extract nutrients and energy from fruit pulp while carrying an indigestible seed ballast. Potential relationships between the nutritious reward and the seed load are one of the basis for discerning patterns of costs and benefits in fruit-frugivore interactions (Snow 1971, McKey 1975, Herrera 1981). On the basis of theoretical grounds it can be expected that large seeded fruits should have more nutritious pulps than small seeded fruits (Snow 1971, Herrera 1981). Therefore, it was of interest to examine possible cost and benefit relationships within the set of fruit used by Oilbirds in our study area. Contrary to theoretical expectations, there was no clear relationship between rewarding characteristics of fruits, such as the energy or nitrogen content of the pulp, and seed mass.

Pulp composition and its consequences

The most distinctive characteristics of most of the pericarps processed by Oilbirds, when compared to other fruits, are a high lipid content, a low water content and a high energy content per unit of dry or fresh mass (Table 2). These properties of the fruits have important consequences for the frugivorous habits of the Oilbird as well as for its interaction with its food plants.

Although analysis of the energetic value of bird's food are generally made in terms of the energy content per unit of dry mass, birds guts process fresh, not dry, foodstuffs. Therefore, comparisons between the energy of bird's foodstuffs are more meaningful in terms of units of fresh mass. The fruits that Oilbird process have an energy content that ranks among the highest of bird foods (see Table 2 in Karasov 1990). The fraction of that energy that can be transformed into usable energy depends on the digestive efficiency of the bird. Oilbirds extract approximately 64 % of the total energy in the food (Bosque & Parra 1992). Therefore, the average metabolizable energy of Lauraceae pulp consumed by Oilbirds is approximately 8.4 $kJ \cdot g^{-1}$ fresh, and that of palms 7.1 $kJ \cdot g^{-1}$ fresh. In contrast, metabolizable energy of succulent fruits consumed by many other frugivores ranges from 1.9 to 3.7 $kJ \cdot g^{-1}$ fresh pulp [estimated from a metabolizable energy value of 12.4 $kJ \cdot g^{-1}$ dry (Karasov 1990), and an average water content of 70—85 % (Moermond & Denslow 1985, Jordano 1992)].

The use of such an energetic food source has important consequences regarding the frugivorous habits of Oilbirds. Oilbirds commonly raise 2 or 3 chicks on a diet of fruit only. During the period of their peak energy demand chicks are provisioned with approximately 160 g of fruit (including seeds) per night, about 45 % of the chick's body mass (Thomas *et al.* 1993). Thus, a pair of Oilbirds feeding two chicks will have to transport about 160 g each (about 39 % of its body mass), apart from their own food requirements. In contrast, frugivores that process succulent, energy dilute pulps must consume daily quantities of fruit approaching double their body mass for maintenance alone (Moermond & Denslow 1985, Studier *et al.* 1988). Adaptations to an energy rich diet is one of the key features that allows Oilbirds to subsist on a totally frugivorous diet.

In the Oilbird efficient utilization of dietary energy must be linked to a competent extraction of lipids. The digestion and absorption of lipids is a complex process involving emulsification of fats by bile, hydrolysis of fatty acids and esters, and absorption of hydrolized products (Castro 1985, Duke 1986). To process lipid-rich fruits birds must possess a number of gastrointestinal traits that permit efficient fat extraction (Place & Stiles 1992, Bosque & Parra 1992, Martínez del Rio & Restrepo 1993, Stiles 1993). In the Oilbirds one of these traits is a high retention time of the food in the gut which allows for a more complete digestion and absorption of lipids (Bosque & Parra 1992). Oilbird nestlings extract approximately 80 % of the pulp's lipids, but since young birds have immature guts it is possible that adult birds extract a larger fraction (Bosque & Parra 1992). Digestive features seemingly related to the Oilbird's lipid rich diet contrast with those of most other frugivores so far studied. Frugivores that feed on succulent fruits typically have rapid passage rates which allows them to process large quantities of pulp that is rich in easily absorbed nutrients (*see* summaries *in* Levey 1993, Martínez del Rio & Restrepo 1993).

It is important to note that average energy content of Lauraceae pulp reported in this work (31.8 $kJ \cdot g^{-1}$ AFDM) is considerably higher than those previously reported in the comprehensive reviews of Moermond & Denslow (1985) and Jordano (1992). Moermond and Denslow estimated an average of 12.7 $kJ \cdot g^{-1}$ dry mass (3.03 $Kcal \cdot g^{-1}$) and Jordano 18.1 $kJ \cdot g^{-1}$ dry mass (4.337 $Kcal \cdot g^{-1}$) for 24 and 27 species of Lauraceae respectively. The difference between these figures and our values are largely due to differences in the methods involved in calculations. Moermond and Denslow estimated energy content of pulp by using energy conversion factors for protein, lipid and carbohydrate constituents of the fruits's pericarps. Since only 40.5 % of the dry mass was accounted for in their calculation of Lauraceae, their estimated energy contents are unusually low. In fact, the caloric value estimated for Lauraceae, as well as those of several other families, is lower than that of any foodstuff component (*see* Table 2.1 *in* Robbins 1993). Jordano's value is likely to be similarly affected since he used the data from Moermond and Denslow (see footnote of Appendix in Jordano 1992). In turn, bomb calorimetry values given in this study include the heat of combustion of fiber most of which might not be energetically available to Oilbirds.

In comparison to other foods consumed by birds, fruits have a low protein content (*see* Table 5.3 *in* Jordano 1992). Because of its low protein content, or because of a low ratio of protein to calories, fruits have been considered inadequate to meet maintenance requirements of birds (Berthold 1976) or to support their rapid nestling growth (Snow 1962, Foster 1978, Ricklefs 1983).

In our study area Oilbirds feed on fruits that, on average, have similar protein (N) content to that of fruits belonging to many other plant families (Table 2). Nevertheless, like many other fruits, the pulps of Lauraceae and palms in our sample show a marked nutritional imbalance in their nitrogen to energy ratio. Compared to other fruits this is largely because of the very high energy content of those pericarps rather than because of a low nitrogen content (Table 2). The pericarps of Burseraceae and Araliaceae have a higher protein: calorie ratio (Table 2). The energy:protein imbalance of fruit pulp led Foster (1978) to propose that dry matter intake in totally frugivorous nestlings might be determined by nitrogen, rather than by energy, needs. According to this view Oilbird nestlings would have to assimilate more energy than required, thus accumulating extensive fat deposits. This "excess energy hypothesis" has been critically examined by Thomas *et al.* (1993) by comparing energy and nitrogen intake and expenditure during the nestling period. Their findings supported the excess energy hypothesis for the first half of the growth period but during the latter part, chicks continue to deposit fat at a rate that exceeds that predicted on the basis of nitrogen controlled intake.

Oilbirds have a number of apparent adaptations to enable them to subsist, as well as grow, on their relatively nitrogen poor fruit diet. Nestling growth is slow, thus lowering daily nitrogen requirements (White 1974, Ramírez 1987). Nitrogen maintenance requirements are low (Bosque & Parra 1992). Assimilation of dietary protein is high and conversion efficiency of dietary protein to tissue is also high (White 1974, Bosque & Parra 1992). Oilbirds however do not consume fruits that have very low nitrogen contents such as those eaten by frugivorous pteropodid bats which typically contain less than 0.12 % N fresh mass (Thomas 1984, Steller 1986).

As a whole, the fruits consumed by Oilbirds in Venezuela share most of the characteristics of plants considered to be involved in specialized dispersal systems (summary *in* Howe 1993). Many of them are large seeded (e.g., > 1 g), are not mechanically tough, have a highly nutritious pulp and have an extend fruiting season of several weeks or months. In addition, the large seeded species have low annual fecundities, producing crops of probably less than 1,000 fruits/ year (*pers. observ.*). Oilbirds in turn regurgitate seeds whole without any evident damage, depend wholly on fruit with no use of animal food and only consume a small number of species. It is not, however evident that Oilbirds provide for "high quality" seed dispersal, at least during the breeding season.

Perspectives for conservation

In Venezuela the Oilbird is not currently a threatened species. The Sociedad Venezolana de Espeleología has explored in the country more than 50 caves where Oilbirds breed and roost, several of them support colonies of several thousand birds (Bosque 1978, Bosque 1986). Only three small colonies of few individuals are known to have gone extinct, all of them located in the north-central most heavily "developed" part of the country (Bosque 1986).

Nevertheless, their highly specialized frugivorous diet makes Oilbirds a vulnerable species. Massive post-breeding exoduses of birds from the Caripe area some years, but not others, might be related to reduced food availability in the midst of the extensive agricultural areas where the Guácharo cave is located. Likewise, foraging trips of more than 100 Km in a single night (Roca & Gutierrez 1991) are likely to be related to conditions of low local food availability. Fortunately, improvement of our knowledge of the Oilbird biology in the Caripe area has led to the recent expansion of the Guácharo National Park, incorporating into it an additional 40,000 Ha. of largely undisturbed forest.

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