



## DIGESTIVE EFFICIENCY AND RATE OF FOOD PASSAGE IN OILBIRD NESTLINGS<sup>1</sup>

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**Abstract.** Oilbirds (*Steatornis caripensis*) of South America are unusual in raising their young exclusively on a fruit pulp diet. In order to determine the ability of Oilbird nestlings to extract energy and nutrients from the diet, we studied their digestive function under laboratory conditions. We used total balance feeding trials to determine the Metabolizable Energy Coefficient (MEC\*) and digestibility of the components of an avocado-based diet. Oilbird nestlings extract an average of 80% of dietary lipids and 88% of dietary nitrogen. They also metabolize some of the ingested fiber. Mean MEC\* (64%) was similar to that of other frugivores. Nitrogen requirements for maintenance (determined from the regression between nitrogen intake and excretion) were considerably lower (less than  $0.075 \text{ g N kg}^{-0.75} \text{ day}^{-1}$ ) than estimates for non-passerines. Efficient utilization of dietary nitrogen is considered an essential adaptation for nestlings on a nitrogen-poor diet. In contrast to all other frugivores so far studied, Oilbird fledglings have a long digesta retention time. Mean retention time of plastic markers mixed in the experimental diets averaged 377 min. This may be attributable to the high lipid content of their diet. Our results help to explain the nutritional and energetic adaptations to frugivory in this species.

**Key words:** Frugivory; Oilbird; *Steatornis*; growth; Venezuela; nitrogen; digesta retention time.

### INTRODUCTION

Most species of birds that regularly include fruit as part of their diet are unable to maintain body mass when fed fruit only (e.g., Berthold 1976, Izhaki and Safriel 1989). Other, more specialized frugivores, such as manakins (Pipridae) (Worthington 1989) or the Phainopepla (*Phainopepla nitens*) (Walsberg 1975), are able to subsist on an all-fruit diet, but only a few species raise their nestlings on such a diet. Most fruit is considered an energetically and nutritionally poor diet for birds (e.g., Moermond and Denslow 1985, Karasov and Levey 1990) and in most cases not adequate to support the rapid post-natal growth of birds (Morton 1973, Ricklefs 1976, Foster 1978).

Nevertheless, in the New World tropics some of the cotingas (Cotingidae) (B. K. Snow 1970), the Oilbird (*Steatornis caripensis*) (Snow 1961, 1962), and some of the tanagers (Thraupidae) (Ricklefs 1976) feed only fruit to their nestlings. The differences between the more specialized frugivores and the more omnivorous bird species are not fully understood; however, recent studies have shown that differences in the degree of frugivory between bird species can be explained in terms of differences in the digestive physiology of the birds and the nutrient composition of their food plants (Levey 1987, Studier et al. 1988, Izhaki and Safriel 1989, Martínez del Río et al. 1989, Karasov and Levey 1990, Martínez del Río and Karasov 1990, Levey and Grajal 1991).

The results presented here are part of a broader study on energetic and nutritional aspects of

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TABLE 1. Composition and energy content of experimental diets fed to Oilbird nestlings.

Diet type	Composition (percent of dry mass)					Water <sup>a</sup>	Energy <sup>b</sup>
	Crude fat	Crude fiber	Nitrogen	Ash			
D1	66.8	13.0	1.2	4.6		81.4	30.9
D2	58.2	21.7	2.8	5.7		82.1	29.6
D3	49.1	15.6	3.8	4.6		81.0	27.8

<sup>a</sup> Percent of fresh mass.

<sup>b</sup>  $\text{kJ g}^{-1}$  AFDM.

growth in the Oilbird to understand how Oilbirds grow on a diet of only fruit pulp. In this paper, we examine aspects of the digestive function of Oilbird nestlings under laboratory conditions to determine their ability to extract energy and nutrients from the diet. Our specific objectives were to determine digestibility of fruit pulp, energy assimilation efficiency, nitrogen requirements for maintenance, and digesta residence time in nestling Oilbirds. In addition, we compare the Oilbird to other frugivorous birds which typically have a low energy assimilation efficiency and a short digesta retention time (Castro et al. 1989, Karasov 1990, Karasov and Levey 1990).

The Oilbird is the only nocturnal frugivorous bird and most of what is known of it is due to Snow's (1961, 1962) fascinating account of the species in Trinidad. Oilbirds (about 415 g) are mainly distributed along mountain chains from Trinidad to Perú and Bolivia (Hilty and Brown 1986). They nest and roost in the high ledges of caves where they orient themselves by echolocation (Griffin 1953, Suthers and Hector 1985). At night they leave their roosting caves, sometimes by the thousands, to feed on the lipid- and energy-rich fruits of Lauraceae, Palmae and Burseraceae in the surrounding forests (Snow 1961, White 1974, Tannenbaum and Wrege 1978, B. K. Snow 1979). After removing the pulp of the fruits in the stomach they regurgitate the seeds. Nestlings, usually between one and three, develop slowly, spending more than 110 days in the nest, and deposit extensive fat reserves, becoming approximately 50% heavier than the adults before fledging (Snow 1961, White 1974, Ramirez 1987). Both the slow growth rate and the fat deposits are considered a consequence of feeding on a lipid-rich but nitrogen-poor diet (Snow 1962, White 1974, Ricklefs 1976).

Because the protein content of fruits is generally low, protein—rather than energy—seems to limit growth in this species (Snow 1962) and in frugivores in general. Therefore, as an adap-

tation to the low protein content of the diet we anticipated that use of dietary nitrogen would be highly efficient. Specifically, we expected that protein digestibility would be high and that nitrogen maintenance requirements would be low.

## METHODS

Oilbird nestlings were obtained from a breeding cave, "Cueva del Guácharo," near Caripe Estado Monagas in northeastern Venezuela, during the breeding season of 1989. This cave hosts a population of several thousand birds (Bosque and Ramirez 1988) that breed from April to September of each year (Tannenbaum and Wrege 1978).

## DIGESTION TRIALS

We estimated the minimum combined nitrogen losses from fecal and urinary origin and nitrogen balance of nestling Oilbirds by comparing nitrogen intake to total excretion scaled to metabolic mass ( $\text{kg}^{0.75}$ ) (Robbins 1981, 1983). These trials used the total balance method in which all food ingested and excreta produced are weighed and analyzed. This procedure required feeding nestlings diets of different protein content. Diet D1 consisted of unsupplemented avocado pulp, and diets D2 and D3 were supplemented with protein by adding respectively 1.32 and 2.64 g of casein from bovine milk (Sigma No. C-0376) to 100 g of fresh avocado pulp. Different diets were prepared from different batches of avocado. Composition and caloric content of the diets are given in Table 1. After mixing in a blender, avocado mash of each diet type was force-fed directly to the stomach of each of three nestlings by means of a catheter attached to a large syringe. This procedure lasted only a few seconds and food was never regurgitated. Daily rations were divided into approximately three equal portions and fed to the nestlings at around 19:30, midnight, and 6:00 the next morning. This schedule roughly corresponds to that of their natural feeding (Snow 1961). Individual birds were confined

in metabolic cages (35 × 25 × 20 cm) that allowed for complete collection of the excreta. Excreta were collected three times nightly at the same time as the birds were fed. Nestlings were fed each of the assigned diets for three (D1) or two (D2 and D3) days before the beginning of the digestion trials which lasted for three (D1) or two (D2 and D3) days. Each nestling was fed only one diet type.

We selected nestlings of at least 320 g (average body mass of all nine nestlings was 378 g). At this size, they are well covered with down, have good thermoregulatory abilities (Thomas and Bosque, in press), and already have well-developed fat deposits. We tried to feed the birds enough pulp to support a slight body mass gain, as previously determined by preliminary feeding trials. On average birds were fed 1,631 kJ kg<sup>-0.75</sup> day<sup>-1</sup>, and body mass change averaged 0.75% for all nine birds during the experimental period. Birds were weighed twice daily at 12-hr intervals. During the experiments birds were housed in a dark room where daily temperatures fluctuated between 24 and 16°C. Cave temperature is relatively constant around 19.5°C. At the end of the experiments birds were returned to their original nests. The number and duration of our trials were largely determined by availability of fresh avocado in Caripe.

Because of the amounts of fruit involved in the experiments, it was not feasible to use the fruits that Oilbirds normally consume. We chose avocado because it belongs to the same genus (*Persea*) as that of *P. caerulea* and *P. rigens*, two of the fruits commonly consumed by Oilbirds in our study area (Tannenbaum and Wrege 1978, Ramírez 1987, pers. observ.). Avocado pulp is similar in nutrient composition to these natural diets and we have been previously able to maintain Oilbirds in captivity on an avocado-based diet.

#### CALORIC CONTENT AND CHEMICAL ANALYSIS

Subsamples of the experimental diets and of the pooled excreta of each individual bird were analyzed to determine metabolizable energy coefficient (Kendeigh et al. 1977), digestibility of the pulp's components and metabolizable energy of the diets.

Samples were kept frozen in air-tight bags until ready for analysis and were dried in a forced-convection oven at 55°C to constant mass to de-

termine moisture content. Ash (mineral) content was determined by mass change after combustion for 6 hr in a muffle furnace at 500°C. The combustion energy of the food and excreta was measured in a Parr adiabatic bomb calorimeter calibrated with benzoic acid. Ash-free combustion energy values were corrected for heat of combustion of fuse wire (Parr 45C10 nickel-chromium) and acid formation according to the specifications of the manufacturer. All samples were run in triplicate and coefficient of variation was always less than 5%. Average ash-free dry mass values (AFDM) are given in the results.

Chemical analysis was done according to methods of the American Organization of Analytical Chemists (Horwitz 1984). Nitrogen was determined by micro-Kjeldahl with a Tecator model 1003 and the lipid fraction (hereafter called crude fat) was extracted with anhydrous ether in a Labconco Goldfish apparatus. All samples were analyzed in duplicate or until the difference between replicates was less than 5%. Average values are given in the results.

#### URINARY AND FECAL NITROGEN

The measurement of protein, or nitrogen, digestibility in birds is complicated since feces, which contain the undigested protein, are mixed in the cloaca with urine, which contains nitrogenous waste. To estimate nitrogen digestibility, therefore, uric acid was separated in the form of urate with the use of the Benedict and Hitchcock reagent (Terpstra and de Hart 1974) and fecal nitrogen was determined by micro-Kjeldahl from the supernatant. Nitrogen from uric acid was then determined by the difference between total nitrogen in the excreta and fecal nitrogen. Since other nitrogen products of metabolism, such as ammonia, are not precipitated by the Benedict and Hitchcock reagent our nitrogen digestibilities represent minimum estimates. When the proportion of excretory nitrogen occurring in the urine and in the feces was known, the energy content of the urine fraction was estimated (results) and used to correct apparent metabolizable energy and metabolizable energy coefficients.

#### DIGESTA RESIDENCE TIME

Digesta residence time is a general term for various expressions such as mean retention, transit and passage times (Karasov and Levey 1990). Each of five fledgling Oilbirds was fed avocado mash in the same manner, as previously ex-

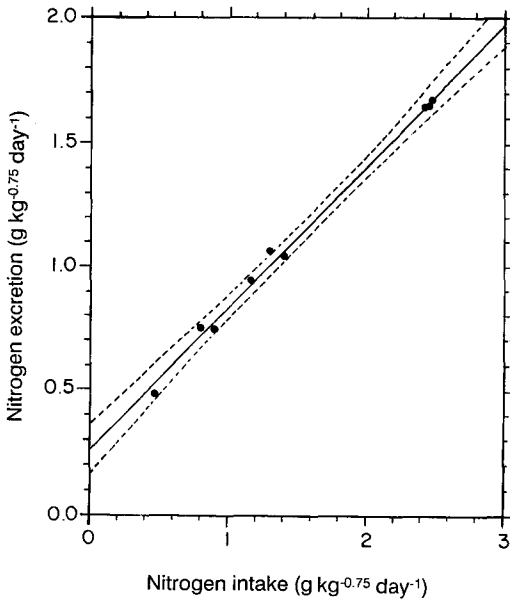


FIGURE 1. Relationship between total nitrogen excretion and dietary nitrogen intake in Oilbird nestlings. The dashed lines give the 95% confidence limits for the regression equation represented by the solid line; the regression equation is  $Y = 0.020 + 0.572X$  ( $r = 0.997$ ,  $P < 0.001$ ).

plained, for two days before the beginning of the trial. On the night of the trial they were fed a dose of avocado mash containing about 450 red markers of 1–2 mm<sup>2</sup> cut from plastic flagging tape (specific gravity = 1.01, Grajal et al. 1989). To simulate their natural feeding routine birds were not fed for 12 hr before the beginning of the experimental period and were not fed again until its conclusion. They were kept under the conditions described above and were quickly transferred to a clean cage at the moment of collecting the excreta. We tried to minimize disturbance to the birds since it is known that this affects passage times in chicks (Tuckey et al. 1958). There were no abnormal excretions associated with the handling of the birds. All excreta were collected, weighed, and the numbers of markers counted at each of the following intervals after feeding: 0.5, 1, 1.5, 2, 2.5, 3, 4, 5, 6, 7, 10, 13, 16 and 24 hr. Dry matter of excreta of each interval was later determined in order to correct for chance variations in defecation (Coombe and Kay 1965, Warner 1981). Recovery of the markers averaged 93.9% at the end of the test period. We plotted cumulative marker excretion against time and

TABLE 2. Breakdown of average ( $\pm$ SEM) daily excretory nitrogen into feces and urine for Oilbird nestlings fed three experimental diets.

Diet fed	Nitrogen excreted (g N kg <sup>-0.75</sup> day <sup>-1</sup> )	
	Feces	Urine
D1	0.123 $\pm$ 0.028	0.219 $\pm$ 0.021
D2	0.132 $\pm$ 0.008	0.848 $\pm$ 0.030
D3	0.168 $\pm$ 0.014	1.168 $\pm$ 0.089
K-W <sup>a</sup>	2.49	7.20
P	ns	*

<sup>a</sup> Differences between diets, Kruskal-Wallis test statistic; \* =  $P < 0.05$ , ns = not significant.

calculated several parameters describing digesta residence time.

To minimize nest disturbance, the five birds that we used for residence time experiments were found on the cave floor where they had fallen from their nests. These birds were abandoned by their parents and were consequently below the normal weight for their age. However, due to their extensive fat deposits, nestling Oilbirds can support long periods of fasting. The fledglings that we used were well-feathered and capable of short flights in the cave and in our laboratory. At the end of the experiment they were returned to the cave.

## RESULTS

### NITROGEN EXCRETION AND MAINTENANCE REQUIREMENTS

A nestling must assimilate enough nitrogen for growth in excess of its maintenance requirements. Maintenance is achieved when intake balances nitrogen losses in the feces and urine (Robbins 1983). Fecal nitrogen consists of undigested protein from the food and of endogenous sources while urinary nitrogen represents the end-products of nitrogen metabolism. Feces and urine (hereafter called excreta) are mixed in the cloaca and voided together. Maintenance requirements for dietary nitrogen can be indirectly determined from the regression between daily specific nitrogen intake and excretion (Robbins 1981, 1983). When the regression line is extrapolated to zero nitrogen intake, the intercept also estimates minimal losses in the feces and urine since all nitrogen excreted must then be of animal origin (endogenous).

Nitrogen excreted (the sum of fecal and urinary wastes) per unit metabolic mass increased linearly with nitrogen intake (Fig. 1) and extrapo-

TABLE 3. Average ( $\pm$ SEM) composition of the excreta (feces and urine) of Oilbird nestlings fed three experimental diets.

Diet fed	Percent of dry mass			
	Crude fat	Crude fiber	Nitrogen	Ash
D1	28.6 $\pm$ 1.2	25.6 $\pm$ 1.1	1.7 $\pm$ 0.0	17.4 $\pm$ 3.9
D2	24.6 $\pm$ 1.7	20.2 $\pm$ 1.8	3.8 $\pm$ 0.1	11.8 $\pm$ 1.1
D3	24.0 $\pm$ 2.2	19.9 $\pm$ 1.3	5.0 $\pm$ 0.1	10.2 $\pm$ 1.0
Mean	25.7 $\pm$ 1.1	22.1 $\pm$ 1.2		13.1 $\pm$ 1.6
K-W <sup>a</sup>	3.29	5.14	7.2	3.82
P	ns	ns	*	ns

<sup>a</sup> Differences between diets, Kruskal-Wallis test statistic; \* =  $P < 0.05$ , ns = not significant.

lation of the relationship to zero nitrogen intake gave an estimate for the nitrogen losses of 0.02 g N kg<sup>-0.75</sup> day<sup>-1</sup> (SE of the estimate = 0.028). The 95% confidence limits of the relationship are narrow and are also shown in Figure 1. Nitrogen balance, the point at which intake and excretion are equal, can be deduced from the regression equation and was determined to be 0.05 g N kg<sup>-0.75</sup> day<sup>-1</sup>. Growth requires a nitrogen intake in excess of such an amount. These estimates of nitrogen requirement are considerably lower than estimates for nonpasserines: 0.07 g N kg<sup>-0.75</sup> day<sup>-1</sup> at zero nitrogen intake and 0.43 g N kg<sup>-0.75</sup> day<sup>-1</sup> at nitrogen balance for all birds (Robbins 1981, 1983).

The distribution of fecal and urinary nitrogen in the excreta shows that the increase in total nitrogen excretion with dietary protein intake was mainly due to the increase of nitrogen excreted in the urine (Table 2). Daily amount of urinary nitrogen excreted per kg<sup>0.75</sup> significantly increased with protein content of the diet (Kruskal-Wallis test statistic = 7.2, df = 2,  $P = 0.027$ ), suggesting that protein intake exceeded requirements for the high protein diets. Daily fecal nitrogen eliminated per kg<sup>0.75</sup> also increased with protein concentration of the diet (Table 2); however, differences were not statistically significant

(Kruskal-Wallis test statistic = 2.49, df = 2,  $P > 0.05$ ). Overall, for all birds and trials, the average of the percentages showed that 20.6% of the excreted nitrogen was found in the feces. This value is quite similar to that determined for poultry (approximately 18%) by Terpstra and Janssen (1976; in Zwartz and Blomert 1990).

#### DIGESTIBILITY OF DIET COMPONENTS

Apparent digestibilities are defined as the relative amounts of nutrient or dry matter that do not appear in the feces, and were determined by the following equation (Robbins 1983):

$$100[(\text{Amount consumed} - \text{Fecal excretion}) \div (\text{Amount consumed})].$$

This coefficient is called "apparent" because it is not corrected for endogenous losses. We assumed that fat was not excreted in the urine to any appreciable extent and therefore considered all fat in the excreta to have fecal origin. Average composition of the excreta of nestlings fed each of the diet types is presented in Table 3.

Apparent digestibility of the components of the avocado pulp are given in Table 4. There were no significant differences in the apparent digestibilities of dry matter, fat or nitrogen in relation to diet (Kruskal-Wallis test,  $P > 0.05$  in

TABLE 4. Average ( $\pm$ SEM) digestibilities of pulp components fed to Oilbird nestlings.

Diet type	Apparent digestibility (%)			
	Dry matter	Crude fat	Crude fiber	Crude protein
D1	56.7 $\pm$ 0.8	81.5 $\pm$ 0.9	14.5 $\pm$ 4.6	72.9 $\pm$ 4.3
D2	57.9 $\pm$ 0.6	82.2 $\pm$ 1.4	60.7 $\pm$ 2.7	92.3 $\pm$ 0.3
D3	55.4 $\pm$ 3.3	76.7 $\pm$ 6.0	43.0 $\pm$ 4.7	92.6 $\pm$ 0.7
Mean	56.7 $\pm$ 1.1	80.1 $\pm$ 2.0		87.6 $\pm$ 2.7
K-W <sup>a</sup>	0.62	0.27	6.25	5.6
P	ns	ns	*	ns

<sup>a</sup> Differences between diets, Kruskal-Wallis test statistic; \* =  $P < 0.05$ , ns = not significant.

TABLE 5. Average ( $\pm$ SEM) energy utilization efficiencies of Oilbird nestlings and metabolizable energy content of the diets.

Diet type	Metabolizable energy coefficient (%)		Metabolizable energy (kJ g <sup>-1</sup> AFDM)	
	Apparent	"Corrected" <sup>a</sup>	Apparent	"Corrected" <sup>a</sup>
D1	61.6 $\pm$ 0.3	62.3 $\pm$ 0.3	19.1 $\pm$ 0.1	19.3 $\pm$ 0.1
D2	66.9 $\pm$ 0.7	68.7 $\pm$ 1.7	19.8 $\pm$ 0.2	20.3 $\pm$ 0.2
D3	64.7 $\pm$ 3.7	67.4 $\pm$ 3.5	18.3 $\pm$ 1.5	19.1 $\pm$ 1.5
Mean	64.4 $\pm$ 1.3	66.1 $\pm$ 1.4	19.1 $\pm$ 0.5	19.6 $\pm$ 0.5
K-W <sup>b</sup>	0.661	0.661	2.76	2.76
P	ns	ns	ns	ns

<sup>a</sup> "Corrected" values consider urinary energy as metabolized energy, see text.

<sup>b</sup> Differences between diets, Kruskal-Wallis test statistic; ns = not significant.

all cases) (Table 4). Ash-free dry matter digestibility was low and averaged 56.7%. Fat was highly digestible, averaging 80.1% for all birds and trials combined.

Apparent digestibility of crude fiber was statistically related to diet type (Kruskal-Wallis test statistic = 6.25, *df* = 2, *P* = 0.044). We cannot interpret this finding. Among individuals, apparent digestibility of fiber was highly variable and ranged from 5 to 85%, a range of variation not encountered in the digestibility of any of the other components of the diet. Although the crude fiber component of the proximate analysis has neither a uniform composition nor a predictable digestibility (Robbins 1983), it appears that Oilbirds are able to digest some structural carbohydrates.

Once urinary losses of nitrogen are accounted for, it is evident that Oilbird nestlings digest and absorb most of the dietary protein available to them. Digestibility averaged 87.6% and was higher for the high protein diet, but it was statistically independent of diet type (Kruskal-Wallis test statistic = 5.6, *df* = 2, *P* > 0.05). Since our methods did not account for endogenous fecal losses, our estimates of digestibilities should be slight underestimates of the "true" values.

#### METABOLIZABLE ENERGY AND METABOLIZABLE ENERGY COEFFICIENT

The apparent metabolizable energy coefficient (MEC\*), the proportion of the gross energy intake extracted by the birds not accounting for endogenous losses, was estimated by (Kendeigh et al. 1977, Karasov 1990):

$$\text{MEC}^*(\%) = 100[(\text{GE}_i)(Q_i) - (\text{GE}_e)(Q_e)]/[(\text{GE}_i)(Q_i)],$$

where  $\text{GE}_i$  and  $\text{GE}_e$  are the gross energy content

of the food (Table 1) and the excreta (Table 3), respectively, and  $Q_i$  and  $Q_e$  are the amounts of food consumed and excreta produced, respectively.

Average MEC\* for all nestlings and trials combined was 64.4% (Table 5). This value is similar to that determined by Karasov (1990) for a number of birds fed fruit pulp and skin. There were no significant differences among the MEC\* of birds fed different diets (Kruskal-Wallis test statistic = 2.49, *df* = 2, *P* > 0.05).

Apparent metabolizable energy (AME), a measure of the energy available from the diet, uncorrected for endogenous losses, was estimated by (Miller and Reinecke 1984):

$$\text{AME} = [(\text{GE}_i)(Q_i) - (\text{GE}_e)(Q_e)]/(Q_i).$$

Avocado pulp is a rich energy source for Oilbirds, the average AME of avocado for Oilbirds was 19.1 kJ g<sup>-1</sup> dry mass (Table 5) or 3.6 kJ g<sup>-1</sup> fresh mass, and was not statistically related to diet type (Kruskal-Wallis test statistic = 2.76, *df* = 2, *P* > 0.05).

In addition, since we separated urinary and fecal nitrogen from the total nitrogen of the excreta, "corrected" metabolizable energy coefficients (MEC) and "corrected" metabolizable energy (ME) of the diet could be calculated. Both of these corrected quantities recognize endogenous urinary losses as metabolized energy and therefore are a more accurate measure of energy availability from the diet. These values are seldom calculated in studies of bird digestion.

The correction equation used for MEC from MEC\* was:

$$\text{MEC} = \text{MEC}^* + (E_e)/[(\text{GE}_i)(Q_i)],$$

where  $E_e$  is the endogenous loss of energy from the urine. Likewise, ME was estimated by cor-

TABLE 6. Percentage (mean  $\pm$  SEM) of the organic and energy content of the excreta estimated to be in the urine of Oilbird nestlings fed different diets.

Diet fed	Percentage of the excreted AFDM in the urine	Percentage of the excreted energy in the urine
D1	4.2 $\pm$ 0.5	1.8 $\pm$ 0.2
D2	11.3 $\pm$ 0.4	5.5 $\pm$ 0.1
D3	14.6 $\pm$ 0.7	7.6 $\pm$ 0.3
K-W <sup>a</sup>	7.2	7.2
P	*	*

<sup>a</sup> Differences between diets, Kruskal-Wallis test statistic; \* =  $P < 0.05$ .

recting for urinary endogenous losses by the following equation:

$$ME = [(GE_i)(Q_i) - ((GE_e)(Q_e) - (E_c))]/(Q_i).$$

Therefore, to estimate our corrected values of MEC and ME it was necessary to estimate the urinary energy loss from the excreta. The total energy content of the birds' urinary ash-free dry mass (AFDM) was deduced from the percentage of urinary nitrogen in the AFDM of the excreta (as calculated from the data in Tables 2 and 3) and the energy content of birds' urine. For the latter, we used an estimated value of 34.4 kJ g<sup>-1</sup> N (see Zwartz and Blomert 1990, for details of calculations). This value depends on the energy content and chemical composition (uric acid, urea, ammonia, creatine and creatinine) of the urine; however, it is little affected even assuming that uric acid was the sole constituent of the urine (34.5 kJ g<sup>-1</sup> N) and differences should have little effect on the estimates of the MECs (Karasov 1990).

Corrected MEC values (Table 5) were independent of the diet type fed (Kruskal-Wallis test statistic = 2.4, df = 2,  $P > 0.05$ ) and averaged 66.1% for all birds and trials combined. Corrected MEC values were between 1.01 and 1.04 times higher than MEC\*. Apparent coefficients are generally 1 to 3% below "true" coefficients, which account for all endogenous losses for birds near maintenance levels (Karasov 1990). Corrected ME of the avocado diets for Oilbirds averaged 19.6 kJ g<sup>-1</sup> (Table 5) and was independent of diet type (Kruskal-Wallis test statistic = 2.76,  $P > 0.05$ ). Corrected ME was between 1 and 4% higher than AME. Miller and Reinecke (1984) compared true metabolized energy, which accounts for all endogenous losses, and AME from a number of studies and found differences ranging from 1 to 40%.

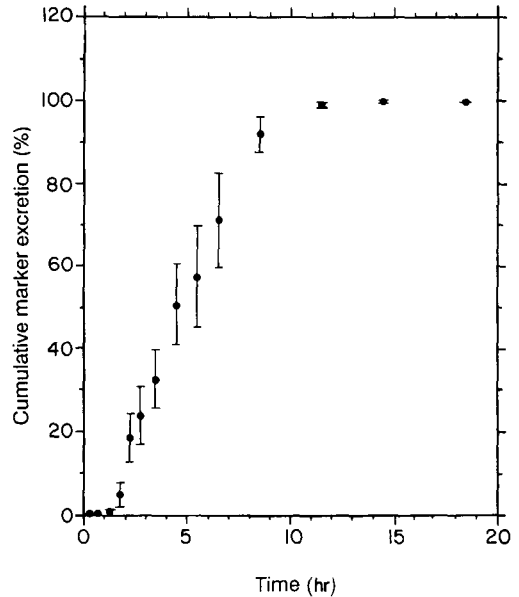


FIGURE 2. Excretion of plastic markers by fledgling Oilbirds as a function of time since food containing the markers was fed. Each point is the mean for five birds; vertical bars indicate SEM.

These data allowed us to estimate the percentage of the excreted energy and of the excreted organic mass (assuming 3 g uric acid/g N excreted; Karasov 1990) in the urine. The percentage of the excreted organic mass in the urine increased significantly with the protein content of the diet, but was always low, ranging from 4.2 to 14.6% (Table 6). The percentage of excretory energy estimated to be in the urine was consequently quite low, ranging between 1.8 and 7.6% (Table 6).

#### DIGESTA RESIDENCE TIME

Oilbird fledglings excreted plastic markers, fed to them in the fruit pulp, in a sigmoid fashion (Fig. 2). Mean retention time averaged 377 min (Table 7). This value, as well as all other estimates of digesta residence time (Table 7), is unusually high for a bird and particularly high for a frugivore (e.g., Herrera 1984, Jordano 1987, Karasov and Levey 1990). In birds, mean retention time of the food in the digestive tract increases with body mass and can be approximated by the following equation (Karasov 1990):  $Y = 29.37 \text{ mass in } g^{0.215}$ . This equation predicts that for birds of the average size used in the experiments mean retention time should be about 102

TABLE 7. Average ( $\pm$ SEM) residence times of markers in the digestive tract of Oilbird fledglings.

Body mass (g)	Appearance time* (min)				Mean retention time <sup>b</sup> (min)
	First	5%	50%	95%	
324 $\pm$ 15	108 $\pm$ 19	112 $\pm$ 13	295 $\pm$ 44	532 $\pm$ 57	377 $\pm$ 26

\* Average time of appearance of first, 5%, 50%, and 95% of markers fed to five Oilbird fledglings. Appearance times (except first) were read for each bird from its individual accumulative excretion curve (not shown).

<sup>b</sup> Calculated by  $t_r = \sum m_i \cdot f_i / \sum m_i$ , where  $m_i$  is the amount of marker excreted at the  $i$ th defecation at time  $t_i$  after dosing and  $f_i$  is the total amount of dry matter excreted from the time of dosing to the time  $t_i$ , divided by the average rate of excretion of dry matter during the experiment (Warner 1981).

min. If the birds had not been below their normal mass (see methods) the expected value, calculated for a bird of 450 g, would have been 109 min. Since frugivores have mean retention times shorter than those of other birds (Karasov and Levey 1990), the expected value for the Oilbird should have been even smaller than that predicted from the equation for all birds. We conclude that Oilbird fledglings have a mean retention time at least 3.7 times longer than that expected for a bird of its size.

#### ENERGY BALANCE

Although our experiments were not designed to study the energy balance of the nestlings, there was enough variation in their daily body masses to permit an estimation of their maintenance energy requirements.

The maintenance energy requirement was calculated from the linear regression of metabolizable energy intake on percent change in body mass (Fig. 3). From the regression equation it was estimated that a metabolizable daily energy intake of  $980 \text{ kJ kg}^{-0.75}$  is necessary to maintain a constant body mass. This amount of energy should be provided by a gross energy intake of approximately  $1,500 \text{ kJ kg}^{-0.75} \text{ day}^{-1}$ . Growth requires an energy intake in excess of such an amount.

Our estimate of the ratio of gross nitrogen intake needs (0.05 g), to gross energy intake needs ( $1,550 \text{ kJ}$ ) per day per  $\text{kg}^{0.75}$  to maintain conditions of equilibrium is quite low and should be easily met by fruits consumed by Oilbirds. In Trinidad Oilbird fruits have an average nitrogen content of 1.92% dry mass and an average of  $23.2 \text{ kJ/g}$  dry pulp (White 1974); in our study area Lauracea consumed by Oilbirds have an average of 1.5% nitrogen and  $32 \text{ kJ g}^{-1}$  dry pulp (unpubl. data). Therefore, Oilbird fruits provide several times the protein requirements needed for balance under our experimental conditions, while satisfying energy balance requirements.

## DISCUSSION

### NITROGEN REQUIREMENTS

Raising chicks exclusively on a diet of fruit is very rare among birds (Morton 1973, Foster 1978). Although there is little knowledge on the energy and nutrient requirements of growing frugivorous and omnivorous birds, fruit is generally considered a poor diet for supporting tissue growth. Either because of its low protein content (Snow 1962, B. K. Snow 1970) or because of an unbalanced ratio of protein to calories (Ricklefs 1976, 1983; Foster 1978), a pure fruit diet cannot support rapid growth in birds. Given the nitrogen

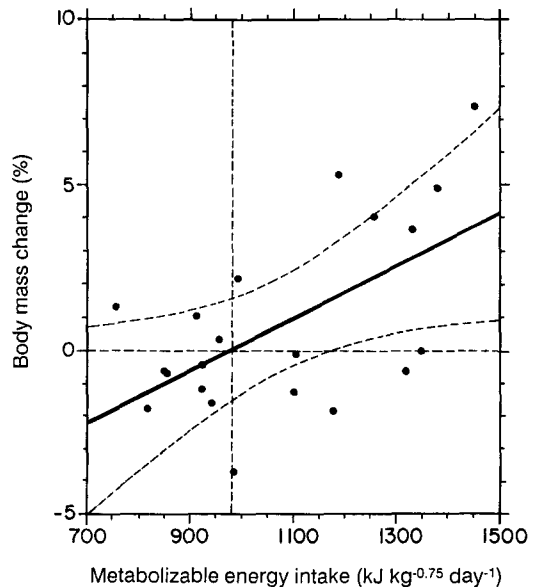


FIGURE 3. Relationship between daily body mass change and metabolizable energy intake in Oilbird nestlings. Maintenance requirements ( $980 \text{ kJ kg}^{-0.75} \text{ day}^{-1}$ ) is indicated by the broken vertical line at no body mass change. The dashed, curved, lines give the 95% confidence limits for the regression equation, represented by the solid line; the regression equation is  $Y = -7.7 + 0.008X$  ( $r = 0.587$ ,  $P = 0.005$ ,  $n = 21$ )



limitations of their diet, we would expect that frugivorous nestlings should have a very efficient utilization of dietary nitrogen. That is, frugivorous nestlings should maximize their conversion efficiency of dietary protein to tissue. Accordingly, White (1974) estimated that protein conversion efficiency of Oilbirds (63%) is several times higher than that of nestlings of other species. A high conversion efficiency of protein to tissue is possible only if absorption of protein is high and the percentage of nitrogen allocated to maintenance is small in relation to that deposited in new tissue.

Our results support these expectations. Digestibility of nitrogen (protein) was high, although not complete, and our estimates of minimum endogenous losses and intake needed for nitrogen balance are quite low. Extrapolated nitrogen loss at zero nitrogen intake is less than one third of that expected for a nonpasserine (Robbins 1983). The maintenance nitrogen requirement ( $0.05 \text{ g N kg}^{-0.75} \text{ day}^{-1}$ ) is almost half of that of the Emu (*Dromaius novaehollandiae*,  $0.09 \text{ g N kg}^{-0.75} \text{ day}^{-1}$ ) (Dawson and Herd 1983), the lowest value reported previously in birds. Maintenance dietary nitrogen requirements of poultry (Leveille and Fisher 1958) and Japanese Quail (*Coturnix*) (Yamane et al. 1979) are 0.34 and  $0.40 \text{ g N kg}^{-0.75} \text{ day}^{-1}$ , respectively.

Our estimates, however, should be taken with reservations when compared to other species. Nestlings of the body mass range used in our trials have around 20% fresh mass of fat (Ramirez 1987, and unpubl. data). Adipose tissue has a low metabolic rate (Schmidt-Nielsen 1979) and a low nitrogen content; therefore, its nitrogen maintenance requirements must also be low when compared to lean tissue. In addition, there are two potential sources of error in our determinations. First, drying of excreta at  $55^\circ\text{C}$  might produce losses of urinary nitrogen (Manoukas et al. 1964, Blem 1968, Dawson and Herd 1983). We did not correct for this error, which can decrease determinations of urinary nitrogen up to 20%. Second, it was not possible to control completely for unwanted changes in body mass. Nevertheless, even assuming a urinary nitrogen loss of 20% and expressing nitrogen requirements in terms of estimated lean mass, our estimate for nitrogen balance would be approximately  $0.075 \text{ g N kg}^{-0.75} \text{ day}^{-1}$ . This is still very low, in accordance to our original expectation.

Dawson and Herd (1983) postulated that re-

cycling of the urinary nitrogen from the cloaca to the upper colon and caeca might be implicated in the Emu's low maintenance requirement for nitrogen. Oilbirds have paired long caeca, but we have not studied their function.

#### DIGESTIBILITY OF THE PULP'S COMPONENTS

*Protein.* As noted above, a high digestibility of protein should characterize nestling frugivores and probably adults as well. There are no comparable data on the assimilation of dietary protein for any other highly frugivorous species. In the Wild Turkey (*Meleagris gallopavo*) crude protein assimilation, corrected for uric acid excreted, is highly variable and ranges from 11.4 to 88.32% for adult and juvenile birds fed a number of fruits (Billingsley and Arner 1970). Among herbivores, digestibility of protein approaches 100% in Willow Ptarmigan (*Lagopus lagopus*) (Moss 1977) and geese (*Branta*) (Buchsbaum et al. 1986). Estimates of digestibility of animal protein by birds are also uncommon. Zwartz and Blomert (1990) estimate protein digestibility as 74.2% in Whimbrels (*Numenius phaeopus*) feeding on fiddler crabs (*Uca tangeri*), and 70% for Eurasian Kestrel (*Falco tinnunculus*) and Western Screech-Owls (*Otus kennicottii*).

Because young birds have immature guts and might be less efficient than adults at extracting energy and nutrients (e.g., Karasov 1990) and because our nitrogen digestibilities are minimum estimates, Oilbird nestlings seem efficient in extracting the available nitrogen from their diet, even at concentrations higher than those encountered in their natural diet.

*Fat.* Oilbirds frequently select fruits with high lipid content. In Trinidad, three species of Lauracea eaten by Oilbirds had lipid contents from 19 to 44% dry mass (Snow 1962) and in our study area nine species of Lauracea ranged from 33 to 67% and averaged 50% dry mass (unpubl. data). Some of the palms and Burseraceae consumed by Oilbirds also have high lipid content. Since protein content of their fruits is generally low, it has been postulated that, in order to accumulate enough nitrogen for growth, nestlings must accommodate large quantities of energy in their fat deposits (Snow 1962, Ricklefs 1976). In addition, nestling Oilbirds could selectively eliminate undigested fat to bring the ratio of nitrogen to energy of the diet more in line with their needs (Ricklefs 1976). Apparent digestibility of fat

should therefore be low and certainly lower than digestibility of protein.

Our data are in accord with this prediction since digestibility of fat (80%) was lower than digestibility of protein (87.6%). However, both digestibilities were high and no firm conclusion can be reached. That animal and plant fat can be completely digested, or nearly so, is indicated by the high digestibilities reported for several species: 99.8% for Whimbrel feeding on fiddler crabs, 96 and 92% of soybean oil and lard, respectively, by growing chicks (Renner and Hill 1961), up to 94% of fatty acids by hens (Hurwitz et al. 1973), 96.8 to 98.6% of the wax and triacylglycerols fed to Wilson's Storm Petrels (*Oceanites oceanicus*) (Obst 1986) and up to 96% by Wild Turkeys fed various fruits (Billingsley and Arner 1970). Low digestibilities of fat have been reported for the frugivorous Phainopepla (62%) (Walsberg 1975), Wild Turkeys fed greenbrier (*Smilax rotundifolia*) fruits (68–74%) (Billingsley and Arner 1970), and chicks fed tallow (69%) (Renner and Hill 1961). In both species, Whimbrels (Zwartz and Blomert 1990) and Wild Turkeys (Billingsley and Arner 1970), for which digestibility of fat and protein has been measured, the former was considerably higher than the latter for all food types. This contrasts with Oilbirds.

*Fiber.* Unlike other components of the pulp, crude fiber digestibility was highly variable and rather erratic (Table 4). It is unlikely that this is due to insufficient time for the digestion trials. The length of our collection periods (48–72 hr) was 7.6 to 11.5 times the mean retention time of the markers, which should allow for two to three complete cycles (98% of meal clearance (Karasov et al. 1986, Karasov 1990). This time should also be sufficient for the metabolic processing of nutrients and excretion of urinary wastes (Karasov 1990). Therefore, we conclude that Oilbird nestlings digested and assimilated part of the structural carbohydrates of their diet (Table 4). Since crude fiber does not have a uniform composition (Robbins 1983), we can only speculate on this. Lignin is among the most refractory parts of fiber (Parra 1978), and normally has a low concentration in fruits (Table 1 in Cork and Foley, in press), so it is unlikely that lignin is digested to any appreciable extent. Alternatively, hemicellulose can be affected by acid hydrolysis or enzymatic digestion (Parra 1978) in the stomach (Dawson et al. 1989, Buchsbaum et

al. 1986). How this may be accomplished deserves further study, since Snow (1962) suspected that in Oilbirds no digestion takes place in the stomach. Long retention time of the digesta (see below) should favor conditions for fiber digestion in this species.

#### DIGESTA RESIDENCE TIME

Rate of food passage through the digestive tract determines the amount of food processed and the length of time that it is available to the digestive enzymes and to absorptive surfaces (Sibly 1981, Mateos et al. 1982), and as such can influence the amount of energy (e.g., Martínez del Río and Karasov 1990) or nutrients (e.g., Larbier et al. 1977) extracted from the digesta. Therefore, the rate of passage of the digesta is an important parameter in the digestive physiology of birds. If birds were to maximize the net energy or nutrients obtained from their food then, under certain constraints, there should be an optimum retention time of the digesta (Sibly 1981, Martínez del Río and Karasov 1990). Numerous studies have shown that frugivorous birds have short digesta residence times (Cvitanic 1958, Borowski 1966, Walsberg 1975, Sorensen 1984, Herrera 1984, Holthuijzen and Adkisson 1984, Jordano 1987, Snow and Snow 1988, Worthington 1989), and comprehensive reviews indicate that their residence time is shorter than that of birds feeding on other diets (Karasov 1990, Karasov and Levey 1990).

Oilbird nestlings and adults feed on a number of single-seeded fruits. They strip off pericarps by muscular action of the stomach and the pulp is then passed to the intestine while the seeds are regurgitated (Snow 1962). Complete regurgitation of seeds by nestlings may take up to 3–5 hr after ingestion (Snow 1961, pers. observ.); however, seeds begin to be regurgitated shortly after ingestion. Without information on the relative contribution of each part of the gut to the total throughput time, it is possible that our estimates of residence time are to a large extent influenced by the storage capacity and pericarp stripping action of the birds (Martínez del Río and Karasov 1990). Since we fed blended pulp without skin or seeds to the nestlings, our estimates of digesta residence time should be lower than those obtained if we had fed whole fruits to the birds and therefore the effect of storage capacity should be minimal. In addition, the time of first appearance of markers in the excreta (mean = 108

min, Table 7) is considerably longer than that of any other frugivore studied (Appendix II in Karasov 1990). Time of first appearance is the best estimator of throughput time when there is no information on the time that the digesta is retained in the stomach. Therefore, we conclude that digesta residence time of Oilbird fledglings properly reflects a long average time of the digesta in contact with digestive and absorptive surfaces.

When corrected for body mass, Oilbirds have a longer 50% excretion time ( $69.7 \pm 10.7$  min  $g^{-0.25}$ ) than frugivores, herbivores, granivorous wild birds, and hummingbirds (respectively, 12.4, 28.1, 35.5 and 36 min  $g^{-0.25}$ ; from data summarized by Karasov and Levey 1990). In addition, food passes through the alimentary canal of young birds faster than through adults (Thornton et al. 1956, Warner 1981).

Current knowledge of the digestive function of Oilbirds is not sufficient to provide a complete explanation for our finding. We can, however, suggest possibilities for future research. The most distinctive feature of the pulp of most Oilbird fruits is its high lipid (approximately 50% dry mass for Lauracea), and therefore energy, content. This high lipid content sets their fruits apart from those of most other frugivores. Digestion and absorption of dietary lipids in the duodenum is a complex process involving the emulsification of fats by bile (Duke 1986) and the hydrolysis of triglycerides to diglycerides, monoglycerides, fatty acids, and glycerol (Sklan et al. 1975).

The effect of dietary fat on transit time of the digesta has been tested experimentally in leghorn hens by Mateos and Sell (1981) and Mateos et al. (1982). Average time of first appearance of markers in the excreta increased linearly, and considerably, from 193 min to 271 min for diets containing from 0 to 30% supplemental fat, respectively. A similar effect has also been induced in chicks by Larbier et al. (1977). In chicks which had their diets supplemented with only 3 to 4.5% of fat, recovery of marker from the excreta, four hours after ingestion, was about 24% lower for chicks eating unsupplemented diets. In a series of carefully conducted experiments with growing chicks, Tuckey et al. (1958) did not find a consistent effect of high levels of dietary fat when different dietary adjustments concomitant with the inclusion of fat in the diet were made. Nevertheless, fat significantly lengthened the time of first appearance of the marker in the excreta. In

turkeys, the introduction of fat into the duodenum decreases stomach motility (Duke and Evanson 1972). This, in turn, influences the rate of food passage. Inhibition of fats on gastric and intestinal motility also occurs in mammals (Laplace 1975, in Larbier et al. 1977, Borella and Lipmann 1980). We propose that high digesta retention time in Oilbirds is similarly related to a slow process of hydrolysis, absorption of the very rich fat diet, or both. That fat absorption might be limited by the extent of digestion was suspected by Sklan et al. (1975). If a model like Sibly's (1981), based on the maximization of energy assimilation (or that of any particular nutrient) were to apply to Oilbirds, it would imply that food, although very energy rich, takes a long time to digest and absorb.

#### FRUGIVORY IN THE OILBIRD

Although most omnivorous birds cannot subsist on a diet of fruit exclusively, a pair of Oilbirds can raise up to three nestlings in a single nesting attempt. How can we interpret these differences in terms of the birds' physiological adaptations or the characteristics of the fruits that the birds consume?

The evidence suggests that net energy or nitrogen extraction rate of frugivores is limited by the rate at which fruit can be processed (Berthold 1976, Karasov and Levey 1990, Levey and Grajal 1991). Rapid transit time of the digesta seems to be a functional adaptation that allows frugivores to process bulky, energetically and nutritionally poor fruit at a fast enough rate to satisfy their energy or nutrient requirements (Walsberg 1975, Herrera 1984, Snow and Snow 1988, Worthington 1989, Karasov and Levey 1990, Levey and Grajal 1991). This short digesta retention time would, however, compromise the ability to extract the nonrefractory components of the fruit resulting in the relatively low assimilation efficiency of frugivores (Karasov 1990, Karasov and Levey 1990). The crux of these arguments lies in the constraints of gut volumes to process a bulky diet with a low metabolizable energy value per unit of fresh mass.

Oilbirds do not fully conform to this general pattern. First, they process an energetically rich diet slowly and second, they show a high utilization efficiency of the fruits' nutrients. Once the undigestible seed has been regurgitated, Oilbirds not only process a very energy-rich food source but also have the digestive adaptations to extract

large quantities of energy from it, as it is evident from the metabolizable energy value of its food. Our pulp diets, which had energy and lipid contents within the range of other Lauracea in the natural diet of the birds, had a metabolizable energy content of more than  $19 \text{ kJ g}^{-1}$  dry mass.

The pulps of Lauracea have a relatively low water content. Those from our study area have approximately 58% fresh mass (unpubl. data for 10 species). Hence on average, metabolizable energy of the seedless Lauracea pulp should be around  $8 \text{ kJ g}^{-1}$  fresh pulp. In contrast, metabolizable energy of succulent fruits consumed by most other frugivores ranges from approximately 1.9 to  $3.1 \text{ kJ g}^{-1}$  fresh pulp (estimated from a metabolizable energy value of  $12.4 \text{ kJ g}^{-1}$  dry [Karsov 1990] and an average dry matter content of 15 to 25%) which agrees well with measured values (e.g., Studier et al. 1988, Worthington 1989, Izhaki and Safriel 1989, Sakai and Carpenter 1990). If undigestible seeds were also passed to the intestine, metabolizable energy of the diet would drop to 1.7 to  $2.8 \text{ kJ g}^{-1}$  fresh mass (estimated from a metabolizable energy value of  $11 \text{ kJ g}^{-1}$  dry mass for pulp and seeds [Karsov 1990]). Oilbirds then process fruit pulps which, after voiding the seed, have from 2.6 to 4.7 times the metabolizable energy content per unit of fresh mass than succulent fruits consumed by most other frugivores. Therefore, Oilbirds must process considerably smaller amounts of pulp per unit of body mass than other frugivores to meet their energy and growth requirements. The significance of this difference can be appreciated by the fact that in the wild or in captivity, frugivorous birds must process daily quantities of fruit approaching double their body mass for maintenance alone (e.g., Moermond and Denslow 1985, Snow and Snow 1988, Studier et al. 1988). From our energy balance regression, we estimate that energy expenditure of a 300 g nestling is balanced by a gross energy intake of 608 kJ, which is provided by about 83 g of fresh Lauracea pulp, or nearly one-fourth of body mass. Snow (1961, 1962) estimated that growing nestlings receive from one-half to one-third of their body mass per night.

The validity of these arguments depends on the assumption that separation of the seed from the fruit and its regurgitation do not importantly limit processing rate, contrary to the suggestion of Moermond and Denslow (1985). We have no data to support this contention, but processing

of the digesta requires such a long time that it is unlikely that stripping the soft pericarp from the smooth seed of Lauracea could limit the net extraction rate of energy or other nutrients. This is further supported by the observation that when Oilbirds are not breeding, virtually no seeds are brought into the cave. This suggests that seeds can be disposed of quickly. Large neotropical frugivores have been observed to regurgitate large-seeded Lauracea within an hour after ingestion (Moermond and Denslow 1985). The combination of these factors—the need to process proportionally much smaller quantities of pulp of a high metabolizable energy, and the non-limiting disposal of the bulky seeds—should ameliorate the constraints imposed by gut volume on rate of energy or nutrient intake.

In addition, if energy intake in frugivores is limited by gut volume and digestion (e.g., Karsov and Levey 1990, Levey and Grajal 1991), then allometric considerations should become important. Since in birds gut mass is proportional to body mass (Peters 1983) and daily energy consumption is proportional to metabolic body mass ( $\text{kg}^{0.75}$ ), then frugivory should be facilitated by larger body size such as that of the Oilbird. This aspect of frugivory has not been adequately investigated, although degree of frugivory has been reported to be related to body size and many specialized frugivores such as some cotingas, hornbills (Bucerotidae), and fruit-pigeons (Columbidae) have large body sizes (Herrera 1984, Jordano 1987, Snow and Snow 1988).

In addition to energetic considerations, it has been suggested that frugivores are protein-limited, either because of low content of protein in fruits (Berthold 1976) or because of secondary compounds that reduce the efficiency of the birds' nitrogen metabolism (Izhaki and Safriel 1989). The limitations of frugivores to maintain an adequate nitrogen balance are not clear. This is particularly so if rapid transit time compromises nitrogen extraction efficiency from the digesta. Nevertheless, rapid transit time has also been considered a functional adaptation of frugivores to overcome the protein shortage of their diet (Herrera 1984, Jordano 1987, Izhaki and Safriel 1989). As with energy, it has been postulated that maximization of protein intake could be achieved by accelerating food turnover rate (Izhaki and Safriel 1989). Since digesta retention is proportionally long in Oilbirds, it is possible that potential compromises between energy and nitro-

gen extraction efficiency are less important in this species. Interestingly, amino acid absorption in chickens increases in lipid-supplemented diets (Larbier et al. 1977), probably because of the decreased passage rate. Slow passage rate may improve the digestibility of nutrients in the diet (Duke 1986, Mateos et al. 1982).

Finally, we note that we have compared digestive characteristics of the Oilbird, a nonpasserine, with those of passerine frugivores. However, it is unlikely that this taxonomic difference is important in interpreting our results. Available information shows that differences in the retention time of the digesta and assimilation efficiency in birds are related to diet type rather than to taxon (Castro et al. 1989, Karasov 1990, Karasov and Levey 1990).

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