



DIET OF OILBIRDS (*STEATORNIS CARIPENSIS*) IN CUEVA DE LOS GUÁCHAROS NATIONAL PARK (COLOMBIA): TEMPORAL VARIATION IN FRUIT CONSUMPTION, DISPERSAL, AND SEED MORPHOLOGY

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Abstract · Oilbirds (*Steatornis caripensis*) are specialized nocturnal frugivores that inhabit Neotropical forests and have the potential to play key ecological roles as seed dispersers. In this study, we focused on type and quantity of seeds dispersed by a population of Oilbirds in Cueva de Los Guácharos National Park (Colombia). We assessed temporal variation in diet composition, fruit nutrient composition and measured seed morphology. To do this, we used 5–10 seed traps in a cave from 2011 to 2016, conducting a 5-day census 1–4 times each year. In 2015, we performed a census in all 12 months to document within year variation. We found seeds of 52 species (including 17 named species, 12 identified just to family, and 23 morphospecies). We found a clear dominance of Arecaceae and Lauraceae families. Intra-annual variation in species richness reflects the fact that more biomass and higher seed numbers are deposited in the cave in periods of nesting (January–June), as well as during seasonal fruiting patterns in the region. Data on fruit contents from published literature indicated that oilbird diet includes a high representation of lipid-rich fruits. Consumed seed size varied enormously (range: 0.01–5.99 g dry mass), the largest seeds being up to 29 mm wide and 54 mm long. Regurgitated seeds showed a negative allometric relationship between width and length. Overall, we found a diverse diet and that Oilbirds provide efficient seed dispersal in terms of seed quantity; however, many aspects of dispersal quality remain to be determined.

Resumen · Dieta de los Guácharos (*Steatornis caripensis*) en el parque nacional Cueva de Los Guácharos (Colombia): variación temporal en la cantidad de la dispersión y morfología de semillas

Los guácharos (*Steatornis caripensis*) son aves nocturnas frugívoras especializadas que habitan bosques neotropicales y que tienen el potencial de desempeñar roles ecológicos claves como dispersoras de semillas. En este trabajo, estudiamos la dieta y la cantidad de semillas dispersadas por una población de guácharos en el Parque Nacional Natural Cueva de los Guácharos (Colombia). Para ello, evaluamos la variación temporal, comparamos la composición de lípidos y medimos la morfología de las semillas. De 2011 a 2016 dispusimos 5–10 trampas de semillas en la cueva principal del parque y llevamos a cabo censos de usualmente 5 días, 1–4 veces cada año. Adicionalmente, en 2015 hicimos censos mensuales durante todo el año. En la dieta de los guácharos encontramos semillas de 52 especies de plantas (incluyendo 17 especies, 12 taxones identificados hasta familia y 23 morfoespecies), en las cuales se reflejó una clara dominancia de las familias Arecaceae y Lauraceae. La variación intranual en la riqueza de especies de las semillas depositadas en la cueva mostró que en los periodos de anidación de los guácharos (enero a junio) se presentó el mayor número de semillas y la mayor biomasa, además una alta riqueza de especies en el primer semestre es coherente con los patrones de fructificación en la región. La dieta del guácharo incluyó una alta representación de frutos ricos en lípidos, lo cual fue inferido de la literatura publicada. Los tamaños de las semillas dispersadas variaron enormemente (peso seco entre 0.01 y 5.99 g), siendo las semillas más grandes de 29 mm de ancho y 54 mm de largo. Las semillas que fueron dispersadas mostraron una relación alométrica negativa entre el ancho y el largo. Aunque, nosotros reportamos que los guácharos tienen una dieta diversa y proveen una eficiente dispersión de semillas en términos de la cantidad, aún deben determinarse muchos aspectos de la calidad de la dispersión.

Key words: Arecaceae · Feeding behavior · Frugivory · Fruit morphology · Lauraceae · Lipids · Seed dispersal · Seed morphology

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INTRODUCTION

Tropical mountains contain some of the most diverse ecosystems on Earth, due to their high degree of ecological heterogeneity and endemism (Aldrich et al. 2000) and are one of the most threatened biomes in the Neotropical realm (Armenteras et al. 2003). The destruction of forest to create croplands and cattle ranches causes habitat loss and fragmentation, which reduces biodiversity and changes biotic communities (Hobbs & Yates 2003, Stevenson & Aldana 2008). In this scenario, long distance dispersal may contribute to the colonization of new habitats (i.e., Clark et al. 1998) and genetic flux within populations (e.g., González-Quevedo et al. 2010). The seed dispersal process is mostly achieved by animals in many tropical forests and contributes to determining the plant community composition (Domínguez-Domínguez et al. 2006, Chapman et al. 2016). However, when animals undertake seed dispersal roles, each species usually has a characteristic effect on plant reproductive success, depending on diet breadth and the components of seed dispersal efficiency (SDE) (Schupp et al. 2010). SDE includes the quantity of dispersed seeds, as well as manipulation, gut treatment, and possibility that dispersed seeds reach adequate sites for their establishment.

Steatornis caripensis Humboldt 1799 (Aves: Caprimulgiformes), commonly known as the Oilbird (or Guácharo), is the only nocturnal frugivorous bird inhabiting Guyana, Trinidad, Venezuela, Colombia, Ecuador, Peru, and Bolivia (Thomas 1999). Oilbirds live in caves and canyons in tropical forests, occupying both mountains and lowlands (Thomas 1999, Tello et al. 2008). Although aspects of their behavior and diet have been studied for nearly a century (McAtee 1922, Snow 1962), few ecological studies have been conducted in the last several decades. For example, in Venezuela diet consisted of fruits from at least 32 plant species (Bosque et al. 1995) and nesting time was associated with a lipid-rich fruit diet (Tannenbaum & Wrege 1978). This preference for oily fruits has been reported in early studies (Snow 1962) suggesting the possibility that the birds have been co-evolving with these plants (Snow 1971, Howe 1993). Based on this theory, plant-frugivore interactions should result either in specialized or generalized dispersal systems (Howe 1993). This implies that specialized birds should prefer plants with larger seeds, lower fecundity, extended crops, higher lipid (or protein) contents, and higher removal and dispersal rates than generalized consumers. In addition, endozoochory may affect plant traits such as seed and fruit morphology. For instance, it has been suggested that as fruits and seeds become larger during evolution, the width increases more slowly than the length, generating a negative allometric relationship (Mazer & Wheelwright 1993). This is explained by the fact that fruit width is the most important dimension allowing fruit swallowing and passage through the digestive tract of frugivores.

Although interactions between plants and animals do not usually fit into generalized and specialized systems (e.g., Stevenson et al. 2015), frugivore specialists - such as Oilbirds - tend to feed from nutrient-rich fruits and may disperse large seeds (McAtee 1922, Amico & Aizen 2005). Some dispersed seeds may be up to 2 cm in width, and can be swallowed only by the largest living frugivore in the Neotropics (Peres & Van Roosmalen 2002, Stevenson et al. 2005). Therefore, it is possible that Oilbirds may perform key ecological roles as seed dispersal agents. However, Oilbirds usually use caves as refuge during the day, and many seeds are regurgitated or defecated in dark conditions and at high densities, which are inappropriate for plant establishment (Janzen 1970). In addition, they search for fruits over long distances, getting as far as 44–300 km from the caves (Holland et al. 2009, Karubian et al. 2012), and in order to reach those distances, Oilbirds must spend some days away from the cave, resting in trees and traveling on average 30 km per night (Holland et al. 2009). Furthermore, they might discharge some of the seeds in resting areas that could be safe sites for plant establishment and far away from parental trees (Karubian et al. 2012). Overall, the impact that Oilbirds may have on plant dispersal will depend on the negative effects caused in seeds when deposited in caves and if transported to inadequate habitats, as well as on the positive effects provided by: (1) avoiding negative-density and distance dependence processes (Janzen 1970, Connell 1971), (2) potential secondary dispersal away from the caves, or (3) colonizing suitable habitats and allowing gene flow.

Our main aim was to describe the diet composition of Oilbirds at Cueva de Los Guácharos National Park (Colombia), to answer the following questions: (1) What are the most frequent plant species consumed by this population?; (2) Are there changes in diet composition within and between years?; (3) Does the amount of dropped seeds vary depending on cave occupancy and nesting periods?; (4) Are Oilbirds choosing lipid-rich fruits?; and (5) What is the general shape of the seeds swallowed and is there a negative allometric relationship between seed width and length? From previous studies (Snow 1962, Tannenbaum & Wrege 1978, Mazer & Wheelwright 1993, Bosque et al. 1995), we expected to find a diverse diet dominated by lipid rich fruits, changes in dispersal quantity along the year and positively associated with cave occupancy, and negative allometry between seed width and length. Although no previous study has addressed seasonal variation in the diet of Oilbirds, we predict temporal changes as result of phenological changes in fruit production in the forest around the cave (Vargas et al. 2014), and in nearby areas (e.g., Stevenson et al. 1998). Fruit production in the region has been characterized as seasonal, and results from fruit-trap and transect studies have shown a high abundance at the beginning of the year (January–May), followed by a decrease with lowest values at the end of the year (September–December)

(Stevenson 2004a, Stevenson & Vargas 2008, Vargas & Stevenson 2009).

METHODS

Study area. The study site is located at Cueva de Los Guácharos National Park, Huila department in Colombia (1°36.14"N, 76°8.13"W, Appendix 1). The park size is 9000 ha and the altitudinal range is between 1700 and 2900 m a.s.l. The main cave (Cueva Grande) was formed by Suaza River, which still flows through the cave. Surrounding forests include primary and secondary sub-Andean forests, harboring at least 74 families of woody plants (Prada & Stevenson 2016), the most abundant being Arecaceae, Lauraceae, Melastomataceae, Rubiaceae, Euphorbiaceae, Juglandaceae, Clusiaceae, and Fagaceae.

Sampling design. To examine fruit diet and seed dispersal patterns, during April 2011 we initially assembled 10 seed traps inside the main cave; five less than 5 m from the cave wall and five near the center of the cave. Seed rain was several times higher near the wall than at the center (70 vs. 18 seeds.m⁻².day⁻¹, Appendix 2), suggesting that most seeds were discharged while resting in the nests. We therefore used for each sampling period just five or six traps near the walls and in the same area of the cave. Each trap was a concave nylon net of 0.64 m², tied to four vertical supports at about 1 m in height (Stevenson & Vargas 2008). The mesh could retain seeds of minimum 1 mm in length. One sampling period consisted on five days per month, when the content of each trap was collected daily. This was done during one month in 2011 (April) and 2016 (September), two months in 2012 (January and February) and 2013 (April and September), 4 months in 2014 (January, April, July, and September), and all 12 months in 2015 to determine within-year variation. The density of seeds dropped in the traps was regressed against the number of active nesting birds in the cave, which were counted by the park's staff monthly (by counting nests on the cave wall, using a painted subdivision of the walls).

Trap contents were removed and washed, and seeds were identified or assigned to a morphotype. Taxonomic determinations were based on our own plant collection in the park (i.e., about 1130 vouchers, including more than 206 tree species), or using fruit and seed guides (Stevenson et al. 2000, Cornejo & Janovec 2010). We also included taxa determined at genus level, because plant identification at species level based just on seeds morphology is difficult, and fruit traits within the same genus show low variation (Jordano 1995). Hence, in Lauraceae and Humiriaceae we provided a combination of two or more letters to each seed based on its morphotype (see Table 1 for details) since most of them could not be properly referred to an already known species (study in prep. by authors).

To determine the lipid content of the fruit consumed by Oilbirds, first, we gathered information

from the literature on the percentage of lipids in the pulp of fruit species consumed. We used mean values found in the literature (Bosque et al. 1995, Bernal & Correa 1998; Rojas 2012, 2015) and averaged mean values for species belonging to one genus. In addition, we compared this distribution with the lipid content of many fruit species available in the forests of Tinigua National Park (Stevenson 2004b), where Oilbirds have been reported and is the only nearby site, where fruit nutritional contents have been measured for a large variety of species (N = 83).

Finally, the morphology of the seeds dispersed by Oilbirds was studied by selecting five to ten seeds per species, and by measuring seed mass using a precision balance of 0.1 g (after reaching constant weight in a portable oven at 50–70 °C), as well as length and width using calipers (N = 280 seeds of 37 species).

Statistical analyses

Diet and seed quantity. To assess which plant species were more important in Oilbirds diet during 2015, we estimated an index of seed dispersal importance (SDII), at species–morphospecies and family level. The index was based on the sum of relative seed numbers (RSD_{*i*} = percentage of seeds belonging to the species *i* divided by the total number of dispersed seeds), the relative frequency (RF_{*i*} = percentage of months when the seeds of species *i* were dispersed, ln transformed), and the relative dominance (RD_{*i*} = percentage of the dry seed mass belonging to species *i* divided by the total mass of dispersed seeds):

SDII_{*i*} (Seed Dispersal Importance Index) = RSD_{*i*} + ln RF_{*i*} + RD_{*i*}. This index includes number of seeds, because each seed is a potential new plant; relative dominance, because large heavy seeds have a high chance of establishment under the shade continuous canopy forests (Harms et al. 2000) where small seeds do not recruit (Stevenson & Guzman-Caro 2013); and relative frequency, i.e., assessing how often the seeds are dispersed (which is ln-transformed to provide similar weight to each component).

To quantify abundance and richness of seeds moved to the cave by Oilbirds, we calculated seed density, biomass, and seed richness to examine monthly differences in the number of seeds dispersed for 2015, using Kruskal-Wallis test and *post hoc* (Mann-Whitney *U* test) pairwise comparisons. We considered seed density as the number of seeds daily deposited in traps per trap area, biomass as seed mass in grams per trap area, and seed richness as the number of plant species–morphospecies registered.

Diet composition. To explore species composition in Oilbirds diet by season and across years, we performed Nonmetric Multidimensional Scaling (NMDS) using Bray-Curtis distance. We distinguished three seasons. (1) Dry season: January to April, which usually corresponds to a period with high fruit abundance (Stevenson et al. 1998); (2) early wet season: May to August, when fruit abundance tends to

Table 1. Relative density, frequency, and dominance, and the derived importance index for plants species of Oilbird (*Steatornis caripensis*) diet recorded in 2015 in the main cave of Cueva de Los Guácharos National Park (Huila, Colombia). Capital letters indicate specific seed morphotypes (RR = stripes and rounded, RGI = stripes and big, RC = stripes and brown, PG = big and elongated, PEG = big and pear shaped, PALO = large and stick shaped, M = macadamia shape, LR = stripes and small, GUA = round, brown with black spots, CAL = pumpkin shaped, AG = very large). Bold and bold numbers indicate overall family scores.

Species	Family	Relative Density (%)	Relative Frequency (ln%)	Relative Dominance (%)	Importance Index
<i>Prestoea acuminata</i>	Arecaceae	35	4.61	13.23	52.84
<i>Geonoma undata</i>	Arecaceae	18.66	4.61	2.04	25.31
<i>Chamaedorea linearis</i>	Arecaceae	1.71	4.07	1.62	7.4
<i>Bactris</i> sp.	Arecaceae	1.01	4.07	1.18	6.26
<i>Euterpe precatoria</i>	Arecaceae	3.69	4.2	3.46	11.35
<i>Oenocarpus mapora</i>	Arecaceae	1.04	4.32	1.44	5.76
<i>Oenocarpus bataua</i>	Arecaceae	1.28	4.32	1.1	5.42
<i>Aiphanes horrida</i>	Arecaceae	0.1	3.22	0.19	3.51
Total	Arecaceae	62.49	33.42	24.26	117.85
<i>Rhodostemonodaphne grandis</i>	Lauraceae	0.22	3.51	1.59	5.32
<i>Persea</i> sp.	Lauraceae	0.79	3.51	1	5.3
<i>Nectandra</i> sp.	Lauraceae	4.19	4.52	1.89	10.6
<i>Nectandra</i> cf. <i>purpurea</i>	Lauraceae	2.76	4.32	8.33	15.41
Lauraceae sp. RR	Lauraceae	2.6	4.32	0.76	7.68
Lauraceae sp. RGI	Lauraceae	0.32	2.12	1.54	3.98
Lauraceae sp. RC	Lauraceae	0.08	2.12	0.48	2.68
Lauraceae sp. PG	Lauraceae	4.03	4.07	19.47	27.57
Lauraceae sp. PEG	Lauraceae	0.66	2.12	0.64	3.42
Lauraceae sp. PALO	Lauraceae	0.06	3.22	0.05	3.33
Lauraceae sp. M	Lauraceae	1.33	4.32	2.33	7.98
Lauraceae sp. LR	Lauraceae	26.03	4.42	7.92	38.37
Lauraceae sp. GUA	Lauraceae	0.26	4.07	0.17	4.5
Lauraceae sp. CAL	Lauraceae	2.04	3.91	0.87	6.82
Lauraceae sp. AG	Lauraceae	0.73	3.51	5.09	9.33
Total	Lauraceae	46.1	54.06	52.13	152.29
<i>Dacryodes</i> sp.	Burseraceae	1.94	4.42	12.19	18.55
<i>Trattinnickia</i> sp.	Burseraceae	0.53	2.78	0.29	3.6
Total	Burseraceae	2.47	7.2	12.48	22.15
<i>Hedyosmum cuatrecazanum</i>	Chloranthaceae	4.41	4.61	0.05	9.07
<i>Dendropanax macrocarpus</i>	Araliaceae	1.82	4.52	0.07	6.41
<i>Humiria</i> sp.	Humiriaceae	0.18	3.91	0.41	4.5

decrease and (3) late wet season: September to December, corresponding the lowest fruit productivity of the year. We also ran an Analysis of Similarities (ANOSIM) to determine if species composition in diet varied between the three seasons, including all sampling periods.

Effect of nesting periods. To examine whether Oilbirds nest occupancy may explain seed abundance in

the cave, we performed a simple regression analysis between nest quantity and seed biomass.

Nutritional content. To assess whether Oilbirds choose lipid-rich fruits, we used a Wilcoxon test to compare the pulp lipid content between fruits consumed by Oilbirds in Cueva de Los Guácharos Park and fruits of a large variety of species reported in Tinigua National Park.

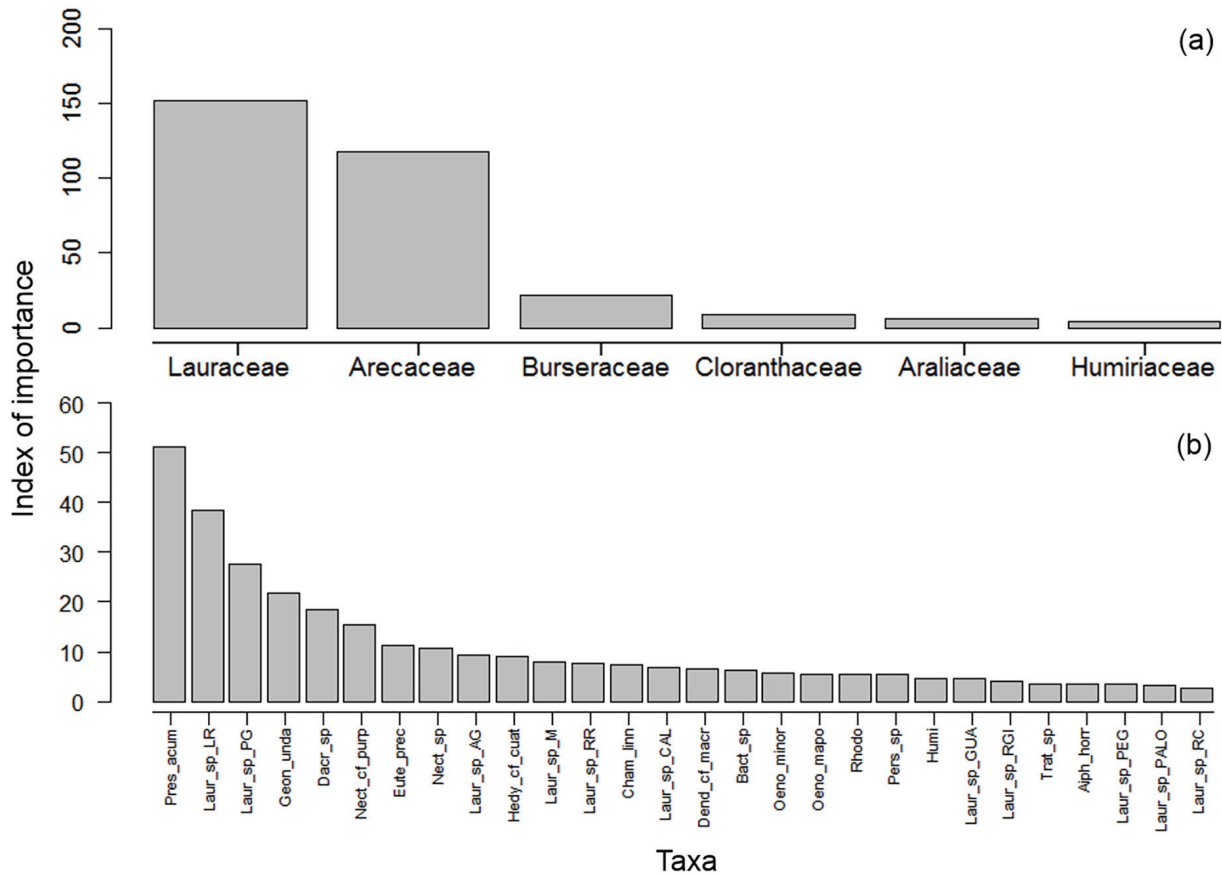


Figure 1. (a) Most important families and (b) Species consumed by Oilbirds (*Steatornis caripensis*) and voided in the main cave in Cueva de Los Guácharos National Park (Huila, Colombia), based on an index of importance considering seed density, frequency of dispersal, and seed mass (see Table 1). Capital letters in Lauraceae indicate specific seed morphotypes (species indet.; cf. Table 1). Pres_acum = *Prestoea acuminata*, Laur_sp_LR = Lauraceae sp. LR, Laur_sp_PG = Lauraceae sp. PG, Geon_unda = *Geonoma undata*, Dacr_sp = *Dacryodes* sp., Nect_cf_purp = *Nectandra* cf. *purpurea*, Eute_prec = *Euterpe precatoria*, Nect_sp = *Nectandra* sp., Laur_sp_AG = Lauraceae sp. AG, Hedy_cf_cuat = *Hedyosmum cuatrecazanum*, Laur_sp_M = Lauraceae sp. M, Laur_sp_RR = Lauraceae sp. RR, Cham_linn = *Chamaedorea linnearis*, Laur_sp_CAL = Lauraceae sp. CAL, Dend_cf_macr = *Dendropanax* cf. *macrocarpus*, Bact_sp = *Bactris* sp., Oeno_mapo = *Oenocarpus mapora*, Oeno_bata = *Oenocarpus bataua*, Rhodo = *Rhodostemonodaphne* sp., Pers_sp = *Persea* sp., Humi = Humiriaceae, Laur_sp_GUA = Lauraceae sp. GUA, Laur_sp_RGI = Lauraceae sp. RGI, Trat_sp = *Trattinnickia* sp., Aiph_horr = *Aiphanes horrida*, Laur_sp_PEG = Lauraceae sp. PEG, Laur_sp_PALO = Lauraceae sp. PALO, Laur_sp_RC = Lauraceae sp. RC.

Seed shape. We performed a simple regression analysis to assess the allometric relationship between seed longitude and width and we examined the fit for an exponential function and for a linear relationship, using the Akaike criterion. All statistical analyses were performed using R version 3.3.1 (R Core Team 2017).

RESULTS

Overall, Oilbirds dropped seeds of 52 species (including 17 named species, 12 identified to family level, and 23 morphospecies that were not assigned to family level), from a total of 13,704 seeds representing at least six plant families (Table 1). Arecaceae and Lauraceae were the dominant plant families in the diet of Oilbirds (Figure 1a), followed by Burseraceae and Chloranthaceae. At species level, two palm species (*Prestoea acuminata*, *Geonoma undata*) and

three Lauraceae species obtained the highest index of importance (Figure 1b). Most Lauraceae species (87%) that could not be identified at species level, except for *Nectandra purpurea* (a very common local species in Cueva de Los Guácharos Park) being the only determined member of that family within the top-ten most important taxa. Only two members of other genera within the top-ten did not belong to Arecaceae and Lauraceae, i.e., *Dacryodes* sp. (Burseraceae) and *Hedyosmum cuatrecazanum* (Chloranthaceae).

When comparing all years, Oilbirds diet composition varied between sampling periods in different seasons and the NMDS analysis showed a significant seasonal aggregation (ANOSIM $R = 0.39$, $P = 0.002$, Figure 2a). In addition, when comparing diet composition across years, diet in late wet season (i.e., fruit scarcity), was more dissimilar between samples than at other periods when fruit availability was higher.

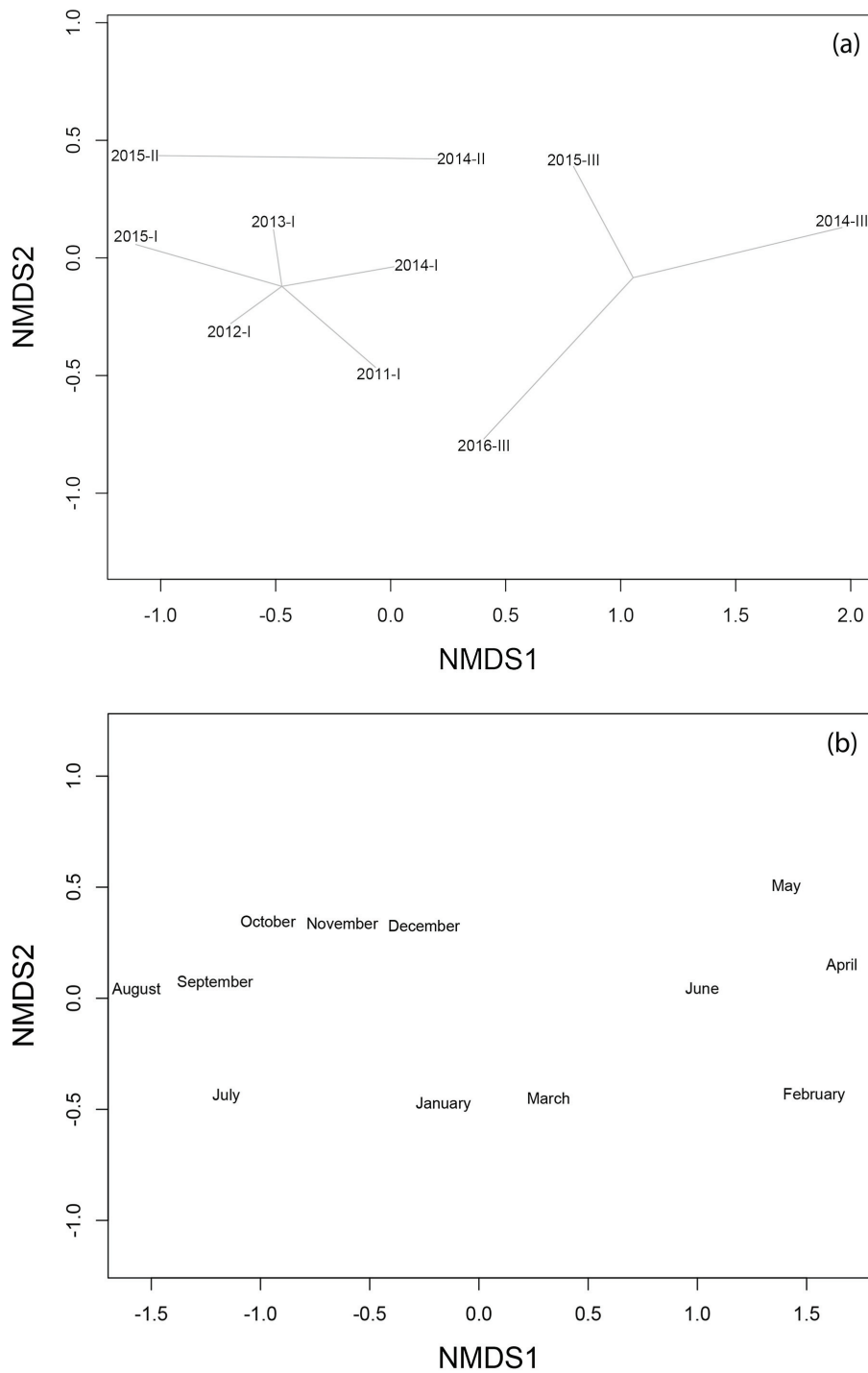


Figure 2. NMDS ordination analysis showing Oilbird (*Steatornis caripensis*) diet composition in Cueva de Los Guácharos National Park (Huila, Colombia): (a) According to three seasonal periods between 2011 and 2015: I. Dry period, II. Early wet period, III. Late wet period. Samples from the same season are joined by lines to the centroid (stress 0.1). (b) Months within a year (2015).

Within 2015 (when all months were sampled), we also found seasonal differences in diet composition, corresponding to three different groupings: July–December, January–March, and April–June (Figure 2b).

The abundance of seeds in the cave varied during 2015 (Figure 3a and 3b). In terms of seed density, April showed the highest value (Kruskal-Wallis, $\chi^2 =$

52.1, $P < 0.001$), followed by May and June, differing significantly from all months except May ($P > 0.05$). Similarly, in terms of seed mass April showed the highest value (Kruskal-Wallis, $\chi^2 = 50.9$, $P < 0.001$), where seed rain was higher in this month in comparison with all others, and some other months of the first semester (March and May) showed higher seed mass than in the second semester. Species richness in

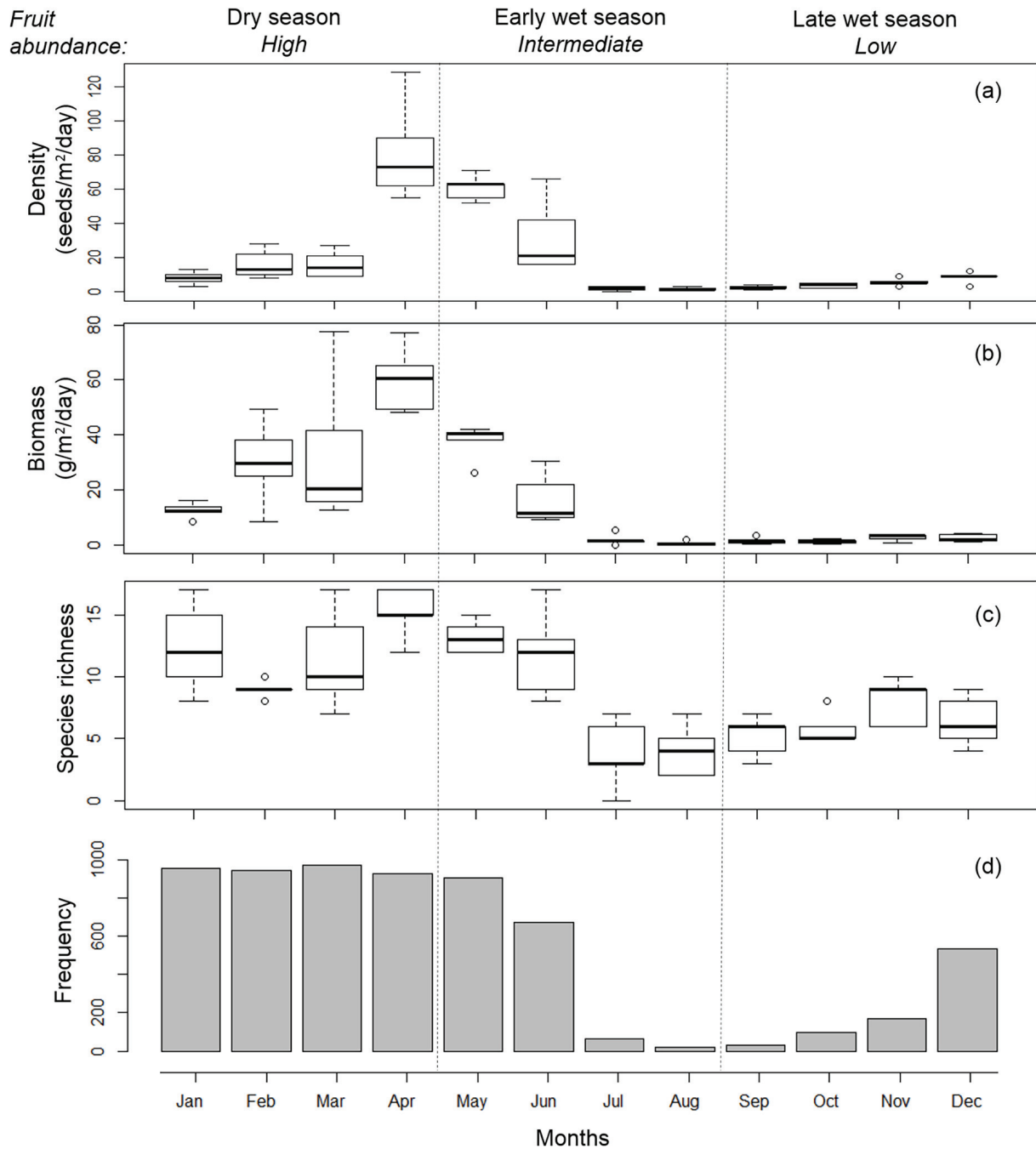


Figure 3. Within-year variation in dispersal quantity and diet diversity of Oilbirds (*Steatornis caripensis*) in Cueva de Los Guácharos National Park (Huila, Colombia) during 2015. (a) Density of seeds (number of seeds.m⁻².day⁻¹), (b) Seed biomass (g.m⁻².day⁻¹), (c) Species richness, and (d) Frequency of occupied Oilbird (*Steatornis caripensis*) nests in the main cave.

diet also varied (Kruskal-Wallis, $\chi^2 = 45.4$, $P < 0.001$), showing likewise a peak in April but few species between July and December (Figure 3c).

August showed the lowest level of seed deposition and the lowest number of occupied nests (Figure 3d). We found a positive association between the biomass of seeds found in traps and the number of occupied nests by Oilbirds, with regression analyses showing that most of the variation in seed abundance may be explained by nest occupancy ($R^2 = 0.81$, $P < 0.05$, $\ln \text{ seed biomass} = 1.005 \times \ln \text{ nest occupancy} + 0.37$).

According to the literature review, fruits of many species in the diet of Oilbirds, such as Lauraceae spp., *Oenocarpus* spp., and *Guarea* spp., are rich in lipid content (Table 2). When comparing the percentage of lipids in the diet of Oilbirds with that of fruits from Tinigua National Park, we found that the species consumed by Oilbirds are richer in lipids (Wilcoxon Test, $W = 840$, $P = 0.032$, Figure 4).

Oilbirds dispersed seed ranging between 0.01 and 5.99 g including mostly ellipsoid (63%) and spherical seeds (31%). The largest seeds belonged to *Rodostemonodaphne grandis* (5.4 x 2.9 cm) and

Table 2. Lipid content of fruits known to be eaten by Oilbirds (*Steatornis caripensis*) in different studies.

Species	Family	Lipids (%)	Reference
<i>Bactris gasipaes</i>	Arecaceae	5.4	Rojas 2012
<i>Bactris gasipaes</i>	Arecaceae	4.6	Bernal & Correa 1998
<i>Bactris gasipaes</i>	Arecaceae	4.4	Bernal & Correa 1998
<i>Bactris gasipaes</i>	Arecaceae	0.8	Bernal & Correa 1998
<i>Bactris setulosa</i>	Arecaceae	28.3	Bosque et al. 1995
<i>Ceroxylon quindiuense</i>	Arecaceae	2.4	Rojas 2012
<i>Chamaedorea linearis</i>	Arecaceae	1.8	Rojas 2012
<i>Euterpe precatoria</i>	Arecaceae	0.3	Rojas 2012
<i>Euterpe precatoria</i>	Arecaceae	8	Bosque et al. 1995
<i>Prestoea acuminata</i>	Arecaceae	1.1	Bosque et al. 1995
<i>Geonoma densa</i> (= <i>G. undata</i>)	Arecaceae	5.5	Bosque et al. 1995
<i>Geonoma weberbaueri</i> (= <i>G. undata</i>)	Arecaceae	1.5	Rojas 2012
<i>Oenocarpus bataua</i>	Arecaceae	12.4	Rojas 2012
<i>Oenocarpus bataua</i>	Arecaceae	19.7	Bosque et al. 1995
<i>Persea caerulea</i>	Lauraceae	10.3	Bosque et al. 1995
<i>Aniba perutilis</i>	Lauraceae	2.3	Bosque et al. 1995
<i>Nectandra acutifolia</i>	Lauraceae	32	Bosque et al. 1995
<i>Beilschmiedia sulcata</i>	Lauraceae	33.3	Bosque et al. 1995
<i>Nectandra</i> aff. <i>laurel</i>	Lauraceae	63.2	Bosque et al. 1995
<i>Nectandra membranacea</i>	Lauraceae	67.8	Bosque et al. 1995
<i>Nectandra turbacensis</i>	Lauraceae	60.2	Bosque et al. 1995
<i>Ocotea</i> aff. <i>austini</i>	Lauraceae	54.8	Bosque et al. 1995
<i>Ocotea floribunda</i>	Lauraceae	52.4	Bosque et al. 1995
<i>Ocotea</i> sp.	Lauraceae	36	Bosque et al. 1995
<i>Persea caerulea</i>	Lauraceae	46.5	Bosque et al. 1995
<i>Phoebe cinnamomifolia</i> (= <i>Cinnamomum triplinerve</i>)	Lauraceae	34	Bosque et al. 1995
<i>Dacryodes trinitensis</i>	Burseraceae	2.5	Bosque et al. 1995
<i>Myrcianthes leucoxylla</i>	Myrtaceae	1	Rojas 2012
Araliaceae sp.	Araliaceae	3.6	Bosque et al. 1995

Lauraceae sp. AG (4.1 x 1.5 cm), while the smallest seeds were *Dendropanax macrocarpus* (0.9 x 0.5 cm) and *Hedyosmum cuatrecasum* (0.5 x 0.3 cm). In terms of biomass, we found that both small and large seeds were dispersed and that distribution is skewed for relatively heavy seeds (Figure 5a). Moreover, there is a negative allometric relationship (a slope < 1) between seed length and seed width (Figure 5b), confirming that in larger seeds width increases more slowly than length. The isometric linear fit was less good ($R^2 = 0.65$) than the exponential fit ($R^2 = 0.74$) and the exponential model had a lower AIC value (17.6) than the linear model (80.4), showing that width increase in large seeds is more constrained than length increase.

DISCUSSION

Across 22 months of sampling, we found that Oilbirds swallow seeds of a variety of plant species, mostly from Arecaceae and Lauraceae families, including at least 52 species and morphospecies, the largest list so far reported (i.e., Tannenbaum & Wrege 1978: 30 species in 8 months, Bosque et al. 1995: 32 species in 30 months, Rojas 2015: 16 species in 9 months). However, it is possible that our list is still incomplete because the cumulative number of species in longer sampling periods (10 days), as the ones used in our study (5 days), does not reach an asymptote (Cardona 2016). The diverse diet may be in part explained by the long-term nature of our study and the diversity of tropical forests visited

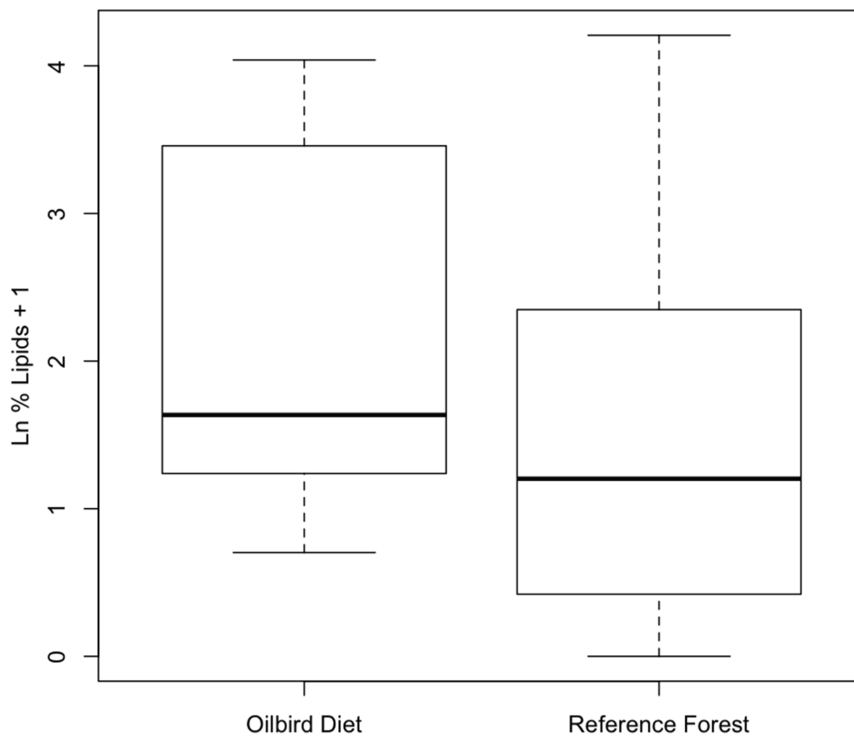


Figure 4. Comparison of pulp lipid content in the diet of Oilbirds (*Steatornis caripensis*) in Cueva de Los Guácharos National Park (Huila, Colombia) and a reference forest (Tinigua National Park, Meta, Colombia).

by Oilbirds of the study colony in southern Colombia.

At population level, we found within-year differences in the patterns of seed deposition in the main cave, which are depending on Oilbirds. We did not register seeds usually dispersed by bats, such as *Cecropia*, *Ficus*, *Piper*, or *Solanum* spp. (Fleming & Heithaus 1981). In general, seed quantity in traps was highest in April, a month that tends to show high fruit productivity, especially in lowland forests (Stevenson et al. 1998, Vargas & Stevenson 2009) and when there are many Oilbirds nesting in the cave (up to 976 occupied nests). In fact, 81% the variation in seed quantity in the cave depends just on the number of birds occupying nests. Similarly, in some other systems (such as primate-plant interactions), it is common that the quantity of seed dispersal is highly dependent on the density of individuals (González & Stevenson 2014), with less variation between adult individuals (e.g. males vs. females: Stevenson et al. 2005, Ramírez et al. 2014).

The estimate of seeds dropped by Oilbirds near the cave wall was 80 seeds.m⁻².day⁻¹ during the nesting period. In addition, about 900 nests were occupied in this period with two mature individuals per nest, and nesting walls had approximately 120 m in perimeter, resulting in ca. 7.5 nests.m⁻¹. Therefore, about 15 Oilbirds (7.5 nests x 2 individuals per nest) are dropping at least 80 seeds each day into the cave, implying that each individual is dropping c. 5.3 seeds per day into a seed trap near the cave wall. Since they drop 74.3% of the seeds near the wall (5.3 seeds per

day) and 25.7% (c. 1.8 seeds per day) in the center of the cave (Appendix 2), in total one Oilbird should move c. 7.1 seeds per day in the cave. From a study using GPS devices, we know that they spend 48% of the time inside the cave during nesting periods (Cardona 2016), and 52% outside the caves; dispersing c. 7.7 seeds per day to the exterior, allowing us to estimate a total of 14.8 seeds moved per day at the individual level. Although this estimate is based on several assumptions, it provides the first estimate of seed dropping per individual. Other kind of approaches have been used to estimate dispersal quantity for other frugivores. For instance, Umbrellabirds (*Cephalopterus* spp.) are involved in seed dispersal into reproductive leks, resulting in six times more seeds deposited in traps located in leks than in surrounding control areas (Karubian et al. 2012). In primates, individual woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park disperse on average 800 seeds each day, much higher than estimates for Oilbirds (e.g., Stevenson 2007). Part of this difference may depend on the fact that woolly monkeys are larger animals (up to 9 kg) and most seeds dispersed by woolly monkeys are small seeded, which are present in large numbers in fecal droppings (Stevenson 2000). These very small seeds of genera such as *Cecropia* and *Ficus* are not dispersed by Oilbirds, limiting their value as seed dispersers in terms of quantity, but not in terms of the biomass of dispersed seeds (Figure 5a).

Diet composition was remarkably similar to that which was found in other studies, including sites

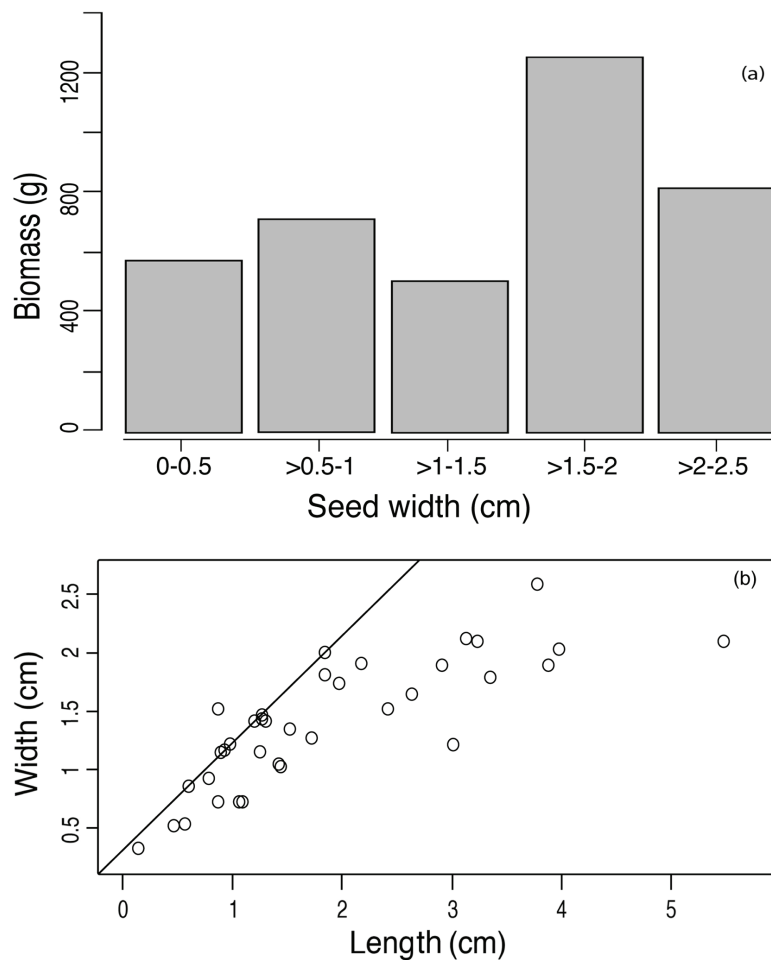


Figure 5. Morphology of seeds recovered in traps inside main cave of Cueva de Los Guácharos National Park (Huila, Colombia). (a) Frequency of dispersal in terms of seed biomass and (b) Relationship between seed length and width. The line represents an isometric relationship and the dots show the observed values, indicating a negative isometric relationship.

located far from Cueva de Los Guácharos. For instance, in central Colombia the dominant species also belong to Arecaceae and Lauraceae, followed by Burseraceae (Rojas 2015), and the same species are present in other oilbird sites in Colombia and Venezuela (i.e., *Oenocarpus bataua*, *Prestoea acuminata*, *Geonoma undata*, and *Euterpe precatoria*) (Bosque et al. 1995, Rojas 2015). However, our temporal analyses revealed changes in fruit diet composition along fruiting periods. In addition, species richness in the cave showed higher numbers during the first semester than on the second semester of the year, consistent with the general patterns of production in surrounding forests (Stevenson et al. 1998). This result suggests that diet diversity in Oilbirds, to a large extent, depend on the diversity of fruits in the environment, which has been reported in other large sized frugivore birds such as cracids. For example, Cauca Guans (*Penelope perspicax*) ingest fruits in proportion to their availability but favor some species with high fruit production or prolonged fruiting (Muñoz et al. 2007). On the other hand, Oilbirds are capable of traveling many kilometers each night, and it seems likely that these birds can optimize feeding

intake by visiting productive fruit patches (Charnov 1976), perhaps using spatial maps (Griffin 1986). Interestingly, during periods of nesting, seed rain was dominated by the palm *Prestoea acuminata*, which occurs in sub Andean forests surrounding the cave (Prada & Stevenson 2016).

Overall, our results showed that Oilbirds consume a large variety of fruits, however, the latter do not represent a random sampling of the fruits present in the environment. First, selected items have a higher lipid content than the average of fruits available in forests. Previous studies have suggested that the ingestion of lipid-rich fruits is important for nestlings, for nutritional purposes, and for maintaining body heat under the climatic conditions of mountain forests (Bosque & Parra 1992, Roca 1994, Rojas 2015). Additionally, during the breeding period, foraging movements of parent birds are more constrained than at other times of their life cycle (Lenz et al. 2015). A possible explanation is that it is unprofitable for breeding birds to fly far away from their nests to search for fruit-rich patches (Blendinger et al. 2015). Second, only two of the 10 most productive endozoochorous fruits in forest surrounding the cave were

consumed by Oilbirds (Cifuentes et al. 2013), despite they were available for extended periods. In fact, fruit productivity in surrounding forests is a poor predictor of the density of seeds dropped in the cave ($R^2 = 0.005$, $P = 0.69$, $N = 170$).

As each pair lays between one and three eggs and nestlings are fed for more than 110 days (Bosque & Parra 1992, Roca 1994, Bosque et al. 1995, Herrera 2002, Rojas 2015), this implies relatively constant visits to the cave, where presumably most seeds will die. This will certainly be the case for seeds from other environments (such as lowland species taken to about 1900 m a.s.l.) and even for local plants germinating inside the cave. However, possible secondary dispersal by abiotic agents or rodents (Jansen et al. 2012), should be studied to accurately determine the effect of Oilbird's seed consumption on plant fitness. In addition, some seeds may be voided outside the cave, where seeds may be established.

Oilbirds have been known to disperse very large seeds (McAttee 1922, Snow 1962, Bosque et al. 1995), and this study supported these findings. For instance, large frugivores, such as ateline primates (e.g., *Lagothrix*, *Ateles*, and *Brachyteles*), are known to disperse large seeds up to 20 mm wide (Peres & Van Roosmalen 2002, Stevenson 2004a), similar in size to the largest defecated by Oilbirds and only surpassed by those dispersed by tapirs (*Tapirus terrestris*) (Fragoso & Huffman 2000). In addition, frugivore populations are declining (Stevenson et al. 2015, Peres et al. 2016), and their dispersal roles may be disappearing in many disturbed and hunted areas. In fact, seed dispersal of large-seeded species is the most vulnerable process in plant regeneration (Neuschulz et al. 2016). In this sense, it is possible that Oilbirds disperse seeds at very long distances, and they are possibly the only animal vector capable of maintaining gene flow in plants with larger-sized seeds across isolated forest patches along elevational gradients. In consequence, this process may be of great importance to maintain patterns of plant diversity in Neotropical forests.

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